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IUCN Global Ecosystem Typology 2.0

Descriptive profiles for biomes and ecosystem functional groups

David A. Keith, Jose R. Ferrer-Paris, Emily Nicholson and Richard T. Kingsford (editors)

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IUCN is pleased to acknowledge the support of its Framework Partners who provide core funding: Ministry for Foreign Affairs of Finland; Government of France and the French Development Agency (AFD); the Ministry of Environment, Republic of Korea; the Norwegian Agency for Development Cooperation (Norad); the Swedish International Development Cooperation Agency (Sida); the Swiss Agency for Development and Cooperation (SDC); and the United States Department of State.

This publication has been made possible in part by funding from: IUCN Commission on Ecosystem Management Red List of Ecosystems Thematic Group; The Centre for Ecosystem Science, University of NSW, Sydney; The PLuS Alliance; Australian Research Council (LP170101143).

Published by: IUCN, Gland, Switzerland

Citation: Keith, D.A., Ferrer-Paris, J.R., Nicholson, E. and Kingsford, R.T. (eds.) (2020). *The IUCN Global Ecosystem Typology 2.0: Descriptive profiles for biomes and ecosystem functional groups*. Gland, Switzerland: IUCN.
Individual chapters/sections within this report should be cited as: Author(s) (2020). 'Title of chapter/section'. In: D.A. Keith, J.R. Ferrer-Paris, E. Nicholson and R.T. Kingsford (eds.) (2020). *The IUCN Global Ecosystem Typology 2.0: Descriptive profiles for biomes and ecosystem functional groups*. Gland, Switzerland: IUCN.

ISBN: 978-2-8317-2077-7

DOI: https://doi.org/10.2305/IUCN.CH.2020.13.en

Cover photos: **Left:** The Earth (NASA). **Right (top to bottom):** Clouds (Adrian Korpal on Unsplash); Freshwater falls, Iguazu (David Keith); Thorny Desert, Catavina (David Keith); Coral reefs, Red Sea (Francesco Ungaro); and Cave system, Yucatán (Alison Perkins). **Back cover:** Dove Lake in Cradle Mountain National Park, Tasmania (Dixanstudio).

Layout and design: Diwata Hunziker

Available from: IUCN, International Union for Conservation of Nature
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Executive summary

Ecosystems are critically important components of Earth's biological diversity and as the natural capital that sustains human life and well-being. Yet all of the world's ecosystems show hallmarks of human influence, and many are under acute risks of collapse, with consequences for habitats of species, genetic diversity, ecosystem services, sustainable development and human well-being. A systematic typology that encompasses all of Earth's ecosystems, representing the diversity of both ecosystem function and biodiversity, is essential for marshalling knowledge to inform effective action to sustain this critical natural capital. Accordingly, at the World Conservation Congress Marseille 2020, the IUCN membership voted strongly in favour of Motion 074, now Resolution 061, for adoption of the Global Ecosystem Typology to support global, regional and national efforts to assess and manage risks to ecosystems (WCC Resolution 061).

The IUCN Global Ecosystem Typology is a hierarchical classification system that, in its upper levels, defines ecosystems by their convergent ecological functions and, in its lower levels, distinguishes ecosystems with contrasting assemblages of species engaged in those functions. This report describes the three upper levels of the hierarchy, which provide a framework for understanding and comparing the key ecological traits of functionally different ecosystems and their drivers. An understanding of these traits and drivers is essential to support ecosystem management. By sharing research and management experiences about ecosystem functions, dependencies and responses to management, the typology can facilitate knowledge transfer that improves management outcomes for both biodiversity and ecosystem services.

The top level of the Global Ecosystem Typology divides the biosphere into **five global realms:** i) terrestrial; ii) subterranean; iii) freshwater (including saline water bodies on land); iv) marine; and v) the atmosphere.

The interfaces between these core realms are recognised as transitional realms, accommodating ecosystems, such as mangroves, that depend on unique conditions and fluxes between contrasting environments. At Level 2, the typology defines **25 biomes** – components of a core or transitional realm united by one or a few common major ecological drivers that regulate major ecological functions. These include familiar terrestrial biomes, such as tropical/subtropical forests and deserts, as well functionally distinctive groupings that fall outside the traditional scope of the biome concept, including lentic and lotic freshwater biomes, pelagic and deep sea benthic marine biomes, subterranean freshwater biomes, and several anthropogenic biomes. Ecosystems in this latter group are created by human activity, which continues to drive and maintain their assembly. Level 3 of the typology includes **108 Ecosystem Functional Groups** that encompass related ecosystems within a biome that share common ecological drivers and dependencies, and thus exhibit convergent biotic traits. Examples include temperate deciduous forests, annual croplands, seasonal upland streams, intertidal forests, epipelagic ocean waters, and deep sea trenches and troughs.

This report contains descriptive profiles for the 25 biomes and 108 Ecosystem Functional Groups in version 2.0 of the Global Ecosystem Typology, with a glossary and synopsis of the rationale and methods for development. The profiles describe the ecological traits and key drivers that distinguish groups of related ecosystems from one another, illustrated by exemplar images and diagrammatic models of ecosystem assembly, with indicative maps of global distribution and sources of further information. The descriptions, images and maps are also available on an interactive website https://global-ecosystems.org/.

Version 2.0 of the Global Ecosystem Typology is the outcome of critical review and input by an extensive international network of ecosystem scientists.

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Acknowledgements

We are grateful to IUCN peer reviewers, Sean Porter and Neil Burgess, for their critical appraisal of the manuscript and the concepts within, which improved the content. Dr Lucie M. Bland scrupulously copy-edited the manuscript.

We also thank the organisations listed below that contributed logistic support, funding and time to see this project to successful completion.

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Development of the Global Ecosystem Typology was supported by:
IUCN Commission on Ecosystem Management Red List of Ecosystems Thematic Group
IUCN Commission on Ecosystem Management
The Centre for Ecosystem Science, University of New South Wales, Sydney, Australia
Provita, Caracas, Venezuela
The PLuS Alliance
Australian Research Council (Grant No. LP170101143)

Glossary of selected terms and acronyms used in ecosystem descriptions

Allochthonous energy	Energy imported into an ecosystem from external sources in the form of organic material.
Ambient environment	Non-resource environmental factors that modify the availability of resources or the ability of organisms to acquire them.
Aphotic	A zone where light intensity is too low to support photosynthesis.
Autochthonous energy	Energy captured from abiotic sources in situ by autotrophs living within an ecosystem.
Autotroph	An organism that fixes carbon from its surroundings, manufacturing complex energy-storing organic compounds, generally using energy from light (photosynthesis) or inorganic chemical reactions (chemosynthesis). Autotrophs are primary producers in trophic webs.
Basin fill	Unconsolidated to moderately consolidated subterranean sediments that bear aquifers. They are composed of gravel, sand, silt and clay deposited on antecedent alluvial fans, pediments, flood plains and playas.
Biofilm	Periphyton. A complex layer composed of algae, cyanobacteria and heterotrophic microbes embedded in a mucopolysaccharide matrix cohering to submerged aquatic surfaces. Important food source for aquatic animals.
Biogenic	A structure created by living organisms (e.g. a coral reef, tunnels in soils or sediment).
C_3	The most common photosynthetic pathway in plants based only on the Calvin cycle with associated energy loss to photorespiration and dependence on daytime CO_2 uptake. This pathway is dominant in environments with abundant moisture and cool temperatures.
Cauliflory	An arrangement of flowers and fruits in which they are borne directly on the main stems of a tree.
C_4	A photosynthetic pathway with a supplementary C-fixation pathway that minimises photorespiration, reduces CO_2 demand and increases water use efficiency, often dominating in warm and dry environments.
CAM	A specialised C_4 photosynthetic pathway in which CO_2 uptake and fixation occur during the night, followed by internal release in daytime when light-dependent photosynthesis can take place. Stomatal closure occurs during the day, reducing moisture loss and enabling survival in very hot and dry conditions.
Chemoautotroph	An organism that fixes carbon from its surroundings using energy from inorganic chemical reactions.
C:N ratio	Carbon-to-nitrogen ratio in biological tissues. Reflects differences in tissue composition related to nitrogen availability and capture as well as woodiness in plants (Pérez-Harguindeguy et al., 2013).
C:N:P (Redfield) ratio	The consistent ratio of Carbon-to-Nitrogen-to-Phosphorus in marine phytoplankton of deep seas, related to a homeostatic protein-to-ribosomal RNA ratio present in both prokaryotes and eukaryotes-
Dimicitic lakes	Lakes with waters that mix from top to bottom twice per year, before and after surface freezing in winter.
Disturbances	Sequences or 'regimes' of environmental events that destroy living biomass, liberate and redistribute resources and trigger life history processes in some organisms (e.g. fires, floods, storms, mass movement).

Dystrophic	Waters with low levels of dissolved nutrients, high acidity, brown colouration and low light penetration due to tannins, organic acids and undecayed plant matter, usually originating from peaty substrates.
Emergent	A large tree, emerging above the height of a main forest canopy.
Engineer	Ecological or ecosystem engineers are organisms that directly or indirectly alter the biotic or abiotic structure of ecosystems and resource availability, making it suitable for habitation by other organisms (Jones et al., 1994).
Epicormic resprouting	New shoots on trees emerging from meristematic tissues beneath the bark on large stems and trunks, usually after death of canopy foliage.
Ericoid leaves	Small, sclerophyllous leaves with thick cuticles and typically crowded on the branchlets; resembling those of heather.
Euphotic	A zone with abundant light that can support photosynthesis.
Heterotroph	An organism that cannot manufacture its own food by carbon fixation and therefore derives its intake of nutrition from other sources of organic carbon, mainly plant or animal matter. In the food chain, heterotrophs are secondary and tertiary consumers. Heterotrophs are consumers in trophic webs, including decomposers, detritivores, herbivores and predators.
LAI	Leaf Area Index, the projected area of leaves as a proportion of the area of land compared to which it is measured. Useful in remote sensing for describing vegetation density (Pérez-Harguindeguy et al., 2013).
Leaf sizes	Terms describing leaf size follow Raunkiaer (1934) except ‘Notophyll’. Size class: Leaf area Megaphyll: >164,025 mm^2 Macrophyll: 18,225–164,025 mm^2 Mesophyll: 2,025–18,225 mm^2 [Notophyll: 2,025–4,500 mm^2] Microphyll: 225–2,025 mm^2 Nanophyll: 25–225 mm^2 Leptophyll: <25 mm^2
Mass movement	Bulk movements of soil and/or rock debris down slope or vertically downwards in response to gravity.
Mesophotic	A zone of moderate light intensity that can support photosynthesis.
Meromictic lakes	Lakes with waters that rarely mix from top to bottom, and thus remaining semi-permanently stratified into stable layers with contrasting temperature and hydrochemistry and biota.
Monomictic lakes	Lakes with waters that mix from top to bottom once per year, regardless of whether the surface freezes in winter, although the seasonal timing of mixing depends on whether surface freezing occurs.
Peat	A deposit of partially decayed organic matter in the upper soil horizons.
Periphyton	Biofilm. A complex layer composed of algae, cyanobacteria and heterotrophic microbes embedded in a mucopolysaccharide matrix cohering to submerged aquatic surfaces. Important food source for aquatic animals.
Photoautotroph	An organism that fixes carbon from its surroundings using energy from light.
Phreatic	Related to groundwater or aquifers.
Polymicitic lakes	Lakes with waters that mix continuously from top to bottom, and thus are never vertically stratified, usually due to their shallow depth.

Primary productivity*	The amount of chemical energy (expressed as carbon biomass) that autotrophs create in a given length of time.
Resources	Five fundamental resources in the environment that are essential to sustaining all life: water, nutrients, oxygen, carbon and energy.
Ruderal	Plants with a combination of life-history traits that enable colonisation of open post-disturbance environments. Traits and related trade-offs include rapid growth, high fecundity, wide propagule dispersal, short life-span, high demands for nutrients and intolerance of competition.
Sclerophyll	Plants or vegetation bearing leaves hardened by an abundance of woody tissue (sclerenchyma) and thick cuticles. Typically associated with environments that experience limited nutrients or water or cold stress.
Secondary productivity	Biomass of heterotrophic (consumer) organisms generated in a given length of time, driven by the transfer of organic material between trophic levels.
Serotinous	Refers to seedbanks that are held in woody fruits retained on the parent plant for later release, which may occur spontaneously or en masse in response to fire or adult mortality.
Semelparous	Plant life cycle with a single reproductive episode before death.
SLA	Specific Leaf Area, the ratio of area of a fresh leaf to its dry mass. Positively related to plant relative growth rate (Pérez-Harguindeguy et al., 2013).
Succulent	Having tissues (usually leaves or stems of plats) engorged with water, as a mechanism for drought tolerance or salt dilution.
Ultramafic	Rocks and derivative soils with low silica content, also low in Potassium, but with high concentrations of Magnesium and Iron.
Xeromorphic	Plants and animals possessing traits that enable them to tolerate drought by storing water, enhancing uptake and reducing loss. Example traits include nocturnal activity, deep roots, etc.

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*Descriptive profiles use ordinal descriptors (high, medium, and low) of productivity (such as for Net Primary Productivity), unless otherwise stated. For terrestrial and transitional realms, these descriptors are based on estimates from an ensemble of global vegetation models (Cramer et al., 1999; Kicklighter et al., 1999; Huston & Wolverton, 2009). For marine surface systems, they are based on estimates of chlorophyll a concentration for the upper 30 m of the water column (Sarmiento et al., 2004; Huston and Wolverton, 2009):

High: >2,000 g dry mass m^{-2}.yr^{-1} for terrestrial and transitional ecosystems; >8 mg.m^{-3} chlorophyll a concentration for marine ecosystems.
Medium: 500–2,000 g dry mass m^{-2}.yr^{-1} for terrestrial and transitional ecosystems; 0.1–8 mg.m^{-3} chlorophyll a concentration for marine ecosystems.
Low: <500 g dry mass m^{-2}.yr^{-1} for terrestrial and transitional ecosystems; <0.1 mg.m^{-3} chlorophyll a concentration for marine ecosystems.

Introduction

The conservation and management of ecosystems has never been more central to the future of biodiversity and human well-being on Earth. The Convention on Biological Diversity post-2020 agenda (CBD, 2020) and UN Sustainable Development Goals (UN, 2015) mandate global action that depends on ecosystem assessment. Ecosystems are integral components of biodiversity, along with species and genes. Rapidly developing information infrastructure to support these global policy initiatives includes the UN System of Environmental-Economic Accounting – Experimental Ecosystem Accounting (SEEA EEA), listing criteria for the IUCN Red List of Ecosystems (RLE) and Key Biodiversity Areas (KBA), among several other initiatives. All of these require a standardised, globally consistent, spatially explicit typology and terminology for managing the world's ecosystems and their services.

IUCN's Commission on Ecosystem Management is leading a global initiative to develop a new functional typology for the world's ecosystems. The IUCN recently adopted its Global Ecosystem Typology to support global, regional and national efforts to assess and manage risks to ecosystems (Motion 074, IUCN World Conservation Congress, Marseillle 2020). By supporting the organisation of knowledge on both ecosystem functions and compositional features, this typology will help identify the ecosystems most critical to biodiversity conservation and supply of ecosystem services, as well as those at greatest risk of collapse, informing sustainable ecosystem management into the future. It will provide a comprehensive and consistent global framework for reporting on post-2020 CBD targets (CBD, 2020), SDGs, natural capital accounting, as well as structuring global risk assessments for the Red List of Ecosystems (Keith et al., 2013; 2015).

Key features of the IUCN Global Ecosystem Typology include:

- A hierarchical structure that represents functional features of ecosystems in three upper levels and compositional features in three lower levels;
- Comprehensive coverage of earth's biosphere, encompassing terrestrial, subterranean, freshwater, marine and atmospheric environments;
- Top-down construction of upper levels to ensure global consistency and bottom-up construction of lower levels to promote local accuracy and ownership;
- Structural integration of established national classifications, which form the lowest level of the hierarchy (Level 6);
- Detailed documentation, including illustrated descriptive profiles for 108 Ecosystem Functional Groups (Level 3);
- Indicative global maps of Ecosystem Functional Groups (Level 3), to be developed into high resolution digital models;
- Standard terminology and definitions to promote consistent application; and
- Strong scientific foundations in community assembly theory.

One of the major innovations of the typology is its dual representation of ecosystem functionality and composition. These two components are integrated into the hierarchical structure of the classification, with functional variation among ecosystems primarily represented in the top three levels of classification, and compositional variation represented in the lower three levels of classification. The purpose of the typology is not to revisit or duplicate existing biogeographic classifications, but to complement them in a framework that supports a broader utility for conservation management and other applications.

The typology is founded on a conceptual ecosystem model that draws on community assembly theory (Keith et al., in review). We adapted this generic model to help resolve biological and physical properties that distinguish functionally different groups of ecosystems from one another, and different ecological drivers that come to the fore in structuring their assembly. Hence, each functional group has a diagrammatic representation of its key traits and processes.

The purpose of this report is to provide technical descriptive details of the upper three levels of the Global Ecosystem Typology v2.0. Hence, its focus is on functional properties of ecosystems, rather than biogeographic and compositional features, which are represented in the three lower levels of the typology to be addressed in forthcoming publications.

Part I

Rocky shore, Seilebost, Isle of Harris, Scotland.
Source: Helen Hoston/Alamy Stock Photo

1 Development of the typology

The typology has been through an extensive development and review process initiated and co-ordinated by the IUCN Commission on Ecosystem Management. The initial structure of the typology was developed at a forum attended by 48 specialists in marine, freshwater and terrestrial ecosystems at Kings College London in May 2017. Lead contributors among the workshop participants then drafted descriptive profiles for each Ecosystem Functional Group in consultation with other experts. The definition and arrangement of units within the typological hierarchy was iteratively reviewed and adapted by workshop participants as the profiles were prepared (out of session, post-workshop) to ensure coverage of the range of variation in ecosystems throughout the biosphere.

The IUCN Commission on Ecosystem Management co-ordinated an extensive global consultation, review, testing and revision process in four phases. The first phase of consultation involved presentations describing the objectives, conceptual basis and structure of the typology at a series of international meetings designed to elicit input on those aspects and to engage participants in refining the description of the units. The 16 presentations and associated discussions were held at dedicated workshops arranged by IUCN Commission on Ecosystem Management and international conference symposia, each attended by 20–100 participants, at the following locations and dates:

- London, UK May 2017– IUCN workshop/meeting
- Cartagena, Colombia, July 2017 – IUCN workshop/meeting
- Cartagena, Colombia, July 2017 – ICCB symposium
- Naypyidaw, Myanmar, Sept 2017 – IUCN workshop/meeting
- Newcastle, Australia, November 2017 – ESA symposium
- Canberra, Australia, May 2018 – Boden conference
- Davos Switzerland, June 2018 – Polar2018 symposium
- Gland Switzerland June 2018 – IUCN workshop/meeting
- Amman, Jordan, September 2018 – IUCN workshop/meeting

- Dubai, UAE, Oct 2018 – Eye ON Earth symposium
- Kuala Lumpur, Malaysia July 2019 – ICCB symposium
- Maputo, Mozambique, March 2019 – IUCN workshop/meeting
- Mombasa, Kenya March 2019 – IUCN workshop/meeting
- New York, USA, June 2019 – UN SEEA-EEA forum of experts

Based on input from working group members and from the participants in consultation meetings, v1.0 of the Global Ecosystem Typology was completed in October 2019, with descriptions and indicative maps for 102 Ecosystem Functional Groups arranged within 25 biomes and five realms. In February 2020, v1.01 of the typology with one additional functional group was published in a report made available through the IUCN Red List of ecosystems website.

The second phase was an intensive peer review of the descriptive profiles and maps by leading ecosystem scientists whose expertise spanned all biomes in the typology. The peer review process was managed by Associate Professor Emily Nicholson (Deakin University). A total of 48 specialists undertook 235 reviews of profiles. Their contributions represent the collective views of global research networks numbering hundreds of experts. A comprehensive revision of the typology and the descriptive profiles was undertaken in response to reviewer comments. The revisions included the addition of five Ecosystem Functional Groups to the typology to encompass variation that was not well unaccounted for in v1.01, major revisions to profiles of four existing Ecosystem Functional Groups and a large number of fine adjustments to the text, diagrammes and maps across all remaining Ecosystem Functional Groups. In addition, a global review of map data sets available for ecosystems enabled the coarse-scale indicative maps of EFGs to be replaced with maps of greater spatial resolution, which were standardised to a 30 arc-second latitudinal and longitudinal grid. These revisions were incorporated into v2.0 of the typology (this report).

The third phase involved testing the typology by developing cross-walks with established national classifications of ecological units. The majority of these classifications were for terrestrial environments based on features of surface vegetation, some were for freshwater environments and a few covered marine environments. The cross-walks were based on expert elicitation. Experts were asked to estimate membership values (0–1) for each unit of a national classification, representing their degree of confidence that it belongs to each global functional group (e.g. membership values of '1' represent no reasonable doubt that national unit 'X" belongs to functional group 'Y'; '0' represents no reasonable doubt that national unit 'X" DOES NOT belong to functional group 'Y', and intermediate values indicate varying levels of uncertainty in membership). The detailed methods and results of this work will be published elsewhere. Information on uncertain membership relationships was used to resolve ambiguities in the description of Ecosystem Functional Groups and develop a description for one additional group. These revisions were incorporated into v2.0 of the typology (this report).

The fourth phase was a further peer review. Two experts, one terrestrial specialist and one marine specialist, were engaged to review the entire report, including descriptive profiles for Ecosystem Functional Groups within their respective areas of expertise. The revisions arising from these reviews were incorporated into v2.0 of the typology (this report).

The process outlined above involved up to six iterations of review and revision for each descriptive profile, and sometimes involved significant addition of content, revision of group definitions or recognition of additional groups. All profiles were reviewed and edited for conceptual consistency by the lead author, and subject to a final production edit by Dr Lucie Bland.environmental variables) and appropriate methods for spatial interpolation (Guisan & Zimmermann, 2000).

2 Design principles

'Ecological' typology is defined as a classification of land or water intended to represent variation in the expression of multiple ecological features. Traditional approaches to ecological classification have been based on biogeography or biophysical attributes, with approaches differing between terrestrial, freshwater and marine disciplines. Ecosystem classifications are specific kinds of ecological typologies based on units that conform to the definition of ecosystems (e.g. ecological units that comprise a biotic complex, an abiotic complex, the interactions between and within them, and occupy a finite physical space; Keith et al., 2013).

Six design criteria for a global ecosystem typology were developed to serve the dual needs for conservation and sustainability of ecosystem services (Table 1). Critically, an ecosystem typology must represent both ecosystem

Table 1. Design principles for a global ecosystem typology

	PRINCIPLE	DESCRIPTION	RATIONALE
1	**Representation of ecological processes**	Groupings reflect major ecological processes, shaping ecosystem assembly and maintaining their defining characteristics and traits.	Enables generalisations and predictions about ecosystem functions and dynamics; responses to environmental change and management actions. Major ecosystem components, drivers, states and transitions should be consistent within a group.
2	**Representation of biota**	Within groups, ecosystems distinguishable through differences in the identity (composition) of their biota.	Enables generalisations and predictions about biodiversity for conservation and management applications. Units reflect not only functions, but the identity of engaged biota.
3	**Conceptual consistency throughout the biosphere**	The typology should encompass all components of the biosphere within a single theoretical framework.	Promotes comprehensive coverage of ecosystems from all environments, logical consistency, robust ecosystem identification and comparison between units.
4	**Scalable structure**	Groupings should be arranged in a hierarchical or nested structure to reflect the nature and magnitude of their similarities.	Enables representation of different features at particular hierarchical levels and facilitates applications across a range of spatial and organisational scales.
5	**Spatially explicit units**	Distributions of units should be mappable through any practical combination of ground observation, remote sensing and spatial modelling.	Enables comparative spatial analyses and time series analyses of ecosystem extent and distribution for monitoring and reporting.
6	**Parsimony & utility**	The typology should be no more complex than required to achieve other specifications and should use simple, accessible and clearly defined terminology.	Facilitates wide usage among people with varied objectives, skills and backgrounds.

functions and the biota engaged in them. In addition, for application across the globe's diverse ecosystems, users and scales of analysis, it must be conceptually consistent throughout the biosphere, have a scalable structure, spatially explicit units and avoid superfluous complexity.

Prior to developing the typology, a sample of 23 ecological typologies was reviewed, finding none that met all of the design principles (Keith et al., in review). None explicitly represented both ecological functions and biota, limiting the ability of ecosystem managers to learn from related ecosystems with similar operating mechanisms and drivers of change. Furthermore, only three typologies encompassed the whole biosphere. For some ecological typologies, a limited or poorly articulated theoretical basis constrains their ability to generalise about properties of ecosystems grouped together. Many existing typologies also failed to describe their units in sufficient detail for reliable identification or required diagnostic features that are hard to observe.

One of the major innovations of the typology is its dual representation of ecosystem functionality and composition, which are integrated into the hierarchical structure of the classification. Functional variation among ecosystems is primarily represented in the top three levels of classification, and compositional variation is represented in the lower three levels. This report focuses on the upper three levels of the typology, hence the emphasis on function, rather than composition or biogeographic patterns. The purpose is not to revisit or duplicate existing biogeographic classifications, but to complement them in a framework that supports a broader utility for conservation management and other applications related to ecosystem function. As an example, tropical forests, like other biomes, are functionally convergent across land masses – they share many functional traits even though they share few species (or even genera). Different biogeographic expressions of functionally convergent ecosystems are important (for conservation and other purposes), and are recognised as separate units at increasingly finer thematic scales within Levels 4–6 of the typology. At Level 4, for example, different expressions of tropical lowland rainforests are recognised within different ecoregions, which serve as templates for dividing that functional group into biogeographically (and thus compositionally) distinctive units. Level 3 units are therefore identified as '**functional groups**' of different ecosystem types, i.e. the members of the group are not 'the same'.

3 Levels of classification within the Global Ecosystem Typology

The typology comprises a nested hierarchy of units (Figure 1; Table 2) to facilitate application at different organisational scales and enable integration of existing classifications where possible (Principle 4, Table 1). Groupings in three upper levels of the typology (Table 2) represent ecosystems that share functional properties, irrespective of the biota engaged in the functions (Principle 1). The units of these upper levels were developed from the top-down (Figure 1), with successive division to ensure global consistency and comprehensive coverage (Principle 3). We use codes M, F, T, S and A for systematic labelling of ecosystem units within the Marine, Freshwater, Terrestrial, Subterranean and Atmospheric realms, respectively, and combinations of these for labelling ecosystems transitional between the realms.Three lower levels of the typology (Table 2) were designated to represent units with similarities in functions but contrasting biotic composition (Principle 2, Table 1). The units of these progressively finer levels will be elaborated in future publications. The units of Level 4 will be developed top-down by division of Level 3 units (Figure 1). In contrast, Levels 5 and 6 facilitate integration of established local classifications into the global framework. Integration will progress from the bottom-up (Figure 1) to exploit local data, detailed knowledge and local ownership vested in established national and subnational typologies, are already in use, or to be developed in the future.

The overall structure of the typology is a simple hierarchy, with groups of units at each level nested within a broader unit at the level above. An important variation to this simple structure involves the units at Levels 4 and 5, which are both nested within level 3 units (Figure 1; Table 2). In other words, Level 4 (derived from the top-down) and level 5 (derived from the bottom-up) represent alternative pathways below Level 3. Thus, units at Levels 5 and 6 are nested directly within Level 3, not within Level 4.

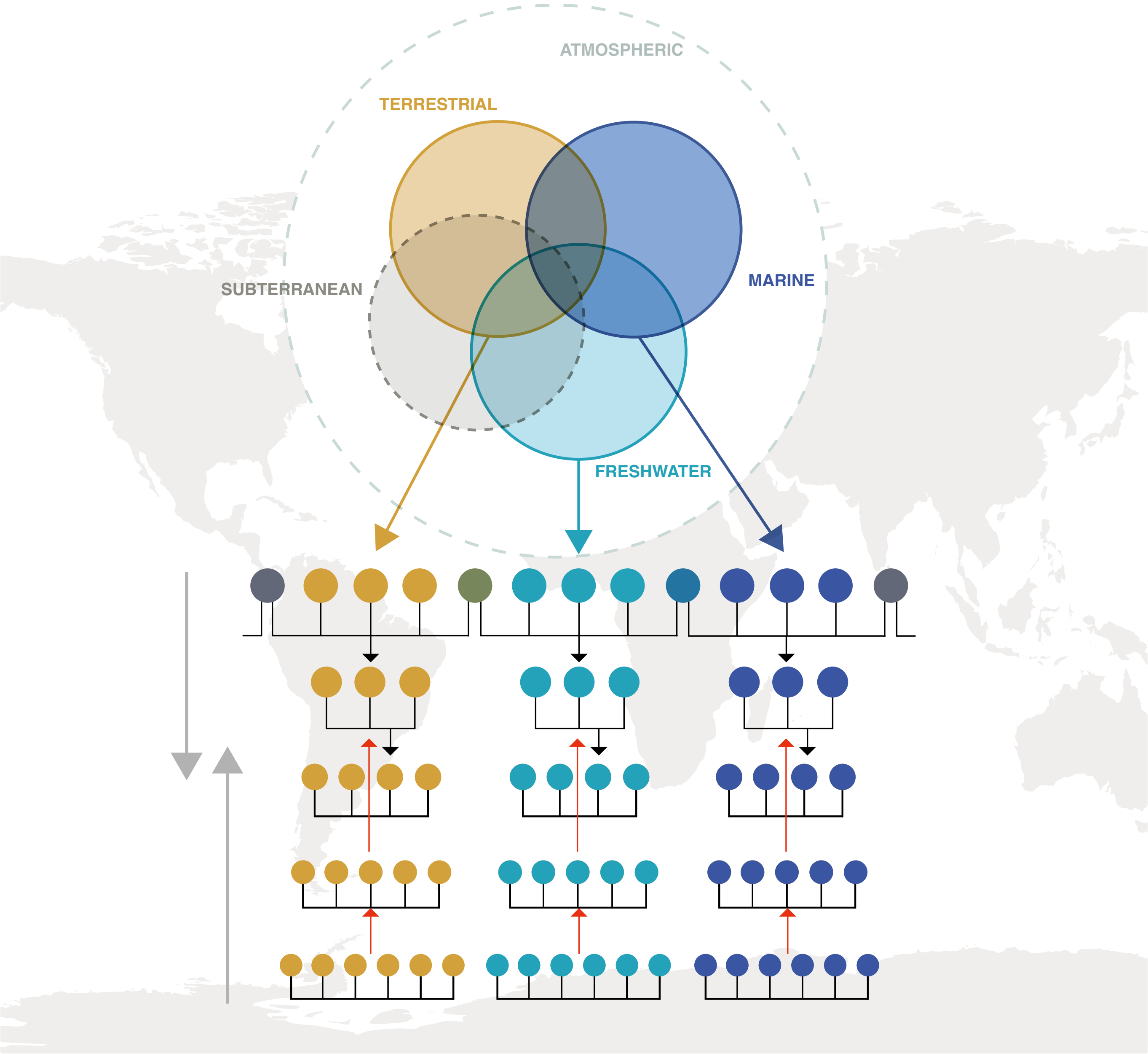
3.1 Realms

The five realms represent all parts of the biosphere. A conceptual model of ecosystem assembly (Keith et al., in review) was used to describe and compare the ecological drivers and traits that characterise the five realms. This comparative analysis helped to identify major gradients of variation and informed the definition of functional biomes (Level 2) and Ecosystem Functional Groups (Level 3) within each realm. Examples of these gradients are illustrated in Figure 2. The comparative analysis was refined iteratively as Levels 2 and 3 of the typology were developed, enabling a synopsis of ecosystem drivers and traits that shape contrasting functional groups of ecosystems within each realm (Table 3) and a comprehensive overview of ecosystem function across the biosphere.

The **terrestrial realm** includes all dry land, its vegetation cover, proximate atmosphere and substrate (soils, rocks) to the rooting depth of plants, and associated animals and microbes. Water and nutrients are the principle resource drivers, with energy, oxygen and carbon rarely limiting (Table 3). Temperature and its variability on interannual, seasonal and diurnal time scales, is a major ambient environmental driver, with ecosystem function and structure responding to global latitudinal and altitudinal climatic gradients. Fire is a major ecosystem driver, essentially unique to the terrestrial realm, although it may occur rarely in the subterranean realm. In addition to direct environmental filtering, gradients in these key resources, ambient environmental factors (notably temperature) and disturbance regimes influence biotic interactions, with the strength of competition, predation and pathogenicity varying greatly across the realm. Human activity is a key driver through structural manipulations associated with land use, but also through movement of biota and anthropogenic climate change. The complexity of trophic webs is similarly variable, with vegetation a key feature in the expression of different ecosystem types within the realm.

The **subterranean realm** includes the earth's crust and subsurface voids characterised by an absence or very low intensity of sunlight. Energy is therefore a major

Figure 1 Hierarchical structure of Global Ecosystem Typology



Top cluster shows thematic overlaps of all five realms, recognising the continuous nature of variation.The expanded structure of three of the realms is elaborated (Atmospheric and Subterranean realms are not shown to simplify the diagramme). The biomes of three core realms and associated transitional biomes are shown in different colours. Units in three upper levels (five realms, 25 biomes and 108 Ecosystem Functional Groups) are distinguished based on ecosystem function, irrespective of compositional differences in biota (Table 2). The bottom three levels (biogeographic ecotypes, global ecosystem types and subglobal ecosystem types) represent units with progressively finer compositional distinctions within groups of functionally similar ecosystems. Black arrows show top-down delineation of four upper levels by successive splitting, in contrast to Levels 5 and 6 aggregated from the bottom-up and assigned to Level 3 units (shown with red arrows). Hence, note that Levels 4 and 5 represent alternative classificatory pathways beneath Level 3, such that Level 5 is not nested within Level 4.

Source: Keith et al. (in review).

resource driver in these ecosystems, although other resources, such as water and carbon, may sometimes be limiting (Table 3). The ambient environment is relatively stable, although extreme temperatures occur in local areas influenced by vulcanism and substrate type influences the availability of nutrients and seepage of moisture. Disturbances are rare and limited to mass movement or subterranean fires restricted to coal, oil or gas strata, with combustion rates limited by oxygen. Subterranean trophic webs are truncated, lacking photoautotrophs, herbivores and large predators. The microbial biota is a key feature in the expression of different subterranean ecosystems.

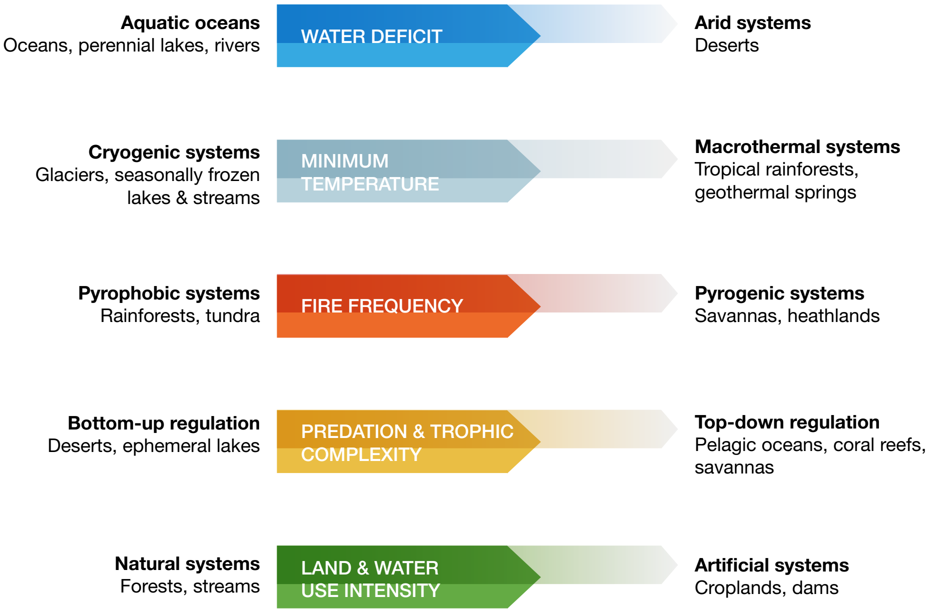
The **freshwater realm** includes all permanent and temporary freshwater bodies as well as saline water bodies that are not directly connected to the oceans. Although some authorities describe this same unit as 'inland water bodies', we follow a conventional interpretation that includes saline water bodies as 'freshwater' for nomenclatural brevity and to avoid implications that freshwaters are always distant from the coast. Hydrological regimes defined by flow velocity and frequency, duration, depth and extent of inundation are critical to the structure and function of these 'freshwater' ecosystems. They regulate allochthonous inputs of water and nutrients from catchments, as well as inundation and drying regimes, and turbulence (Table 3). Catchment geomorphology, substrates and climate are key components of the ambient environment that regulate resource inputs and disturbance regimes. Trophic complexity increases with the size and connectivity of the water body. Biota of the benthos and the water column are closely associated with flow regimes and catchments in the diverse expressions of freshwater ecosystems.

The **marine realm** includes all connected saline ocean waters characterised by waves, tides and currents (Table 3).

Table 2 Definitions of hierarchical levels within the global ecosystem typology

	LEVEL	DEFINITION
1	**Realm**	One of five major components of the biosphere that differ fundamentally in ecosystem organisation and function: terrestrial, freshwater, marine, subterranean, atmospheric
2	**Functional biome**	A component of a realm united by one or a few common major ecological drivers that regulate major ecological functions. Biomes are derived from the top-down by subdivision of realms (Level 1).
3	**Ecosystem Functional Group**	A group of related ecosystems within a biome that share common ecological drivers promoting convergence of biotic traits that characterise the group. Functional groups are derived from the top-down by subdivision of biomes (Level 2).
4	**Biogeographic ecotype**	An ecoregional expression of an ecosystem functional group derived from the top-down by subdivision of Ecosystem Functional Groups (Level 3). They are proxies for compositionally distinctive geographic variants that occupy different areas within the distribution of a functional group.
5	**Global ecosystem type**	A complex of organisms and their associated physical environment within an area occupied by an Ecosystem Functional Group. Global ecosystem types grouped into the same Ecosystem Functional Group share similar ecological processes, but exhibit substantial difference in biotic composition. They are derived from the bottom-up, either directly from ground observations or by aggregation of sub-global ecosystem types (Level 6).
6	**Sub-global ecosystem type**	A subunit or nested group of subunits within a global ecosystem type, which therefore exhibit a greater degree of compositional homogeneity and resemblance to one another than global ecosystem types (Level 5). These represent units of established classifications, in some cases arranged in a sub-hierarchy of multiple levels, derived directly from ground observations.

Figure 2 Examples of major ecosystem assembly filters represented as gradients segregating functionally contrasting ecosystems



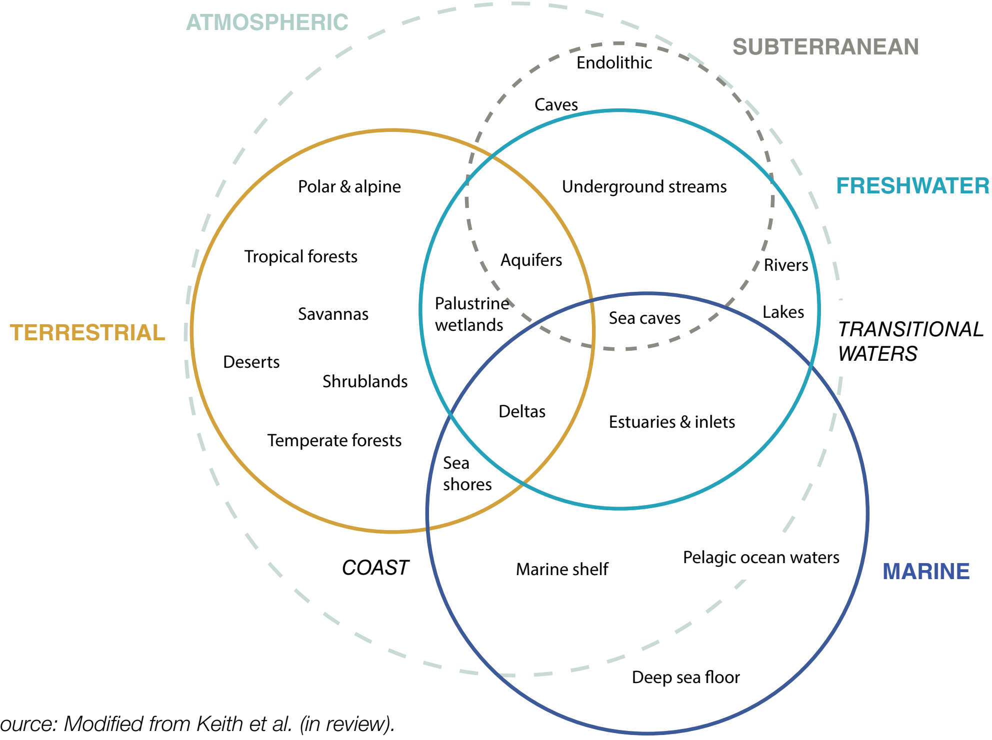
Source: Keith et al. (in review).

These processes transport resources and biota over short temporal and local spatial scales (waves), while global circulation occurs over centuries via deep ocean currents. The availability of light and nutrients diminishes along depth gradients. Oxygen may be locally limited in zones of high heterotrophic activity. Salient ambient environmental factors, such as substrate type (hard vs soft), influence the traits of benthic fauna and geomorphology, as well as the movement of deep currents and local or regional upwelling. Upwelling is critical to supply of nutrients to euphotic waters, and hence productivity and trophic complexity. Water temperature influences metabolic rates of most marine biota, and regional and local temperature gradients are therefore critical to their distributions. Primary productivity is contributed mainly by planktonic algae, but benthic macrophytes can make important contributions on parts of the marine shelf. Trophic interactions are critical to the structure of many marine ecosystems through top-down regulation.

The **atmospheric realm** includes the gaseous medium and its suspended particulate liquids and solids above the terrestrial realm, extending to the altitudinal limits of life. Altitudinal gradients strongly structure the diminishing availability of water, nutrients and oxygen, coincident with declines in ambient temperatures and barometric pressure, and increasing UV-B radiation (Table 3). Nonetheless, atmospheric ecosystems are among the most dynamic over time scales of days to decades driven by planetary oscillations. We deferred resolution of lower levels within the atmospheric realm, because knowledge of the biotic components of these ecosystems is currently poor. Additional challenges to classifying atmospheric ecosystems are posed by their sparse and itinerant biota, represented mainly by dispersive life stages. Meteorological classifications based on patterns of weather and air masses suggest a way forward to identify distinguishing drivers and traits of atmospheric ecosystems.

Transitional realms accommodate continuous variation among the core units (Figure 3). The interface between terrestrial and freshwater realms is occupied by palustrine wetlands, some of which accumulate peat under impeded substrate drainage. The freshwater-marine transitional realm is occupied by brackish aquatic ecosystems on marine coasts. The marine-terrestrial transitional realm is characterised by steep environmental gradients in desiccation, temperature, salinity and wave and tide disturbance, occupied by contrasting shoreline ecosystems. The interface of marine and terrestrial ecosystems is sometimes influenced by seepage or outflow of freshwater, supporting intertidal wetlands and deltaic systems. Unique ecosystems also occur where the subterranean realm meets the interface of freshwater and marine realms, respectively.

Figure 3 Continuous variation and transitions states among realms. Broken lines represent overlaps of Subterranean (grey) and Atmospheric realms (light blue) in a fourth dimension. Transitional realms and biomes shown in italics.



Source: Modified from Keith et al. (in review).

3.2 Biomes

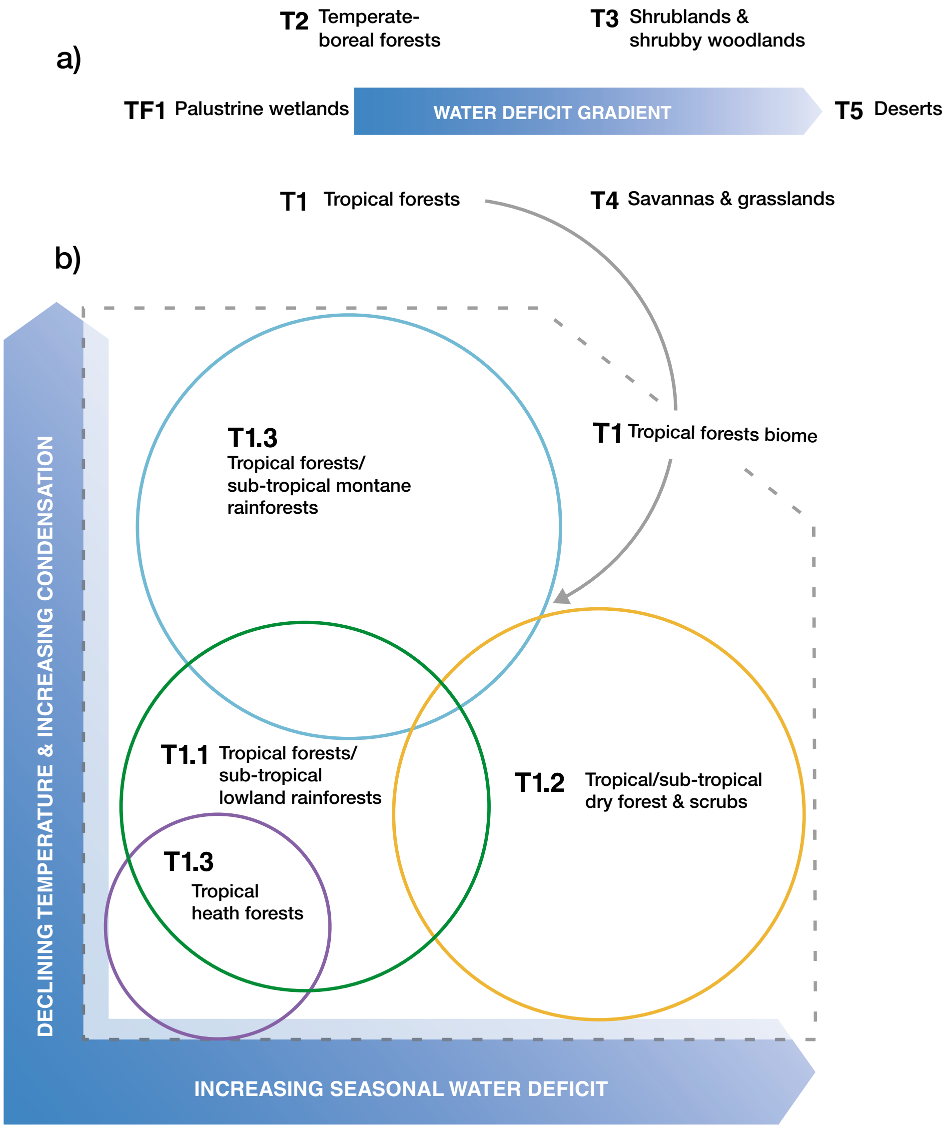
The biome concept evolved from its original application to continental-scale vegetation units associated with major climate types, to units reflecting functional and evolutionary processes, albeit still with an emphasis on terrestrial vegetation (Mucina, 2019). Here, elements of the functional biome concept proposed by Moncrieff et al. (2016) and generalised by Mucina (2019) were adopted. A deductive approach to definition of units was taken, using the report's conceptual model to focus a priori on convergent ecosystem functions and traits that are shaped by one or more dominant assembly processes (Keith et al., in review; Table 3).

The focus on traits and the ecological drivers that shape them, albeit qualitative, enabled the extension of the traditional scope of the biome concept from vegetation-climate relationships on land (Ricklefs & Relye, 2018) to the entire biosphere. For example, functional distinctions justify recognition of different biomes on marine shelfs and the deep sea floor. Marine shelfs host diverse photoautotroph communities of benthic macrophytes, symbiotic algae, epiphytic algae and planktonic algae, compared to the deep sea floor, where a lack of sunlight precludes the existence of any photoautotrophs. The pelagic ocean waters, with exclusively planktonic autotrophs that diminish with depth (due to sunlight attenuation), define a third functionally distinctive biome in the oceans. Conceptually, such distinctions in ecosystems are analogous to those between traditionally recognised terrestrial biomes. For example, tropical forests and deserts show marked contrasts in structural features of their autotroph communities that are shaped by the availability of water. In both cases, the functional differences between biomes rests on a diagnosis of major assembly filters that come to the fore in shaping functional traits of the ecosystems. Although the diagnoses involve subjective judgements, a common conceptual model (Keith et al., in review) is critical to clear justification and recognition of separate biomes.

The 25 biomes recognised in v2.0 of the IUCN Global Ecosystem Typology are described in Part II. As noted above, many conform to 'traditional' terrestrial biomes (e.g. Whittaker, 1975; Ricklefs & Relye, 2018) because of the close interrelations between functional traits and plant dominant growth forms. Other functionally distinctive groupings fall outside the traditional scope of the biome concept, including lentic and lotic freshwater biomes, pelagic and benthic marine biomes, and several anthropogenic biomes. Ecosystems in this latter group are created by human activity, which continues to drive and maintain their assembly (Ellis et al., 2010).

Figure 4

a) Relationships of terrestrial biomes to a major assembly filter represented by a water deficit gradient (five of seven terrestrial biomes shown).
b) Relationships of four ecosystem functional groups to two environmental gradients (representing major assembly filters) elaborated within the Tropical forests biome (T1). A third filter related to an edaphic gradient differentiates group T1.4 from T1.1 (not shown here).



Source: Modified from Keith et al. (in review).

3.3 Ecosystem Functional Groups

Expert working groups for each realm delineated candidate Ecosystem Functional Groups (EFG) (Level 3) through a development and review process described above (see section 1). They identified gradients in key assembly filters for each biome and major ecosystem and species traits that vary among them (Table 3). In terrestrial environments, key assembly gradients include water deficit, seasonality, temperature, nutrient deficiency, fire activity and herbivory. In subterranean environments, substrate structure is a major factor. In freshwater environments, gradients in flow continuity and velocity, water body size, seasonal freezing and salinity are key assembly filters. In marine environments, depth gradients in light, vertical and horizontal movement of nutrients, temperature gradients and stability, and substrate stability and particle size are major assembly filters.

Experts delineated candidate functional groups by identifying distinctive sets of traits associated with particular segments of the assembly filter space defined by the gradients. An example for tropical forests in Figure 4 illustrates how Ecosystem Functional Groups were delineated using reasoning based on the conceptual model of ecosystem assembly (Keith et al., in review).

In the Terrestrial realm, variation in ecosystem functions is closely related to a water deficit gradient (Figure 4a). Water surplus occurs at the interface with the Freshwater realm, an environmental space occupied by the Palustrine Wetlands biome. Several biomes replace one another along the gradient of increasing water deficit, with the Tropical/subtropical forests biome occupying a mesic segment of this gradient. Within that biome, we identified seasonal water deficit and temperature as two specific assembly filters that enable recognition of three functional groups of forest characterised by distinctive combinations of traits (Figure 4b). Tropical/subtropical lowland rainforests (Functional group T1.1) develop under water surplus for most of the year and consistently warm temperatures (limited frost incidence). They are characterised by high diversity and endemism, a dense evergreen tree canopy, high structural complexity and several other traits (see description of T1.1 for details). Tropical heath forests (Functional group T1.4) occupy a similar, but more restricted hydrological and thermal niche with respect to the environmental gradients in Figure 4b, but are differentiated by a third assembly filter related to a gradient in soil acidity and nutrient status (not shown in Figure 4b). As the seasonal water deficit increases, these humid forests are replaced by Tropical/subtropical dry forests (Functional group T1.2). The distinctive traits of these dry forests include seasonal phenology (including deciduousness), reduced leaf area, and scarcity of certain life forms such as ferns and bryophytes, etc. (see description of T1.2 for details). A fourth functional group (T1.3) occurs in tropical montane environments that experience cooler temperatures, moderate frosts and regular fogs. These forests are distinguished by their simpler evergreen tree canopies with a smaller range of leaf sizes, high epiphyte loading, an abundance of ferns and bryophytes, high local endemism and lower plant and animal diversity (see description of T1.3 in Part II for details).

For each of the 108 EFGs recognised in v2.0 of the typology, we represented the key drivers and traits in simplified conceptual models derived from the generic assembly model (Keith et al., in review) as a basis for review and description. We adjusted and augmented descriptions based on published reviews (see cited references in the descriptive profiles below) and in consultation with broader networks of specialists (see section 1, Development of the typology).

Finally, we prepared indicative global distribution maps for each EFG from available spatial data. In some cases, modifications were made to the source data sets where it was necessary to align the mapped entities with the concept of EFGs (as described in the profiles) or to accommodate comments of expert reviewers. The full details of map compilation for each functional group are given below (see 'Indicative distribution maps').

3.4 Lower levels of classification

The three lower levels of the typology are designed to represent different compositional expressions of functionally convergent groups of ecosystems. They will be developed progressively through two contrasting approaches that involve different trade-offs, strengths and weaknesses. Firstly, Level 4 units (Biogeographic ecotypes) will be developed from the top-down, by subdividing EFGs using an ecoregional template. Ecoregionalisations (e.g. Spalding et al., 2007; Abell et al., 2008; Dinerstein et al., 2017) serve as simple and accessible proxies for biotic composition based on biogeographic boundaries and have recently been shown to delineate biodiversity patterns effectively, at least on land (Smith et al., 2018). The efficacy of spatial proxies for biodiversity is underpinned by niche differentiation and variation in species' interactions along regional gradients, insularity and historical legacies of vicariance and dispersal (Chase, 2003; Maestre et al., 2009; Nekola & White, 2009). Assuming two to five functional groups may be represented in each ecoregion, we estimate 3,000–7,500 units could be identified across the biosphere at Level 4. An important limitation of this approach is that ecoregional proxies impose the same fixed spatial template across all Ecosystem Functional Groups. The lack of flexibility limits the scope for adjustment of units even where a more evidence-based delineation of units is possible.

The second approach addresses this problem by developing Levels 5 and 6 of the typology (global and sub-global ecosystem types, respectively) from the bottom-up. In practice, sub-global ecosystem types will be based on established local classifications (e.g. Mucina & Rutherford, 2006). These benefit from the abundance of direct observational data and expertise available at local scales. Incorporating these classifications into a global framework acknowledges the value of substantial investments in data acquisition and development, as well as the integration of these classifications into policy instruments and management plans. Improved local accuracy and precision however, are traded off against inconsistencies that inevitably exist between local classifications based on different data sets and methods of construction. Sub-global ecosystem types will be aggregated into global ecosystem types (Level 5) based on compositional similarities. This will help resolve some of the inconsistencies between different classifications. In turn, global ecosystem types (Level 5) will be assigned to EFGs (Level 3) based on their key ecological traits and drivers.

As noted previously, Level 5 units are not nested within Level 4 units because they are alternative pathways for representation of variation in biotic composition within Ecosystem Functional Groups (Level 3). The more complex, non-nested relationship between units of Levels 4 and 5, including one to many, many to one and one to one, could ultimately be mapped in a cross-walk based on methods identified in the next section.

Table 3 Assembly filters and ecological traits distinguishing ecosystems within the five realms of the biosphere*

REALM	TERRESTRIAL	SUBTERRANEAN	FRESHWATER	MARINE	ATMOSPHERIC
Substrate	Soil/Rock	Rock	Separate fresh and saline waters and benthos	Connected saline waters and benthos	Atmospheric gases
RESOURCE FILTERS					
Water	Climatic and topographic gradients, sometimes limiting	Diffusion gradients, sometimes limiting	Climatic & topographic gradients, sometimes limiting	Not limiting	Convection and turbulence, limited to vapour and condensation
Nutrients	Topographic and substrate gradients, sometimes limiting, climatic leaching	Substrate and seepage gradients, sometimes limiting	Catchment substrates and stratification gradients, sometimes limiting	Sometimes limiting along depth and mixing gradients; deviations from the C:N:P Redfield ratio	Limited to aerosols
Energy	Euphotic, rarely limiting except at high latitude or by autotrophic competition	Aphotic, principally chemical sources, limiting	Mostly euphotic-mesophotic (rarely aphotic), depth and turbidity gradients, sometimes limiting	Euphotic-aphotic, depth, turbidity and benthic geomorphology (influencing lateral and vertical flux of organic carbon) gradients, often limiting	Not limiting
Oxygen	Rarely limiting	Diffusion and depth gradients, sometimes limiting	Turbulence, diffusion, depth and consumption gradients, sometimes limiting	Depth, mixing & consumption gradients, sometimes limiting (oxygen minimum zones)	Not limiting
Carbon	Not limiting	Diffusion gradients, often limiting	Inflow and mixing gradients, sometimes limiting	Depth and nutrient gradients, often limiting	Allochthonous sources, limiting
AMBIENT ENVIRONMENTAL FILTERS					
Temperature	Extended hot-cold climatic gradients altered locally by topography and altitude, limiting metabolic function & growing season	Geothermal heat gradients, sometimes heat-limited but typically not cold-limited	Limited climatic & depth gradients, rarely heat-limited and rarely below freezing	Latitudinal & depth gradients influence metabolism, productivity and growth, some systems heat-limited but rarely below freezing	Extended altitudinal and regional gradients

* See Figure 1.

Table 3 (continued)

REALM	TERRESTRIAL	SUBTERRANEAN	FRESHWATER	MARINE	ATMOSPHERIC
Geomorphology	Landforms influence water, nutrients, light (high latitudes)	Landform influences surface connectivity, hence water, nutrients and carbon	Topography defines catchment extent & form, water flow direction and velocity, influencing water & nutrient supply & flood regimes	Bathymetry influences currents and habitat structure, hence nutrients, carbon, oxygen & biotic processes	Topography regulate orographic uplift, hence water and atmospheric instability
Solid substrate	Soil chemistry, texture and depth gradients influence nutrients & water percolation	Lithology influences nutrients and structure	Catchment & benthic substrates influence nutrients and water percolation	Hard/soft sediment gradients define habitat structure, influence nutrients and mobility of benthic life forms	No solid substrates
Fluid circulation	Surface flow influences fine-scale nutrient and water patterns	Fluid connectivity to surface influences water, nutrients, carbon and dispersal	Directional flows and mixing influence oxygen, nutrients and biotic dispersal	Tidal regimes and currents influence nutrients, oxygen, carbon sediment transport, biotic reproduction and dispersal	Convection, wind influence water and biotic dispersal
Seasonality	Influences water, energy, temperature and phenology in many systems	Influences water in surface-connected systems	Influences flow and filling/ drying regimes, water, nutrients, temperature in many systems	Seasonal productivity of surface layers influences vertical flux of nutrients and carbon through water column and to benthos	Seasonal weather patterns influence water, temperature and wind
Interannual variability	Very high interannual variability drives boom/bust supply of water and nutrients at extremes	Low variability except in connected streams	Very high interannual variability drives boom/bust supply of water and nutrients at extremes	Low variability in most systems, but interannual climate cycles (e.g El Niño, Indian Ocean Dipole) and forage fish may drive trophic fluctuations	Regional scale cycles, such as El Niño, drive large fluctuations
UV-B radiation	May limit function at extremes of altitudinal and latitudinal gradients	Not applicable	Rarely limiting	Rarely limiting on function, diminishes with depth and turbidity	May limit function in some biota

Table 3 (continued)

REALM	TERRESTRIAL	SUBTERRANEAN	FRESHWATER	MARINE	ATMOSPHERIC
Salinity	Groundwater salinity may limit water and nutrient uptake	Rarely influential	High groundwater salinity limits uptake of water and nutrients	Relatively stable except on shorelines, rarely limiting	Not limiting
Geothermal flux	Strong influence at local scales on nutrients and temperature	Rarely influential	Local gradients influence nutrients, toxins & temperature	Local gradients influence nutrients, toxins & temperature	Not applicable
DISTURBANCE REGIME FILTERS					
Fires	Strong climatic and flammability gradients and feedbacks consume biomass and influence life histories, water and nutrients	Surface fires may influence flux of nutrients and carbon, subterranean fires rare	Catchment fires influence water and nutrient fluxes, turbidity, sedimentation rates	Rarely influential except on some shorelines	Smoke plume gradients influence convection, nutrients, carbon and other particulates
Floods	Rare events and biomass destruction may initiate regime shifts	Rare events may alter structure, remove biomass	Flood regime gradients influence life histories, lateral connectivity and flux of water, nutrients and carbon	Not influential except at river outflows	Not applicable
Storms	Climatic storm gradients influence biomass destruction, biotic dispersal, may initiate succession and regime shifts	Not applicable	Climatic storm gradients influence biomass destruction, turbidity and biotic dispersal, may initiate succession and regime shifts	Climatic storm gradients influence surface and shoreline systems, nutrient mixing, turbidity, biotic dispersal	Climatic storm gradients influence distribution of water, nutrients and biotic dispersal
Volcanism	Strong influence in local areas on nutrients and regime shifts	Structures lava tube systems; rare events my alter structure, remove biomass	Strong influence in local areas on nutrients, chemical energy and regime shifts	Strong influence in local areas on nutrients, chemical energy and regime shifts	Transient influence on particulate matter and greenhouse effects
Mass movement	Strong influence in locally steep areas, biomass destruction, succession, regime shifts	Infrequent but strong influence on ecosystem structure, connectivity	Localised but strong influence ecosystem structure, connectivity	Strong influence in tectonically active areas on nutrients, chemical energy, biomass destruction, shoreline & benthos structure	

Table 3 (continued)

REALM	TERRESTRIAL	SUBTERRANEAN	FRESHWATER	MARINE	ATMOSPHERIC
BIOTIC INTERACTIONS & FILTERS					
Autotrophic competition	Strongly vertically structured in many systems, related to resource gradients	Weak or absent	May be strong in eutrophic systems and shorelines	Limited except in a few shelf systems dominated by autotrophs (also some sessile heterotrophs)	Mostly absent
Herbivory & predation	Strong influence in many systems, related to resource gradients	Weak in most systems except the most productive	Influential on structure in some systems	Strongly influential on structure in most systems	Herbivores mostly absent, predators itinerant but potentially influential on trophic structure
Ecosystem engineers	Sessile autotrophs engineer biogenic structure and influence light, water and nutrients in most systems, animals manipulate structure in some systems	Rarely influential	Sessile plants and fish engineer structure and resources influencing oxygen and light (via turbidity)	Benthic autotrophs and consumers influence biogenic structure and sediment structure	Unlikely to be influential
Mutualisms & symbioses	Host-dependent interactions influential on survival and reproduction in most systems	Rarely influential	Host-dependent interactions influential on survival and reproduction in some systems	Host-dependent interactions influential on survival and reproduction in many systems	Unlikely to be influential
Detritivory	Invertebrate detritivores prominent in the soils of most systems, nutrient and carbon cycling	Invertebrate detritivores prominent in resource-rich hotspots, nutrient & carbon cycling	Vertebrate and invertebrate detritivores mainly on benthos, nutrient and carbon cycling	Vertebrate and invertebrate detritivores mainly on benthos, major component in some deep and transitional systems, nutrient & carbon cycling	Mostly absent
Decomposition	Fungal, archaean and bacterial decomposers prominent in soils of most systems, nutrient & carbon cycling	Archaean and bacterial decomposers are major ecosystem components, nutrient and carbon cycling	Archaean and bacterial decomposers, nutrient and carbon cycling	Archaean and bacterial decomposers, abundant in some deep systems, nutrient and carbon cycling	Physical agents (i.e. UV-radiation) likely to be more important than biological agents of decomposition

Table 3 (continued)

REALM	TERRESTRIAL	SUBTERRANEAN	FRESHWATER	MARINE	ATMOSPHERIC
ANTHROPOGENIC FILTERS					
Structural transformation	Vegetation and landform transformation via land use, excavation, ploughing, construction	Structural transformation via tunnels and mines	Bank, channel and benthos transformation via canalisation and earthworks	Transformation of biogenic, shoreline and benthic structure via engineering, bottom trawling, marine mining and dumping	Not applicable
Water extraction, diversion & impoundment	Sediment redistribution; desiccation or flooding	Desiccation or flooding	Altered flow and filling regimes	Reduced freshwater inflow to coastal systems	Not applicable
Pollution	Nutrient and toxin release, night lights	Artificial light, nutrient and toxin seepage	Eutrophication, toxin release, increased turbidity, reduced light penetration	Eutrophication and toxin release, micro- and macroplastics, increased turbidity	Release of greenhouse gases, particulates, toxins, CFCs
Assisted biotic migration	Managed and incidental translocations of organisms and propagules	Incidental introductions of microbes and invertebrates	Managed and incidental translocations of organisms and propagules	Mostly incidental translocations via shipping or aquaculture	Incidental movement mostly of propagules, i.e. via convection of urban heat
Climate change	Warming and alteration of precipitation patterns, increased variability and extreme events	Limited influence	Altered flow and filling regimes, warming, marine incursions	Warming sea surface, reduced oxygen, ocean acidification, altered circulation, upwelling processes and nutrient cycling, sea-level rise, increased storm frequency	Warming and altered air circulation, increased frequency and intensity of extreme weather
ECOLOGICAL TRAITS					
Energy Sources	Mostly autochthonous	Allochthonous	Mixed	Mixed, but allochthonous at depth	Allochthonous
Trophic structure	Autotrophs support multiple heterotrophic levels; complexity varies with resources	Truncated, no autotrophs, few predators, weak interactions	Complexity varies with water body size	Complexity varies along depth and resource gradients	Simple and truncated, weak trophic interactions
Productivity	Varies greatly with resource gradients and temporally in some systems	Low and stable, but varies with connectivity	Varies greatly with resource gradients and temporally with flow and filling regimes	Varies greatly with resource gradients and ocean circulation	Low and variable with weather

Table 3 (continued)

REALM	TERRESTRIAL	SUBTERRANEAN	FRESHWATER	MARINE	ATMOSPHERIC
Autotroph traits	Complex differentiated organs and phenology	Microbial or absent	Mostly simple organisms or unicellular, specialised organisms in some systems	Mostly simple organisms or unicellular	Microbial or absent
Biogenic structure	Complex and vertically stratified in most systems, but complexity varies along resource gradients	Simple biofilms	Simple vertical structure mostly with one, sometimes more strata: biofilm, submerged, floating, emergent	Complex plant or animal foundations in some benthic systems, soft sediments mostly with simple structure	Absent
Heterotroph diets	Heterotrophs with diverse diets	Detritivores and decomposers dominant, few predators	Heterotrophs with diverse diets	Heterotrophs with diverse diets	Few, but specialised predators
Body sizes	Small-large	Small only	Small-medium	Small-very large	Small only
Phenology	Seasonal growth, mortality and reproduction in many systems, deciduous organs in some systems	Limited seasonality influenced by connectivity to surface	Life histories cued to seasonality of flows and filling regimes	Seasonality of currents on surface drives variation in productivity throughout	Seasonal winds and precipitation influence dispersal
Salinity tolerance and regulation	Osmotic regulation in rare cases	Osmotic regulation in some species	Salt exclusion and excretion, osmotic regulation increasing along salinity gradients	Osmotic regulation pervasive across all taxa	Not applicable
Water conservation	Diverse morphological, dietary, digestive, life-history, physiological and behavioural traits	Physiological traits in some taxa	Diverse morphological, dietary, digestive, life-history, physiological & behavioural traits in systems with intermittent water	Few taxa with traits except on shorelines	Morphological traits to promote water retention
Buoyancy	Few traits except in propagules of some species	Few species with traits except aquatic vertebrates	Many species with morphological and physiological water-buoyancy traits	Many species with morphological and physiological water-buoyancy traits	Many species with morphological air-buoyancy traits

4 Reflections on the approach to typology development

4.1 Theoretical foundations

The biome concept has terrestrial foundations, with a focus on global climatic relationships, vegetation structure and physiognomy (Walter, 1973; Mucina, 2019). Broadening its scope to encompass a more diverse suite of traits and selection filters in the context of assembly theory (Keith et al., in review) enables a logical extension of this powerful concept to freshwater and marine realms. A model of ecosystem function based on assembly theory offers a deductive framework to identify the key ecological processes that sustain the identity of ecosystems characterised by different traits.

Some biomes and Ecosystem Functional Groups identified through this approach have proved difficult to reconcile with traditional climate-centric biome concepts (Moncrieff et al., 2016). For example, the global distribution of tropical and subtropical savanna ecosystems (recognised at Level 3 of the typology) could not be predicted from climate in the absence of fire (Bond et al., 2005). Similarly, Orians & Milewski (2007) highlighted the profound influence of nutrient poverty, somewhat independent of climatic variation, in structuring traits and functions of some shrub-dominated and temperate forest systems recognised at Level 3 of the typology.

Strong theoretical foundations of this ecosystem typology should also make the overall framework robust to advances in data quality and availability. Nonetheless, adjustments to the circumscriptions and descriptions of units will be needed as knowledge of assembly processes improves for particular types of ecosystems. Notably, ecosystem processes and variation in traits within the atmospheric realm need further research before that component of the typology can be resolved.

4.2 Top-down and bottom-up construction

The combination of top-down and bottom-up approaches to classification in the IUCN typology (Figure 1) serves to balance consistency with realism. A top-down approach, subdividing functionally contrasting biomes within realms and functional groups within biomes, is guided by assembly theory and is critical to: i) consistent and comprehensive global coverage (Principle 3; Table 1); ii) integrating both ecosystem function and composition (Principles 1 and 2) into a single classificatory framework; and iii) for scalability to different applications (Principle 4). A bottom-up approach to grouping compositionally similar units at lower levels and assigning them to functional groups promotes realism by incorporating local data and expertise. This flexibility to define compositional relationships from the bottom-up is critical to local ownership and wide use of the typology (Principle 6) because: i) expertise and data on compositional relationships reside primarily at national and subnational levels; and ii) ecosystem management and biodiversity conservation is implemented through locally-based on-ground action.

The combination of top-down and bottom-up approaches to construction of the typology has two advantages. First, it enables explicit linkages with finer scale classifications that catalogue local expressions of global biomes and functional groups. Second, it provides two alternative options for global analysis based on Levels 4 and 5, which have complementary strengths and weaknesses. Concordance between these options allows inferences to be drawn that are robust to uncertainties in ecosystem classification, while discordance highlights a need for additional data to resolve uncertainties.

Effective coupling of top-down and bottom-up units of classification requires Ecosystem Types (Level 5) to be assigned to Functional Groups (Level 3), either quantitatively or qualitatively, using methods designed to handle inherent uncertainty. Quantitative methods, such as fuzzy sets (De Cáceres et al., 2010) and model-based approaches (Lyons et al., 2016), can be applied if suitable attribute data are available. Where formal data are lacking, structured expert elicitation provides a repeatable method to reduce subjective biases in cross-walking classifications (Hemming et al., 2018).

4.3 Discrete representation of continuous patterns in nature

Like any ecological classification, the IUCN Global Ecosystem Typology artificially compartmentalises natural continua (Keith, 2015; Riesch et al., 2018). Although continua between units of classification are recognised (Figures 3 and 4), they generate uncertainties related to 'vagueness', a form of linguistic uncertainty pertaining to boundary cases in which there is no objective, determinate way to resolve whether objects are inside or outside one category or another (Regan et al., 2002). Vagueness also occurs in other taxonomic classifications (e.g. species, soils, etc.). It is reducible through lucid descriptions, but cannot be eliminated. Practitioners nevertheless find the classification of nature into 'discrete' units cognitively attractive for interpretation and communication of patterns and relationships. We therefore concluded that the benefits of wide uptake outweighed the limitations of adopting a discrete model of ecosystem variation.

4.4 Classification and mapping

We separated the tasks of constructing the typology and defining its units from mapping their distribution. This liberates the definition of units from constraints imposed by current availability of spatial data, and allows for progressive improvement of maps representing spatial expression of conceptually stable ecosystem types. Maps are, however, essential to many applications, including ecosystem risk assessment and management (Principle 5). Classification units at all levels of the typology have spatial distributions and are therefore mappable, aided by recent advances in global spatial data and cloud computing (Murray et al., 2018). Mapping at any level of the typology requires spatially explicit ground observations, interpretive expertise, spatial predictors (including remote sensing data and environmental variables) and appropriate methods for spatial interpolation (Guisan & Zimmermann, 2000).

5 Descriptive profiles for Ecosystem Functional Groups

The descriptive profiles in Part II provide brief summaries of key ecological traits and processes for each functional group of ecosystems to enable any ecosystem type to be assigned to a group. The profiles describe features that distinguish different functional groups to inform diagnosis and identification.

Inevitably, there are inherent uncertainties in assigning ecosystem types to unique functional groups because ecological classifications, in general, simplify complex variation in nature by segmenting and categorising continuous gradients in multiple features (see section 4). Thus, any given ecosystem type may possess a suite of features that are typical of different functional groups. Users should assess and weigh evidence on all features to identify the most likely functional group and report the nature of uncertainties in group membership.

5.1 Nomenclature

Names of functional groups are vernacular —names and descriptors frequently applied in the literature that reflect key functional features are adopted. A vernacular (rather than systematic) approach to nomenclature is intended to exploit terms (e.g. rainforest, lake or reef) that are familiar to a wide range of users, recognising regional variations and conventions in terminology.

5.2 Text descriptions

The text describes key ecological traits that characterise each functional group and help distinguish it from other groups. The descriptions include ecosystem-level traits (e.g. productivity, energy sources, trophic structure, physical structure, bottom-up and top-down organisational processes) as well as species-level traits that are represented among the component biota of ecosystem types within the group (e.g. life forms, life-history traits, specialised organs, and characteristic behaviours and mobility). Where possible, variability in traits is noted. While efforts have been made to simplify descriptions, some technical terms are necessary to describe ecosystem features accurately; a glossary defines selected terms used in the profiles.

5.3 Exemplary photographs

Each profile is illustrated with a photograph that shows some of the ecological features mentioned in the text. Although representative examples were chosen for illustration, they may not represent the range of variability in features expressed within each functional group, some of which have extensive global distributions.

5.4 Major ecosystem drivers

The text identifies key ecological drivers that shape the ecological character of ecosystem types within a functional group. Abiotic drivers and processes include ambient environmental features and disturbance regimes that directly or indirectly influence resource availability. Biotic drivers include a range of interactions and dependencies that in some profiles are described alongside the ecological traits that underpin them. Human influence is only addressed in anthropogenic EFGs even though it affects most ecosystems on earth. These effects vary greatly in type, intensity and spatially in a manner that reflects social, cultural and economic norms and opportunities, technology and access as well as ecosystem characteristics. Specific influences of anthropogenic processes vary with ecosystem state and will therefore be addressed in IUCN Red List of Ecosystems assessments.

5.5 Diagrammatic assembly models

For each EFG, a generic ecosystem assembly model was adapted to illustrate key ecological traits and assembly filters (i.e. drivers that shape ecosystem traits). Only the major features are shown and anthropogenic processes are only shown for anthropogenic functional groups (encompassing ecosystems that are shaped and maintained by humans). In the diagrammatic representations of the models, ecological traits are listed in green circles at the centre, while drivers are identified in peripheral boxes using the following colours:

aquamarine: resources
blue: ambient environmental factors that influence resource availability or uptake
red: environmental disturbance regimes
yellow: biotic interactions
brown: human activities

Connecting arrows show influences of and interactions among drivers (only major connections are shown and feedbacks are generally not shown).

5.6 Indicative distribution maps

Separate distribution maps were developed for each EFG, largely independently of one another. This multi-layer format to the spatial data enabled us to incorporate more spatial information on EFG distributions than is possible in a single composite map. It also enabled us to accommodate different levels of data quality and uncertainty, different degrees of spatial dynamism over relatively short time scales, and spatial juxtapositions with other EFGs. The multi-layered format allows occurrences of two or more EFGs to be represented within the same spatial unit (i.e. grid cells). Interactive versions of the maps are available at https://global-ecosystems.org/.

The maps show areas of the world containing major (in red) or minor occurrences (in yellow) of each EFG. Minor occurrences are areas where an EFG is scattered in patches within matrices of others or where they occur in substantial areas but only within a segment of a larger region. Small but important occurrences are identified with a black ellipse.

The maps were designed to be indicative of global distribution patterns and are not intended to represent fine-scale patterns. The spatial grain of map rasters varies from 10 minutes to 1 degree of latitude and longitude, depending on the resolution of available base layers (Table 4). For most EFGs, the spatial resolution is 30 arc seconds, approximately 1 km^2 at the equator. Given bounds of resolution and accuracy of source data, the maps should be used to query which EFG are likely to occur within areas, rather than which occur at particular point locations.

Initially, existing spatial data were first searched on map units that aligned with the concept of individual EFGs by comparing descriptions in metadata or associated publications to the EFG descriptive profiles. Matching data sets were found for 27 EFGs comprising either polygons or rasters (e.g. MT1.2, T7.4, M1.3; Table 4) or point records (i.e. MFT1.1). For eight of those EFGs, direct maps were supplemented with biogeographic regions likely to contain minor occurrences (i.e. TF1.1).

In some cases, maps were found to align with key features of EFGs, but applied them over a broader range of environments or locations. In those cases (12 EFGs), environmental spatial data or biogeographic regions were used to clip the broader mapped extent to achieve closer alignment with the EFG concept (e.g. F1.1, T1.1). For 34 EFGs that had no direct mapping, maps were assembled from simple combinations of remote sensing and/or environmental proxies, clipped by biogeographic regions where necessary. For the remaining 33 EFGs that had no suitable environmental proxies or remote sensing, indicative maps were developed based on biogeographic regions, informed by a variety of non-spatial and spatial sources (Table 4 for details) to create envelopes plausibly containing the EFG distribution (i.e. T4.5). One EFG (S1.2) was not mapped due to its distribution throughout the Earth's crust.

Although ecoregions (Spalding et al., 2007; Abell et al., 2008; Dinerstein et al., 2017) are one of numerous spatial data sets used in the construction of some of the maps, it must be emphasised that EFGs are conceptually different entities to ecoregions. We used ecoregions in mapping as a template to constrain the extent mapped from remote sensing and environmental proxies. Consequently, when EFGs are aggregated into functional biomes (Level 2 of the Global Ecosystem Typology), spatial patterns may differ from those of biogeographic biomes as mapped and described in respective ecoregion classifications (provinces of Spalding et al., 2007; major habitat types of Abell et al., 2008; biomes of Olson et al., 2001; and Dinerstein et al., 2017). Differences reflect distinctions between functional and biogeographic interpretations of the term 'biome' (Mucina, 2019).

5.7 Use of references

Key references are listed as sources of further information for each functional group. Preference has been given to recent global reviews and where these are not available, regional reviews or publications addressing characteristic ecological processes are provided for respective ecosystem groups. Older literature was cited where it addressed key features more directly than recent literature.

5.8 Updates

The Global Ecosystem Typology will be updated periodically as new information comes to light. Updates to version 1.0 incorporated in version 1.01 include:

- a expanded glossary of terms;
- a full copy edit of descriptive profiles; and
- inclusion of a new EFG, F2.10 Subglacial Lakes.

Version 2.0 is the outcome of further major review and revision of the typology by 48 ecosystem specialists. Updates to version 1.01 incorporated in version 2.0 include:

- addition of five new EFGs to Level 3 of the typology in response to reviewers' recommendations (one freshwater group F1.7, one anthropogenic terrestrial group T7.5, two subterranean freshwater groups SM1.2 and SM1.3, and one artificial subterranean-freshwater group SF2.2);
- major revisions to four existing profiles for freshwater EFGs (F1.2, F1.4, F1.5, F3.2);
- amendments to diagrammatic models for 28 EFGs in response to recommendations from specialist reviewers;
- thematic adjustments to distribution maps for 12 EFGs;
- addition or replacement of references in 12 EFGs;
- minor edits to text in profiles for all EFGs to improve clarity and detail;
- substantial expansion of the glossary; and
- comprehensive upgrade of broad-scale indicative maps to higher resolution maps based directly on remote sensing, or point locations, or indirectly on environmental proxies.

An interactive interface to the Global Ecosystem Typology, its hierarchical structure, descriptive profiles and maps is available at https://global-ecosystems.org/.

Future updates will also be available at this site.

Table 4 Methods and source data for indicative maps of each Ecosystem Functional Group (EFG)

EFG	DESCRIPTION
T1.1 / T1.2 / T2.1 / T2.2 / T2.6 / T3.4 / T4.1 / T5.1 / T5.2 / T5.3 / T5.4 / T5.5 / T6.5 / T7.5	Major and minor occurrences were initially identified using consensus land-cover maps (Tuanmu & Jetz, 2014) and then cropped to selected terrestrial ecoregions (Dinerstein et al., 2017) at 30 arc second spatial resolution. Ecoregions were selected if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile.
S2.1 / T1.4 / T2.3 / T2.4 / T3.1 / T3.2 / T4.2 / T4.3 / T4.4 / T4.5 / T6.4 / TF1.2 / TF1.3 / F1.6 / TF1. 7	Terrestrial ecoregions containing major or minor occurrences of this ecosystem functional group were identified by consulting available ecoregion descriptions (Dinerstein et al., 2017), global and regional reviews, national and regional ecosystem maps, locations of relevant examples, and proofed by expert reviewers. Consequently, they are coarse-scale indicative representations of distribution, except where they occupy small ecoregions. Ecoregions were mapped at 30 arc seconds spatial resolution.
T1.3	The distribution of tropical montane rainforest was approximated from a model of environmental suitability based on climatic variables and cloud cover (Wilson & Jetz, 2016). Occurrences were aggregated to half degree spatial resolution and cells reclassified as major occurrences (>25% of cell area) and minor occurrences (< 25% of cell area).
T2.5	Remote sensing estimates of canopy height were used as a direct indicator of the distribution of this group of tall forest ecosystems (Armston et al., 2015: Tang et al., 2019). We selected all areas with tree canopies taller than 40 m, and clipped to the spatial extent of temperate climate types (Beck et al., 2018). Mapped occurrences were then aggregated to half degree spatial resolution and reclassified as major occurrences (>20% of cell area) and minor occurrences (< 20% of cell area).
T3.3	Major and minor occurrences were identified using consensus land-cover maps (Tuanmu & Jetz, 2014; Latifovic et al., 2016), then cropped to selected terrestrial ecoregions at 30 arc seconds spatial resolution (Dinerstein et al., 2017; CEC, 1997). Ecoregions were selected if they contained areas mentioned or mapped in published regional studies (Loidi et al., 2015; Luebert & Pliscoff, 2017), or if: i) their descriptions mentioned features consistent with those identified in the profile of the Ecosystem Functional Group; and ii) if their location was consistent with the ecological drivers described in the profile.
T6.1	Areas of permanent snow where identified from consensus land-cover maps (Tuanmu & Jetz, 2014), glacier inventories (Raup et al., 2007; NSIDC, 2005–2018) and the Antarctic Land Cover map for 2000 (Hui et al., 2017). A composite map was created at 30 arc seconds spatial resolution in geographic projection, occurrences were then aggregated to half degree spatial resolution and reclassified as major occurrences (cells with > 22% snow coverage) and minor occurrences (cells with at least one occurrence).
T6.2	Known locations of prominent ice-free rock in glacial and alpine environments were selected from global geographical gazeteers (GeoNames, 2020), glacier inventories (Raup et al 2007; NSIDC, 2005–2018) and the Antarctic Land Cover map for 2000 (Hui et al., 2017). Further areas with mixed occurrence of barren and snow/ice cover were identified from the Circumpolar Arctic Vegetation Map (Raynolds et al., 2019), the USGS EROS LandCover GLCCDB, version 2 (Loveland et al., 2000) and a 1-km consensus land-cover map (Tuanmu & Jetz, 2014). A composite map was created at 30 arc seconds spatial resolution in geographic projection, occurrences were then aggregated to half degree cells. Cells containing at least one known location were designated as major occurrences, while those mapped as mixed barren and snow/ice cover were designated as minor occurrences if snow/ice covered at least 2.5% of the cell area.
T6.3	Areas corresponding to the tundra climatic zone according to the Köppen-Geiger classification system (Beck et al., 2018) were first identified. Additional areas were then selected in high latitudes corresponding with low annual solar radiation (values <1800 in Beckmann et al., 2014). A union of these maps was created at 30 arc seconds spatial resolution in geographic projection, occurrences were then aggregated to half degree spatial resolution and reclassified cells as major occurrences (>80% of cell area) and minor occurrences (30%-80% of cell area).

Table 4 (continued)

EFG	DESCRIPTION
T7.1	Major occurrences of croplands were taken from the map of Habitat type 14.1 by Jung et al. (2020) based on the IUCN Habitats Classification Scheme (version 3.1) (IUCN, 2012). We compared this to cropping areas in consensus land-cover maps (Tuanmu & Jetz, 2014) and found that maps of Jung et al. (2020) more closely matched the concept of T7.1. Occurrences were extracted from fractional aggregated 1 km resolution base data (Jung et al. 2020), approximating 30 arc seconds spatial resolution.
T7.2	The presence of sown pastures was approximated by selecting areas of overlap between existing irrigation infrastructure (Siebert et al., 2005; 2013) and presence of major livestock (Gilbert et al., 2018). Occurrences were aggregated to half degree spatial resolution and reclassified as major occurrences (>60% cell area) and minor occurrences (<60% cell area).
T7.3	Major occurrences of plantations were taken from the map of Habitat type 14.3 by Jung et al. (2020) based on the IUCN Habitats Classification Scheme v3.1 (IUCN, 2012). We compared this to cropping areas in consensus land-cover maps (Tuanmu & Jetz, 2014) and found that maps of Jung et al. (2020) more closely matched the concept of T7.3. Occurrences were extracted from fractional aggregated 1-km resolution base data (Jung et al., 2020), approximating 30 arc seconds spatial resolution.
T7.4	The indicative distribution of Urban and infrastructure lands was estimated using spatial data for night light brightness (values >0) (NOAA/NCEI, 2019; Cinzano et al., 2019).
S1.1 / SF1.1	Distributions of aerobic caves and underground streams and pools were based on mapped area of carbonate rock outcrop (Williams & Ting Fong, 2016) mapped at 30 arc seconds spatial resolution. This provides an upper limit on the area of exposed karst terrain, as not all carbonate rocks are karstified. Lava tubes and other rocks that may contain these ecosystem functional groups are not shown on this indicative map, but are less extensive than those in carbonate rock.
S1.2	Global distribution throughout the earth's crust. Not mapped.
SF1.2	Indicative global maps of Groundwater aquifers were based on BGR & UNESCO (2012) with colour ramp showing type of aquifer by recharge rate, only in major groundwater basins (type 11 (minor occurrences) to type 15 (major occurrences).
SF2.2	Point records of flooded mines were compiled from public databases (UNEXMIN, n.d.)), an internet search for "flooded mines" and locations of deep mines inferred from world mineral resources spatial data (USGS, n.d.). Terrestrial ecoregions (Dinerstein et al., 2017) with concentrations of these records were selected to represent an indicative global distribution of flooded mines at 30 arc seconds spatial resolution.
SF2.1	Freshwater ecoregions (Abell et al., 2008) containing urban and industrialised areas with water transfer infrastructure were identified by consulting available ecoregion descriptions (TNC & WWF, n.d.), maps of irrigation and other water infrastructure, and expertise of authors. Due to uncertainty and limited verification and likely limited spatial extent within mapped areas, all inferred occurrences were shown as minor at 30 arc seconds spatial resolution.
SM1.1 / SM1.2	Indicative distributions of anchialine caves and pools were based on mapped areas of carbonate rock outcrop (Williams & Ting Fong, 2016) and lava flows intersecting the coast, which were aggregated within a template of 1-degree grid cells.
SM1.3	Marine ecoregions (Spalding et al., 2008) containing occurrences of rocky coastline (see MT1.1) were verified by inspection of imagery available in Google Earth to identify an envelope of potential distribution for sea caves. The coastlines within these ecoregions were summarised using a template of 1-degree grid cell intersected with the coast. As caves represent a small portion of such coastlines, all mapped areas were designated as minor occurrences.
TF1.1	Major occurrences of tropical swamp forest and flooded forest were taken from the map of Habitat type 1.8 by Jung et al. (2020) based on the IUCN Habitats Classification Scheme v3.1 (IUCN, 2012). We compared this to areas of tropical swamp forest and flooded forest mapped Global Lakes and Wetlands Database (Lehner & Döll, 2004) as well as ecoregions with such forests mentioned in their description (Dinerstein et al., 2017), and found that maps of Jung et al. (2020) more closely matched the concept of TF1.1. Occurrences were extracted from fractional aggregated 1-km resolution base data (Jung et al. 2020), approximating 30 arc seconds spatial resolution.

Table 4 (continued)

EFG	DESCRIPTION
TF1.4	Major occurrences of freshwater marshes and floodplains were taken from the Global Lakes and Wetlands Database (Lehner & Döll, 2004). Occurrences in boreal and polar climates were excluded by removing Köppen-Geiger classes>26 in Beck et al., (2018). Additional areas with minor occurrences identified in selected freshwater ecoregions (Abell et al., 2008). Ecoregions were selected if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. Occurrences were aggregated to half degree spatial resolution.
TF1.5	Locations of pan, brackish and saline wetlands were taken from the Global Lakes and Wetlands Database GLWD3 class 7 from Lehner & Döll (2004). Occurrences were aggregated to half degree spatial resolution.
F1.1	Freshwater ecoregions (Abell et al., 2008) were initially identified as containing permanent upland streams if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. The selected ecoregions were then clipped to exclude cold or dry climates (mean temperature of coldest quarter >0°C, mean annual precipitation >300 mm) based on data from Karger et al. (2017). Major occurrences were mapped by intersecting the selected ecoregions with the distribution of 1st–3rd order streams taken from the RiverATLAS (v1.0) database at 30 arc seconds spatial resolution (Linke et al., 2019). The remaining areas within selected ecoregions (excluding freeze/thaw areas) were designated as minor occurrences.
F1.2 / F1.5	Freshwater ecoregions (Abell et al., 2008) were identified as containing occurrences of these functional groups if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. Within these areas, major occurrences were mapped using stream orders 4–9 taken from the RiverATLAS (v1.0) database (Linke et al. 2019) combined with global estimates of surface water phenology (classes 1, 2 and 7 from Pekel et al., 2016). The remaining area of selected ecoregions was designated as minor occurrences. Occurrences were aggregated to 10-minute spatial resolution.
F1.3	The distribution of freeze-thaw rivers and streams was mapped from the Global River Classification database (Ouellet Dallaire et al., 2018), including all reaches with minimum temperature below 0°C. Occurrences were aggregated to 10-minute spatial resolution.
F1.4	Freshwater ecoregions (Abell et al., 2008) were identified as containing occurrences of these functional groups if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. Within the selected ecoregions, major occurrences were mapped using 1st–4th order streams (3-km buffer) taken from the RiverATLAS (v1.0) database (Linke et al., 2019). The remaining areas of selected ecoregions were mapped as minor occurrences. Occurrences were aggregated to 10-minute spatial resolution.
F1.6	Freshwater ecoregions (Abell et al., 2008) were identified as containing occurrences of these functional groups if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. Within the selected ecoregions, remote sensing estimates of ephemeral surface water (classes 4, 5 and 8 from Pekel et al., 2016) were used to identify major occurrences at 0.5 minute spatial resolution. The remaining areas of selected ecoregions were mapped as minor occurrences.
F1.7	The distribution of large lowland rivers was taken from the Global River Classification database (Ouellet Dallaire et al., 2018). Reaches with flow > 10,000 m^3/s were mapped with a 20-km buffer as major occurrences, clipped to exclude those with seasonal freezing temperatures (mean temperature of coldest quarter <0°C).
F2.1	Locations of large lakes (>100 km^2) were taken from the HydroLAKES database (Messager et al., 2016) and combined with global estimates of permanent surface water surfaces (classes 1, 2 and 7 from Pekel et al., 2016). Freeze/thaw lakes in boreal and polar climates (temperature of coldest quarter > -10°C) were excluded (Beck et al., 2018) (see F2.3). Occurrences were aggregated to 30 arc seconds spatial resolution.

Table 4 (continued)

EFG	DESCRIPTION
F2.2 / F2.3 / F2.8 / F2.9	Freshwater ecoregions (Abell et al., 2008) were identified as containing occurrences of these functional groups if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. Within those areas, locations of small lakes (<100 km^2), excluding artificial lakes (inclusion on types 1 and 3 only), were taken from the HydroLAKES database (Messager et al., 2016) and combined with global estimates of surface water phenology (classes 1, 2 and 7 from Pekel et al., 2016), occurrences were aggregated to 10 minutes spatial resolution.
F2.4	Location of small and large natural lakes was taken from the HydroLAKES database (types 1 and 3 in Messager et al., 2016). We included all lakes with minimum temperature below 0°C (Linke et al., 2019). Occurrences were aggregated to 10-minute spatial resolution.
F2.5	Location of natural ephemeral freshwater lakes was taken from global lake databases (Lehner & Döll, 2004; types 1 and 3 from Messager et al., 2016), excluding those from endorheic basins cf. F2.7 (Linke et al., 2019), and intersected with estimates of ephemeral surface water (classes 9 and 10 from Pekel et al., 2016). Occurrences were aggregated to 10 minutes spatial resolution.
F2.6	Major occurrences were compiled from a list of known salt lakes in Wurtsbaugh et al., (2017) and augmented by authors, then matched with names in the HydroLAKES database to identify natural lakes (types 1 and 3 of Messager et al., 2016). Minor occurrences were mapped within arid and semi-arid parts of selected freshwater ecoregions (Abell et al., 2008) by clipping ecoregions to exclude areas with mean annual rainfall >250 mm (Harris et al., 2014a). Freshwater ecoregions (Abell et al., 2008) were selected if they contained occurrences of permanent salt, or soda lakes, if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. Occurrences were aggregated to 10 minutes spatial resolution.
F2.7	Location of ephemeral lakes was taken from global lake databases (Lehner & Döll, 2004; types 1 and 3 from Messager et al., 2016), intersected with estimates of ephemeral surface water (classes 9 and 10 from Pekel et al., 2016) and the distribution of arid and semi-arid, endorheic basins (Linke et al., 2019). Occurrences were aggregated to 10 minutes spatial resolution. Occurrences were aggregated to 10 minutes spatial resolution.
F2.10	Major occurrences of subglacial lakes were mapped as 0.5 degree cells containing the point records of Wright & Siegert (2012), Bowler et al., (2019), Marteinsson et al. (2013) and Livingstone et al. (2016). Unmapped lakes are likely to occur within areas with permanent snow and ice cover and were mapped as minor occurrences based on permanent snow and ice from Dinerstein et al. (2017) and Tuanmu et al. (2014).
F3.1	Point locations of large reservoirs were obtained from water bodies tagged as ‘reservoirs' in ‘reservoirs’ in vector layers GLWD1 and GLWD2 of Lehner & Döll (2004). These were mapped with a spatial buffer of 15 minutes, enabling reservoirs to be represented in 0.5 degree grid cells.
F3.2 / F3.4 / F3.5	Freshwater ecoregions (Abell et al., 2008) were identified as containing major or minor occurrences of these functional groups if: i) their descriptions mentioned features consistent with those identified in the profile of the EFG; and ii) if their location was consistent with the ecological drivers described in the profile. The selections were check by expert reviewers. Occurrences were mapped at 30 arc seconds spatial resolution.
F3.3	The distribution of rice paddies was estimated from the percentage of rice cover at a 5 arc minute resolution based on Monfreda et al. (2008). Cells with > 10% rice cover were designated as major occurrences, and those with 1%–10% rice cover were designated as minor occurrences.
FM1.1	Known locations of fjords where selected from a global geographical gazetteer (GeoNames, 2020) and the composite gazetteer of Antarctica (SCAR, 1992-2020). We further selected related coastal areas from a global coastal typology (Type IV in Dürr et al., 2011) and the adjacent marine shelfs to 2,000 meter depth (Becker et al., 2009). A composite map was created at 30 arc seconds spatial resolution in geographic projection, occurrences were then aggregated to half degree spatial resolution and reclassified as major occurrences (cells with at least one known occurrence) and minor occurrences (cells with > 5% occurrence of coastal/marine shelf areas). Minor occurrences were clipped to a 50-km buffer along the coast to remove inland and oceanic areas.

Table 4 (continued)

EFG	DESCRIPTION
FM1.2 / FM1.3	Marine ecoregions (Spalding et al., 2008) containing major or minor occurrences of each EFG were identified by consulting global and regional reviews, maps of relevant ecosystems, imagery available in Google Earth and expertise of authors. Occurrences were converted to 30 arc seconds spatial resolution and clipped to a 50-km buffer along the coastline to exclude inland and offshore areas of the ecoregions.
M1.1	Indicative maps of Seagrass meadows were obtained from UNEP-WCMC & Short (2017) based on Green & Short (2003). Occurrences were converted to 30 arc seconds spatial resolution.
M1.2	Ecoregions with major and minor occurrences of Kelp forests were identified by overlaying a global map of kelp systems (Wernberg & Filbee-Dexter, 2019) on marine ecoregions (Spalding et al., 2008), and then clipping to bathymetry with <80 m deep (Becker et al., 2009). Clipped ecoregions were assigned to major and minor occurrences based on information in Wernberg & Filbee-Dexter (2019) and author expertise, and proofed by specialist reviewers. Occurrences were converted to 30 arc seconds spatial resolution.
M1.3	Indicative maps of Photic coral reefs were obtained from IMaRS/USF et al. (2011). Occurrences were converted to 30 arc seconds spatial resolution.
M1.4	Major and minor occurrences of shellfish beds and reefs were identified by overlaying a global map of oyster reefs (Beck et al., 2011) on marine ecoregions (Spalding et al., 2008), and then clipping to the extent of the marine 'shelf' base layer as mapped by Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M1.5 / M1.6 / M1.7 / M1.8	These are EFGs that are widespread through the global extent of the marine shelf biome. Reliable data on their precise distribution are limited. To represent regional uncertainty, their indicative distributions were mapped in as minor occurrences through the full extent of the marine 'shelf' base layer as mapped by Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M1.9	Marine ecoregions (Spalding et al., 2008) with major and minor occurrences of Upwelling zones were identified by consulting global and regional reviews (cited in descriptive profile), maps of relevant ecosystems and expertise of authors, proofed by specialist reviewers. The identified ecoregions were then clipped to the extent of the marine 'shelf' base layer as mapped by Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M2.1 / M2.2 / M2.3 / M2.4	Indicative distributions of the marine pelagic EFGs were derived from bathymetric spatial data obtained from Becker et al. (2009) using depth range thresholds cited in respective descriptive profiles for each functional group. Occurrences were mapped at 30 arc seconds spatial resolution.
M2.5	Indicative distributions of sea ice were obtained from Fetterer et al. (2017). To approximate the maximum annual global extent, we used the monthly extent for March 2019 for the northern hemisphere, and the monthly extent for September 2018 for the southern hemisphere. Occurrences were mapped at 30 arc seconds spatial resolution.
M3.1	Major occurrences of continental and island slopes were based on the 'slope' geomorphic unit of Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M3.2	Major occurrences of submarine canyons was based on the 'canyons' geomorphic unit of Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M3.3	Major occurrences of Abyssal plains was based on the 'plains' and 'hills' classes within the abyssal geomorphic unit of Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M3.4	Major occurrences of seamounts, ridges and plateaus was based on the 'mountains' classes within the abyssal geomorphic unit of Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M3.5	The distribution of deepwater biogenic beds was based on the 'mountains' and 'hills' classes within the abyssal geomorphic unit of Harris et al. (2014b). These were mapped in yellow as minor occurrences to acknowledge considerable uncertainties in the distribution of biogenic beds within these geomorphic units. Occurrences were converted to 30 arc seconds spatial resolution.

Table 4 (continued)

EFG	DESCRIPTION
M3.6	Major occurrences of Hadal trenches and troughs was based on the 'hadal' and 'trenches' geomorphic units of Harris et al. (2014b). Occurrences were converted to 30 arc seconds spatial resolution.
M3.7	Major occurrences of Chemosynthetic-based ecosystems was based on the distribution of hydrothermal vents on spreading plate boundaries mapped in 'Plate lines and polygons' data by USGS, ESRI (n.d.). Occurrences were converted to 30 arc seconds spatial resolution. The distribution of cold seeps is poorly known and was not mapped.
M4.1	Marine ecoregions that include occurrences of submerged artificial structures were identified by overlaying a mapped distribution of shipwrecks (Monfils, 2004) on marine ecoregions (Spalding et al., 2008). Occurrences were converted to 30 arc seconds spatial resolution. In many cases these ecoregions encompassed other submerged structures such as energy infrastructure. To represent uncertainty, indicative distributions were mapped as minor occurrences.
M4.2	Marine ecoregions (Spalding et al., 2008) containing marine aquafarms were identified by consulting global and regional reviews, suitability maps (Gentry et al., 2017) and expertise of authors, proofed by specialist reviewers. These were clipped to the extent of the marine 'shelf' base layer as mapped by Harris et al. (2014b) and converted to 30 arc seconds spatial resolution. Occurrences were aggregated to half degree spatial resolution.
MT1.1 / MT1.4	Marine ecoregions (Spalding et al., 2008) containing rocky shorelines and boulder and cobble shorelines, respectively, were identified by consulting regional substrate maps, imagery available in Google Earth (to exclude ecoregions with extensive sandy or muddy shores) and expertise of authors, proofed by specialist reviewers. Occurrences were aggregated to 1 degree spatial resolution.
MT1.2	Tidal flats were mapped directly from remote sensing time series and aggregated to 1 degree spatial resolution by Murray et al. (2018). Major occurrences were mapped in 1-degree cells with >200 km^2 mudflat extent, and minor occurrences were mapped in cells with 5 km^2–200 km^2 mudflat extent.
MT1.3	The indicative map of Sandy shorelines was based on point records of sandy coastlines mapped by Vousdoukas et al. (2020) aggregated to 1 degree spatial resolution. Cells with >50 points were reclassified as major occurrences, and those with 1–50 points were reclassified as minor occurrences.
MT2.1	Coastlines were mapped between 60°S and 60°N with a 20-km buffer applied.
MT3.1	Marine ecoregions (Spalding et al., 2008) containing major and minor occurrences of urbanised shorelines were identified from the map of night lights (see T7.4), imagery available on Google Earth and expertise of authors. Occurrences were aggregated to 1 degree spatial resolution and intersected with the coastline to exclude areas inland and in the open ocean.
MFT1.1	The extent of major coastal deltas was taken directly from Tessler et al. (2015), which was checked for completeness against point locations shown in Figure 1 of Goodbred & Saito (2012) and found to be inclusive of major occurrences. The data from Tessler et al. (2015) were at 30 arc seconds spatial resolution.
MFT1.2	The indicative map for Intertidal forests and shrublands was based on mapping by Giri et al. (2011) summarised within a template of 1-degree grid cells. Cells with >200 km^2 of intertidal woody cover were reclassified as major occurrences, and those with 5 km^2–200 km^2 of intertidal woody cover were reclassified as minor occurrences.
MFT1.3	The indicative map for Coastal saltmarshes was based on mapping by McOwen et al. (2017) summarised within a template of 1-degree grid cells. Cells with >5% cover of marsh vegetation were reclassified as major occurrences, and those with non-zero cover up to 5% were reclassified as minor occurrences.

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Appendix 1. List of Ecosystem Functional Groups by realms and biomes

REALM	BIOME		ECOSYSTEM FUNCTIONAL GROUP (EFG)	
TERRESTRIAL	T1	Tropical-subtropical forests	T1.1	Tropical-subtropical lowland rainforests
			T1.2	Tropical-subtropical dry forests and thickets
			T1.3	Tropical-subtropical montane rainforests
			T1.4	Tropical heath forests
TERRESTRIAL	T2	Temperate-boreal forests & woodlands	T2.1	Boreal and temperate high montane forests and woodlands
			T2.2	Deciduous temperate forests
			T2.3	Oceanic cool temperate rainforests
			T2.4	Warm temperate laurophyll forests
			T2.5	Temperate pyric humid forests
			T2.6	Temperate pyric sclerophyll forests and woodlands
TERRESTRIAL	T3	Shrublands & shrubby woodlands	T3.1	Seasonally dry tropical shrublands
			T3.2	Seasonally dry temperate heaths and shrublands
			T3.3	Cool temperate heathlands
			T3.4	Rocky pavements, screes and lava flows
TERRESTRIAL	T4	Savannas and grasslands	T4.1	Trophic savannas
			T4.2	Pyric tussock savannas
			T4.3	Hummock savannas
			T4.4	Temperate woodlands
			T4.5	Temperate subhumid grasslands
TERRESTRIAL	T5	Deserts and semi-deserts	T5.1	Semi-desert steppes
			T5.2	Thorny deserts and semi-deserts
			T5.3	Sclerophyll hot deserts and semi-deserts
			T5.4	Cool deserts and semi-deserts
			T5.5	Hyper-arid deserts
TERRESTRIAL	T6	Polar-alpine	T6.1	Ice sheets, glaciers and perennial snowfields
			T6.2	Polar-alpine rocky outcrops
			T6.3	Polar tundra and deserts
			T6.4	Temperate alpine grasslands and shrublands
			T6.5	Tropical alpine grasslands and shrublands

Appendix 1 (continued)

REALM	BIOME		ECOSYSTEM FUNCTIONAL GROUP (EFG)	
TERRESTRIAL	T7	Intensive land-use systems	T7.1	Annual croplands
			T7.2	Sown pastures and fields
			T7.3	Plantations
			T7.4	Urban and industrial ecosystems
			T7.5	Derived semi-natural pastures and oldfields
SUBTERRANEAN	S1	Subterranean lithic systems	S1.1	Aerobic caves
			S1.2	Endolithic systems
			S2.1	Anthropogenic subterranean voids
SUBTERRANEAN-FRESHWATER	SF1	Subterranean freshwaters	SF1.1	Underground streams and pools
			SF1.2	Groundwater ecosystems
	SF2	Anthropogenic subterranean freshwaters	SF2.1	Water pipes and subterranean canals
			SF2.2	Flooded mines and other voids
SUBTERRANEAN-MARINE	SM1	Subterranean tidal systems	SM3.1	Anchialine caves
			SM3.2	Anchialine pools
			SM3.1	Sea caves
FRESHWATER-TERRESTRIAL	TF1	Palustrine wetlands	TF1.1	Tropical flooded forests and peat forests
			TF1.2	Subtropical/temperate forested wetlands
			TF1.3	Permanent marshes
			TF1.4	Seasonal floodplain marshes
			TF1.5	Episodic arid floodplains
			TF1.6	Boreal, temperate and montane peat bogs
			TF1.7	Boreal and temperate fens
FRESHWATER	F1	Rivers and streams	F1.1	Permanent upland streams
			F1.2	Permanent lowland rivers
			F1.3	Freeze-thaw rivers and streams
			F1.4	Seasonal upland streams
			F1.5	Seasonal lowland rivers
			F1.6	Episodic arid rivers
			F1.7	Large lowland rivers

Appendix 1 (continued)

REALM	BIOME		ECOSYSTEM FUNCTIONAL GROUP (EFG)	
FRESHWATER	F2	Lakes	F2.1	Large permanent freshwater lakes
			F2.2	Small permanent freshwater lakes
			F2.3	Seasonal freshwater lakes
			F2.4	Freeze-thaw freshwater lakes
			F2.5	Ephemeral freshwater lakes
			F2.6	Permanent salt and soda lakes
			F2.7	Ephemeral salt lakes
			F2.8	Artesian springs and oases
			F2.9	Geothermal pools and wetlands
			F2.10	Subglacial lakes
FRESHWATER	F3	Artificial fresh waters	F3.1	Large reservoirs
			F3.2	Constructed lacustrine wetlands
			F3.3	Rice paddies
			F3.4	Freshwater aquafarms
			F3.5	Canals, ditches and drains
FRESHWATER-MARINE	FM1	Semi-confined transitional waters	FM1.1	Deepwater coastal inlets
			FM1.2	Permanently open riverine estuaries and bays
			FM1.3	Intermittently closed and open lakes and lagoons
MARINE	M	Marine shelfs	M1.1	Seagrass meadows
			M1.2	Kelp forests
			M1.3	Photic coral reefs
			M1.4	Shellfish beds and reefs
			M1.5	Photo-limited marine animal forests
			M1.6	Subtidal rocky reefs
			M1.7	Subtidal sand beds
			M1.8	Subtidal mud plains
			M1.9	Upwelling zones

Appendix 1 (continued)

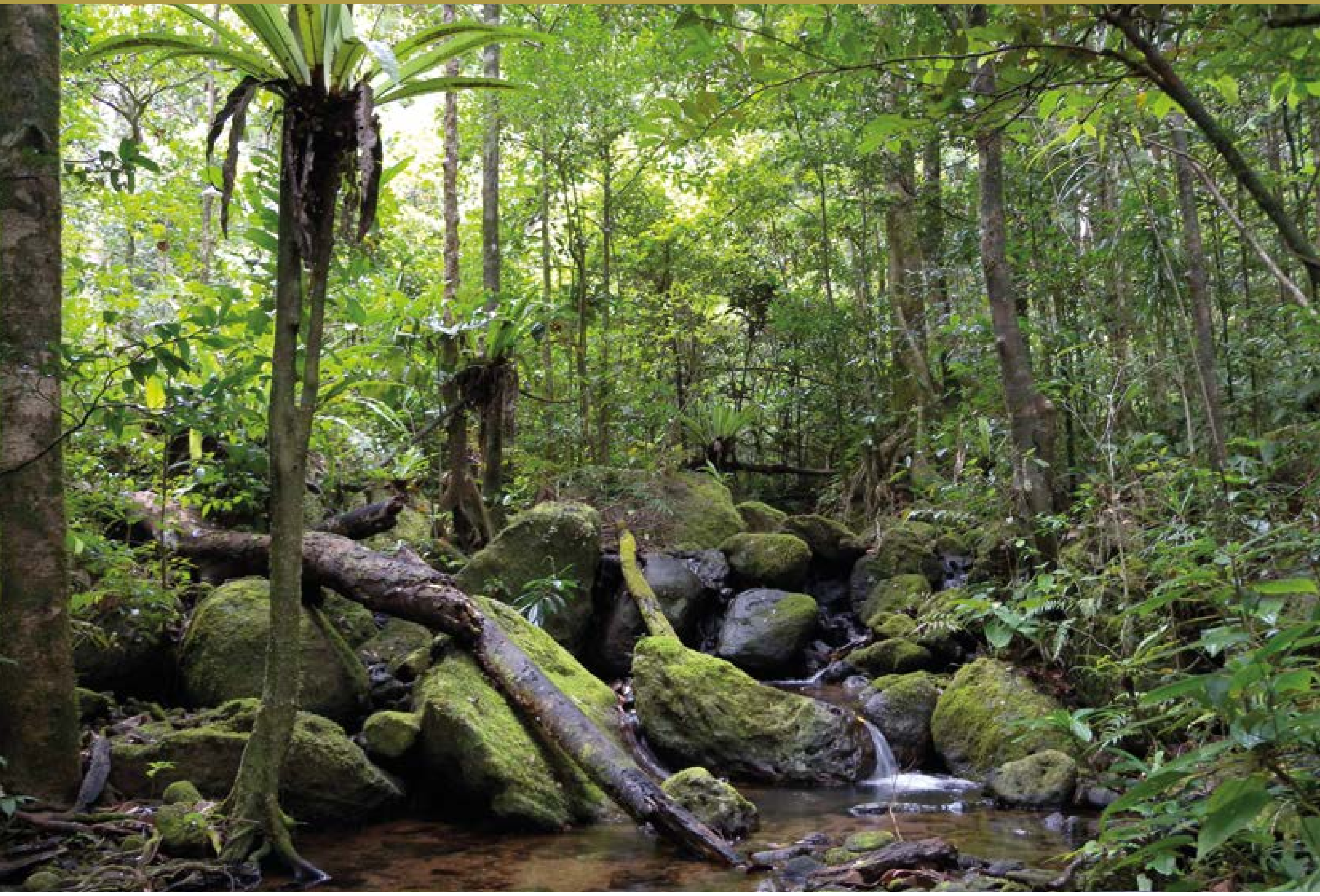
REALM	BIOME		ECOSYSTEM FUNCTIONAL GROUP (EFG)	
MARINE	M2	Pelagic ocean waters	M2.1	Epipelagic ocean waters
			M2.2	Mesopelagic ocean waters
			M2.3	Bathypelagic ocean waters
			M2.4	Abyssopelagic ocean waters
			M2.5	Sea ice
MARINE	M3	Deep sea floors	M3.1	Continental and island slopes
			M3.2	Marine canyons
			M3.3	Abyssal plains
			M3.4	Seamounts, ridges and plateaus
			M3.5	Deepwater biogenic beds
			M3.6	Hadal trenches and troughs
			M3.7	Chemosynthetically-based ecosystems
MARINE	M4	Anthropogenic marine systems	M4.1	Submerged artificial structures
			M4.2	Marine aquafarms
MARINE-TERRESTRIAL	MT1	Shoreline systems	MT1.1	Rocky shores
			MT1.2	Muddy shores
			MT1.3	Sandy shores
			MT1.4	Boulder and cobble shores
	MT2	Supralittoral coastal systems	MT2.1	Coastal shrublands and grasslands
	MT3	Anthropogenic shorelines	MT3.1	Artificial shores
MARINE-FRESHWATER-TERRESTRIAL	MFT1	Brackish tidal systems	MFT1.1	Coastal river deltas
			MFT1.2	Intertidal forests and shrublands
			MFT1.3	Coastal saltmarshes and reedbeds

Part II

Mirror lakes at the head of Milford Sound, New Zealand.
Source: Christopher Meder

Note: The content of Part II is taken from Keith et al. (in review). For further information regarding methods and source data for maps, please see Table 4.

T1 Tropical-subtropical forests biome



Masoala National Park, Madagascar.
Source: Frank Vassen (2008)

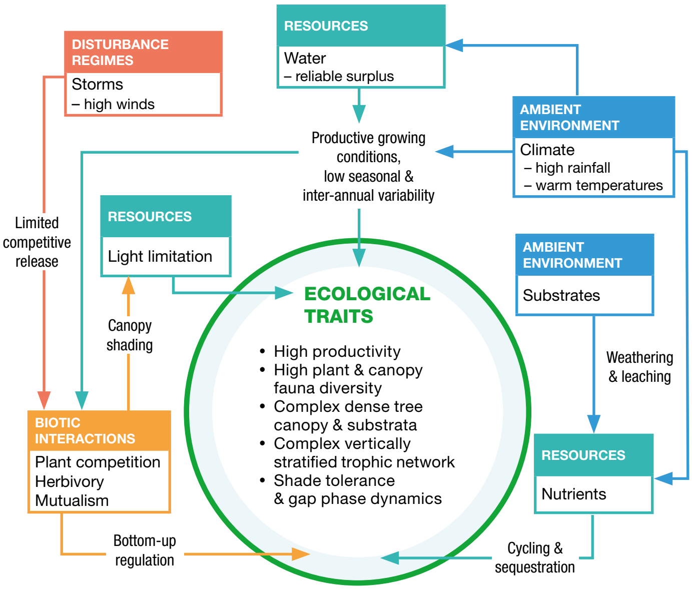
The Tropical-subtropical forests biome includes moderate to highly productive ecosystems with closed tree canopies occurring at lower latitudes north and south of the equator. Fragmented occurrences extend to the subtropics in suitable mesoclimates. High primary productivity is underpinned by high insolation, warm temperatures, relatively low seasonal variation in day length and temperature (increasing to the subtropics), and strong water surpluses associated with the intertropical convergence zone extending to wetter parts of the seasonal tropics and subtropics. Productivity and biomass vary in response to: i) strong rainfall gradients associated with seasonal migration of the intertropical convergence zone; ii) altitudinal gradients in precipitation, cloud cover, and temperatures; and iii) edaphic gradients that influence the availability of soil nutrients. Species diversity and the complexity of both vegetation and trophic structures are positively correlated with standing biomass and primary productivity; however, trophic webs and other ecosystem processes are strongly regulated from the bottom-up by the dominant photoautotrophs (trees), which fix abundant energy and carbon, engineer habitats for many other organisms, and underpin feedbacks related to nutrient and water cycling and regional climate. Complex nutrient cycling and/or sequestering mechanisms are common, countering the high potential for soil nutrient leaching due to high rainfall. Plant species exhibit leaf plasticity, shade tolerance and gap-phase dynamics in response to the periodic opening of canopy gaps initiated by tree death, storm damage, and lightning strikes. Fires may occur in ecotonal areas between these forests and savannas. Biogeographic legacies result in strong compositional distinctions and consequently some functional differences among land masses within the biome.

T1.1 Tropical subtropical lowland rainforests

BIOME: TROPICAL-SUBTROPICAL FORESTS
REALM: TERRESTRIAL

Contributors: D.A. Keith, K.R. Young, R.T. Corlett

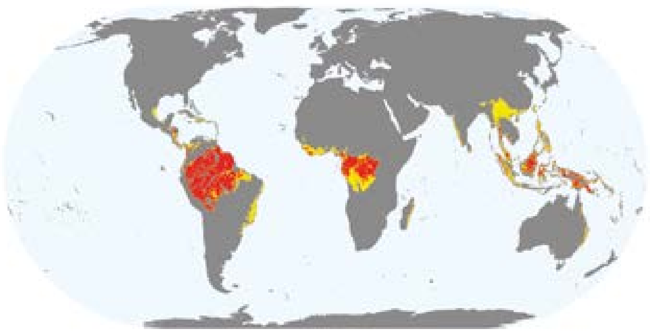
Tropical rainforest, Daintree, northeast Australia.
Source: David Keith (2009)



ECOLOGICAL TRAITS: These closed-canopy forests are renowned for their complex structure and high primary productivity, which support high functional and taxonomic diversity. At subtropical latitudes they transition to warm temperate forests (T2.4). Bottom-up regulatory processes are fuelled by large autochthonous energy sources that support very high primary productivity, biomass and Leaf Area Index (LAI). The structurally complex, multi-layered, evergreen tree canopy has a large range of leaf sizes (typically macrophyll-notophyll) and high SLA, reflecting rapid growth and turnover. Diverse plant life forms include buttressed trees, bamboos (sometimes abundant), epiphytes, lianas and ferns, but grasses and hydrophytes are absent or rare. Trophic networks are complex and vertically stratified with low exclusivity and diverse representation of herbivorous, frugivorous and carnivorous vertebrates. Tree canopies support a vast diversity of invertebrate herbivores and their predators. Mammals and birds play critical roles in plant diaspore dispersal and pollination. Growth and reproductive phenology may be seasonal or unseasonal, and reproductive masting is common in trees and regulates diaspore predation. Fungal, microbial and diverse invertebrate decomposers and detritivores dominate the forest floor and the subsoil. Diversity is high across taxa, especially at the upper taxonomic levels of trees, vertebrates, fungi and invertebrate fauna. Neutral processes as well as micro-niche partitioning may have a role in sustaining high diversity, but evidence is limited. Many plants are in the shade, forming seedling banks that exploit gap-phase dynamics initiated by individual tree-fall or stand-level canopy disruption by tropical storms in near coastal forests. Seed banks regulated by dormancy are uncommon. Many trees exhibit leaf form plasticity enabling photosynthetic function in deep shade, dappled light or full sun, even on a single individual. Some species germinate on tree trunks, gaining quicker access to canopy light, while roots absorb microclimatic moisture until they reach the soil.

KEY ECOLOGICAL DRIVERS: Precipitation exceeds evapotranspiration with low intra- and inter-annual variability, creating a reliable year-round surplus, while closed tree canopies maintain humid microclimate and shade. Temperatures are warm with low-moderate diurnal and seasonal variation (mean winter minima rarely <10°C except in subtropical transitional zones). Soils are moist but not regularly inundated or peaty (see TF1.3) Most nutrient capital is sequestered in vegetation or cycled through the dynamic litter layer, critical for retaining nutrients that would otherwise be leached or lost to runoff. In some coastal regions outside equatorial latitudes (mostly >10° and excluding extensive forests in continental America and Africa), decadal regimes of tropical storms drive cycles of canopy destruction and renewal.

DISTRIBUTION: Humid tropical and subtropical regions in Central and West Africa, Southeast Asia, Oceania, northeast Australia, Central and tropical South America and the Caribbean.



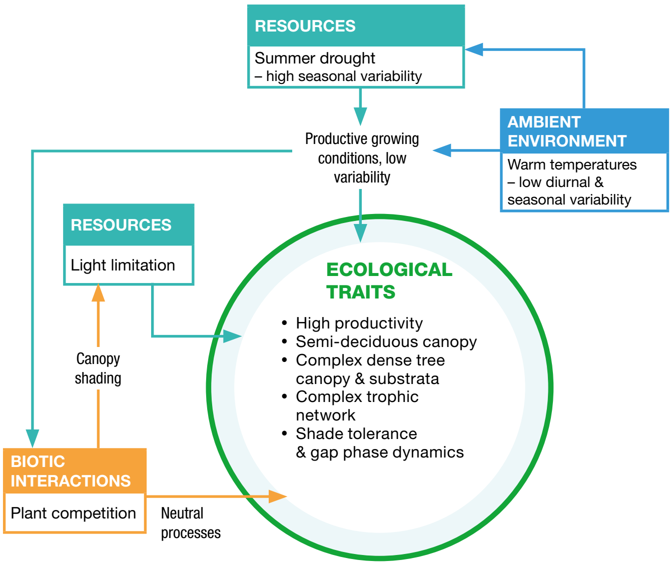
Reference:
Ashton, P.S., Seidler, R. (2014). On the Forests of Tropical Asia: Lest the memory fade. Kew, UK: Royal Botanic Gardens.
Corlett, R.T., Primack, R.B. (2011). Tropical Rain Forests: An Ecological and Biogeographical Comparison. Second Edition. Chichester, UK: Wiley-Blackwell.

T1.2 Tropical subtropical dry forests and thickets

BIOME: TROPICAL-SUBTROPICAL FORESTS
REALM: TERRESTRIAL

Contributors: R.T. Pennington, J. Franklin, N.A. Brummitt, A. Etter, K.R. Young, R.T. Corlett, D.A. Keith

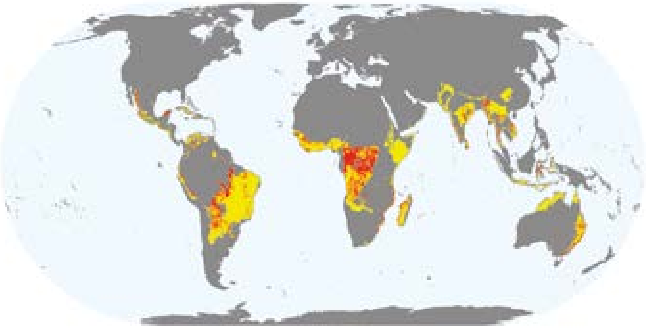
Tropical dry forest, northern Minas Gerais, Brazil.
Source: Toby Pennington (2015)



ECOLOGICAL TRAITS: These closed-canopy forests and thickets have drought-deciduous or semi-deciduous phenology in at least some woody plants (rarely fully evergreen), and thus seasonally high LAI. Strongly seasonal photoautotrophic productivity is limited by a regular annual water deficit/surplus cycle. Diversity is lower across most taxa than T1.1, but tree and vertebrate diversity is high relative to most other forest systems. Plant growth forms and leaf sizes are less diverse than in T1.1. Grasses are rare or absent, except on savanna ecotones, due to canopy shading and/or water competition, while epiphytes, ferns, bryophytes and forbs are present but limited by seasonal drought. Trophic networks are complex with low exclusivity and diverse representation of herbivorous, frugivorous, and carnivorous vertebrates. Fungi and other microbes are important decomposers of abundant leaf litter. Many woody plants are dispersed by wind and some by vertebrates. Most nutrient capital is sequestered in vegetation or cycled through the litter layer. Trees typically have thin bark and low fire tolerance and can recruit in shaded microsites. Plants are tolerant of seasonal drought but can exploit moisture when it is seasonally available through high SLA and plastic productivity. Gap-phase dynamics are driven primarily by individual tree-fall and exploited by seedling banks and vines (seedbanks are uncommon). These forests may be involved in fire-regulated stable-state dynamics with savannas.

KEY ECOLOGICAL DRIVERS: Overall water surplus (or small deficit <100 mm), but a substantial seasonal deficit in winter in which little or no rain falls within a 4–7-month period. Warm temperatures (minima rarely <10°C) with low-moderate diurnal and seasonal variability in the tropics, but greater seasonal variability in subtropical continental areas. Diverse substrates generally produce high levels of nutrients. Tropical storms may be important disturbances in some areas but flammability is low due to limited ground fuels except on savanna ecotones.

DISTRIBUTION: Seasonally dry tropical and subtropical regions in Central and West Africa, Madagascar, southern Asia, north and northern and eastern Australia, the Pacific, Central and South America and the Caribbean.



References:
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Pennington, R.T., Lewis, G., Ratter, J. (2006). *Neotropical Savannas and Dry Forests. Plant Diversity, Biogeography and Conservation*. Florida, USA: CRC Press.
Murphy, P.G. and Lugo, A.E. (1986). 'Ecology of tropical dry forest'. *Annual Review of Ecology and Systematics* 17: 67–88.
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T1.3 Tropical-subtropical montane rainforests

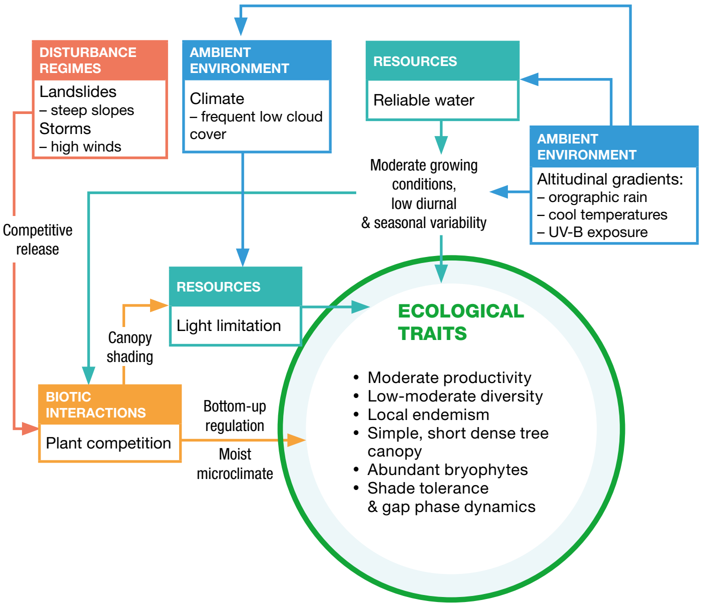
BIOME: TROPICAL-SUBTROPICAL FORESTS
REALM: TERRESTRIAL

Contributors: D.A. Keith, N.A. Brummitt, K.R. Young, R.T. Corlett, A. Etter

Cloud forest, Mt Gower, Lord Howe Island, Oceania.
Source: David Keith (2018)

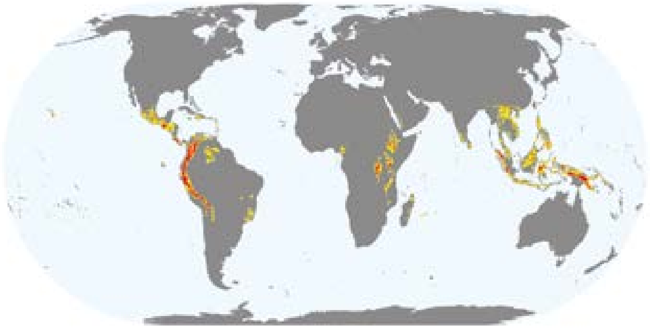
ECOLOGICAL TRAITS: Closed-canopy evergreen forests on tropical mountains usually have a single-layer low tree canopy (~5–20 m tall) with small leaf sizes (microphyll-notophyll) and high SLA. They transition to lowland rainforests (T1.1) with decreasing altitude and to warm temperate forests (T2.4) at subtropical latitudes. Structure and taxonomic diversity become more diminutive and simpler with altitude, culminating in elfinwood forms. Conspicuous epiphytic ferns, bryophytes, lichens, orchids and bromeliads drape tree branches and exploit atmospheric moisture (cloud stripping), but grasses are rare or absent, except for bamboos in some areas. Moderate productivity is fuelled by autochthonous energy, limited by cool temperatures, possibly by high exposure to UV-B radiation, and sometimes by shallow soil and/or wind exposure. Growth and reproductive phenology is usually seasonal. Plant propagules are dispersed mostly by wind and territorial birds and mammals. Taxonomic diversity is moderate to low, especially in the tree canopy, but there is often high local endemism at higher altitudes in most groups, especially amphibians, birds, plants and invertebrates. Gap-phase dynamics are driven by individual tree-fall or lightning strikes, more rarely by extreme wind storms in some areas. Seedling banks are common (seedbanks are uncommon) and most plants are shade tolerant and can recruit in the shade.

KEY ECOLOGICAL DRIVERS: Substantial cloud moisture and high humidity underpin a reliable year-round rainfall surplus over evapotranspiration. Altitudinal gradients in temperature, precipitation and exposure are pivotal in ecosystem structure and function. Frequent cloud cover from orographic uplift and closed tree canopies maintain a moist microclimate and shady conditions. Temperatures are mild-cool with occasional frost. Seasonal variability is low-moderate but diurnal variability is moderate-high. Winter monthly mean minima may be around 0°C in some areas. Landslides are a significant form of disturbance that drive successional dynamics on steep slopes and is exacerbated by extreme rainfall events.



Mountains experience elevated UV-B radiation with altitude and, in some regions, are exposed to local or regional storms.

DISTRIBUTION: Humid tropical and subtropical regions in East Africa, East Madagascar, Southeast Asia, west Oceania, northeast Australia, Central and tropical South America.



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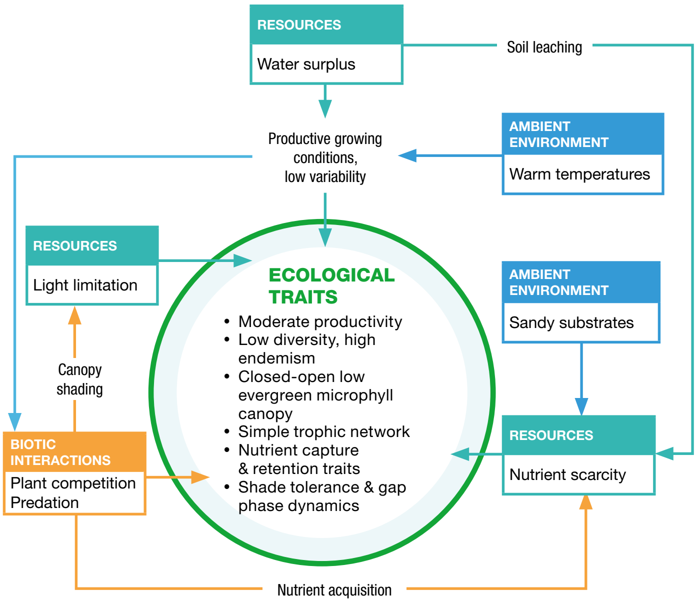
T1.4 Tropical heath forests

BIOME: TROPICAL-SUBTROPICAL FORESTS
REALM: TERRESTRIAL

Contributors: D.A. Keith, R.T. Young, A. Etter

Kerangas forest, Bako National Park, Sarawak, Malaysia.
Source: Bernard Dupont (2007)



ECOLOGICAL TRAITS: Structurally simple evergreen forests with closed to open canopies, typically 5–20 m tall and uniform with a moderate to high LAI. Productivity is lower than in other tropical forests, weakly seasonal and limited by nutrient availability and in some cases by soil anoxia, but decomposition rates are high. Plant traits, such as insectivory and N-fixing microbial associations, are well represented, suggesting adaptive responses to nitrogen deficiency. Aside from plant insectivory, trophic networks are simple compared to other tropical forests. Diversity of plant and animal taxa is also relatively low, but endemism is proportionately high. Tree foliage is characterised by small (microphyll-notophyll) leaves with lower SLA than other tropical forests. Leaves are leathery and often ascending vertically, enabling more light penetration to ground level than in other tropical forests. Tree stems are slender (generally <20 cm in diameter), sometimes twisted, and often densely packed and without buttresses. Epiphytes are usually abundant but lianas are rare and ground vegetation is sparse, with the forest floor dominated by insectivorous vascular plants and bryophytes.

KEY ECOLOGICAL DRIVERS: These forests experience an overall water surplus, but productivity is limited by deep sandy low-nutrient acidic substrates, which are leached by high rainfall. Most nutrients are retained in the vegetation. Downward movement of clay and organic particles through the soil profile results in a deep, white sandy horizon capped by a thin grey surface horizon (typical of podzols), limiting the capacity of the soil to retain nutrients (especially nitrogen) and moisture within the shallow rooting zone. Hence they are prone to inter-annual droughts, but waterlogging may occur where the water table is close to the surface, resulting in periodic anoxia within the root zone. Landscape water-table gradients result in surface mosaics in which heath forests may be juxtaposed with more waterlogged peat forests (TF1.1) and palustrine wetland systems (TF1.4).

DISTRIBUTION: Scattered through northwest and west Amazonia, possibly Guyana, and Southeast Asia, notably in the Rio Negro catchment and southern Kalimantan. Not known in Africa, but possibly in the Congo region.

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T2 Temperate-boreal forests and woodlands biome

Petworth, Sussex, England.
Source: David Keith

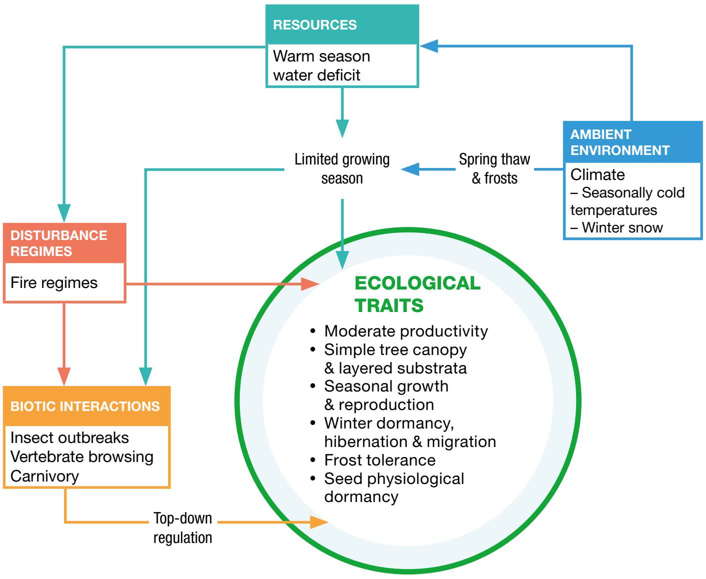
Temperate-boreal forests and woodlands biome include moderate to highly productive tree-dominated systems with a wide range of physiognomic and structural expressions distributed from warm-temperate to boreal latitudes. Although generally less diverse than Tropical-subtropical forests (T1) in taxa such as flowering plants, primates, and birds, these Temperate-boreal forests exhibit greater temporal and spatial variability in productivity, biomass, phenology, and leaf traits of trees. Temporal variability is expressed primarily through seasonal variation in water balance and/or temperature, which regulate the length and timing of growing and breeding seasons. Inter-annual variation is usually less important than in some other biomes (i.e. T5), but nonetheless may play significant roles in resource availability and disturbance regimes (e.g. fire and storms). Gradients in minimum temperatures, soil nutrients, and fire regimes differentiate ecosystem functional groups within this biome. These influence traits such as leaf form (broadleaf vs. needleleaf), leaf phenology (evergreen vs. deciduous), ecophysiological and morphological traits promoting nutrient acquisition and conservation, and morphological traits related to flammability, fire resistance, and recovery. The dominant photoautotrophs (trees) engineer habitats and underpin trophic webs. Resource gradients exert strong bottom-up controls on trophic processes, but in some temperate forests, fires are significant top-down consumers of biomass, as well as influencing flammability feedbacks and timing of life-history processes, such as reproduction and recruitment.

Boreal forest, Liesjärvi National Park, Tammela, Finland.
Source: Seppo Tuominen (with permission)

T2.1 Boreal and temperate montane forests and woodlands

BIOME: T2 TEMPERATE-BOREAL FORESTS AND WOODLANDS
REALM: TERRESTRIAL

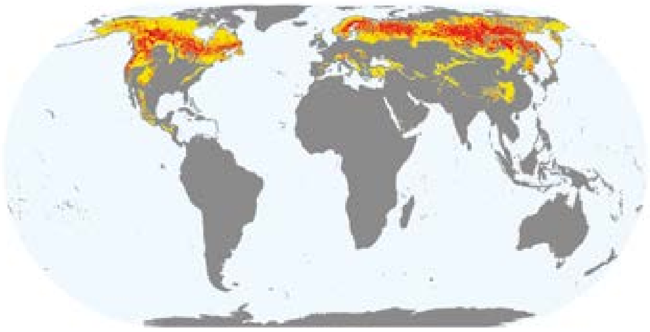
Contributors: D.A. Keith, D. Faber-Langendoen, T. Kontula, J. Franklin, N.A. Brummitt



ECOLOGICAL TRAITS: Evergreen, structurally simple forests and woodlands in cold climates are dominated by needle-leaf conifers and may include a subdominant component of deciduous trees, especially in disturbed sites, accounting for up to two-thirds of stand-level leaf biomass. Boreal forests are generally less diverse, more cold-tolerant and support a more migratory fauna than temperate montane forests. Structure varies from dense forest up to 30 m tall to stunted open woodlands <5 m tall. Large trees engineer habitats of many fungi, non-vascular plants, invertebrates and vertebrates that depend on rugose bark, coarse woody debris, or large tree canopies. Energy is mainly from autochthonous sources, but may include allochthonous subsidies from migratory vertebrates. Primary productivity is limited by seasonal cold and may also be limited by water deficit on coarse textured soils. Forested bogs occupy peaty soils (TF1.6). Seasonal primary productivity may sustain a trophic web with high densities of small and large herbivores (e.g. hare, bear, deer and insects), with feline, canine and raptor predators. Browsers are top-down regulators of plant biomass and cyclers of nitrogen, carbon and nutrients. Forest structure may be disrupted by insect defoliation or fires on multi-decadal cycles. Tree recruitment occurs semi-continuously in gaps or episodically following canopy fires and may be limited by spring frost, desiccation, permafrost fluctuations, herbivory and surface fires. Plants and animals have strongly seasonal growth and reproductive phenology, and possess morphological, behavioural and ecophysiological traits enabling cold-tolerance and the exploitation of short growing seasons. Plant traits include bud protection, extra-cellular freezing tolerance, hardened evergreen needle leaves with low SLA or deciduous leaves with high SLA, cold-stratification seed dormancy, seasonal geophytic growth forms and vegetative storage organs. Tracheids in conifers confer resistance to cavitation in drought by compartmentalising water transport tissues. Some large herbivores and most birds migrate to winter habitats from the boreal zone, and thus function as mobile links, dispersing other biota and bringing allochthonous subsidies of energy and nutrients into the system. Hibernation is common among sedentary vertebrates, while insect life cycles have adult phases cued to spring emergence.

KEY ECOLOGICAL DRIVERS: These systems are driven by large seasonal temperature ranges, cold winters with prolonged winter snow, low light, short growing seasons (1–3 months averaging >10°C) and severe post-thaw frosts. There is an overall water surplus, but annual precipitation can be <200 mm. Soil moisture recharged by winter snow sustains the system through evapotranspiration peaks in summer, but moisture can be limiting where these systems extend to mountains in warm semi-arid latitudes. The acid soils usually accumulate peat and upper horizons may be frozen in winter. Forests may be prone to lightning-induced canopy fires on century time scales and surface fires on multi-decadal scales.

DISTRIBUTION: Boreal distribution across Eurasia and North America, extending to temperate (rarely subtropical) latitudes on mountains.



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Crawford, R.M.M. (2013). *Tundra-Taiga Biology*. Oxford, UK: Oxford University Press.
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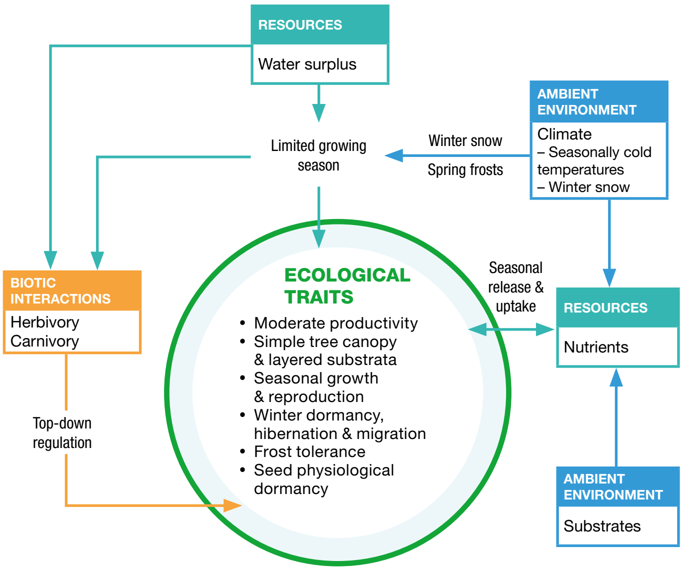
T2.2 Deciduous temperate forests

BIOME: T2 TEMPERATE-BOREAL FORESTS AND WOODLANDS
REALM: TERRESTRIAL

Deciduous forest during autumn leaf fall, Inkoo, Finland.
Source: Anne Raunio (with permission)

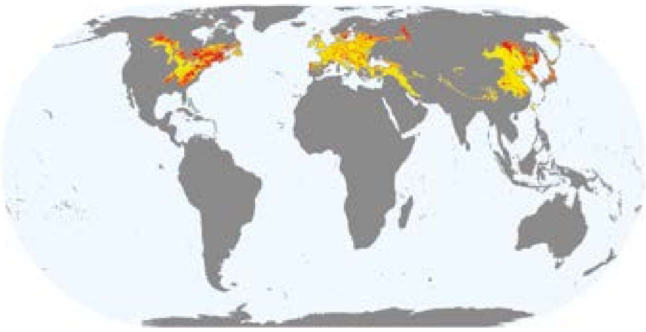
Contributors: D.A. Keith, N.A. Brummitt, F. Essl,
D. Faber-Langendoen



ECOLOGICAL TRAITS: These structurally simple, winter deciduous forests have high productivity and LAI in summer. Winter dormancy, hibernation and migration are common life histories among plants and animals enabling cold avoidance. Local endemism is comparatively low and there are modest levels of diversity across major taxa. The forest canopy comprises at least two-thirds deciduous broad-leaf foliage (notophyll-mesophyll) with high Specific Leaf Area (SLA) and up to one-third evergreen (typically needleleaf) cover. As well as deciduous woody forms, annual turnover of above-ground biomass also occurs some in non-woody geophytic and other ground flora, which are insulated from the cold beneath winter snow and flower soon after snowmelt before tree canopy closure. Annual leaf turnover is sustained by fertile substrates and water surplus, with nutrient withdrawal from foliage and storage of starch prior to fall. Tissues are protected from cold by supercooling rather than extra-cellular freeze-tolerance. Dormant buds are insulated from frost by bracts or by burial below the soil in some non-woody plants. Fungal and microbial decomposers play vital roles in cycling carbon and nutrients in the soil surface horizon. Despite highly seasonal primary productivity, the trophic network includes large browsing herbivores (deer), smaller granivores and herbivores (rodents and hares) and mammalian predators (canids and felines). Most invertebrates are seasonally active. Behavioural and life-history traits allow animals to persist through cold winters, including through dense winter fur, food caching, winter foraging, hibernation, dormant life phases and migration. Migratory animals provide allochthonous subsidies of energy and nutrients and promote incidental dispersal of other biota. Browsing mammals and insects are major consumers of plant biomass and cyclers of nitrogen, carbon and nutrients. Deciduous trees may be early colonisers of disturbed areas (later replaced by evergreens), but are also stable occupants across large temperate regions. Tree recruitment is limited by spring frost, allelopathy and herbivory, and occurs semi-continuously in gaps. Herbivores may influence densities of deciduous forest canopies by regulating tree regeneration. Deciduous leaf fall may exert allelopathic control over tree seedlings and seasonal ground flora.

KEY ECOLOGICAL DRIVERS: Phenological processes in these forests are driven by large seasonal temperature ranges (mean winter temperatures <-1°C, summer means up to 22°C), typically with substantial winter snow and limited growing season, with 4–6 months >10°C, and severe post-thaw frosts. Fertile soils with high N levels and an overall water surplus support deciduous leaf turnover. Fires are uncommon.

DISTRIBUTION: Cool temperate Europe (southwest Russia to British Isles), northeast Asia (northeast China, southern Siberia Korea, and Japan), and northeast America. Limited occurrences in warm-temperate zones of south Europe and Asia and the Midwest USA.



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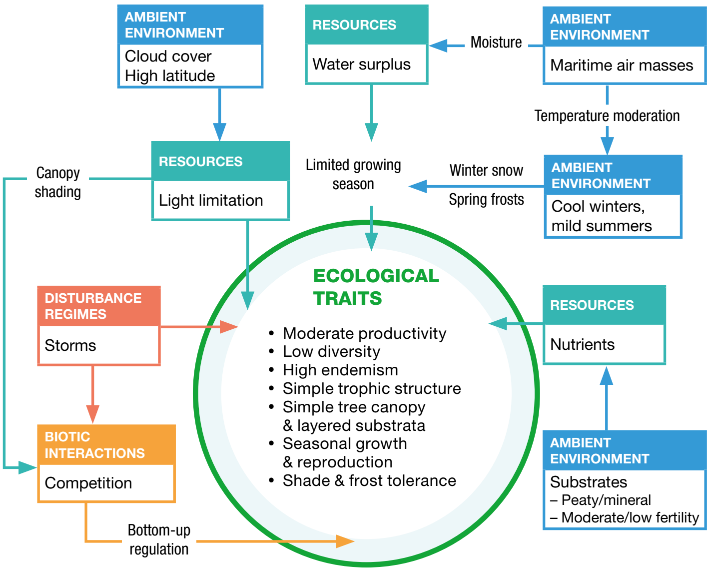
Cool temperate evergreen forest, Hwequehwe, Chile.
Source: David Keith (2017)

T2.3 Oceanic cool temperate rainforests

BIOME: T2 TEMPERATE-BOREAL FORESTS AND WOODLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, S.K. Wiser, N. Brummit, F. Essl, M.S. McGlone, D. Faber-Langendoen



ECOLOGICAL TRAITS: Broadleaf and needleleaf rainforests in cool temperate climates have evergreen or semi-deciduous tree canopies with high LAI and mostly nanophyll-microphyll foliage. Productivity is moderate to high and constrained by strongly seasonal growth and reproductive phenology and moderate levels of frost tolerance. SLA may be high but lower than in T2.2. Evergreen trees typically dominate, but deciduous species become more abundant in sites prone to severe frost and/or with high soil fertility and moisture surplus. The smaller range of leaf sizes and SLA, varied phenology, frost tolerance, broader edaphic association and wetter, cooler climate distinguish these forests from warm temperate forests (T2.4). Local or regional endemism is significant in many taxa. Nonetheless, energy sources are primarily autochthonous. Trophic networks are less complex than in other cool-temperate or boreal forests (T2.1 and T2.2), with weaker top-down regulation due to the lower diversity and abundance of large herbivores and predators. Tree diversity is low (usually <8–10 spp./ha), with abundant epiphytic and terrestrial bryophytes, pteridophytes, lichens, a modest range of herbs, and conspicuous fungi, which are important decomposers. The vertebrate fauna is mostly sedentary and of low-moderate diversity. Most plants recruit in the shade and some remain in seedling banks until gap-phase dynamics are driven by individual tree-fall, lightning strikes, or by extreme wind storms in some areas. Tree recruitment varies with tree masting events, which strongly influence trophic dynamics, especially of rodents and their predators.

KEY ECOLOGICAL DRIVERS: There is a large water surplus, rarely with summer deficits. Rainfall is seasonal, borne on westerly winds peaking in winter months and inter-annual variability is relatively low. Cool winters (minima typically <0–5°C for three months) limit the duration of the growing season. Maritime air masses are the major supply of climatic moisture and moderate winters and summer temperatures. Light may be limited in winter by frequent cloud cover and high latitude. Intermittent winter snow does not persist for more than a few days or weeks. Soils are moderately fertile to infertile and may accumulate peat. Exposure to winter storms and landslides leaves imprints on forest structure in some regions. Fires are rare, occurring on century time scales when lightning (or human) ignitions follow extended droughts.

DISTRIBUTION: Cool temperate coasts of Chile and Patagonia, New Zealand, Tasmania and the Pacific Northwest, rarely extending to warm-temperate latitudes on mountains in Chile, southeast Australia, and outliers above 2,500-m elevation in the Papua New Guinea highlands. Some authors extend the concept to wet boreal forests on the coasts of northwest Europe, Japan and northeast Canada.

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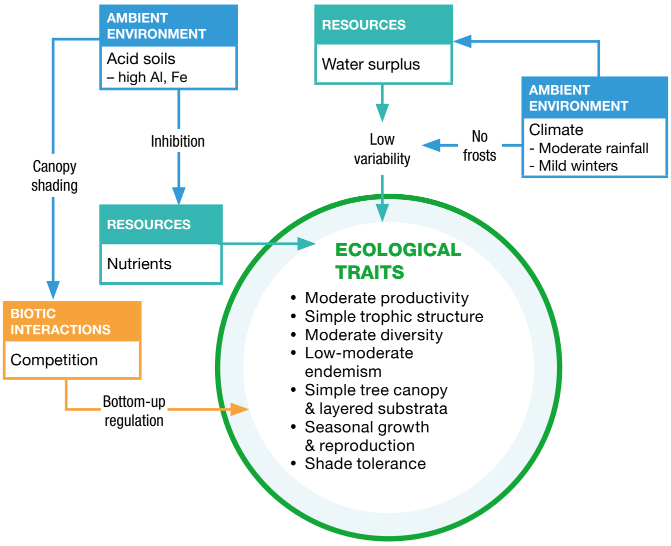
McGlone, M.S., Lusk, C.H., Armesto, J.J. (2016). ‘Biogeography and ecology of south-temperate forests’. *New Zealand Journal of Botany* 54(2): 94–99.

T2.4 Warm temperate laurophyll forests

BIOME: T2 TEMPERATE-BOREAL FORESTS AND WOODLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, N.A. Brummitt, D. Faber-Langendoen, R.T. Corlett, M.S. McGlone

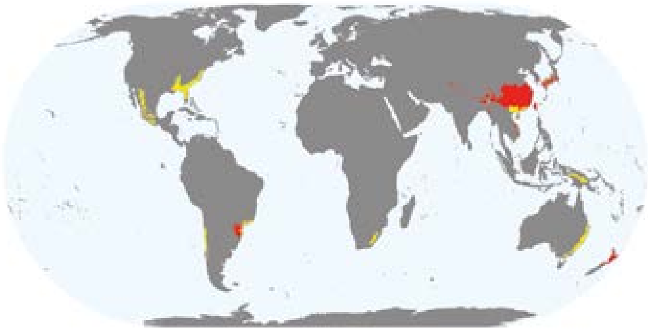
Warm-temperate rainforest, Royal National Park, Australia.
Source: David Keith (2016)



ECOLOGICAL TRAITS: Relatively productive but structurally simple closed-canopy forests with high LAI occur in humid warm-temperate to subtropical climates. The tree canopies are more uniform than most tropical forests (T1.1 and T1.2) and usually lack large emergents. Their foliage is often leathery and glossy (laurophyll) with intermediate SLA values, notophyll-microphyll sizes and prodigiously evergreen. Deciduous species are rarely scattered within the forest canopies. These features, and drier, warmer climates and often more acid soils, distinguish them from oceanic cool temperate forests (T2.3), while in the subtropics they transition to T1 forests. Autochthonous energy supports relatively high primary productivity, weakly limited by summer drought and sometimes by acid substrates. Forest function is regulated mainly by bottom-up processes related to resource competition rather than top-down trophic processes or disturbance regimes. Trophic structure is simpler than in tropical forests, with moderate levels of diversity and endemism among major taxa (i.e. typically <20 tree spp./ha), but local assemblages of birds, bats and canopy invertebrates may be abundant and species-rich, and play important roles in pollination and seed dispersal. Canopy insects are the major consumers of primary production and a major food source for birds. Decomposers and detritivores, such as invertebrates, fungi and microbes on the forest floor, are critical to nutrient cycling. Vertebrate herbivores are relatively uncommon, with low-moderate mammalian diversity. Although epiphytes and lianas are present, plant life-form traits that are typical of tropical forests (T1.1 and T1.2), such as buttress roots, compound leaves, monopodial growth and cauliflory, are uncommon or absent in warm-temperate rainforests. Some trees have ecophysiological tolerance of acid soils (i.e. through aluminium accumulation). Gap-phase dynamics are driven by individual tree-fall and lightning strikes, but many trees are shade-tolerant and recruit slowly in the absence of disturbance. Ground vegetation includes varied growth forms but few grasses.

KEY ECOLOGICAL DRIVERS: The environmental niche of these forests is defined by a modest overall water surplus with no distinct dry season, albeit moderate summer water deficits in some years. Mean annual rainfall is typically 1,200–2,500 mm, but topographic mesoclimates (e.g. sheltered gullies and orographic processes) sustain reliable moisture at some sites. Temperatures are mild with moderate seasonality and a growing season of 6–8 months, and mild frosts occur. Substrates may be acidic with high levels of Al and Fe that limit the uptake of nutrients. These forests may be embedded in fire-prone landscapes but are typically not flammable due to their moist microclimates .

DISTRIBUTION: Patchy warm temperate-subtropical distribution at 26–43° latitude, north or south of the Equator.



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Corlett, R.T. and Hughes, A.C. (2015). 'Subtropical Forests'. In: K.S.-H. Peh, R.T. Corlett, Y. Bergeron (eds.), *Routledge Handbook of Forest Ecology*, Chapter 4, pp. 46–55. Oxford, UK: Routledge.
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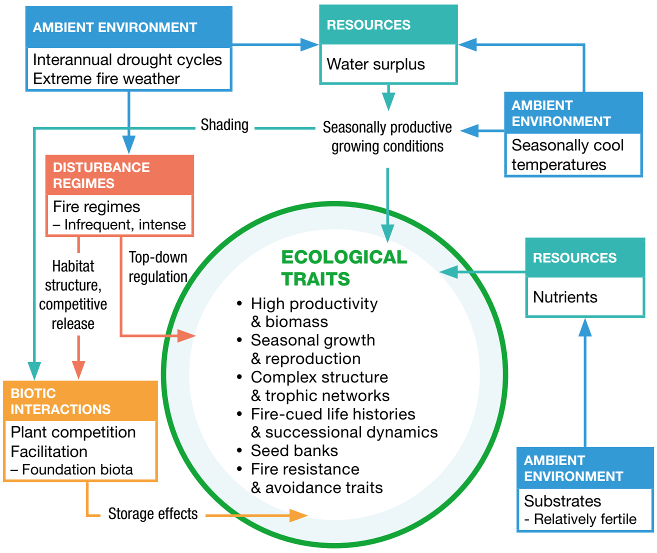
Temperate fire-prone tall forests, Buladelah, Australia.
Source: David Keith (2003)

T2.5 Temperate pyric humid forests

BIOME: T2 TEMPERATE-BOREAL FORESTS AND WOODLANDS
REALM: TERRESTRIAL

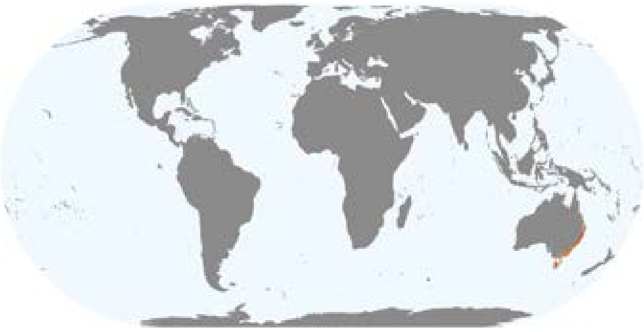
Contributors: D.A. Keith, R.C. Mac Nally



ECOLOGICAL TRAITS: This group includes the tallest forests on earth. They are moist, multi-layered forests in wet-temperate climates with complex spatial structure and very high biomass and LAI. The upper layer is an open canopy of sclerophyllous trees 40–90 m tall with long, usually unbranched trunks. The open canopy structure allows light transmission sufficient for the development of up to three subcanopy layers, consisting mostly of non-sclerophyllous trees and shrubs with higher SLA than the upper canopy species. These forests are highly productive, grow rapidly, draw energy from autochthonous sources and store very large quantities of carbon, both above and below ground. They have complex trophic networks with a diverse invertebrate, reptile, bird and mammal fauna with assemblages that live primarily in the tree canopy or the forest floor, and some that move regularly between vertical strata. Some species are endemic and have traits associated with large trees, including the use of wood cavities, thick or loose bark, large canopies, woody debris, and deep, moist leaf litter. There is significant diversification of avian foraging methods and hence a high functional and taxonomic diversity of birds. High deposition rates of leaf litter and woody debris sustain diverse fungal decomposers and invertebrate detritivores and provide nesting substrates and refuges for ground mammals and avian insectivores. The shade-tolerant ground flora may include a diversity of ferns forbs, grasses (mostly C_3) and bryophytes. The dominant trees are shade-intolerant and depend on tree-fall gaps or periodic fires for regeneration. In cooler climates, trees are killed by canopy fires but may survive surface fires, and canopy seedbanks are crucial to persistence. Epicormic resprouting (i.e. from aerial stems) is more common in warmer climates. Subcanopy and ground layers include both shade-tolerant and shade-intolerant plants, the latter with physically and physiologically dormant seedbanks that cue episodes of mass regeneration to fire. Multi-decadal or century-scale canopy fires consume biomass, liberate resources and trigger life-history processes in a range of biota. Seedbanks sustain plant diversity through storage effects.

KEY ECOLOGICAL DRIVERS: There is an annual water surplus with seasonal variation (peak surplus in winter) and rare major summer deficits associated with inter-annual drought cycles. Multiple tree layers produce a light diminution gradient and moist micro-climates at ground level. Winters are cool and summers are warm with occasional heatwaves that dry out the moist micro-climate and enable periodic fires, which may be extremely intense and consume the canopy. The growing season is 6–8 months; snow is uncommon and short-lived. Soils are relatively fertile, but often limited in Nitrogen.

DISTRIBUTION: Subtropical - temperate southeast and temperate southwest Australia.



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Wardell-Johnson, G., Neldner, J., Balmer, J. (2017). 'Wet sclerophyll forests'. In: D.A. Keith (ed.), *Australian vegetation*, pp. 281–313. Cambridge, UK: Cambridge University Press.

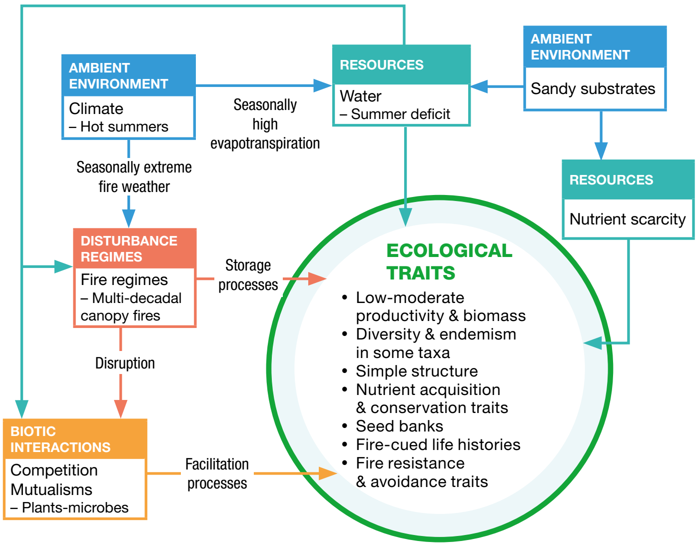
T2.6 Temperate pyric sclerophyll forests and woodlands

BIOME: T2 TEMPERATE-BOREAL FORESTS AND WOODLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, F. Essl, J. Franklin, R. Mac Nally

Dry sclerophyll forest regenerating three years after fire, Royal National Park, Australia.
Source: David Keith (2020)

ECOLOGICAL TRAITS: Forests and woodlands, typically 10–30 m tall with an open evergreen sclerophyllous tree canopy and low-moderate LAI grow in fire-prone temperate landscapes. Productivity is lower than other temperate and tropical forest systems, limited by low nutrient availability and summer water deficits. Abundant light and water (except in peak summer) enable the development of substantial biomass with high C:N ratios. Trees have microphyll foliage with low to very low SLA. Sclerophyll or subsclerophyll shrubs with low to very low SLA foliage form a prominent layer between the trees. A sparse ground layer of C_3 and C_4 tussock grasses and forbs becomes more prominent on soils of loamy texture. Diversity and local endemism may be high among some taxa including plants, birds, and some invertebrates such as dipterans and hemipterans. Low nutrients and summer droughts limit the diversity and abundance of higher trophic levels. Plant traits (e.g. sclerophylly, stomatal invagination, tubers and seedbanks) confer tolerance to pronounced but variable summer water deficits. Plants possess traits that promote the efficient capture and retention of nutrients, including specialised root structures, N-fixing bacterial associations, slow leaf turnover and high allocation of photosynthates to structural tissues and exudates. Consumers have traits that enable the consumption of high-fibre biomass. Mammalian herbivores (i.e. the folivorous koala) can exploit high-fibre content and phenolics. Plants and animals have morphological and behavioural traits that allow tolerance or avoidance of fire and the life-history processes of many taxa are cued to fire (especially plant recruitment). Key fire traits in plants include recovery organs protected by thick bark or burial, serotinous seedbanks (i.e. held in plant canopies), physical and physiological seed dormancy and pyrogenic reproduction. Almost all plants are shade-intolerant and fire is a critical top-down regulator of diversity through storage effects and the periodic disruption of plant competition.



KEY ECOLOGICAL DRIVERS: Hot summers generate a marked but variable summer water deficit, usually with a modest winter surplus, irrespective of whether rainfall is highly seasonal with winter maximum, aseasonal, or weakly seasonal with inter-annually variable summer maxima. Soils are acidic, sandy, or loamy in texture, and low to very impoverished in P and N. Hot summers define a marked season for canopy or surface fires at decadal to multi-decadal intervals. Light frost occurs periodically in some areas but snow is rare.

DISTRIBUTION: Temperate regions of Australia, the Mediterranean, and central California.

References:
Barbour, M., Keeler-Wolf, T. and Schoenherr, A.A. (2007). *Terrestrial vegetation of California. 3rd edition.* Berkeley, USA: University of California Press.
Tozer, M.G., Simpson, C.C., Jansens, I.B., Keith, D.A. (2017). 'Biogeography of Australia's dry sclerophyll forests: drought, nutrients and fire'. In: D.A. Keith (ed.), *Australian vegetation*, pp. 314–338. Cambridge, UK: Cambridge University Press.

T3 Shrublands and shrubby woodlands biome

Anna Bay, Western Australia.
Source: David Keith

The Shrublands and shrub-dominated woodlands biome includes oligotrophic systems occurring on acidic, sandy soils that are often shallow or skeletal. Classically regarded as 'azonal' biomes or 'pedobiomes' (i.e. biomes determined by soils), they are scattered across all landmasses outside the polar regions, generally (but not always) closer to continental margins than to interior regions and absent from central Asia. Productivity and biomass are low to moderate and limited by soil fertility. The effect of nutrient poverty on productivity is exacerbated in tropical to mid-latitudes by water deficits occurring during either winter (tropics) or summer (temperate humid and Mediterranean climates) and by low insolation and cold temperatures at higher latitudes. Trophic networks are simple but the major functional components (photoautotrophic plants, decomposers, detritivores, herbivores and predators) are all represented and fuelled by autochthonous energy sources. Shrubs are the dominant primary producers and possess a diversity of leaf and root traits as well as mutualistic relationships with soil microbes that promote the capture and conservation of nutrients. Recurrent disturbance events exert top-down regulation by consuming biomass, releasing resources, and triggering life-history processes (including recruitment and dispersal) in a range of organisms. Fire is the most widespread mechanism, with storms or mass movement of substrate less frequently implicated. Storage effects related to re-sprouting organs and seed banks appear to be important for maintaining plant diversity and hence structure and function in shrublands exposed to recurring fires and water deficits.

T3.1 Seasonally dry tropical shrublands

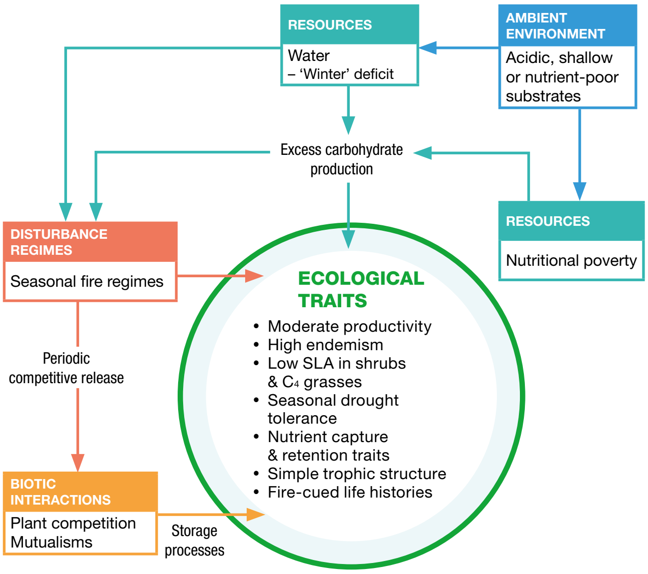
BIOME: T3 SHRUBLANDS & SHRUBBY WOODLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, J. Russell-Smith

Tropical maquis on serpentinite, Pic Maloui, New Caledonia.
Source: Oliver Descouedres (with permission)

ECOLOGICAL TRAITS: These moderate-productivity, mostly evergreen shrublands, shrubby grasslands and low, open forests (generally <6 m tall) are limited by nutritional poverty and strong seasonal drought in the tropical winter months. Taxonomic and functional diversity is moderate in most groups but with high local endemism in plants, invertebrates, birds and other taxa. Vegetation is spatially heterogeneous in a matrix of savannas (T4.2) or tropical dry forests (T1.2) and dominated by sclerophyllous shrubs with small leaf sizes (nanophyll-microphyll) and low SLA. C_4 grasses may be conspicuous or co-dominant (unlike in most temperate heathlands, T3.2) but generally do not form a continuous stratum as in savannas (T4). These systems have relatively simple trophic networks fuelled by autochthonous energy sources. Productivity is low to moderate and constrained by seasonal drought and nutritional poverty. Shrubs are the dominant primary producers and show traits promoting the capture and conservation of nutrients (e.g. sclerophylly, cluster roots, carnivorous structures, and microbial and fungal root mutualisms) and tolerance to severe seasonal droughts (i.e. stomatal invagination). Nectarivorous and/or insectivorous birds and reptiles and granivorous small mammals dominate the vertebrate fauna, but vertebrate herbivores are sparse. Recurring fires play a role in the top-down regulation of ecosystem structure and composition.

KEY ECOLOGICAL DRIVERS: A severe seasonal climatic water deficit during tropical winter months is exacerbated by sandy or shallow rocky substrates with low moisture retention. Nutritional poverty (especially N and P) stems from oligotrophic, typically acid substrates, such as sandstones, ironstones, leached sand deposits, or rocky volcanic or ultramafic substrates. Vegetation holds the largest pool of nutrients. Temperatures are warm, rarely <10°C, with low diurnal and seasonal variation. Dry-season fires recur on decadal or longer time scales, but they are rare in table-top mountains (tepui).



DISTRIBUTION: Brazilian campos rupestres (where grasses are important), Venezuelan tepui, Peruvian tabletops, Florida sands, northern Australia and montane oceanic islands.

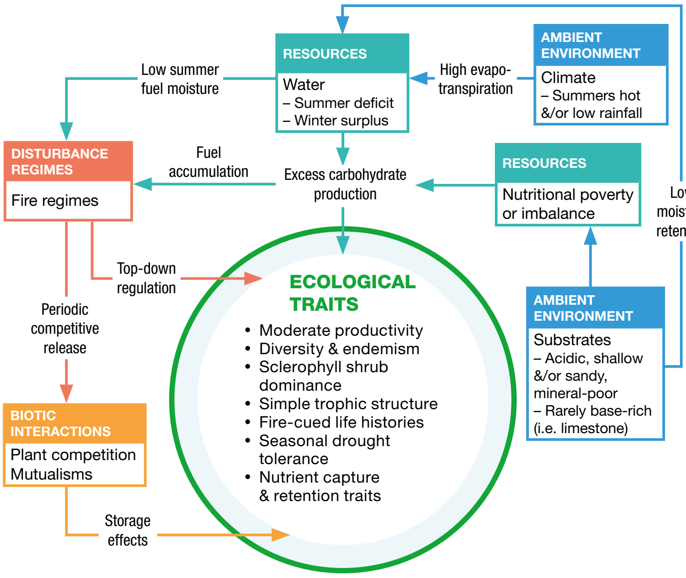
References:
Fernandes, G.W. (2016). *Ecology and Conservation of Mountaintop Grasslands in Brazil.* Berlin, Germany: Springer.
Morellato, L.P.C., Silveira FAO (2018.) 'Plant life in campo rupestre: New lessons from an ancient biodiversity hotspot'. *Flora* 238: 1–10.
Russell-Smith, J., Ryan, P.G., Klessa, D., Waight, G., Harwood, R. (1998). 'Fire regimes, fire-sensitive vegetation, and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia'. *Journal of Applied Ecology* 35(6): 829–846.

T3.2 Seasonally dry temperate heaths and shrublands

BIOME: T3 SHRUBLANDS & SHRUBBY WOODLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, J. Loidi

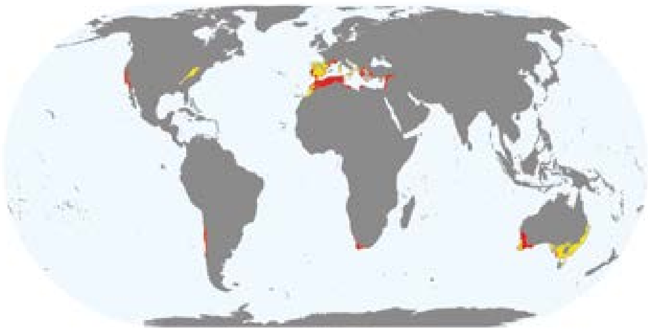
Fynbos, Pakhuispas, Cederberg Mountains, South Africa.
Source: David Keith (2007)



ECOLOGICAL TRAITS: Sclerophyllous, evergreen shrublands are distinctive ecosystems of humid and subhumid climates in mid-latitudes. Their low-moderate productivity is fuelled by autochthonous energy sources and is limited by resource constraints and/or recurring disturbance. Vegetation is dominated by shrubs with very low SLA, high C:N ratios, shade-intolerance, and long-lived, small, often ericoid leaves, with or without a low, open canopy of sclerophyll trees. The ground layer may include geophytes and sclerophyll graminoids, although less commonly true grasses. Trophic webs are simple, with large mammalian predators scarce or absent, and low densities of vertebrate herbivores. Native browsers may have local effects on vegetation. Diversity and local endemism may be high among vascular plants and invertebrate consumers. Plants and animals have morphological, ecophysiological, and life-history traits that promote persistence under summer droughts, nutrient poverty, and recurring fires, which play a role in top-down regulation. Stomatal regulation and root architecture promote drought tolerance in plants. Cluster roots and acid exudates, mycorrhizae and insectivory promote nutrient capture, while cellulose, lignin, exudate production and leaf longevity promote nutrient conservation in plants. Vertebrate herbivores and granivores possess specialised dietary and digestive traits enabling consumption of foliage with low nutrient content and secondary compounds. Decomposition rates are slow, allowing litter-fuel accumulation to add to well-aerated fine fuels in shrub canopies. Life-history traits, such as recovery organs, serotiny, post-fire seedling recruitment, pyrogenic flowering and fire-related germination cues, promote plant survival, growth and reproduction under recurring canopy fires. Animals evade fires in burrows or through mobility. Animal pollination syndromes are common (notably dipterans, lepidopterans, birds, and sometimes mammals) and ants may be prominent in seed dispersal.

KEY ECOLOGICAL DRIVERS: A marked summer water deficit and a modest winter surplus is driven by high summer temperatures and evapotranspiration with winter-maximum or aseasonal rainfall patterns. Winters are mild, or cool at high elevations. Sandy soil textures or reverse-texture effects of clay-loams exacerbate an overall water deficit. Soils are typically acid, derived from siliceous sand deposits, sandstones, or acid intrusives or volcanics, and are low to very low in P, N and mineral cations (though this varies between regions, e.g, base-rich limestones, marl and dolomites in southern Europe). The climate, soils and vegetation promote summer canopy fires at decadal to multi-decadal intervals. Positive feedbacks between fire and vegetation may be important in maintaining flammability.

DISTRIBUTION: Mediterranean-type climate regions of Europe, north and south Africa, southern Australia, western North and South America, and occurrences in non-Mediterranean climates in eastern Australia, the USA, and Argentina.



References:

Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., and Rundel, P.W. (2012). ‘Fire in Mediterranean Ecosystems: Ecology, Evolution and Management’. In: *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management,* pp. 83–112. Cambridge, UK: Cambridge University Press.

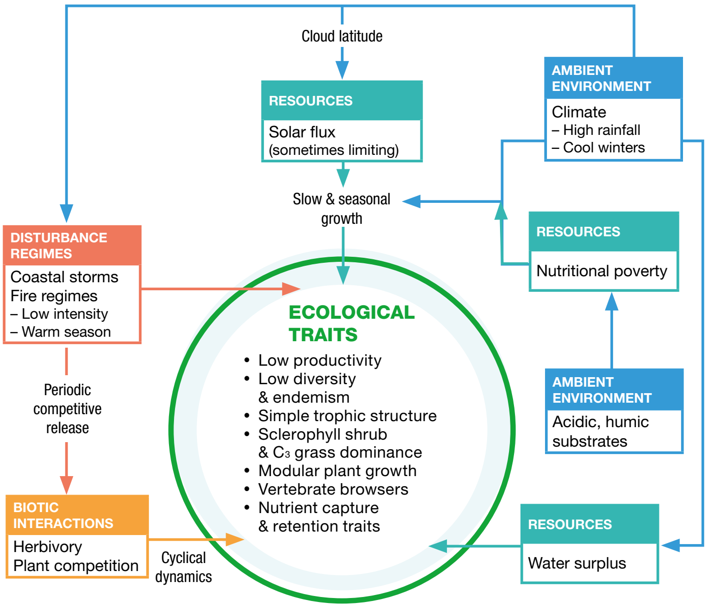
Lamont, B.B., Keith, D.A. (2017). ‘Heathlands and associated shrublands’. In: D.A. Keith (ed.), *Australian vegetation*, pp. 339–368. Cambridge, UK: Cambridge University Press.

T3.3 Cool temperate heathlands

BIOME: T3 SHRUBLANDS & SHRUBBY WOODLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, F. Essl, N.A. Brummitt, J. Loidi

Magellanic heath, Patagonia, Chile.
Source: David Keith (2016)



ECOLOGICAL TRAITS: These mixed graminoid shrublands are restricted to cool-temperate maritime environments. Typically, the vegetation cover is >70% and mostly less than 1 m tall, dominated by low, semi-sclerophyllous shrubs with ferns and C_3 graminoids. Shrub foliage is mostly evergreen and ericoid, with low SLA or reduced to spiny stems. Modular growth forms are common among shrubs and grasses. Diversity and local endemism are low across taxa and the trophic network is relatively simple. Primary productivity is low, based on autochthonous energy sources and limited by cold temperatures and low-fertility acid soils rather than by water deficit (as in other heathlands, T3). Seasonally low light may limit productivity at the highest latitudes. Cool temperatures and low soil oxygen due to periodically wet subsoil limit decomposition by microbes and fungi so that soils accumulate organic matter despite low productivity. Mammalian browsers including cervids, lagomorphs and camelids (South America) consume local plant biomass but subsidise autochthonous energy with carbon and nutrients consumed in more productive forest or anthropogenic ecosystems adjacent to the heathlands. Browsers and recurring low-intensity fires appear to be important in top-down regulatory processes that prevent the transition to forest, as is anthropogenic fire, grazing, and tree removal. Canids and raptors are the main vertebrate predators. Other characteristic vertebrate fauna include ground-nesting birds and rodents. At least some communities exhibit autogenic cyclical patch dynamics in which shrubs and grasses are alternately dominant, senescent and regenerating.

KEY ECOLOGICAL DRIVERS: Unlike most other heathlands, these ecosystems have an overall water surplus, although sometimes with small summer deficits. Mild summers and cold winters with periodic snow are tempered by maritime climatic influences. A short day length and low solar angle limits energy influx at the highest latitudes. Severe coastal storms with high winds occur periodically. Acid soils, typically with high humic content in upper horizons, are often limited in N and P. Low-intensity fires recur at decadal time scales or rarely. Some northern European heaths were derived from forest and return to forest when burning and grazing ceases.

DISTRIBUTION: Boreal and cool temperate coasts of western Europe and America, the Azores and the Magellanic region of South America, mostly at >40° latitude, except where transitional with warm-temperate heaths (e.g. France and Spain).

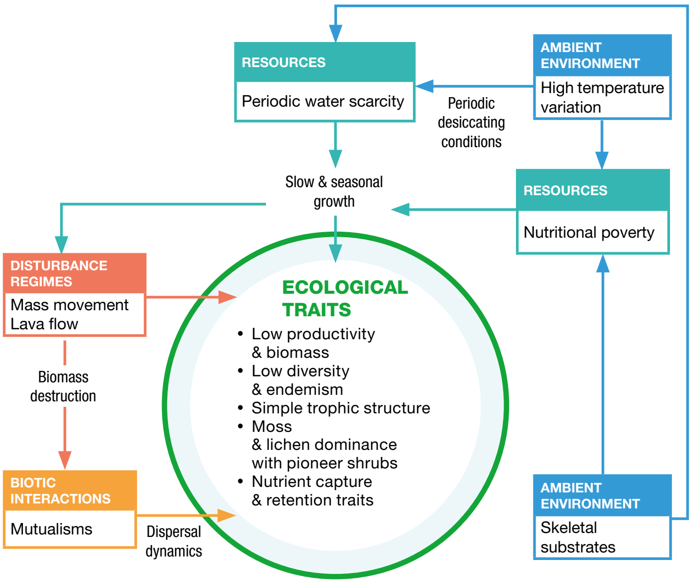
References:
Aerts, R., Heil, G.W. (1993). *Heathlands: Patterns and processes in a changing environment*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
Loidi, J., Biurrun, I, Juan Antonio Campos, J.A., García-Mijangos, I., Herrera, M. (2010). 'A biogeographical analysis of the European Atlantic lowland heathlands'. *Journal of Vegetation Science* 21(5): 832–842.
Watt, A.S. (1947). 'Pattern and process in the plant community'. *Journal of Ecology* 35(1/2): 1-22.

T3.4 Rocky pavements, lava flows and screes

BIOME: T3 SHRUBLANDS & SHRUBBY WOODLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, N.A. Cutler

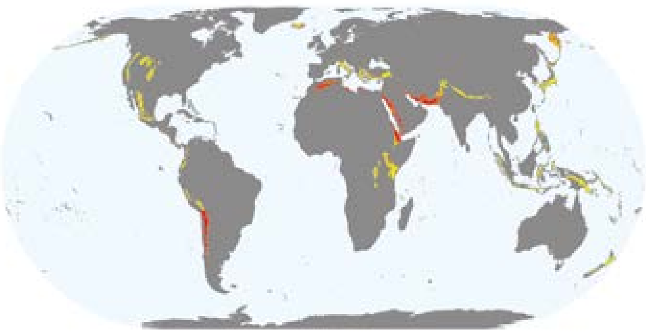
Lava flow, Conguillo National Park, Chile.
Source: David Keith (2017)



ECOLOGICAL TRAITS: Vegetation dominated by cryptogams (lichens, bryophytes), with scattered shrubs- with very low LAI develops on skeletal rocky substrates. These low-productivity systems are limited by moisture and nutrient scarcity, temperature extremes, and periodic disturbance through mass movement. Diversity and endemism is low across taxa and the trophic structure is simple. Reptiles and ground-nesting birds are among the few resident vertebrates. Lichens and bryophytes may be abundant and perform critical roles in moisture retention, nutrient acquisition, energy capture, surface stabilisation and proto-soil development, especially through carbon accumulation. N-fixing lichens and cyanobacteria, nurse plants and other mutualisms are critical to ecosystem development. Rates of ecosystem development are linked to substrate weathering, decomposition and soil development, which mediate nutrient supply, moisture retention and temperature amelioration. Vascular plants have nanophyll-microphyll leaves and low SLA. Their cover is sparse and comprises ruderal pioneer species (shrubs, grasses and forbs) that colonise exposed surfaces and extract moisture from rock crevices. Species composition and vegetation structure are dynamic in response to surface instability and show limited differentiation across environmental gradients and microsites due to successional development, episodes of desiccation and periodic disturbances that destroy biomass. Rates of vegetation development, soil accumulation and compositional change display amplified temperature-dependence due to resource-concentration effects. Older rocky systems have greater micro-habitat diversity, more insular biota and higher endemism, and are classified in other functional groups.

KEY ECOLOGICAL DRIVERS: Skeletal substrates (e.g. lava pavements, scree slopes and rock outcrops) limit water retention and nutrient capital and increase heat absorption, leading to periodically extreme temperatures. High summer temperatures and solar exposure concentrate resources and increase the temperature-sensitivity of biogeochemical processes. Winter temperatures may be cold at high elevations (see T6.2). Recurring geophysical disturbances, such as lava flow, mass movement and geothermal activity, as well as desiccation episodes, periodically destroy biomass and reset successional pathways.

DISTRIBUTION: Localised areas scattered around the Pacific Rim, African Rift Valley, Mediterranean and north Atlantic.



References:
Anderson-Teixeira, K.J., Vitousek, P.M. and Brown, J.H. (2007). 'Amplified temperature dependence in ecosystems developing on the lava flows of Mauna Loa, Hawai'i'. *PNAS* 105(1): 228–233.
Crews, T.E., Kurina, L.M. and Vitousek, P.M. (2001). 'Organic matter and nitrogen accumulation and nitrogen fixation during early ecosystem development in Hawai'i'. *Biogeochemistry* 52: 259–279.
Cutler, N.A., Belyea, L.R., Dugmore, A.J. (2008). 'The spatiotemporal dynamics of a primary succession'. *Journal of Ecology* 96(2): 231–246.

T4 Savannas and grasslands biome

Letaba, Kruger National Park, South Africa.
Source: David Keith

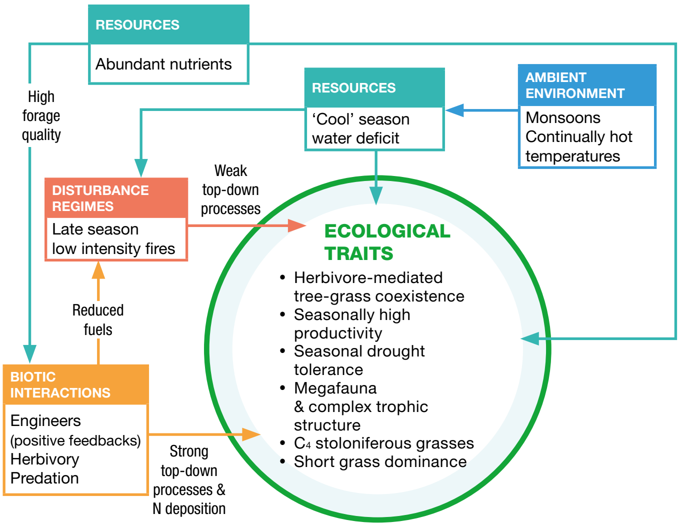
Ecological functions within the Savannas and grasslands biome are closely linked to a mostly continuous ground layer of grasses that contribute moderate to very high levels of primary productivity driven by strongly seasonal water surplus and deficit cycles. The timing of the seasonal cycle of productivity varies with latitude and becomes more variable inter-annually as total rainfall declines. The woody component of the vegetation may be completely absent or may vary to a height and stature that resembles that of a forest. In the tropics and subtropics, productivity peaks in the summer when high rainfall coincides with warm temperatures. At temperate latitudes, summer growth is suppressed by water deficits associated with high evapotranspiration, sometimes exacerbated by weakly seasonal (winter-maximum) rainfall, so that productivity peaks in spring when warming temperatures coincide with high soil moisture accumulated over winter. Co-existence between trees and grasses and between grasses and interstitial forbs is mediated by herbivory and/or fire. These agents are critical in the top-down regulation of grassy ecosystems and in some cases are involved in feedback mechanisms that mediate regime shifts between alternative stable states. Herbivory is the primary driver in highly fertile and productive systems, whereas fire is the primary driver in less fertile and lower productivity systems. Nutrient gradients are exacerbated volatilisation during fire and the loss of nutrients in smoke. The representation of grass species with C_3 and C_4 photosynthetic pathways varies with water availability and temperature over regional and continental climatic gradients. Grasses are rapid responders to seasonal pulses of elevated soil moisture and sustain a complex trophic web with large-bodied mammalian herbivores and their predators. The curing of grasses over the dry season is critical to flammability. Mammal diversity, trophic complexity, and the expression of physical and chemical defences against herbivory also vary with soil fertility.

T4.1 Trophic savannas

BIOME: T4 SAVANNAS & GRASSLANDS
REALM: TERRESTRIAL

Contributors: C.E.R. Lehmann, D.A. Keith

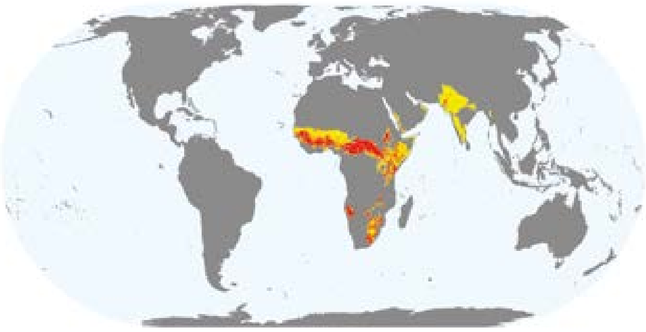
Trophic savanna during wildebeest migration, Serengeti.
Source: http://english.cntv.cn/special/great_migration/homepage/



ECOLOGICAL TRAITS: These grassy woodlands and grasslands are dominated by C_4 grasses with stoloniferous, rhizomatous and tussock growth forms that are kept short by vertebrate grazers. Trophic savannas (relative to pyric savannas, T4.2) have unique plant and animal diversity within a complex trophic structure dominated by abundant mammalian herbivores and predators. These animals are functionally differentiated in body size, mouth morphology, diet and behaviour. They promote fine-scale vegetation heterogeneity and dominance of short grass species, sustaining the system through positive feedbacks and limiting fire fuels. Trees and grasses possess functional traits that promote tolerance to chronic herbivory as well as seasonal drought. Seasonal high productivity coincides with summer rains. The dry season induces grass curing and leaf fall in deciduous and semi-deciduous woody plants. Trees are shade-intolerant during their establishment and most develop chemical (i.e. phenolics) or physical (i.e. spinescence) herbivory defence traits and an ability to re-sprout as they enter the juvenile phase. Their soft microphyll-notophyll foliage has relatively high SLA and low C:N ratios, as do grasses. Robust root systems and stolons/rhizomes enable characteristic grasses to survive and spread under heavy grazing. As well as vertebrate herbivores and predators, vertebrate scavengers and invertebrate detritivores are key components of the trophic network and carbon cycle. Nitrogen fixation, recycling and deposition by animals exceed volatilisation.

KEY ECOLOGICAL DRIVERS: Trophic savannas like pyric savannas are driven by seasonal climates but generally occupy environmental niches with lower rainfall and higher soil fertility. High annual rainfall deficit of 400 mm to >1,800 mm. Annual rainfall generally varies from 300 mm to 700 mm, always with strong seasonal (winter) drought, but these savanna types are restricted to landscapes with sufficient water bodies (rivers and lakes) to sustain high densities of large mammals. Temperatures are warm-hot with low-moderate variability through the year. Low intensity fires have return intervals of 5–50 years, depending on animal densities and inter-annual rainfall variation, usually after the growing season, removing much of the remaining biomass not consumed by herbivores. Soils are moderately fertile and often have a significant clay component.

DISTRIBUTION: Seasonal tropics and subtropics of Africa and Asia.



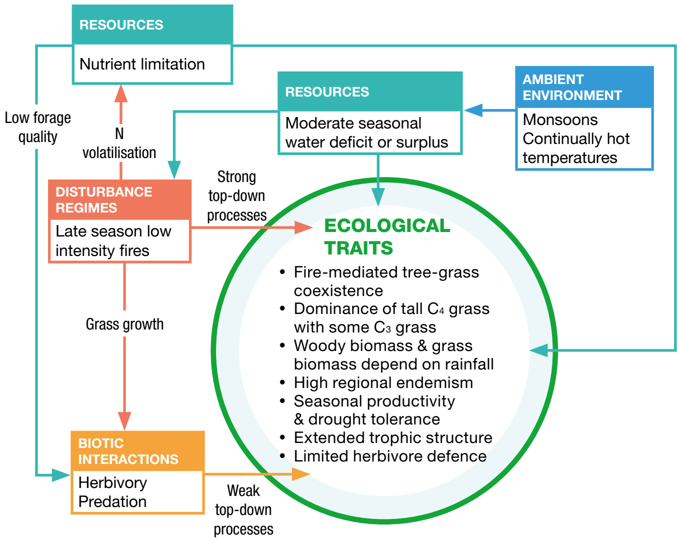
References:
Archibald, S., Hempson, G.P. (2016). 'Competing consumers: Contrasting the patterns and impacts of fire and mammalian herbivory in Africa'. *Philosophical Transactions of the Royal Society B* 371(1703): 20150309.
Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L.M., Moxley, C., Owen-Smith, N., Peel, M.J. et al. (2015). 'Ecology of grazing lawns in Africa'. *Biological Reviews* 90(3): 979–994.

T4.2 Pyric tussock savannas

BIOME: T4 SAVANNAS & GRASSLANDS
REALM: TERRESTRIAL

Contributors: C.E.R. Lehmann, A. Etter, K.R.Young, D.A. Keith

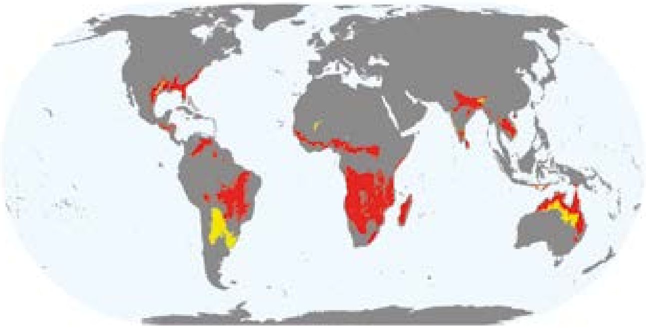
Gran Sabana near Rio Carrao, Venezuela.
Source: David Keith (2012)



ECOLOGICAL TRAITS: Grassy woodlands and grasslands are dominated by C_4 tussock grasses, with some C_3 grasses in the Americas and variable tree cover. In the tropics, seasonally high productivity coincides with the timing of summer rains and grasses cure in dry winters, promoting flammability. This pattern also occurs in the subtropics but transitions occur with temperate woodlands (T4.4), which have different seasonal phenology, tree and grass dominance and fire regimes. Tree basal area, abundance of plants with annual semelparous life cycles and abundant grasses with tall tussock growth forms are strongly dependent on mean annual rainfall (i.e. limited by seasonal drought). Local endemism is low across all taxa but regional endemism is high, especially in the Americas and Australasia. Plant traits, such as deciduous leaf phenology or deep roots, promote tolerance to seasonal drought and rapid resource exploitation. Woody plants have microphyll-notophyll foliage with moderate-high SLA and mostly high C:N ratios. Some C_4 grasses nonetheless accumulate high levels of rubisco, which may push down C:N ratios. Nitrogen volatilisation exceeds deposition because fire is the major consumer of biomass. Woody plant species are shade-intolerant during their establishment and develop fire-resistant organs (e.g. thick bark and below-ground bud banks). The contiguous ground layer of erect tussock grasses creates an aerated flammable fuel bed, while grass architecture with tightly clustered culms vents heat away from meristems. Patchy fires promote landscape-scale vegetation heterogeneity (i.e. in tree cover) and maintain the dominance of flammable tussock grasses over shrubs, especially in wetter climates, and hence sustain the system through positive feedbacks. Fires also enhance efficiency of predators. Vertebrate scavengers and invertebrate detritivores are key components of the trophic network and carbon cycle. Mammalian herbivores and predators are present but exert less top-down influence on the diverse trophic structure than fire. Consequently, plant physical defences against herbivores, such as spinescence, are less prominent than in T4.1.

KEY ECOLOGICAL DRIVERS: An overall rainfall deficit up to ~1,200 mm or a modest surplus of up to 500 mm, always with strong seasonal (winter) drought with continuously warm-hot temperatures through the year even though rainfall become less seasonal in the subtropics. Mean annual rainfall varies from 650 mm to 1,500 mm. Sub-decadal fire regimes of surface fires occur throughout the dry season, while canopy fires occur rarely late in the dry season. Soils are of low-moderate fertility, often with high Fe and Al.

DISTRIBUTION: Seasonally dry tropics and subtropics of the Americas, Australia, Asia, and Africa.



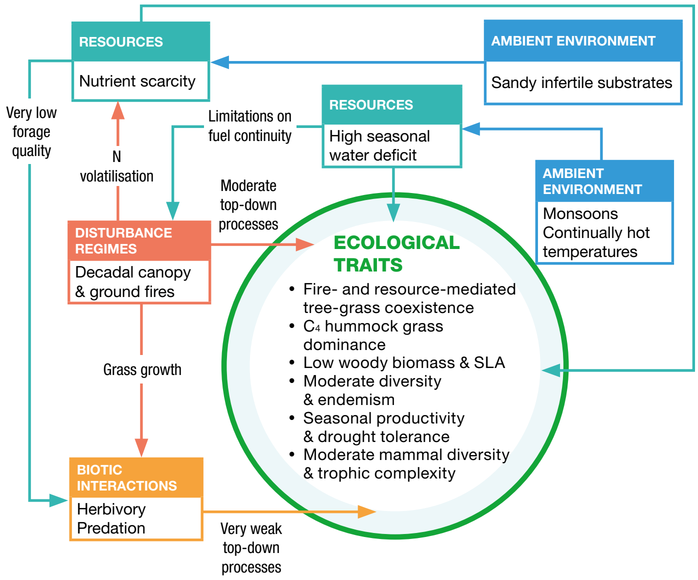
References:
Furley, P.A. (1999). 'The nature and diversity of neotropical savanna vegetation with particular reference to the Brazilian cerrados'. *Global Ecology and Biogeography* 8(3–4): 223–241.
Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Lehmann, C.E., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P. et al. (2014). 'Savanna Vegetation-Fire-Climate Relationships Differ Among Continents'. *Science* 343(6170): 548–552.

T4.3 Hummock savannas

BIOME: T4 SAVANNAS & GRASSLANDS
REALM: TERRESTRIAL

Fire-prone spinifex savanna with low C_4 hummock grasses on stony soils, Hamersley Range, Australia.
Source: Belinda Pellow (1986) with permission

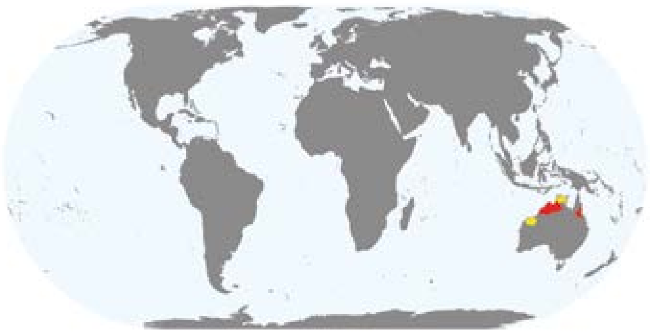
Contributors: D.A. Keith, R.J. Williams



ECOLOGICAL TRAITS: These open woodlands are dominated by C_4 hummock grasses (C_3 and stoloniferous grasses are absent) with sclerophyllous trees and shrubs. Their primary productivity is lower and less regularly seasonal than in other savannas of the subtropics (T4.1 and T4.2), but the seasonal peak nonetheless coincides with summer monsoonal rains. Plant traits promote tolerance to seasonal drought, including reduced leaf surfaces, thick cuticles, sunken stomata and deep root architecture to access subsoil moisture. Deciduous leaf phenology is less common than in other savannas, likely due to selection pressure for nutrient conservation associated with oligotrophic substrates. A major feature distinguishing this group of savannas from others is its ground layer of slow-growing sclerophyllous, spiny, domed hummock grasses interspersed with bare ground. Woody biomass and LAI decline along rainfall gradients. Sclerophyll shrubs and trees are shade-intolerant during establishment and most possess fire-resistant organs (e.g. thick bark, epicormic meristematic tissues and below-ground bud banks). Their notophyll foliage and that of hummock grasses has low SLA and mostly high C:N ratios, although N may be elevated in rubisco-enriched C_4 grasses. Trophic structure is therefore simpler than in others savannas. Mammalian herbivores and their predators are present in low densities, but fire and invertebrates are the major biomass consumers. Fire promotes landscape-scale vegetation heterogeneity but occurs less frequently than in other savannas due to slow recovery of perennial hummock grass fuels. Nitrogen volatilisation exceeds deposition due to recurring fires.

KEY ECOLOGICAL DRIVERS: Large overall rainfall deficit up to ~2,000 mm, always with a seasonal (winter) drought, but in drier areas seasonality is weaker than in other savanna groups. Mean annual rainfall is generally 400–1,000 mm. Climatic water deficit is exacerbated by coarse-textured, usually shallow, rocky soils. These are characteristically infertile. Temperatures are warm-hot with moderate seasonal and diurnal variability. Fires promoted by flammable hummocks may consume the low tree canopies and occur at variable decadal intervals any time when it is dry, but fire spread depends on ground fuel continuity which is limited by rainfall and rocky terrain.

DISTRIBUTION: Rocky areas of the seasonal Australian tropics, extending to the semi-arid zone.



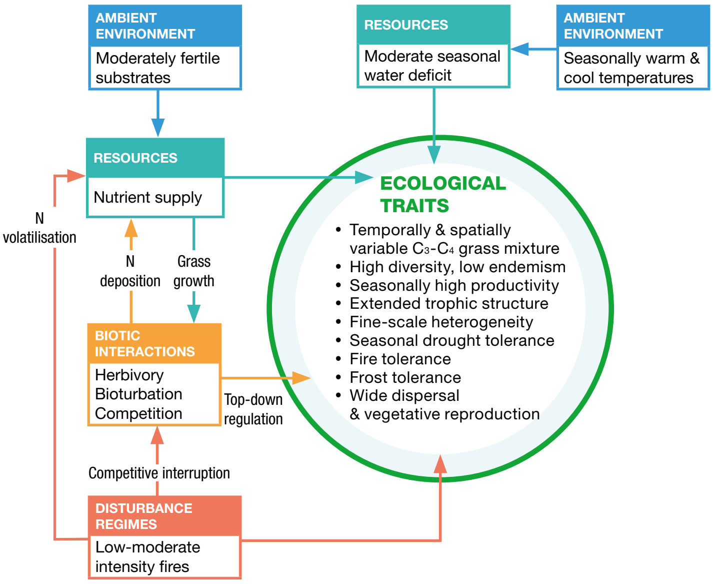
References:
Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Lehmann, C.E., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P. et al. (2014). 'Savanna Vegetation-Fire-Climate Relationships Differ Among Continents'. *Science* 343(6170): 548–552.
Williams, R.J., Cook, G.D., Liedloff, A.C., Bond, W.J. (2017). 'Australia's tropical savannas: Vast ancient and rich landscapes'. In: D.A. Keith (ed.), *Australian vegetation*, pp. 368–388. Cambridge, UK: Cambridge University Press.

T4.4 Temperate woodlands

BIOME: T4 SAVANNAS & GRASSLANDS
REALM: TERRESTRIAL

Contributors: D.A. Keith, D. Faber-Langendoen, J. Franklin

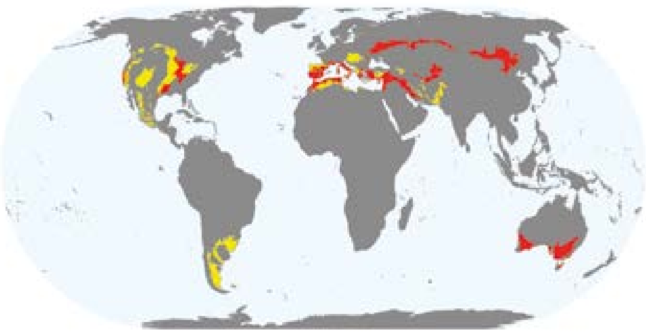
Temperate grassy woodland, Tamworth, Australia.
Source: David Keith (2003)



ECOLOGICAL TRAITS: These structurally simple woodlands are characterised by space between open tree crowns and a ground layer with tussock grasses, interstitial forbs, and a variable shrub component. Grasses with C_3 and C_4 photosynthetic pathways are common, but C_4 grasses may be absent from the coldest and wettest sites or where rain rarely falls in the summer. In any given area, C_4 grasses are most abundant in summer or on dry sites or areas with summer-dominant rainfall, while C_3 grasses predominate in winter, locally moist sites, cold sites, or areas without summer rainfall. The ground flora also varies inter-annually depending on rainfall. Trees generate spatial heterogeneity in light, water and nutrients, which underpin a diversity of microhabitats and mediate competitive interactions among plants in the ground layer. Foliage is mostly microphyll and evergreen (but transmitting abundant light) or deciduous in colder climates. Diversity of plant and invertebrate groups may therefore be relatively high at local scales, but local endemism is limited due to long-distance dispersal. Productivity is relatively high as grasses rapidly produce biomass rich in N and other nutrients after rains. This sustains a relatively complex trophic network of invertebrate and vertebrate consumers. Large herbivores and their predators are important top-down regulators. Bioturbation by fossorial mammals influences soil structure, water infiltration, and nutrient cycling. The fauna is less functionally and taxonomically diverse than in most tropical savannas (T4.1 and T4.2), but includes large and small mammals, reptiles and a high diversity of birds and macro-invertebrates, including grasshoppers, which are major consumers of biomass. Plants and animals tolerate and persist through periodic ground fires that consume cured-grass fuels, but few have specialised traits cued to fire (cf. pyric ecosystems such as T2.6).

KEY ECOLOGICAL DRIVERS: A water deficit occurs seasonally in summer, driven primarily by peak evapotranspiration under warm-hot temperatures and, in some regions, seasonal (winter-maximum) rainfall patterns. Mean annual rainfall is 350–1,000 mm. Low winter temperatures and occasional frost and snow may limit the growing season to 6–9 months. Soils are usually fine-textured and fertile, but N may be limiting in some areas. Fires burn, mostly in the ground layers, during the drier summer months at decadal intervals.

DISTRIBUTION: Temperate southeast and southwest Australia, Patagonia and Pampas of South America, western and eastern North America, the Mediterranean region, and temperate Eurasia.



References:
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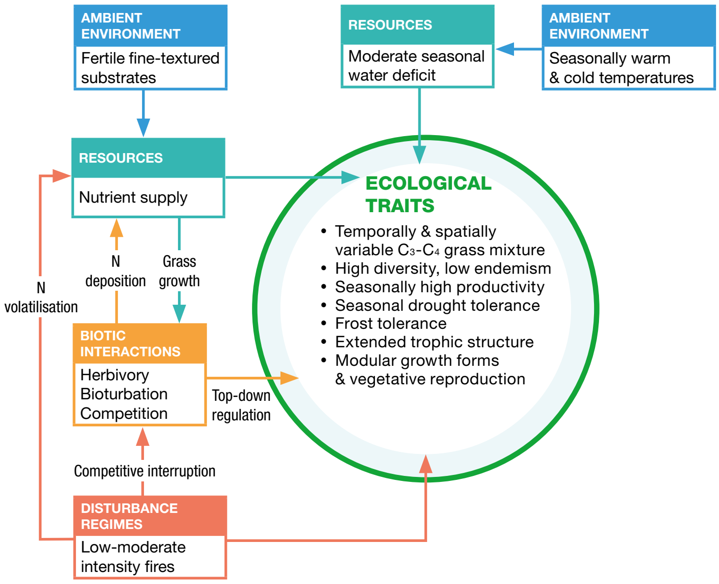
Prober, S.M., Gosper C.R., Gilfedder L., Harwood, T.D., Thiele, K.R., Williams, K.J., Yates ,C.J. (2017). 'Temperate eucalypt woodlands'. In: D.A. Keith (ed.), Australian vegetation, pp. 410–437. Cambridge, UK: Cambridge University Press.
Davis, F.W., Baldocchi, D., Tyler, C. (2016). 'Oak woodlands'. In: H.A. Mooney, E. Zavaleta (eds.), *Ecosystems of California*, pp. 509–534. Berkeley, USA: University of California Press.

Bison on the Great Plains, North Dakota, USA.
Source: Indielista/Shutterstock

T4.5 Temperate subhumid grasslands

BIOME: T4 SAVANNAS & GRASSLANDS
REALM: TERRESTRIAL

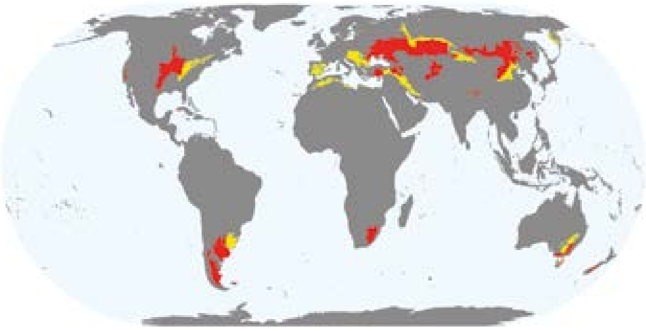
Contributors: D.A. Keith, F. Essl, D.J. Gibson



ECOLOGICAL TRAITS: Structurally simple tussock grasslands with interstitial forbs occur in subhumid temperate climates. Isolated trees or shrubs may be present in very low densities, but are generally excluded by heavy soil texture, summer drought, winter frost, or recurring summer fires. Unlike tropical savannas (T4.1–T4.3), these systems are characterised by a mixture of both C_3 and C_4 grasses, with C_4 grasses most abundant in summer or on dry sites and C_3 grasses predominating in winter or locally moist sites. There are also strong latitudinal gradients, with C_3 grasses more dominant towards the poles. Diversity of plant and invertebrate groups may be high at small spatial scales, but local endemism is limited due to long-distance dispersal. Productivity is high as grasses rapidly produce biomass rich in N and other nutrients after rains. This sustains a complex trophic network in which large herbivores and their predators are important top-down regulators. Fossorial mammals are important in bioturbation and nutrient cycling. Mammals are less functionally and taxonomically diverse than in most savannas. Taxonomic affinities vary among regions (e.g. ungulates, cervids, macropods and camelids), but their life history and dietary traits are convergent. Where grazing is not intense and fire occurs infrequently, leaf litter accumulates from the tussocks, creating a thatch that is important habitat for ground-nesting birds, small mammals, reptiles and macro-invertebrates, including grasshoppers, which are major consumers of plant biomass. Dense thatch limits productivity. Plant competition plays a major role in structuring the ecosystem and its dynamics, with evidence that it is mediated by resource ratios and stress gradients, herbivory and fire regimes. Large herbivores and fires both interrupt competition and promote coexistence of tussocks and interstitial forbs.

KEY ECOLOGICAL DRIVERS: A strong seasonal water deficit in summer driven by peak evapotranspiration under warm-hot temperatures, despite an unseasonal or weakly seasonal rainfall pattern. Mean annual rainfall varies from 250 mm to 750 mm. Cold winter temperatures limit the growing season to 5–7 months, with frost and snow frequent in continental locations. Summers are warm. Soils are deep, fertile and organic and usually fine-textured. Fires ignited by lightning occur in the drier summer months at sub-decadal or decadal intervals.

DISTRIBUTION: Western Eurasia, northeast Asia, Midwest North America, Patagonia and Pampas regions of South America, southeast Africa, southeast Australia, and southern New Zealand.



References:
Gibson, G.J. (2009). *Grasses and grassland ecology.* Oxford, UK: Oxford University Press.

T5 Deserts and semi-deserts biome

Bahía de los Ángeles, Mexico.
Source: David Keith

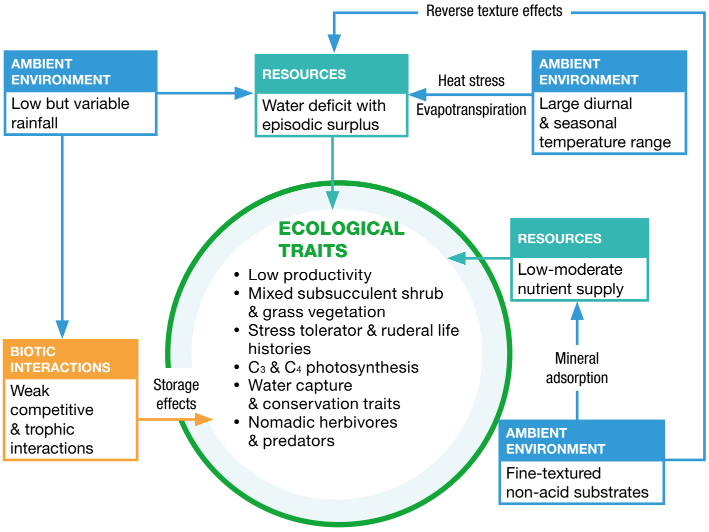
The Deserts and semi-deserts biome includes low to very low biomass ecosystems occurring in arid or semi-arid climates, principally associated with the subtropical high-pressure belts and major continental rain shadows. Primary productivity is low or very low and dependent on low densities of low-stature photoautotrophs that sustain a complete but sparse trophic web of consumers and predators. Productivity is limited by severe water deficits caused by very low rainfall. Rainfall deficits are exacerbated by extremes of temperature and desiccating winds. Resources, productivity and biomass are highly variable in space and time in response to the amount of annual rainfall, the size of individual rainfall events, and the lateral movement of resources from sources to sinks. Landscape heterogeneity and resource gradients are therefore critical to the persistence of desert biota in the context of highly stochastic, unseasonal temporal patterns of rainfall events that drive 'pulse and reserve' or 'boom-bust' ecosystem dynamics. There may be high rates of erosion and sedimentation due to the lack of surface stability provided by the sparse vegetation cover and this can be amplified by the activities of large mammals and people. Extreme and prolonged water deficits, punctuated by short episodes of surplus, impose severe physiological constraints on plants and animals, which exhibit a variety of physiological, morphological, behavioural and life-history traits enabling water acquisition and conservation. The life-history spectra of desert systems are polarised between long-lived drought tolerators with low metabolic rates and opportunistic drought evaders with either high mobility or short-lived active phases and long dormant phases. Mobility enables organisms to track transient resources over large distances. Competitive interactions are weak, although herbivory and predation are more evident in the most productive ecosystems and during the decline in resource availability that follows rainfall events.

T5.1 Semi-desert steppes

BIOME: T5 DESERTS AND SEMI-DESERTS
REALM: TERRESTRIAL

Sagebrush steppe, Seedskadee National Wildlife Refuge, USA.
Source: C. & M. Stuart (2009) CC2.5

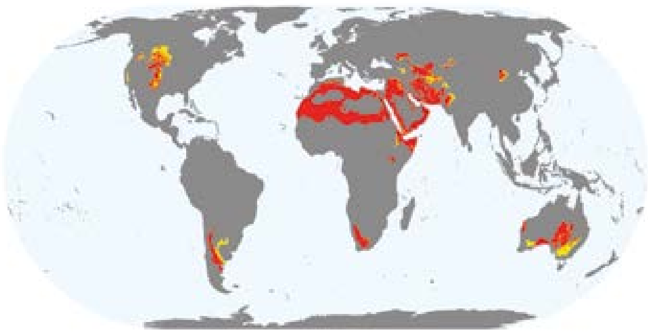
Contributors: M.G. Tozer, D.J. Eldridge, D.A. Keith



ECOLOGICAL TRAITS: These mixed semi-deserts are dominated by suffrutescent (i.e. with a woody base) or sub-succulent (semi-fleshy) perennial shrubs and tussock grasses. Productivity and biomass are limited by low average precipitation, extreme temperatures and, to a lesser extent, soil nutrients, but vary temporally in response to water availability. Vegetation takes a range of structural forms, including open shrublands, mixed shrublands with a tussock grass matrix, prairie-like tall forb grasslands, and very low dwarf shrubs interspersed with forbs or grasses. Total cover varies from 10% to 30% and the balance between shrubs and grasses is mediated by rainfall, herbivory and soil fertility. Stress-tolerator and ruderal life-history types are strongly represented in flora and fauna. Trait plasticity and nomadism are also common. Traits promoting water capture and conservation in plants include xeromorphy, deep roots, and C_4 photosynthesis. Shrubs have small (less than nanophyll), non-sclerophyll, often hairy leaves with moderate SLA. Shrubs act as resource-accumulation sites, promoting heterogeneity over local scales. C_3 photosynthesis is represented in short-lived shrubs, forbs and grasses, enabling them to exploit pulses of winter rain. Consumers include small mammalian and avian granivores, medium-sized mammalian herbivores, and wide-ranging large mammalian and avian predators and scavengers. Abundant detritivores consume dead matter and structure resource availability and habitat characteristics over small scales. Episodic rainfall initiates trophic pulses with rapid responses by granivores and their predators, but less so by herbivores, which show multiple traits promoting water conservation.

KEY ECOLOGICAL DRIVERS: Semi-desert steppes are associated with fine-textured, calcareous soils of low-moderate fertility, and may contain appreciable levels of magnesium or sodium. Clay particles exchange mineral ions with plant roots and have 'reverse texture effects', limiting moisture extraction as soils dry. Indurated subsoils influence infiltration/runoff relationships and vegetation patterns. Semi-desert steppes are not typically fire-prone and occur in temperate-arid climates. Mean annual rainfall ranges from ~150 to 300 mm, with a winter maximum. Evapotranspiration is 2–20 times greater than precipitation, but large rain events bring inter-annual pulses of water surplus. Temperatures are highly variable diurnally and seasonally, often exceeding 40°C in summer and reaching 0°C in winters but rarely with snow.

DISTRIBUTION: Extensive areas across the Sahara, the Arabian Peninsula, west Asia, southwest Africa, southern Australia, Argentina, and the Midwest USA.



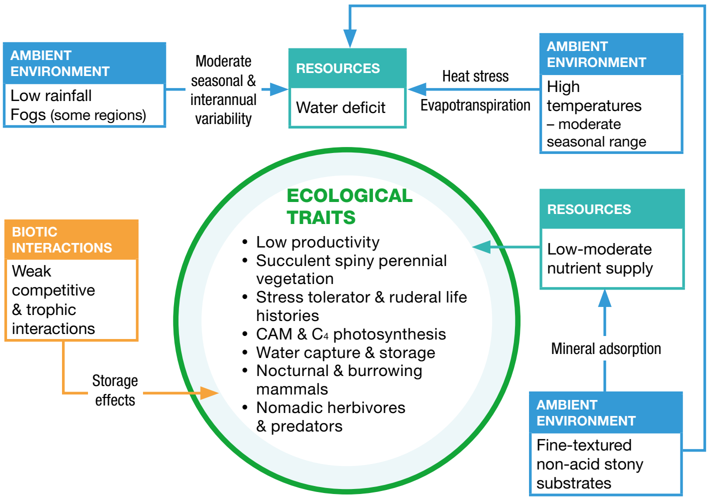
References:
Eldridge, D.J., Travers, S.K., Facelli, A.F., Facelli, J.M., Keith, D.A. (2017). 'The Chenopod shrublands'. In: D.A. Keith (ed.), *Australian vegetation*, pp. 599–625. Cambridge, UK: Cambridge University Press.
West N.E. (1983). 'Comparisons and contrasts between the temperate deserts and semi-deserts of three continents'. In: N.E. West (ed.), *Ecosystems of the World.* Vol. 5, pp. 461–472. Amsterdam, The Netherlands: Elsevier.

Thorny Desert, Cataviña, Mexico.
Source: David Keith (2012)

T5.2 Succulent or Thorny deserts and semi-deserts

BIOME: T5 DESERTS AND SEMI-DESERTS
REALM: TERRESTRIAL

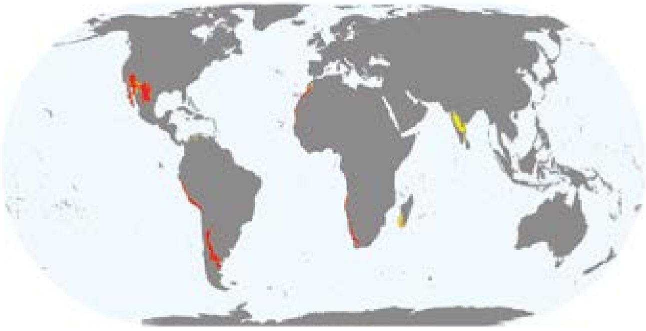
Contributors: M.G. Tozer, D.A. Keith



ECOLOGICAL TRAITS: These deserts are characterised by long-lived perennial plants, many with spines and/or succulent stem tissues or leaves. Local endemism is prominent among plants and animals. Productivity is low but relatively consistent through time and limited by precipitation and extreme summer temperatures. Vegetation cover is sparse to moderate (10–30%) and up to several metres tall. Dominant plants are stress-tolerators with slow growth and reproduction, many exhibiting CAM physiology and traits that promote water capture, conservation and storage. These include deep root systems, suffrutescence, plastic growth and reproduction, succulent stems and/or foliage, thickened cuticles, sunken stomata, and deciduous or reduced foliage. Spinescence in many species is likely a physical defence to protect moist tissues from herbivores. Annuals and geophytes constitute a variable proportion of the flora exhibiting rapid population growth or flowering responses to semi-irregular rainfall events, which stimulate germination of soil seed banks or growth from dormant subterranean organs. Mammalian, reptilian and invertebrate faunas are diverse, with avian fauna less well represented. Faunal traits adaptive to drought and heat tolerance include physiological mechanisms (e.g. specialised kidney function and reduced metabolic rates) and behavioural characters (e.g. nocturnal habit and burrow dwelling). Many reptiles and invertebrates have ruderal life histories, but fewer mammals and birds do. Larger ungulate fauna exhibit flexible diets and forage over large areas. Predators are present in low densities due to the low productivity of prey populations.

KEY ECOLOGICAL DRIVERS: These systems occur in subtropical arid climates with large overall water deficits. Precipitation is 5–20% of potential evapotranspiration, but exhibits low inter-annual variability relative to other desert systems. Inter-annual pulses of surplus are infrequent and atmospheric moisture from fogs may contribute significantly to available water. Temperatures are hot with relatively large diurnal ranges, but seasonal variation is less than in other deserts, with very hot summers and mild winters. Substrates are stony and produce soils of moderate to low fertility. Thorny deserts are generally not fire-prone.

DISTRIBUTION: Mostly subtropical latitudes in the Americas, southern Africa, and southern Asia.



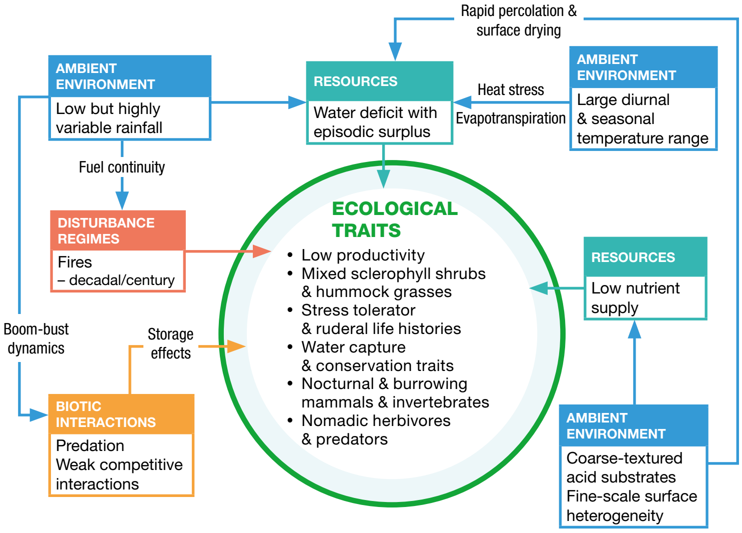
Reference:
Shmida, A., Evenari, M., Noy-Meir, I. (1986). 'Hot desert ecosystems: an integrated view'. In: M. Evenari, I. Noy Meir, D.W. Goodall (eds.), *Hot deserts and arid shrublands. Ecosystems of the World*, pp. 379–387. Amsterdam, The Netherlands: Elsevier.

T5.3 Sclerophyll hot deserts and semi-deserts

BIOME: T5 DESERTS AND SEMI-DESERTS
REALM: TERRESTRIAL

Contributors: M.G. Tozer, D.A. Keith

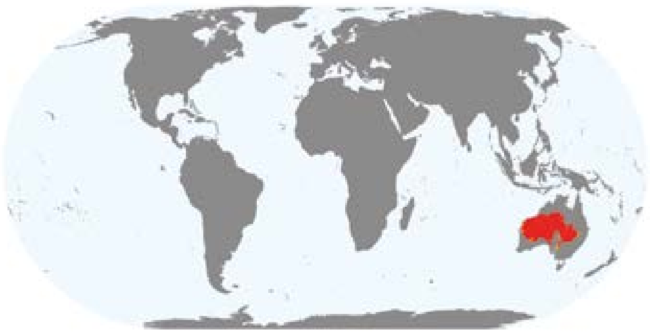
Desert characterised by sclerophyll shrubs and hummock grasses, Uluru National Park, central Australia.
Source: John Coppi/CSIRO



ECOLOGICAL TRAITS: Arid systems dominated by hard-leaved (sclerophyll) vegetation have relatively high diversity and local endemism, notably among plants, reptiles and small mammals. Large moisture deficits and extremely low levels of soil nutrients limit productivity, however, infrequent episodes of high rainfall drive spikes of productivity and boom-bust ecology. Spatial heterogeneity is also critical in sustaining diversity by promoting niche diversity and resource-rich refuges during 'bust' intervals. Stress-tolerator and ruderal life-history types are strongly represented in both flora and fauna. Perennial, long-lived, slow-growing, drought-tolerant, sclerophyll shrubs and hummock (C_4) grasses structure the ecosystem by stabilising soils, acting as nutrient-accumulation sites and providing continuously available habitat, shade and food for fauna. Strong filtering by both nutritional poverty and water deficit promote distinctive scleromorphic and xeromorphic plant traits. They include low SLA, high C:N ratios, reduced foliage, stomatal regulation and encryption, slow growth and reproduction rates, deep root systems, and trait plasticity. Perennial succulents are absent. Episodic rains initiate emergence of a prominent ephemeral flora, with summer and winter rains favouring grasses and forbs, respectively. This productivity 'boom' triggers rapid responses by granivores and their predators. Herbivore populations also fluctuate but less so due to ecophysiological traits that promote water conservation. Abundant detritivores support a diverse and abundant resident reptilian and small-mammal fauna. Small mammals and some macro-invertebrates are nocturnal and fossorial, with digging activity contributing to nutrient and carbon cycling, as well as plant recruitment. The abundance and diversity of top predators is low. Nomadism and ground-nesting are well represented in birds. Periodic fires reduce biomass, promote recovery traits in plants (e.g. re-sprouting and fire-cued recruitment) and initiate successional processes in both flora and fauna.

KEY ECOLOGICAL DRIVERS: Resource availability is limited by a large overall water deficit (rainfall <250 mm p.a., 5–50% of potential evapotranspiration) and acid sandy soils with very low P and N, together with high diurnal and seasonal variation in temperatures. Summers have runs of extremely hot days (>40°C) and winters have cool nights (0°C), rarely with snow. Long dry spells are punctuated by infrequent inter-annual pulses of water surplus, driving ecological booms and transient periods of fuel continuity. Fires occur at decadal- or century-scale return intervals when lightning or human ignitions coincide with fuel continuity.

DISTRIBUTION: Mid-latitudes on sandy substrates of central and northwestern Australia.



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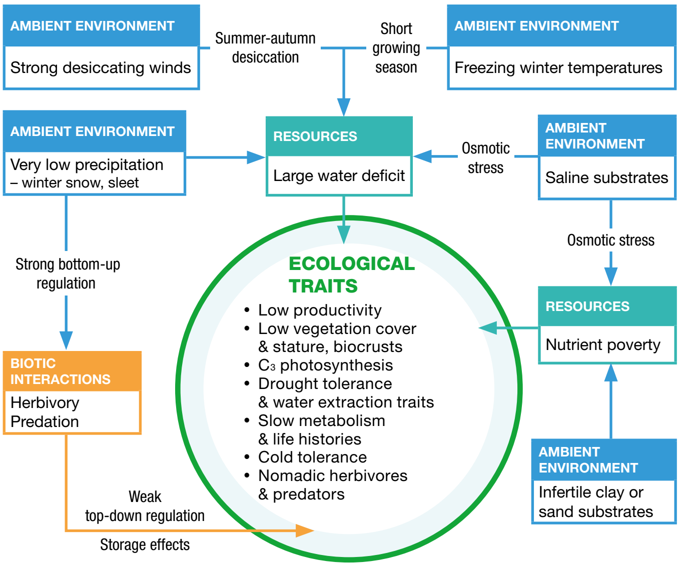
Keith D.A. (2004). *Ocean Shores to Desert Dunes: The Native Vegetation of New South Wales and the ACT.* Sydney, Australia: NSW Department of Environment and Conservation.
Morton, S., Stafford Smith, D.M., Dickman, C.R., Dunkerley, D.L., Friedel, M.H., McAllister, R.R.J., Reid, R.W., Roshier, D.A., Smith, M.A. et al. (2011). 'A fresh framework for the ecology of arid Australia'. *Journal of Arid Environments* 75(4): 313–329.

T5.4 Cool deserts and semi-deserts

BIOME: T5 DESERTS AND SEMI-DESERTS
REALM: TERRESTRIAL

Contributors: M.G. Tozer, D.J. Eldridge, D. Faber-Langendoen, D.A. Keith

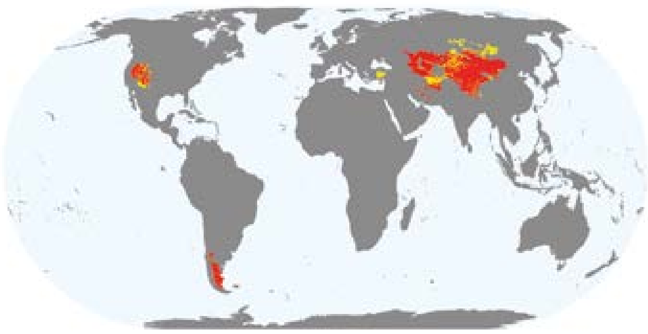
Altai mountains, Gobi Desert, Mongolia.
Source: Bolatbek Gabiden



ECOLOGICAL TRAITS: In these arid systems, productivity is limited by both low precipitation and cold temperatures but varies spatially in response to soil texture, salinity, and water table depth. Vegetation cover varies with soil conditions from near zero (on extensive areas of heavily salinized soils or mobile dunes) to >50% in upland grasslands and shrublands, but is generally low in stature (<1 m tall). The dominant plants are perennial C_3 grasses and xeromorphic suffrutescent or non-sclerophyllous perennial shrubs. Dwarf shrubs, tending to prostrate or cushion forms occur in areas exposed to strong, cold winds. Plant growth occurs mainly during warming spring temperatures after winter soil moisture recharges. Eurasian winter annuals grow rapidly in this period after developing extensive root systems over winter. Diversity and local endemism are low across all taxa relative to other arid ecosystems. Trophic networks are characterised by large nomadic mammalian herbivores. Vertebrate herbivores, including antelopes, equines, camelids and lagomorphs, are important mediators of shrub-grass dynamics, with heavy grazing promoting replacement of grasses by N-fixing shrubs. Grasses become dominant with increasing soil fertility or moisture but may be replaced by shrubs as grazing pressure increases. Fossorial lagomorphs and omnivorous rodents perturb soils. Predator populations are sparse but taxonomically diverse. They include raptors, snakes, bears and cats. Bio-crusts with cyanobacteria, mosses, and lichens are prominent on fine-textured substrates, and become dominant where it is too cold for vascular plants. They play critical roles in soil stability and water and nutrient availability.

KEY ECOLOGICAL DRIVERS: Mean annual precipitation is similar to most warm deserts (<250 mm) due to rain shadows and continentality, however, in cool deserts this falls mainly as snow or sleet in winter rather than rain. Although evapotranspiration is less severe than in hot deserts, a substantial water deficit exists due to low precipitation (mostly 10–50% of evapotranspiration) and strong desiccating winds that may occasionally propagate fires. Mean monthly temperatures may fall below −20°C in winter (freezing the soil surface) and exceed 15°C in summer. Substrates vary from stony plains and uplands to extensive dune fields, with mosaics of clay and sandy regolith underpinning landscape-scale heterogeneity. Large regions were submerged below seas or lakes in past geological eras with internal drainage systems leaving significant legacies of salinity in some lowland areas, especially in clay substrates.

DISTRIBUTION: Cool temperate plains and plateaus from sea level to 4,000 m elevation in central Eurasia, western North America, and Patagonia. Extreme cold deserts are placed in the polar/alpine biome.



References:

Johnson, S.L., Kuske, C.R., Carney, T.D., Housman, D.C., Gallegos-Graves, L.V., Belnap, J. (2012). 'Increased temperature and altered summer precipitation have differential effects on biological soil crusts in a dryland ecosystem'. *Global Change Biology* 18(8): 2583–2593.

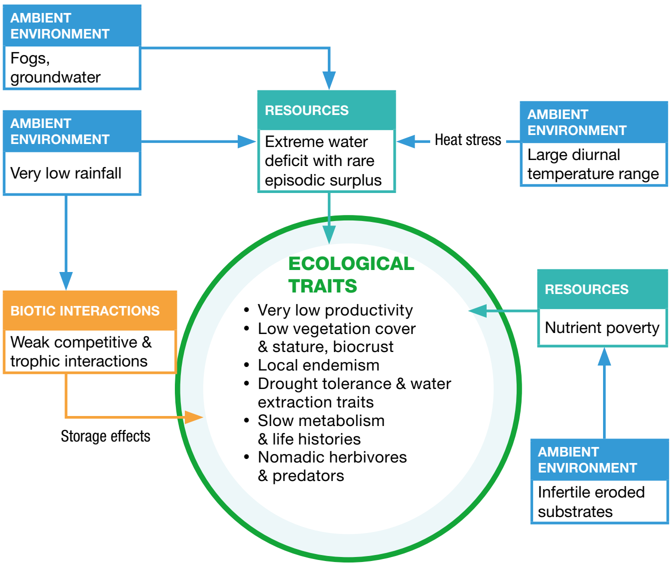
West, N.E. (1983). 'Comparisons and contrasts between the temperate deserts and semi-deserts of three continents'. In: N.E. West (ed.), *Temperate deserts and semi-deserts. Ecosystems of the World. Vol. 5*. Amsterdam, The Netherlands: Elsevier.

T5.5 Hyper-arid deserts

BIOME: T5 DESERTS AND SEMI-DESERTS
REALM: TERRESTRIAL

Contributors: M.G. Tozer, D. Faber-Langendoen, D.A. Keith

Sparsely vegetated, where sea fog is the main source of moisture, Atacama Desert, Peru.
Source: Toby Pennington (with permission)



ECOLOGICAL TRAITS: Hyper-arid deserts show extremely low productivity and biomass and are limited by low precipitation and extreme temperatures. Vegetation cover is very sparse (<1%) and low in stature (typically a few centimetres tall), but productivity and biomass may be marginally greater in topographically complex landscapes within patches of rising ground-water or where runoff accumulates or cloud cover intersects. Trophic networks are simple because autochthonous productivity and allochthonous resources are very limited. Rates of decomposition are slow and driven by microbial activity and UV-B photodegradation, both of which decline with precipitation. Microbial biofilms play important decomposition roles in soils and contain virus lineages that are putatively distinct from other ecosystems. Although diversity is low, endemism may be high because of strong selection pressures and insularity resulting from the large extent of these arid regions and limited dispersal abilities of most organisms. Low densities of drought-tolerant perennial plants (xerophytes) characterise these systems. The few perennials present have very slow growth and tissue turnover rates, low fecundity, generally long life spans, and water acquisition and conservation traits (e.g. extensive root systems, thick cuticles, stomatal regulation, and succulent organs). Ephemeral plants with long-lived soil seed banks are well represented in hyper-arid deserts characterised by episodic rainfall, but they are less common in those that are largely reliant on fog or groundwater. Fauna include both ruderal and drought-tolerant species. Thermoregulation is strongly represented in reptiles and invertebrates. Birds and large mammals are sparse and nomadic, except in areas with reliable standing water. Herbivores and granivores have boom-bust population dynamics coincident with episodic rains.

KEY ECOLOGICAL DRIVERS: Extreme rainfall deficit arising from very low rainfall (150 mm to almost zero and <5% of potential evapotranspiration), exacerbated by extremely hot temperatures and desiccating winds. Principal sources of moisture may include moisture-laden fog, irregular inter-annual or decadal rainfall events, and capillary rise from deep water tables. UV-B radiation is extreme except where moderated by fogs. Temperatures exhibit high diurnal and seasonal variability with extreme summer maxima and sub-zero winter night temperatures. Hyper-arid deserts occur on extensive low-relief plains (peneplains) and mountainous terrain. Substrates may be extensive sheets of unstable, shifting sand or stony gibber with no soil profile development and low levels of nutrients.

DISTRIBUTION: Driest parts of the Sahara-Arabian, Atacama, and Namib deserts in subtropical latitudes.

References:
Zablocki, O., Adriaenssens, E.M., Cowan, D. (2016). 'Diversity and Ecology of Viruses in Hyperarid Desert Soils'. *Applied and Environmental Microbiology* 82(3): 770–777.
Rundel, P.W., Dillon, M.O., Palma, B., Mooney, H.A., Gulmon, S.L., Ehleringer, J.R. (1991). 'The Phytogeography and Ecology of the Coastal Atacama and Peruvian Deserts'. *Aliso* 13(1): Article 2.

T6 Polar-alpine (cryogenic) biome

Mount Cook area, South Island, New Zealand.
Source: David Keith

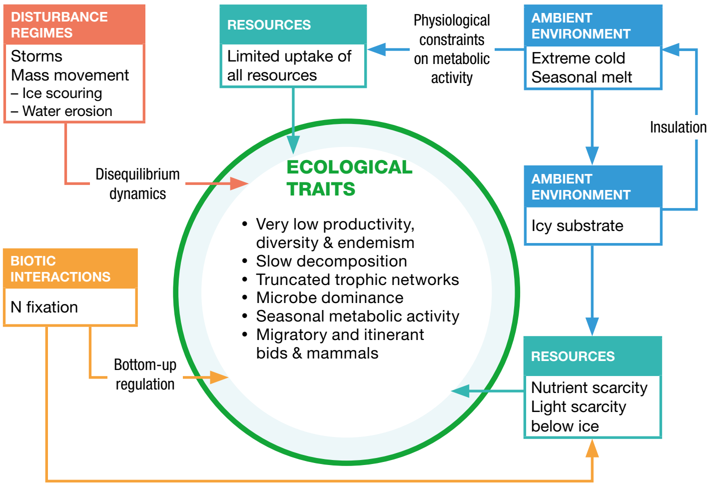
The Polar-alpine biome encompasses the extensive Arctic and Antarctic regions as well as high mountainous areas across all continental land masses. Primary productivity is low or very low, strictly seasonal and limited by conditions of extreme cold associated with low insolation and/or high elevation, further exacerbated by desiccating conditions and high-velocity winds. Low temperatures limit metabolic activity and define the length of growing seasons. Microbial decomposition is slow, leading to peat accumulation in the most productive ecosystems. Regional and local temperature gradients shape ecosystems within the biome. Standing biomass, for example, is low or very low and varies with the severity of cold and insolation. Microbial lifeforms dominate in the coldest systems with perennial snow or ice cover, augmented with crustose lichens, bryophytes, and algae on periodically exposed lithic substrates. Forbs, grasses and dwarf shrubs with slow growth rates and long lifespans become increasingly prominent and may develop continuous cover with increasing insolation and warmer conditions. This vegetation cover provides habitat structure and food for vertebrate and invertebrate consumers and their predators. Trophic webs are simple or truncated and populations of larger vertebrates are generally migratory or itinerant. In these warmer cryogenic systems, snow cover is seasonal (except at equatorial latitudes) and insulates plants and animals that lie dormant beneath it during winter and during their emergence from dormancy prior to spring thaw. While dormancy is a common trait, a diverse range of other physiological, behavioural, and morphological traits that facilitate cold tolerance are also well represented among the biota.

Edge of the Antarctic ice sheet, Paradise Bay.
Source: David Keith (2017)

T6.1 Ice sheets, glaciers and perennial snowfields

BIOME: POLAR-ALPINE (CRYOGENIC ECOSYSTEMS)
REALM: TERRESTRIAL

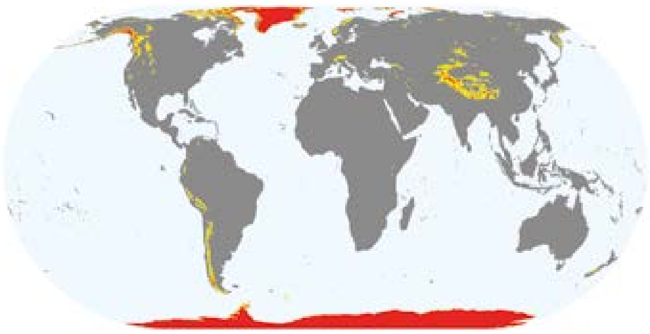
Contributors: D.A. Keith, A. Terauds, A.M.B. Anesio



ECOLOGICAL TRAITS: In these icy systems, extreme cold and periodic blizzards limit productivity and diversity to very low levels, and trophic networks are truncated. Wherever surface or interstitial water is available. life is dominated by micro-organisms, including viruses, bacteria, protozoa and algae, which may arrive by Aeolian processes. Bacterial densities vary from 10^7 to 10^{11} cells.L^{-1}. On the surface, the main primary producers are snow (mainly Chlamydomonadales) and ice algae (mainly Zygnematales) with contrasting traits. Metabolic activity is generally restricted to summer months at temperatures close to zero and is enabled by exopolymeric substances, cold-adapted enzymes, cold-shock proteins and other physiological traits. N-fixing cyanobacteria are critical in the N-cycle, especially in late summer. Surface heterogeneity and dynamism create cryoconite holes, rich oases for microbial life (especially cyanobacteria, prokaryotic heterotrophs and viruses) and active biogeochemical cycling. Most vertebrates are migratory birds with only the emperor penguin over-wintering on Antarctic ice. Mass movement and snow burial also places severe constraints on establishment and persistence of life. Snow and ice algae and cyanobacteria on the surface are ecosystem engineers. Their accumulation of organic matter leads to positive feedbacks between melting and microbial activity that discolours snow and reduces albedo. Organic matter produced at the surface can also be transported through the ice to dark subglacial environments, fuelling microbial processes involving heterotrophic and chemoautotrophic prokaryotes and fungi.

KEY ECOLOGICAL DRIVERS: Permanent but dynamic ice cover accumulates by periodic snow fall and is reduced in summer by melting, sublimation, and calving (i.e. blocks of ice breaking free) in the ablation zone. Slow lateral movement occurs downslope or outwards from ice cap centres with associated cracking. Precipitation may average several metres per year on montane glaciers or less than a few hundred millimetres on extensive ice sheets. Surface temperatures are extremely cold in winter (commonly –60°C in Antarctica) but may rise above 0°C in summer. Desiccating conditions occur during high winds or when water is present almost entirely in solid form. Nutrients, especially N and P, are extremely scarce, the main inputs being glacial moraines, aerosols, and seawater (in sea ice), which may be supplemented locally by guano. Below the ice, temperatures are less extreme, there is greater contact between ice, water and rock (enhancing nutrient supply), a diminished light intensity, and redox potential tends towards anoxic conditions, depending on hydraulic residence times.

DISTRIBUTION: Polar regions and high mountains in the western Americas, central Asia, Europe, and New Zealand, covering ~10% of the earth's surface.



References:
Anesio, A.M., Laybourn-Parry, J. (2012). 'Glaciers and ice sheets as a biome'. *Trends in Ecology and Evolution* 27(4): 219–225.
Anesio, A.M., Lutz, S., Chrismas, N.A.M., Benning, L.G. (2017). 'The microbiome of glaciers and ice sheets'. *npj Biofilms Microbiomes* 3: 10.

T6.2 Polar alpine rocky outcrops

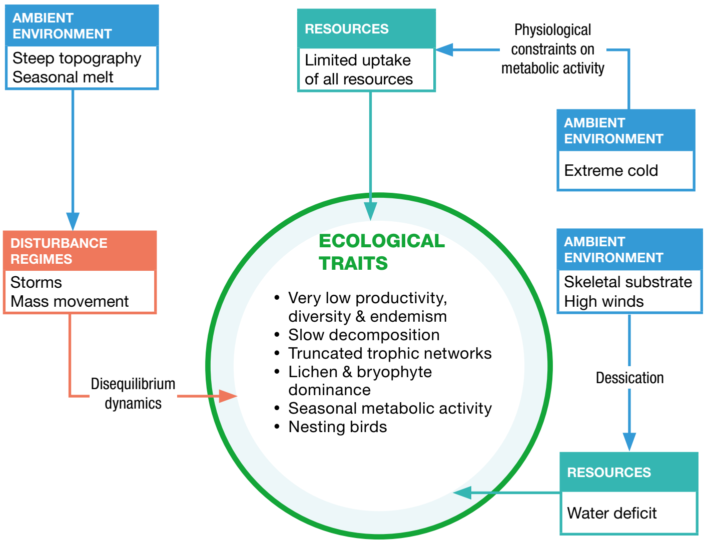
BIOME: POLAR-ALPINE (CRYOGENIC ECOSYSTEMS)
REALM: TERRESTRIAL

Contributors: D.A. Keith, K.R. Young, A. Terauds

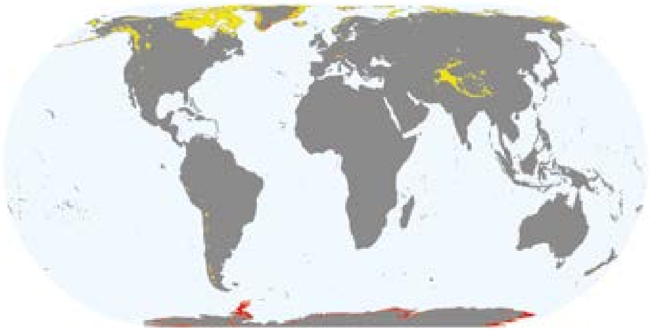
Rocky mountains around Paradise Bay, Antarctica.
Source: David Keith (2017)

ECOLOGICAL TRAITS: Low biomass systems with very low productivity constrained by extreme cold, desiccating winds, skeletal substrates, periodic mass movement and, in polar regions, by seasonally low light intensity. The dominant lifeforms are freeze-tolerant crustose lichens, mosses and algae that also tolerate periodic desiccation, invertebrates, such as tardigrades, nematodes and mites, and micro-organisms, including bacteria and protozoa, and nesting birds that forage primarily in other (mostly marine) ecosystems. Diversity and endemism are low, likely due to intense selection pressures and wide dispersal. Trophic networks are simple and truncated. Physiological traits, such as cold-adapted enzymes and cold-shock proteins, enable metabolic activity, which is restricted to summer months when temperatures are close to or above zero. Nutrient input occurs primarily through substrate weathering supplemented by guano, which along with cyanobacteria is a major source of N. Mass movement of snow and rock, with accumulation of snow and ice during the intervals between collapse events, promotes disequilibrium ecosystem dynamics.

KEY ECOLOGICAL DRIVERS: Extremely cold winters with wind-chill that may reduce temperatures below –80°C in Antarctica. In contrast, insolation and heat absorption on rocky substrates may increase summer temperatures well above 0°C. Together with the impermeable substrate and intermittently high winds, exposure to summer insolation may produce periods of extreme water deficit punctuated by saturated conditions associated with meltwater and seepage. Periodic burial by snow reduces light availability, while mass movement through landslides, avalanches or volcanic eruptions maintain substrate instability and destroy biomass, limiting the persistence of biota.



DISTRIBUTION: Permanently ice-free areas of Antarctica, Greenland, the Arctic Circle, and high mountains in the western Americas, central Asia, Europe, Africa and New Zealand.



Reference:

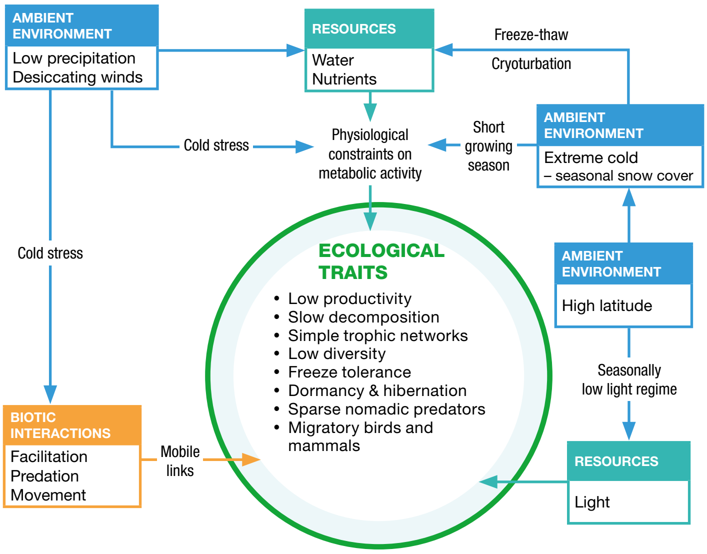
Chown, S.L. Clarke, A., Fraser, C.I., Cary, S.C., Moon, K.L. and McGeoch, M.A. (2015). 'The changing form of Antarctic biodiversity'. *Nature* 522: 431–438.
Convey, P., Stevens, P.I. (2007). 'Antarctic biodiversity'. *Science* 317(5846): 1877–1878.

T6.3 Polar tundra and deserts

BIOME: POLAR-ALPINE (CRYOGENIC ECOSYSTEMS)
REALM: TERRESTRIAL

Contributors: D.A. Keith, F. Essl, K.R. Young, C.H. Körner

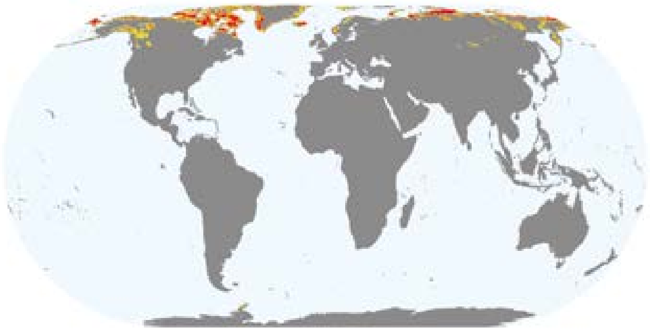
Tundra vegetation at Sydkap, inner Scoresby Sund, East Greenland.
Source: Hannes Grobe (2007) Creative Commons CC2.5



ECOLOGICAL TRAITS: These low productivity autotrophic ecosystems are limited by winter dormancy during deep winter snow cover, extreme cold temperatures and frost during spring thaw, short growing seasons, desiccating winds, and seasonally low light intensity. Microbial decomposition rates are slow, promoting accumulation of peaty permafrost substrates in which only the surface horizon thaws seasonally. Vegetation is treeless and dominated by a largely continuous cover of cold-tolerant bryophytes, lichens, C_3 grasses, sedges, forbs and dwarf and prostrate shrubs. Tundra around the world is delimited by the physiological temperature limits of trees, which are excluded where the growing season (i.e. days >0.9°C) is less than 90–94 days duration, with mean temperatures less than 6.5°C across the growing season. In the coldest and/or driest locations, vascular plants are absent and productivity relies on bryophytes, lichens, cyanobacteria and allochthonous energy sources such as guano. Aestivating insects (i.e. those that lay dormant in hot or dry seasons) dominate the invertebrate fauna. Vertebrate fauna is dominated by migratory birds, some of which travel seasonal routes exceeding several thousand kilometres. Many of these feed in distant wetlands or open oceans. These are critical mobile links that transfer nutrients and organic matter and disperse the propagules of other organisms, both externally on plumage or feet and endogenously. A few mammals in the Northern Hemisphere are hibernating residents or migratory herbivores. Pinnipeds occur in near-coast tundras and may be locally important marine subsidies of nutrients and energy. Predatory canids and polar bears are nomadic or have large home ranges.

KEY ECOLOGICAL DRIVERS: Winters are very cold and dark and summers define short, cool growing seasons with long hours of low daylight. Precipitation falls as snow that persists through winter months. In most areas, there is an overall water surplus, occasionally with small summer deficit, but some areas are ice-free, extremely dry (annual precipitation <150 mm p.a.) polar deserts with desiccating winds. Substrates are peaty or gravelly permafrost, which may partially thaw on the surface in summer, causing cryoturbation.

DISTRIBUTION: Primarily within the Arctic Circle and adjacent subarctic regions, with smaller occurrences on subantarctic islands and the Antarctic coast.



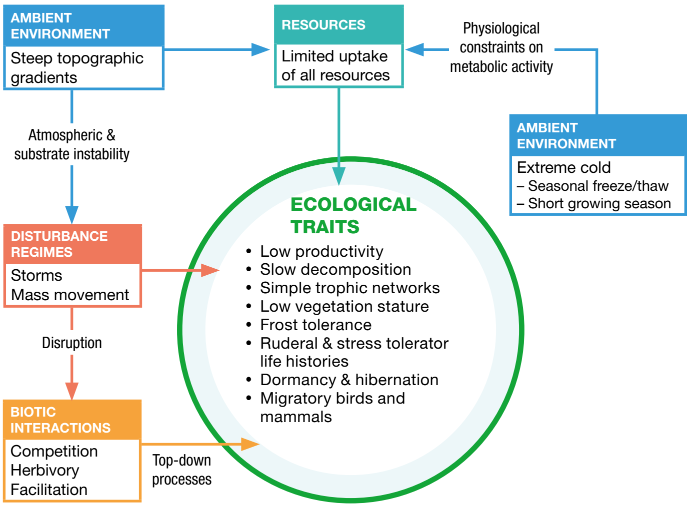
References:
Gough, L. and Asmus, A.L. (2014). 'Tundra-Taiga Biology: Human, Plant, And Animal Survival In The Arctic'. In: R.M.M. Crawford, *Arctic, Antarctic, and Alpine Research*, 46(4): 1011–1012. New York, USA: Oxford University Press.
Paulsen, J., Körner, C. (2014). 'A climate-based model to predict potential treeline position around the globe'. *Alpine Botany* 124(1); 1–12.

T6.4 Temperate alpine grasslands and shrublands

BIOME: POLAR-ALPINE (CRYOGENIC ECOSYSTEMS)
REALM: TERRESTRIAL

Contributors: D.A. Keith, F. Essl, K.R. Young, C.H. Körner

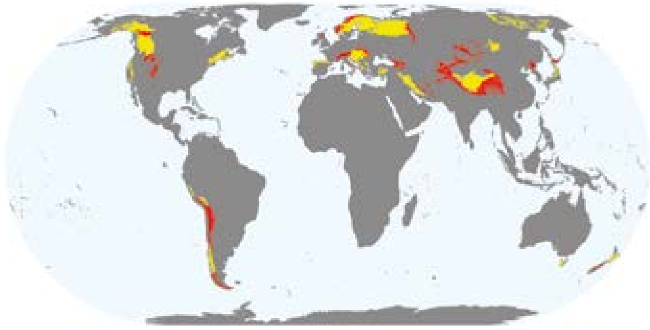
Alpine grassland with diverse herbs, Davos Klosters, Switzerland.
Source: David Keith (2018)



ECOLOGICAL TRAITS: Mountain systems beyond the cold climatic treeline are dominated by grasses, herbs, or low shrubs (typically <1 m tall). Moderate-low and strictly seasonal productivity is limited by deep winter snow cover, extreme cold and frost during spring thaw, short growing seasons, desiccating winds, and, in some cases, by mass movement. Vegetation comprises a typically continuous cover of plants, including bryophytes, lichens, C_3 grasses, sedges, forbs and dwarf shrubs, including cushion growth forms. However, the cover of vascular plants may be much lower in low-rainfall regions or in sites exposed to strong desiccating winds and often characterised by dwarf shrubs and lichens that grow on rocks (i.e. fjaeldmark). Throughout the world, alpine ecosystems are defined by the physiological temperature limits of trees, which are excluded where the growing season (i.e. days >0.9°C) is less than 90–94 days, with mean temperatures less than 6.5°C across the growing season. Other plants have morphological and ecophysiological traits to protect buds, leaves, and reproductive tissues from extreme cold, including growth forms with many branches, diminutive leaf sizes, sclerophylly, vegetative propagation, and cold-stratification dormancy. The vertebrate fauna includes a few hibernating residents and migratory herbivores and predators that are nomadic or have large home ranges. Aestivating insects include katydids, dipterans, and hemipterans. Local endemism and beta-diversity may be high due to steep elevational gradients, microhabitat heterogeneity and topographic barriers to dispersal between mountain ranges, with evidence of both facilitation and competition.

KEY ECOLOGICAL DRIVERS: Winters are long and cold, while summers are short and mild. Seasonal snow up to several metres deep provides insulation to over-wintering plants and animals. Severe frosts and desiccating winds characterise the spring thaw and exposed ridges and slopes. Severe storms may result from orographic-atmospheric instability. Typically there is a large precipitation surplus, but deficits occur in some regions. Steep elevational gradients and variation in micro-topography and aspect promote microclimatic heterogeneity. Steep slopes are subjected to periodic mass movements, which destroy surface vegetation.

DISTRIBUTION: Mountains in the temperate and boreal zones of the Americas, Europe, central Eurasia, west and north Asia, Australia, and New Zealand.



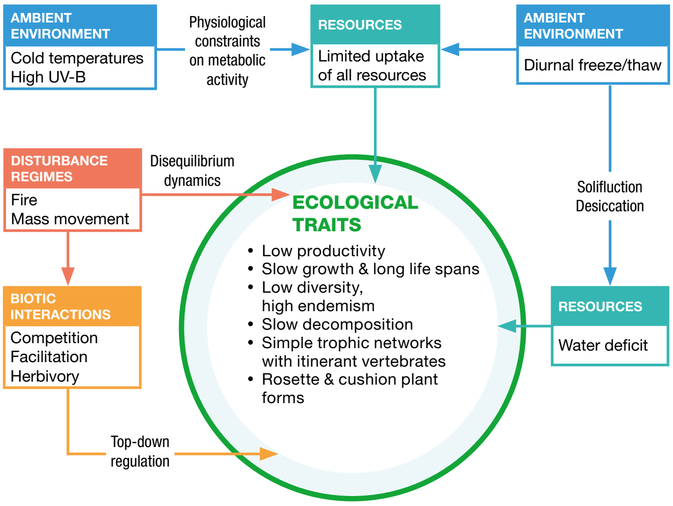
References:
Körner, C. (2004). 'Mountain Biodiversity, Its Causes and Function'. *Ambio* sp1313: 11–17.
_____ (2012). 'High elevation treelines'. In: C. Körner, *Alpine Treelines*, pp. 1–10. Basel, Switzerland: Springer.
Paulsen, J., Körner C.(2014). 'A climate-based model to predict potential treeline position around the globe'. *Alpine Botany* 124(1): 1–12.

T6.5 Tropical alpine grasslands and herbfields

BIOME: POLAR-ALPINE (CRYOGENIC ECOSYSTEMS)
REALM: TERRESTRIAL

Contributors: D.A. Keith, A. Etter

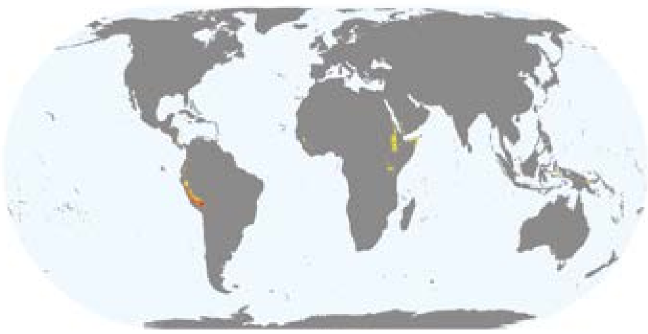
Giant rosettes of Lobelia and Dendrosenecio in alpine herbfields, Rwenzori Mountains, Uganda.
Source: Rowan Donovan (2011) Alamy Stock



ECOLOGICAL TRAITS: Treeless mountain systems dominated by an open to dense cover of cold-tolerant C_3 perennial tussock grasses, herbs, small shrubs and distinctive arborescent rosette or cushion growth forms. Lichens and bryophytes are also common. Productivity is low, dependent on autochthonous energy, and limited by cold temperatures, diurnal freeze-thaw cycles and desiccating conditions, but not by a short growing season (as in T6.4). Elfin forms of tropical montane forests (T1.3) occupy sheltered gullies and lower elevations. Diversity is low to moderate but endemism is high among some taxa, reflecting steep elevational gradients, microhabitat heterogeneity, and topographic insularity, which restricts dispersal. Solifluction (i.e. the slow flow of saturated soil downslope) restricts seedling establishment to stable microsites. Plants have traits to protect buds, leaves and reproductive tissues from diurnal cold and transient desiccation stress, including ramulose (i.e. many-branched), cushion and rosette growth forms, insulation from marcescent (i.e. dead) leaves or pectin fluids, diminutive leaf sizes, leaf pubescence, water storage in stem-pith, and vegetative propagation. Most plants are long-lived and some rosette forms are semelparous. Cuticle and epidermal layers reduce UV-B transmission to photosynthetic tissues. Plant coexistence is mediated by competition, facilitation, herbivory (vertebrate and invertebrate) and fire regimes. Simple trophic networks include itinerant large herbivores and predators from adjacent lowland savannas, as well as resident reptiles, small mammals and macro-invertebrates.

KEY ECOLOGICAL DRIVERS: Cold nights (as low as –10°C) and mild days (up to 15°C) produce low mean temperatures and diurnal freeze-thaw cycles, but seasonal temperature range is small and freezing temperatures are short-lived. Cloud cover and precipitation are unseasonal in equatorial latitudes or seasonal in the monsoonal tropics. Strong orographic effects result in an overall precipitation surplus and snow and fog are common, but desiccating conditions may occur during intervals between precipitation events, with morning insolation also increasing moisture stress when roots are cold. Exposure to UV-B radiation is very high. Substrates are typically rocky and shallow (with low moisture retention capacity) and exposed to solifluction. Micro-topographic heterogeneity influences fine-scale spatial variation in moisture availability. Steep slopes are subjected to periodic mass movements, which destroy surface vegetation. Low-intensity fires may be ignited by lightning or spread upslope from lowland savannas, but these occur infrequently at multi-decadal intervals.

DISTRIBUTION: Restricted mountainous areas of tropical Central and South America, East and West Africa, and Southeast Asia.



Reference:

Smith, A.P. and Young, T.P. (1987). 'Tropical alpine plant ecology'. *Annual Review of Ecology and Systematics* 18: 137–158.

T7 Intensive land-use biome

Tea plantation in Ciwidey, Bandung, Indonesia.
Source: Crisco 1492 on Wikimedia commons

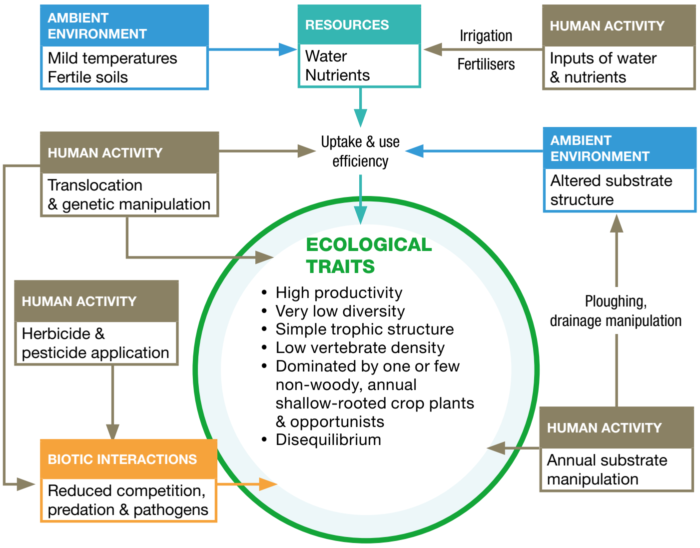
Intensive land-use systems include major anthropogenic enterprises of cropping, pastoralism, plantation farming, and urbanisation. Human intervention is a dominating influence on this biome, also known as the 'anthrome'. Maintenance of these systems is contingent on continuing human interventions, including alterations to the physical structure of vegetation and substrates (e.g. clearing, earthworks and drainage), the supplementation of resources (e.g. with irrigation and fertilisers) and the introduction and control of biota. These interventions maintain disequilibrium community structure and composition, low endemism and low functional and taxonomic diversity. Target biota are genetically manipulated (by selective breeding or molecular engineering) to promote rapid growth rates, efficient resource capture, enhanced resource allocation to production tissues, and tolerance to harsh environmental conditions, predators and diseases. Non-target biota include widely dispersed, cosmopolitan opportunists with short lifecycles. Many intensive land use systems are maintained as artificial mosaics of contrasting patch types at scales of metres to hundreds of metres. Typically, but not exclusively, they are associated with temperate or subtropical climates and the natural availability of freshwater and nutrients from fertile soils on flat to undulating terrain accessible by machinery. The antecedent ecosystems that they replaced include forests, shrublands, grasslands and palustrine wetlands (biomes T1–T4 and TF1). On global and regional scales, intensive land-use systems are engaged in climate feedback processes via alterations to the water cycle and the release of greenhouse gases from vegetation, soils, livestock and fossil fuels. On local scales, temperatures may be modified by human-built structures (i.e. heat-island effects) or may be artificially controlled.

T7.1 Annual croplands

BIOME: T7 INTENSIVE ANTHROPOGENIC TERRESTRIAL ECOSYSTEMS
REALM: TERRESTRIAL

Contributors: D.A. Keith, R. Harper

Wheat crop at harvest time, Hohenberg-Krusemark, Germany.
Source: Heiko Janowski



ECOLOGICAL TRAITS: Structurally simple, very low-diversity, high-productivity annual croplands are maintained by the intensive anthropogenic supplementation of nutrients, water and artificial disturbance regimes (i.e. annual cultivation), translocation (i.e. sowing) and harvesting of annual plants. These systems are dominated by one or few shallow-rooted annual plant species, such as grains (mostly C_3 grasses), vegetables, 'flowers', legumes, or fibre species harvested annually by humans for commercial or subsistence production of food, materials or ornamental displays. Disequilibrium community structure and composition is maintained by translocations and/or managed reproduction of target species and the periodic application of herbicides and pesticides and/or culling to exclude competitors, predators, herbivores and/or pathogens. Consequently, these systems have very low functional, genetic and taxonomic diversity and no local endemism. Productivity is highly sensitive to variations in resource availability. Target biota are genetically manipulated by selective breeding or molecular engineering to promote rapid growth rates, efficient resource capture, enhanced resource allocation to production tissues, and tolerance to harsh environmental conditions, insect predators and diseases. Croplands may be rotated inter-annually with livestock pastures or fallow fields (T7.2). Target biota coexists with a cosmopolitan ruderal biota (e.g. weedy plants, mice and starlings) that exploits production landscapes opportunistically through efficient dispersal, itinerant foraging, rapid establishment, high fecundity and rapid population turnover. When actively managed systems are abandoned or managed less intensively, these non-target biota, especially non-woody plants, become dominant and may form a steady, self-maintaining state or a transitional phase to novel ecosystems.

KEY ECOLOGICAL DRIVERS: The high to moderate natural availability of water (from at least seasonally high rainfall) and nutrients (from fertile soils) is supplemented by human inputs via irrigation, landscape drainage modifications (i.e. surface earthworks) and/or fertiliser application by humans. Intermittent flooding may occur where croplands replace palustrine wetlands. Temperatures are mild to warm, at least seasonally. These systems are typically associated with flat to moderate terrain accessible by machinery. Artificial disturbance regimes (i.e. annual ploughing) maintain soil turnover, aeration, nutrient release and relatively low soil organic carbon content.

DISTRIBUTION: Tropical to temperate humid climatic zones or river flats in dry climates across south sub-Saharan and North Africa, Europe, Asia, southern Australia, Oceania, and the Americas.

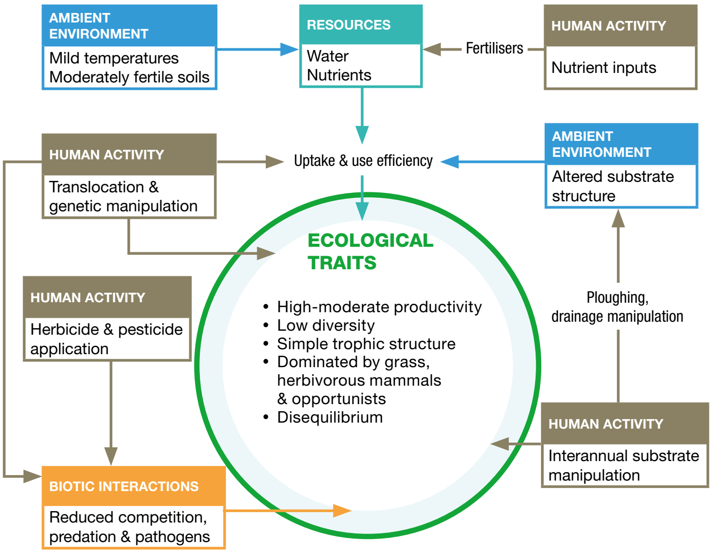
References:
Leff, B., Ramankutty, N., Foley, J.A. (2004). 'Geographic distribution of major crops across the world'. *Global Biogeochemical Cycles* 18(1): GB1009.
Ray, D.K. and Foley, J.A. (2013). 'Increasing global crop harvest frequency: recent trends and future directions'. *Environmental Research Letters* 8(4): 044041.

T7.2 Sown pastures and fields

BIOME: T7 INTENSIVE ANTHROPOGENIC TERRESTRIAL ECOSYSTEMS
REALM: TERRESTRIAL

Contributors: D.A. Keith, R. Harper

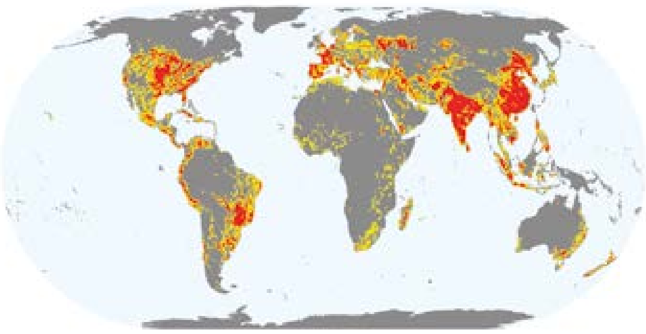
Dairy cattle on sown pasture, Ireland.
Source: Martin Abegglen (2009) Wikimedia Commons



ECOLOGICAL TRAITS: Structurally simple, low-diversity, high-productivity pastures are maintained by the intensive anthropogenic supplementation of nutrients (more rarely water) and artificial disturbance regimes (i.e. periodic ploughing,), translocation (e.g. sowing and livestock movement) and harvesting of animals or plants. They are dominated by one or few selected plant species (C_3 and C_4 perennial pasture grasses and/or herbaceous legumes) and animal species (usually large mammalian herbivores) for commercial production of food or materials, ornamental displays, or, rarely, subsistence. Their composition and structure is maintained by the translocation and/or managed reproduction of target species and the periodic application of herbicides and pesticides and/or culling to exclude competitors, predators, herbivores or pathogens. Consequently, these systems have low functional and taxonomic diversity and no local endemism. Target biota are genetically manipulated to promote rapid growth rates, efficient resource capture, enhanced resource allocation to production tissues, and tolerance to harsh environmental conditions, predators and diseases. They are harvested by humans continuously or periodically for consumption. Major examples include intensively managed production pastures for livestock or forage (i.e. hay), lawns, and sporting fields. Livestock pastures may be rotated inter-annually with non-woody crops (T7.1). Target biota coexist with a cosmopolitan ruderal biota that exploits production landscapes through efficient dispersal, rapid establishment, high fecundity and rapid population turnover. When the ecosystem is abandoned or managed less intensively, non-target biota become dominant and may form a steady, self-maintaining state or a transitional phase to novel ecosystems.

KEY ECOLOGICAL DRIVERS: High to moderate natural availability of water and nutrients is supplemented by human inputs via water management, landscape drainage modifications (i.e. surface earthworks) and/or fertiliser application. Intermittent flooding may occur where pastures replace palustrine wetlands. Temperatures are mild to warm, at least seasonally. Typically associated with moderately fertile substrates, and flat to undulating terrain accessible by machinery. Artificial disturbance regimes (i.e. ploughing for up to five years per decade) maintain soil turnover, aeration and nutrient release.

DISTRIBUTION: Mostly in subtropical to temperate climatic zones and developed countries across Europe, east and south Asia, subtropical and temperate Africa, southern Australasia, north and central America, and temperate south America.



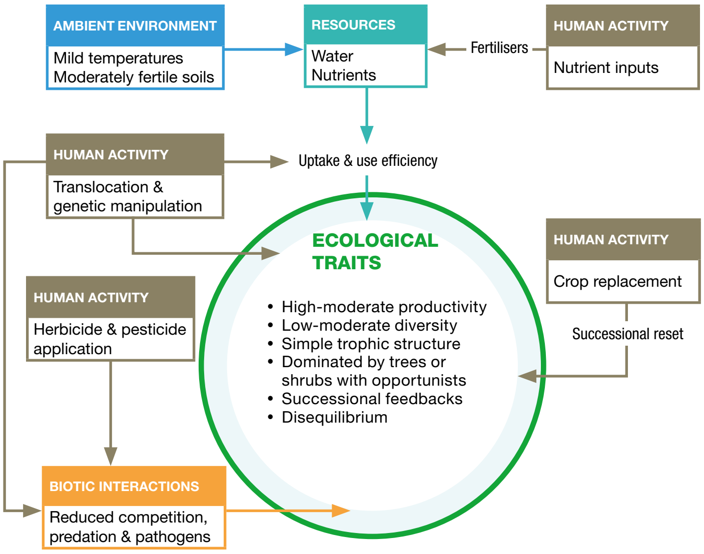
References:
Bernués, A., Ruiz, R., Olaizola, A., Villalba, D., Casasús, I. (2011). 'Sustainability of pasture-based livestock farming systems in the European Mediterranean context: Synergies and trade-offs'. *Livestock Science* 139(1-2): 44–57.
Spedding, C.R.W. (1986). 'Animal production from grass: A systems approach'. In: D.A.J. Cole, G.C. Brander (eds.), *Bioindustrial ecosystems. Ecosystems of the World. Vol. 21*, pp. 107–120. Amsterdam, The Netherlands: Elsevier.

T7.3 Plantations

BIOME: T7 INTENSIVE ANTHROPOGENIC TERRESTRIAL ECOSYSTEMS
REALM: TERRESTRIAL

Contributors: D.A. Keith, K.R. Young

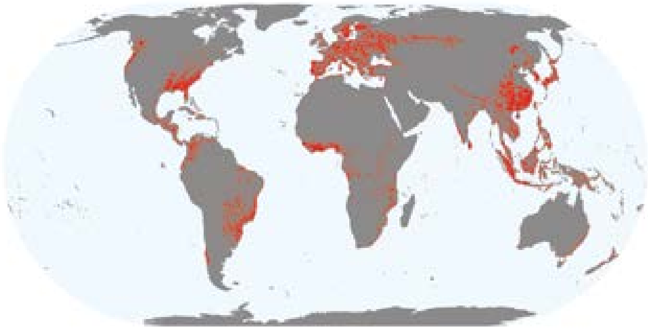
Multi-species plantation (shade coffee), Chikmagalur, India.
Source: Prashantby (2016) Creative Commons



ECOLOGICAL TRAITS: These moderate to high productivity autotrophic systems are established by the translocation (i.e. planting or seeding) of woody perennial plants. Target biota may be genetically manipulated by selective breeding or molecular engineering to promote rapid growth rates, efficient resource capture, enhanced resource allocation to production tissues, and tolerance of harsh environmental conditions, insect predators and diseases. The diversity, structure, composition, function and successional trajectory of the ecosystem depends on the identity, developmental stage, density and traits (e.g. phenology, physiognomy and growth rates) of planted species, as well as the subsequent management of plantation development. Most plantations comprise at least two vertical strata (the managed woody species and a ruderal ground layer). Mixed forest plantings may be more complex and host a relatively diverse flora and fauna if managed to promote habitat features. Cyclical harvest may render the habitat periodically unsuitable for some biota. Mixed cropping systems may comprise two vertical strata of woody crops or a woody and herbaceous layer. Secondary successional processes involve colonisation and regeneration, initially of opportunistic biota. Successional feedbacks occur as structural complexity increases, promoting visits or colonisation by vertebrates and the associated dispersal of plants and other organisms. Crop replacement (which may occur on inter-annual or decadal cycles), the intensive management of plantation structure, or the control of non-target species may reset, arrest, or redirect successional processes. Examples with increasing management intervention include: environmental plantations established for wildlife or ecosystem services; agroforestry plantings for subsistence products or livestock benefits; forestry plantations for timber, pulp, fibre, bio-energy, rubber, or oils; and vineyards, orchards and other perennial food crops (e.g. cassava, coffee, tea, palm oil and nuts). Secondary (regrowth) forests and shrublands are not included as plantations even where management includes supplementary translocations.

KEY ECOLOGICAL DRIVERS: High to moderate natural availability of water and nutrients is supplemented by human inputs of fertiliser or mulch, landscape drainage modifications (i.e. surface earthworks) and, in intensively managed systems, irrigation. Rainfall is at least seasonally high. Temperatures are mild to warm, at least seasonally. Artificial disturbance regimes involving the complete or partial removal of biomass and soil turnover are implemented at sub-decadal to multi-decadal frequencies.

DISTRIBUTION: Tropical to cool temperate humid climatic zones or river flats in dry climates across south sub-Saharan and Mediterranean Africa, Europe, Asia, southern Australia, Oceania and the Americas.



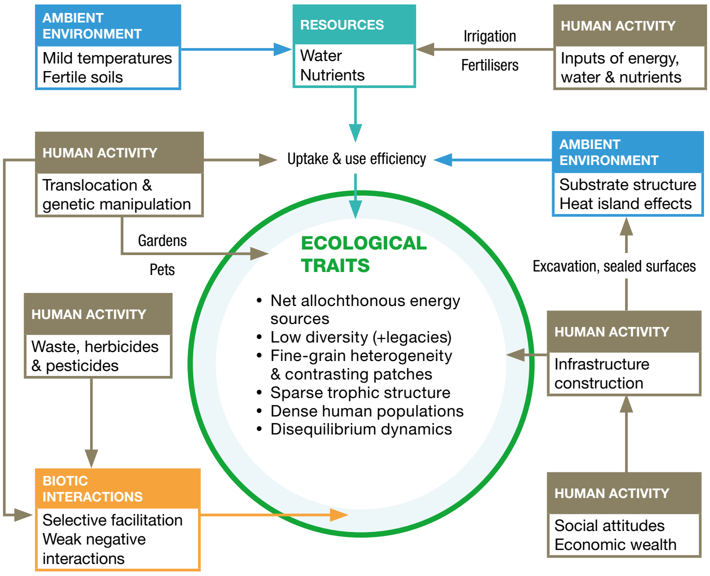
References:
Kanninen, M. (2010). ‘Plantation forests: global perspectives’. In: J. Bauhus, P.J. van der Meer and M. Kanninen (eds.), *Ecosystem goods and services from plantation forests*, pp. 1–15. London, UK: Earthscan.
Monfreda, C.N., Ramankutty, N., Foley, J.A. (2008). ‘Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000’. *Global Biogeochemical Cycles* 22(1): GB1022.

Buildings, roads and city park, São Paulo, Brazil.
Source: Sergio Souza.

T7.4 Urban and industrial ecosystems

BIOME: T7 INTENSIVE ANTHROPOGENIC TERRESTRIAL ECOSYSTEMS
REALM: TERRESTRIAL

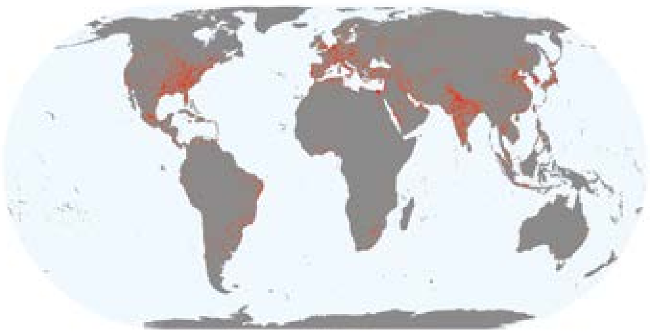
Contributors: D.A. Keith, R.T. Corlett



ECOLOGICAL TRAITS: These systems are structurally complex and highly heterogeneous fine-scale spatial mosaics of diverse patch types that may be recognised in fine-scale land use classifications. These elements include: i) buildings; ii) paved surfaces; iii) transport infrastructure; iv) treed areas; v) grassed areas; vi) gardens; vii) mines or quarries; viii) bare ground; and ix) refuse areas. Patch mosaics are dynamic over decadal time scales and driven by socio-ecological feedbacks and a human population that is highly stratified, functionally, socially and economically. Interactions among patch types and human social behaviours produce emergent properties and complex feedbacks among components within each system and interactions with other ecosystem types. Unlike most other terrestrial ecosystems, the energy, water and nutrient sources of urban systems are highly allochthonous and processes within urban systems drive profound and extensive global changes in land use, land cover, biodiversity, hydrology and climate through both resource consumption and waste discharge. Biotic community structure is characterised by low functional and taxonomic diversity, highly skewed rank-abundance relationships and relict local endemism. Trophic networks are simplified and sparse and each node is dominated by few taxa. Urban biota include humans, dependents (e.g. companion animals and cultivars), opportunists and vagrants, and legacy biota whose establishment pre-dates urbanisation. Many biota have highly plastic realised niches, traits enabling wide dispersal, high fecundity and short generation times. The persistence of dependent biota is maintained by human-assisted migration, managed reproduction, genetic manipulation, amelioration of temperatures, and intensive supplementation of nutrients, food and water. Pest biota are controlled by the application of herbicides and pesticides or culling with collateral impacts on non-target biota.

KEY ECOLOGICAL DRIVERS: Humans influence the availability of water, nutrients, and energy through governance systems for resource importation and indirectly through interactions and feedbacks. Light is enhanced artificially at night. Urban temperature regimes are elevated by the anthropogenic conversion of chemical energy to heat and the absorption of solar energy by buildings and paved surfaces. However, temperatures may be locally ameliorated within buildings. Surface water runoff is enhanced and percolation is reduced by sealed surfaces. Chemical and particulate air pollution, as well as light and noise pollution, may affect biota. Infrastructure development and renewal, driven by socio-economic processes, as well as natural disasters (e.g. storms, floods, earthquakes and tsunami), create recurring disturbances. There is frequent movement of humans and associated biota and matter between cities.

DISTRIBUTION: Extensively scattered through equatorial to subpolar latitudes from sea-level to submontane altitudes, mostly in proximity to the coast, rivers or lakes, especially in North America, Western Europe and Japan, as well as India, China and Brazil. Land use maps depict fine-scale patch types listed above.



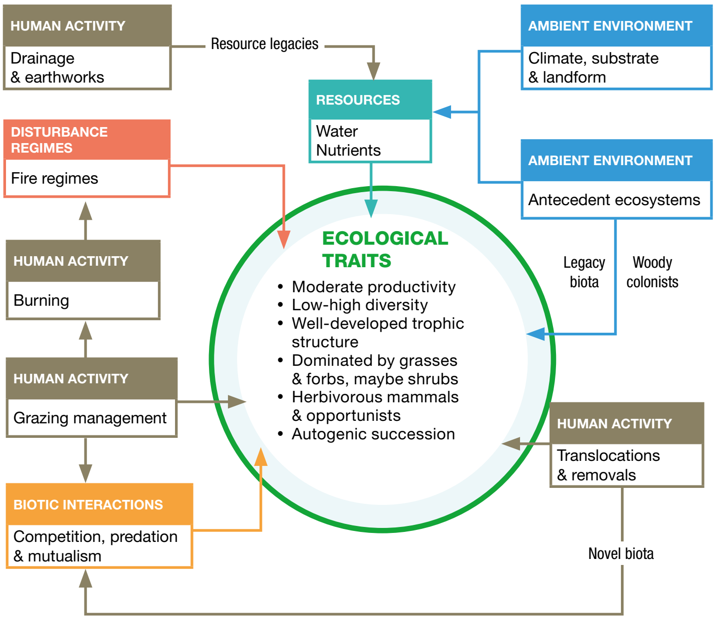
References:
Alberti, M., Marzluff, J.M., Shulenberger, E., Bradley, G., Ryan, C., Zumbrunnen, C. (2003). 'Integrating Humans into Ecology: Opportunities and Challenges for Studying Urban Ecosystems'. *BioScience* 53(12): 1169–1179.
Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M. (2008). 'Global change and the ecology of cities'. *Science* 319(5864): 756–760.

T7.5 Derived semi-natural pastures and old fields

BIOME: T7 INTENSIVE ANTHROPOGENIC TERRESTRIAL ECOSYSTEMS
REALM: TERRESTRIAL

Semi-natural grassland, South Downs, England.
Source: David Keith (2018)

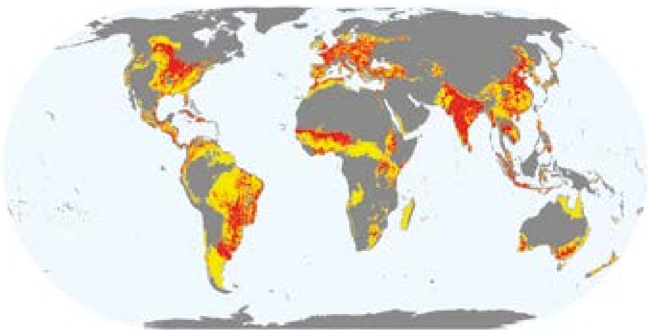
Contributors: D.A. Keith, P.W. Bogaart



ECOLOGICAL TRAITS: Extensive 'semi-natural' grasslands and open shrublands exist where woody components of vegetation have been removed or greatly modified for agricultural land uses. Hence they have been 'derived' from a range of other ecosystems (mostly from biomes T1-T4, a few from T5). Remaining vegetation includes a substantial component of local indigenous species, as well as an introduced exotic element, providing habitat for a mixed indigenous and non-indigenous fauna. Although structurally simpler than the systems from which they were derived, they often harbour an appreciable diversity of native organisms, including some no longer present in 'natural' ecosystems. Dominant plant growth forms include tussock or stoloniferous grasses and forbs, with or without non-vascular plants, shrubs and scattered trees. These support microbial decomposers and diverse invertebrate groups that function as detritivores, herbivores and predators, as well as vertebrate herbivores and predators characteristic of open habitats. Energy sources are primarily autochthonous, with varying levels of indirect allochthonous subsidies (i.e. via surface water sheet flows), but few managed inputs (cf. T7.2). Productivity can be low-high, depending on climate and substrate, but is generally lower and more stable than more intensive anthropogenic systems (T7.1-T7.3). Trophic networks include all levels, but complexity and diversity depends on the species pool, legacies from antecedent ecosystems, successional stage and management regimes. These novel ecosystems may persist in a steady self-maintaining state, or undergo passive transformation (i.e. oldfield succession), unless actively maintained in disequilibrium. For example, removal of domestic herbivores may initiate transition to tree-dominated ecosystems.

KEY ECOLOGICAL DRIVERS: Availability of water and nutrients varies depending on local climate, substrate and terrain (hence surface water movement and infiltration). The structure, function and composition of these ecosystems are shaped by legacy features of antecedent systems from which they were derived, as well as ongoing and past human activities. These activities may reflect production and/or conservation goals, or abandonment. They include active removal of woody vegetation, management of vertebrate herbivores, introductions of biota, control of 'pest' biota, manipulation of disturbance regimes, drainage and earthworks, etc. Fertilisers and pesticides are not commonly applied.

DISTRIBUTION: Mostly in temperate to tropical climatic zones across all land masses.



References:
Cramer, V.A., Hobbs, R.J., Standish, R.J. (2008). 'What's new about old fields? Land abandonment and ecosystem assembly'. *Trends in Ecology & Evolution* 23(2): 104–112.
García-Feced, C., Weissteiner, C.J., Baraldi, A., Paracchini, M.A., Maes, J., Zulian, G., Kempen, M., Elbersen, B., Pérez-Sob, M. (2015). 'Semi-natural vegetation in agricultural land: European map and links to ecosystem service supply'. *Agronomy for Sustainable Development* 35: 273–283.
Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J. et al. (2010). 'Habitat fragmentation causes immediate and time delayed biodiversity loss at different trophic levels'. *Ecology Letters* 13(5): 597–605.

S1 Subterranean lithic biome

Marakoopa caves, Mole Creek, Tasmania, Australia.
Source: Diego Delso on Wikimedia commons, CC BY-SA 3.0

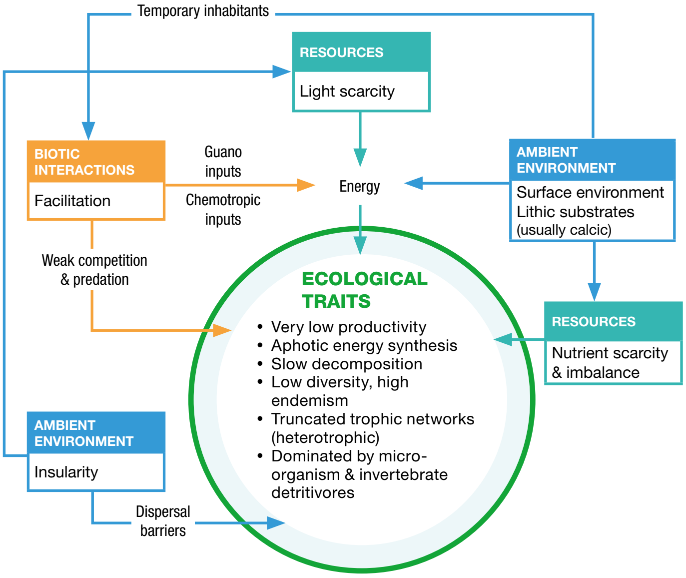
The subterranean lithic biome includes non-aquatic lithic systems beneath the earth's surface. Sunlight is absent or of insufficient intensity to sustain photosynthesis. There is no standing water and moisture is supplied primarily by seepage through the substrate and may be lost by slow diffusion through the atmosphere to cave openings or by vertical or lateral seepage through the substrate. These physically stable systems exhibit low levels of environmental variability. Rarely, mass movements, for example rock falls, may re-organise the physical structure of subterranean ecosystems. Subterranean ecosystems have truncated trophic structures with no photoautotrophs and few obligate predators. Heterotrophic microbes and invertebrates dominate the biota, while chemoautotrophs are the primary energy assimilators. Most have low metabolic rates and prolonged life histories in response to resource limitations, resulting in low overall productivity. The subterranean biome includes dry caves and endolithic systems distributed throughout the earth's crust. Incursions of fresh or marine waters generate transitional biomes (SF, SM).

S1.1 Aerobic caves

BIOME: SUBTERRANEAN LITHIC ECOSYSTEMS
REALM: SUBTERRANEAN

Contributors: D.A. Keith, G.C. Hose

Bats roosting in a cave, Nicaragua.
Source: Grigory Kubatyan (Dreamstime.com)

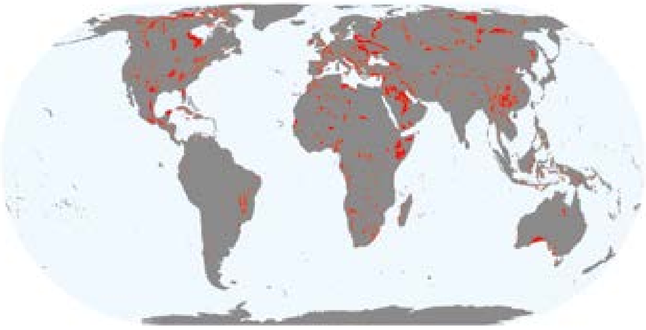


ECOLOGICAL TRAITS: Dark subterranean air-filled voids support simple, low productivity systems. The trophic network is truncated and dominated by heterotrophs, with no representation of photosynthetic primary producers or herbivores. Diversity is low, comprising detritivores and their pathogens and predators, although there may be a few specialist predators confined to resource-rich hotspots, such as bat latrines or seeps. Biota include invertebrates (notably beetles, springtails and arachnids), fungi, bacteria and transient vertebrates, notably bats, which use surface-connected caves as roosts and breeding sites. Bacteria and fungi form biofilms on rock surfaces. Fungi are more abundant in humid microsites. Some are parasites and many are critical food sources for invertebrates and protozoans. Allochthonous energy and nutrients are imported via seepage moisture, tree roots, bats and other winged animals. This leads to fine-scale spatial heterogeneity in resource distribution, reflected in patterns of biotic diversity and abundance. Autochthonous energy can be produced by chemoautotrophs. For example, chemoautotrophic Proteobacteria are prominent in subterranean caves formed by sulphide springs. They fix carbon through sulphide oxidation, producing sulphuric acid and gypsum residue in snottite draperies (i.e. microbial mats), accelerating chemical corrosion. The majority of biota are obligate subterranean organisms that complete their life cycles below ground. These are generalist detritivores and some are also opportunistic predators, reflecting the selection pressure of food scarcity. Distinctive traits include specialised non-visual sensory organs, reduced eyes, pigmentation and wings, elongated appendages, long lifespans, slow metabolism and growth and low fecundity. Other cave taxa are temporary below-ground inhabitants, have populations living entirely above- or below-ground, or life cycles necessitating use of both environments. The relative abundance and diversity of temporary inhabitants decline rapidly with distance from the cave entrance. The specialist subterranean taxa belong to relatively few evolutionary lineages that either persisted as relics in caves after the extinction of above-ground relatives or diversified after colonisation by above-ground ancestors.

Although diversity is low, local endemism is high, reflecting insularity and limited connectivity between cave systems.

KEY ECOLOGICAL DRIVERS: Most caves form from the chemical weathering of limestone, dolomite or gypsum, either from surface waters or from phreatic waters. Caves also derive from lava tubes and other substrates. Characteristics include the absence of light except at openings, low variability in temperature and humidity, and scarcity of nutrients. The high physical fragmentation of cave substrates limits biotic connectivity and promotes insular evolution in stable conditions.

DISTRIBUTION: Scattered worldwide, but mostly in the Northern Hemisphere, in limestone (map), basalt flows, and rarely in other lithic substrates.

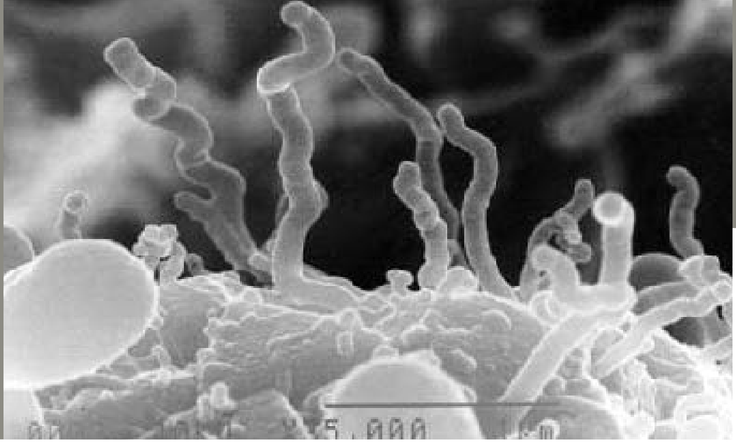


References:
Gibert, J., Deharveng, L. (2002). 'Subterranean Ecosystems: A Truncated Functional Biodiversity'. *BioScience* 52(6): 473–481.
Engel, A.S. (2010). 'Microbial Diversity of Cave Ecosystems'. In: L.L. Barton, M. Mandl and A. Loy (eds.), *Geomicrobiology: Molecular and Environmental Perspective*, pp. 219–238. Dordrecht, The Netherlands: Springer.

S1.2 Endolithic systems

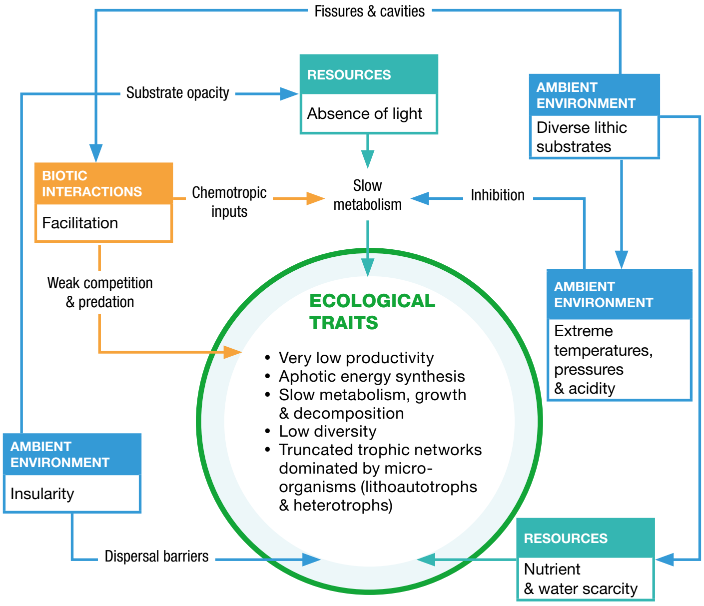
BIOME: SUBTERRANEAN LITHIC ECOSYSTEMS
REALM: SUBTERRANEAN

Contributors: D.A. Keith, T.M. Iliffe, V. Gerovasileiou, B. Gonzalez, D. Brankovits, A. Martínez



Endolithic nanobacteria in sandstone, Australia.
Source: Philippa Uwins

ECOLOGICAL TRAITS: Lithic matrices and their microscopic cracks and cavities host microbial communities. Their very low productivity is constrained by the scarcity of light, nutrients, and water, and sometimes also by high temperatures. Diversity is low and the trophic network is truncated, supporting microscopic bacteria, archaea, viruses and unicellular eukaryotes. Most are detritivores or lithoautotrophs, which derive energy, oxidants, carbohydrates and simple organic acids from carbon dioxide, geological sources of hydrogen and mineral compounds of potassium, iron and sulphur. Some fissures are large enough to support small eukaryotic predators such as nematodes. Photoautotrophs (i.e. cyanobacteria) are present only in the surface layers of exposed rocks. Sampling suggests that these systems harbour 95% of the world's prokaryote life (bacteria and archaea), with rocks below the deep oceans and continents containing similar densities of cells and potentially accounting for a significant proportion of sequestered carbon. Endolithic microbes are characterised by extremely slow reproductive rates, especially in deep sedimentary rocks, which are the most oligotrophic substrates. At some depth within both terrestrial and marine substrates, microbes are sustained by energy from organic matter that percolates through fissures from surface systems. In deeper or less permeable parts of the crust, however, lithoautotrophic microbes are the primary energy synthesisers that sustain heterotrophs in the food web. Methanogenic archaea and iron-reducing bacteria appear to be important autotrophs in sub-oceanic basalts. All endolithic microbes are characterised by slow metabolism and reproduction rates. At some locations they tolerate extreme pressures, temperatures (up to 125°C) and acidity (pH<2), notably in crustal fluids. Little is currently known of endemism, but it may be expected to be high based on the insularity of these ecosystems.



KEY ECOLOGICAL DRIVERS: Endolithic systems are characterised by a lack of light, a scarcity of nutrients, and high pressures at depth. Temperatures vary within the crust from <20°C up to 125°C, but show little temporal variation. The chemical properties and physical structure of lithic matrices influence the supply of resources and the movement of biota. Stable cratonic massifs have minimal pore space for microbial occupation, which is limited to occasional cracks and fissures. Sedimentary substrates offer more space, but nutrients may be scarce, while fluids in basic volcanic and crustal rocks have more abundant nutrients. Chemical and biogenic weathering occurs through biogenic acids and other corrosive agents. The matrix is mostly stable, but disturbances include infrequent and spatially variable earthquakes and volcanic intrusions.

DISTRIBUTION: Throughout the earth's crust, from surface rocks to a predicted depth of up to 4–4.5 km below the land surface and 7–7.5 km below ocean floors. Not mapped.

Reference:
Edwards, K.J., Becker, K. and Colwell, F. (2012). 'The deep, dark energy biosphere: Intraterrestrial life on earth'. *Annual Review of Earth and Planetary Sciences* 40: 551–568.

S2 Anthropogenic subterranean voids biome

Underground mine tunnel.
Source: Maxim

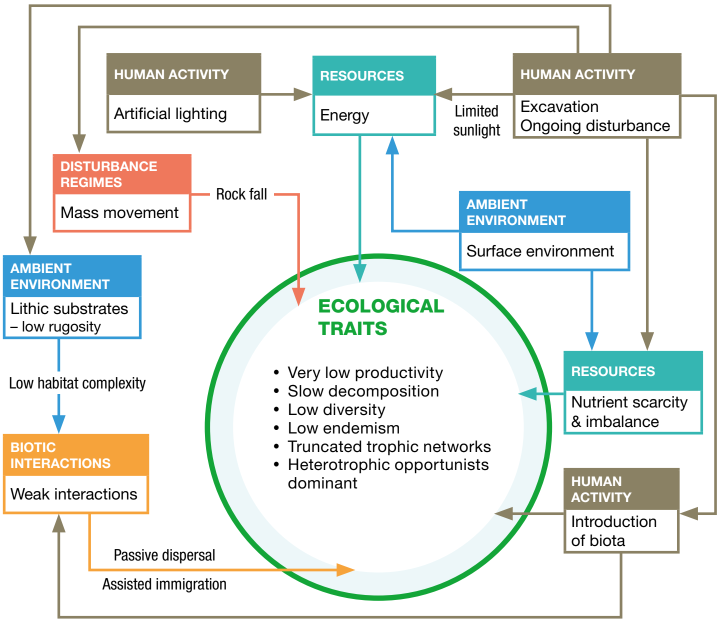
The Anthropogenic subterranean voids biome includes a single functional group of ecosystems that owe their genesis to excavation by humans. They include underground mines, transport tunnels, tombs, defence and energy installations, and other infrastructure. Most are very recent ecosystems constructed with earth-moving machinery during the industrial era, but some were constructed manually up to several millennia ago. Productivity is low and energy generally comes from allochthonous sources via connections to the surface, either by atmospheric diffusion or seepage, but some energy is contributed by chemoautotrophic microbes. While sunlight is absent or highly diffuse, some active voids are artificially lit and this may provide sufficient energy to sustain algal autotrophs. Trophic webs are simple and dominated by opportunistic microbes and invertebrates introduced by machinery or directly by humans, or else colonising spontaneously through openings to the surface. The latter may include small mammals that use the voids as refuges or breeding sites. Microbes from external and endolithic sources rapidly colonise newly exposed lithic surfaces and create biofilms that support detritivores and enhance substrate weathering. The stability of artificial subterranean voids varies depending on their substrate and management, with some prone to collapse and structural change after active use ceases.

S2.1 Anthropogenic subterranean voids

BIOME: ANTHROPOGENIC SUBTERRANEAN VOIDS
REALM: SUBTERRANEAN

Contributors: D.A. Keith, T.M. Iliffe, V. Gerovasileiou, B. Gonzalez, D. Brankovits, A. Martínez García

Goonyella coal mine, near Mackay, Australia.
Source: Newcastle on Hunter



ECOLOGICAL TRAITS: These low-productivity systems in subterranean air-filled voids are created by excavation. Although similar to Aerobic caves (S1.1), these systems are structurally simpler, younger, more geologically varied, and much less biologically diverse with few evolutionary lineages and no local endemism. Low diversity, low endemism, and opportunistic biotic traits stem from founder effects related to their recent anthropogenic origin (hence few colonisation events and little time for evolutionary divergence), as well as low microhabitat niche diversity due to the simple structure of void walls compared to natural caves. The trophic network is truncated and dominated by heterotrophs, usually with no representation of photosynthetic primary producers or herbivores. Generalist detritivores and their pathogens and predators dominate, although some specialists may be associated with bat dung deposits. Biota include invertebrates (notably beetles, springtails and arachnids), fungi, bacteria and transient vertebrates, notably bats, which use the voids as roosts and breeding sites. Bacteria and fungi form biofilms on void surfaces. Many are colonists of human inoculations, with some microbes identified as 'human-indicator bacteria' (e.g. *Escherichia coli*, *Staphylococcus aureus* and high-temperature *Bacillus spp.*). Fungi are most abundant in humid microsites. Some are parasites and many are critical food sources for invertebrates and protozoans. Sources of energy and nutrients are allochthonous, imported by humans, bats, winged invertebrates, other animals, and seepage moisture. Many taxa have long life spans, slow metabolism and growth and low fecundity, but lack distinctive traits found in the biota of natural caves. Some are temporary below-ground inhabitants, have populations that live entirely above- or below-ground, or have life cycles necessitating the use of both environments.

KEY ECOLOGICAL DRIVERS: Excavations associated with tunnels, vaults and mines. While some are abandoned, others are continuously accessed by humans, enhancing connectivity with the surface, resource importation and biotic dispersal. Substrates include a range of rock types as well as artificial surfaces on linings and debris piles. Air movement varies from still to turbulent (i.e. active train tunnels). Light is absent except at openings and where artificial sources are maintained by humans, sometimes supporting algae (i.e. lampenflora). Humidity and temperature are relatively constant, and nutrients are scarce except where enriched by human sources.

DISTRIBUTION: Scattered worldwide, but mostly associated with urban centres, transit corridors and industrial mines.

References:
Gibert, J., Deharveng, L. (2002). 'Subterranean Ecosystems: A Truncated Functional Biodiversity'. *BioScience* 52(6): 473–481.
Engel, A.S. (2010). 'Microbial diversity of cave ecosystems'. In: L.L. Barton, M. Mandl and A. Loy (eds.), *Geomicrobiology: Molecular and Environmental Perspective*, pp. 219–238. Dordrecht, The Netherlands: Springer.

SF1 Subterranean freshwaters biome

Puerto Princesa subterranean river, Palawan, Philippines
Source: Aleksandar Todorovic/Shutterstock

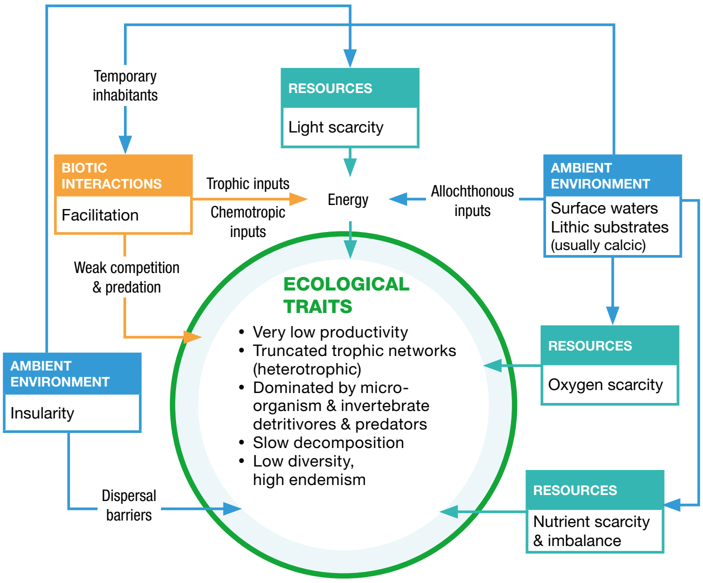
The Subterranean freshwaters biome includes streams, small lakes and aquifers beneath the earth's surface and potentially has the largest volume of water of all the freshwater biomes. In the absence of sunlight, these ecosystems rely on allochthonous energy sourced from surface ecosystems via connected waters and in situ chemoautotrophs. Depending on the mode of connectivity to the surface, water flow-through varies from extremely rapid to slow. Highly connected subterranean streams in monsoonal climates undergo seasonal flooding and drying cycles. In contrast, paleo-aquifers are characterised by slow, low-variability seepage over millennial time scales. Inflowing water is the principal source of dissolved oxygen and mineral nutrients, although some nutrients are liberated by in situ weathering of lithic substrates. The water regime largely determines environmental variability in subterranean freshwaters, but these systems may occasionally be influenced by mass movements. The trophic structure of subterranean waters is typically truncated, although photosynthetically inactive, algae and higher-plant propagules may be transient occupants in systems that are connected to the surface. Chemoautotrophic and heterotrophic microbes in biofilms and the water column dominate the trophic web, supporting small invertebrate detritivores and predators. Small predatory fish may occur in streams and lakes, where voids in the subsurface are of sufficient size. Productivity, metabolic rates, life histories and the diversity of the biota all reflect resource scarcity but may vary depending on water source. Insular systems exhibit high levels of endemism.

SF1.1 Underground streams and pools

BIOME: SF1 SUBTERRANEAN FRESHWATER SYSTEMS
REALM: TRANSITIONAL SUBTERRANEAN-FRESHWATER

Contributors: D.A. Keith, G.C. Hose

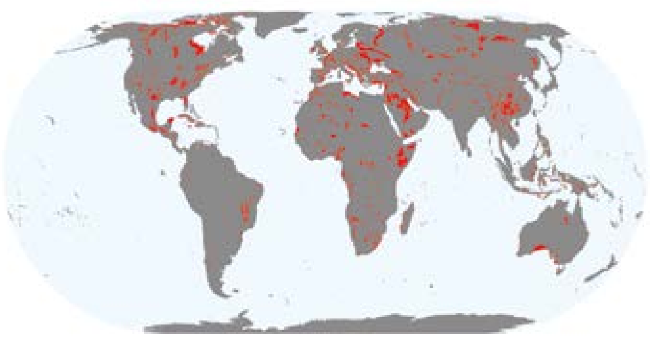
Above: Blind cave fish, southern Madagascar.
Source: Hectonichus CC 3.0
Below: Molnár János cave with drone UX-1, Hungary.
Source: UNEXMIN 2019



ECOLOGICAL TRAITS: Subterranean streams, pools and aquatic voids (flooded caves) are low-productivity systems devoid of light. The taxonomic and functional diversity of these water bodies is low, but they may host local endemics, depending on connectivity with surface waters and between cave systems. The truncated trophic network is entirely heterotrophic, with no photosynthetic primary producers or herbivores. Detritivores and their predators are dominant, although a few specialist predators may be associated with resource-rich hotspots. Microbial mats composed of bacteria and aquatic fungi covering submerged rock surfaces are major food sources for protozoans and invertebrates. Other biota include planktonic bacteria, crustaceans, annelids, molluscs, arachnids and fish in larger voids. Chemoautotrophic proteobacteria are locally abundant in sulphur-rich waters fed by springs but not widespread. Obligate denizens of subterranean waters complete their life cycles entirely below ground and derive from relatively few evolutionary lineages. These make up a variable portion of the biota, depending on connectivity to surface waters. Most species are generalist detritivores coexisting under weak competitive interactions. Some are also opportunistic predators, reflecting selection pressures of food scarcity. Distinctive traits include the absence of eyes and pigmentation, long lifespans, slow metabolism and growth rates and low fecundity. Less-specialised biota include taxa that spend part of their life cycles below ground and part above, as well as temporary below-ground inhabitants. Transient vertebrates occur only in waters of larger subterranean voids that are well connected to surface streams with abundant food.

KEY ECOLOGICAL DRIVERS: Most caves form from chemical weathering of soluble rocks, such as limestone or dolomite, and others include lava tunnels. Cave waters are devoid of light, typically low in dissolved oxygen nutrients, and food, and exhibit low variability in temperature. Water chemistry reflects substrate properties (i.e. high Calcium levels in limestone voids). Resource supply and biotic dispersal depend on connectivity with surface waters and flow velocity and turbulence. In the absence of light, surface-connected streams are major allochthonous sources of energy and nutrients. Disconnected systems are the most biologically insular and oligotrophic, and may also be limited by nutrient imbalance. These features promote insular evolution in stable conditions.

DISTRIBUTION: Scattered worldwide, mostly in the Northern Hemisphere in limestone (map) and more rarely in basalt flows and other lithic substrates.



Reference:

Gibert, J., Deharveng, L. (2002). ‘Subterranean Ecosystems: A Truncated Functional Biodiversity’. *BioScience* 52(6): 473–481.

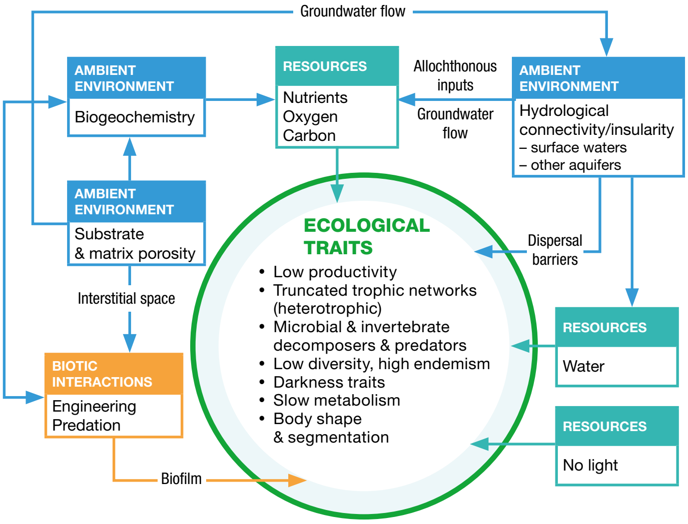
SF1.2 Groundwater ecosystems

BIOME: SF1 SUBTERRANEAN FRESHWATER SYSTEMS
REALM: TRANSITIONAL SUBTERRANEAN-FRESHWATER

Contributors: D.A. Keith, T.M. Iliffe, V. Gerovasileiou, B. Gonzalez, D. Brankovits, A. Martínez, G.C. Hose

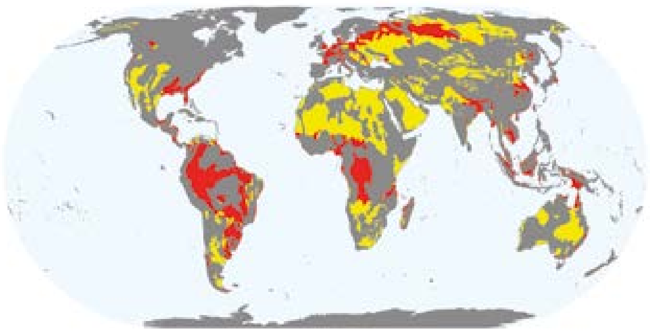
Stygofauna from the Pilbara, Western Australia, clockwise from top left: snail, *Hydrobiidae*; syncarid, *Billibathynella*; amphipod, *Neoniphargidae*; amphipod, *Bogidiellidae*.
Source: Jane McRae/Western Australian Museum

ECOLOGICAL TRAITS: These low-productivity ecosystems are found within or below groundwater (phreatic) zones. They include aquifers (underground layers of water-saturated permeable rock or unconsolidated gravel, sand, or silt) and hyporheic zones beneath rivers and lakes (i.e. where shallow groundwater and surface water mix). Diversity and abundance of biota decline with depth and connectivity to surface waters, as do nutrients (i.e. most meiofauna is limited to 100 m deep). Microbial communities are functionally diverse and invertebrate taxa exhibit high local endemism where aquifers are poorly connected. Trophic networks are truncated and comprised almost exclusively of heterotrophic microbes and invertebrates. Chemoautotrophic bacteria are the only source of autochthonous energy. Herbivores only occur where plant material enters groundwater systems (i.e. in well-connected hyporheic zones). Microbes and their protozoan predators dwell on particle surfaces rather than in pore water. They play key roles in weathering and mineral formation, engineer chemically distinctive microhabitats through redox reactions, and are repositories of Carbon, Nitrogen and Phosphorus within the ecosystem. Meio-faunal detritivores and predators transfer Carbon and nutrients from biofilms to larger invertebrate predators such as crustaceans, annelids, nematodes, water mites and beetles. These larger trophic generalists live in interstitial waters, either browsing on particle biofilms or ingesting sediment grains, digesting their surface microbes, and excreting ‘cleaned’ grains. They have morphological and behavioural traits that equip them for life in dark, resource-scarce groundwater where space is limited. These include slow metabolism and growth, long lifespans without resting stages, low fecundity, lack of pigmentation, reduced eyes, enhanced non-optic sensory organs and elongated body shapes with enhanced segmentation. Much of the biota belongs to ancient subterranean lineages that have diverged sympatrically within aquifers or allopatrically from repeated colonisations or aquifer fragmentation.



KEY ECOLOGICAL DRIVERS: Groundwater ecosystems are characterised by a scarcity of nutrients, Carbon, dissolved oxygen and free space, and an absence of light. They occur within basin fill or other porous geological strata. Groundwater flow, pore size, interstitial biogeochemistry and hydrological conductivity to adjacent aquifers and surface waters determine ecosystem properties. Subsurface water residence times vary from days in shallow, well-connected, coarse-grained hyporheic systems to thousands of years in deep, poorly connected aquifers confined between impermeable rock strata. Lack of connectivity promotes insularity and endemism as well as reductive biogeochemical processes that influence the availability of food and nutrients.

DISTRIBUTION: Globally distributed. Map shows only the major groundwater basins by recharge rates.



References:
Danielopol, D.L., Griebler, C., Gunatilaka, A. and Notenboom, J. (2003). ‘Present state and future prospects for groundwater ecosystems’. *Environmental Conservation* 30(2): 104–130.
Hancock, P.J., Boulton, A.J. and Humphreys, W.F. (2005). ‘Aquifers and hyporheic zones: towards an understanding of groundwater’. *Hydrogeology Journal* 13(1): 98–111.
Struckmeier, W., Richts, A. (2008). *Groundwater resources of the world*. Hanover, Germany: BGR and Paris, France: UNESCO.

SF2 Anthropogenic subterranean freshwaters biome

‘Blue Danube’ subterranean sewer tunnel, Voronezh, Russia.
Source: mulderphoto

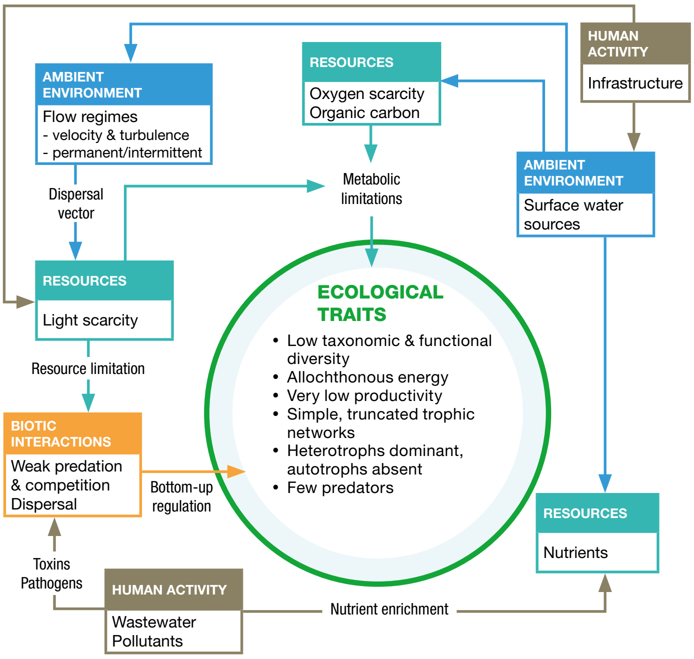
The Artificial subterranean freshwaters biome includes aquatic systems in underground canals, drains, sewers, water pipes and flooded mines constructed by humans. These are usually well connected to surface waters. The availability of resources is largely a function of source waters and the water regime, which varies from permanent to intermittent with low to high flow velocity or, in the case of flooded mines, negligible flow. Sunlight is absent or, if it diffuses through vents and portals (as in some canals), it is generally too dim to support photosynthesis. Algae may nonetheless be transported through these systems depending on the water of source. Although primary productivity is low and energy is supplied from allochthonous sources, secondary productivity by heterotrophic microbes in biofilms and in the water column may be high in sewers and drains where organic Carbon, nutrients and dissolved oxygen are abundant. This may support several tiers of detritivores and predators, including microscopic invertebrates, macro-invertebrates, and small vertebrates, including rodents and fish. Anaerobic bacteria may be important components of the trophic network where organic Carbon and nutrients are abundant but dissolved oxygen is scarce due to either low aeration or high microbial activity. In water supply pipes, low levels of organic carbon and nutrients exacerbate constraints on productivity imposed by the absence of light. Trophic webs within pipes are truncated and simple, and the mostly transitory biota reflects that of source waters.

Water pipes in the Snowy Mountains, Australia.
Source: Shutterstock

SF2.1 Water pipes and subterranean canals

BIOME: SF2 FRESHWATER SUBTERRANEAN SYSTEMS
REALM: TRANSITIONAL SUBTERRANEAN-FRESHWATER

Contributors: D.A. Keith, T.M. Iliffe, V. Gerovasileiou, B. Gonzalez, D. Brankovits, A. Martínez



ECOLOGICAL TRAITS: Constructed subterranean canals and water pipes are dark, low-productivity systems acting as conduits for water, nutrients, and biota between artificial or natural freshwater ecosystems. Energy sources are therefore entirely or almost entirely allochthonous from surface systems. Although similar to underground streams (S2.1), these systems are structurally simpler, younger, and less biologically diverse with few evolutionary lineages and no local endemism. Diversity and abundance are low, often resulting from the accidental transport of biota from source to sink ecosystems. Trophic networks are truncated, with very few or no primary producers and no vertebrate predators except incidental transients. The majority of the resident heterotrophic biota are bacteria, aquatic fungi and protists living in biofilms covering mostly smooth artificial surfaces or cut rock faces. Biofilms constitute food sources for detritivores and predators, including protozoans and planktonic invertebrates, as well as filter feeders such as molluscs. The structure of the biofilm community varies considerably with hydraulic regime, as does the biota in the water column. Transient vertebrates, notably fish, occupy well-connected ecosystems with abundant food and predominantly depend on transported nutrients and prey. A range of organisms may survive in these environments but only some maintain reproductive populations. All biota are capable of surviving under no or low light conditions, at least temporarily while in transit. Other traits vary with hydraulic regimes and hydrochemistry, with physiological tolerance to toxins important in highly eutrophic, slow-flowing drains and tolerance to low nutrients and turbulence typical in high-velocity minerotrophic water pipes.

KEY ECOLOGICAL DRIVERS: Subterranean canals and water pipes are engineered structures designed to connect and move waters between artificial (or more rarely natural) sources. They are united by an absence of light and usually low oxygen levels and low variability in temperatures, but hydraulic regimes, nutrient levels, water chemistry, flow and turbulence vary greatly among ecosystems. Water supply pipes are extreme oligotrophic systems with rapid flow, high turbulence, low nutrients and low connectivity to the atmosphere, often sourced from de-oxygenated water at depth within large reservoirs (F3.1). In contrast, subterranean wastewater or stormwater canals have slower, more intermittent flows, low turbulence and very high nutrient levels and chemical pollutants, including toxins. Many of these eutrophic systems have an in situ atmosphere, but dissolved oxygen levels are very low in connection with high levels of dissolved organic Carbon and microbial activity.

DISTRIBUTION: Common in landscapes with urban or industrial infrastructure, including water supply and sewerage reticulation systems, hydroelectricity, irrigation and other intensive agricultural industries.

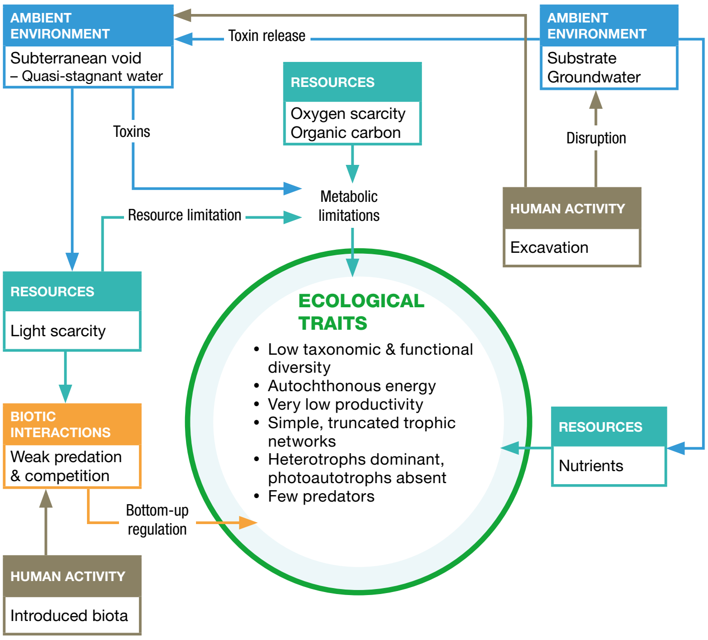
Reference:
Douterelo, I., Sharpe, R.L., Boxall, J.B. (2013). 'Influence of hydraulic regimes on bacterial community structure and composition in an experimental drinking water distribution system'. *Water Research* 47(2): 503–516.

SF2.2 Flooded mines and other voids

BIOME: SF2 FRESHWATER SUBTERRANEAN SYSTEMS
REALM: TRANSITIONAL SUBTERRANEAN-FRESHWATER

Contributors: D.A. Keith, T.M. Iliffe

Flooded iron ore mine, Bell Island, Newfoundland, Canada.
Source Jill Heinerth



ECOLOGICAL TRAITS: Abandoned and now flooded underground mines frequently contain extensive reservoirs of geothermally warmed groundwater, colonized by stygobitic invertebrates from nearby natural subterranean habitats. A fraction of the biota is likely to have been introduced by mining activities. A lack of light excludes photoautotrophs from these systems and low connectivity limits inputs from allochthonous energy sources. Consequently, overall productivity is low, and is likely to depend on chemoautrophic microbes (i.e. sulfate-reducing bacteria) as sources of energy. Few studies have investigated the ecology of the aquatic biota in quasi-stagnant water within mine workings, but trophic networks are truncated and likely to be simple, with low diversity and abundance at all trophic levels, and no endemism. Most of the resident heterotrophic biota are bacteria, aquatic fungi and protists living in biofilms on artificial surfaces of abandoned infrastructure, equipment or cut rock faces. Extremophiles are likely to dominate in waters that are highly acidic or with high concentrations of heavy metals or other toxins. Micro-invertebrates are most likely to be the highest-level predators. Some voids may have simple assemblages of macroinverterbates, but few are likely to support vertebrates unless they are connected with surface waters that provide a means of colonization.

KEY ECOLOGICAL DRIVERS: Like all subterranean ecosystems, light is absent or extremely dim in flooded mines. Unlike subterranean canals and pipes (SF2.1), mine waters are quasi-stagnant and not well connected to surface waters. During mine operation, water is pumped out of the mine forming a widespread cone of water table depression, with oxidation and hydrolysis of exposed minerals changing groundwater chemistry. When mines close and dewatering ceases, water table rebounds and the voids often flood. Some voids are completely inundated, while others retain a subterranean atmosphere, which may or may not be connected to the surface. Further changes in water chemistry occur after flooding due to dissolution and flushing of the oxidation products. Water is often warm due to geothermal heating. After inundation has stabilised, seepage and mixing may be slow, and stratification creates strong gradients in oxygen and solutes. Waters are acidic in most flooded mines. The ionic composition varies depending on mineralogy of the substrate, but ionic concentrations are typically high, and often contain heavy metals at levels toxic to some aquatic biota. Acid mine drainage is a common cause of pollution in surface rivers and streams, where it seeps to the surface.

DISTRIBUTION: Common in in many mineral rich regions of the world.

References:
Nuttall, C.A., Younger, P.L. (2004). 'Hydrochemical stratification in flooded underground mines: an overlooked pitfall'. *Journal of Contaminant Hydrology* 69(1–2): 101–114.
Roesler, A.J., Gammons, C.H., Druschel, G.K., Oduro, H. and Poulson, S.R. (2007). 'Geochemistry of Flooded Underground Mine Workings Influenced by Bacterial Sulfate Reduction'. *Aquatic Geochemistry* 13: 211–235.
Wright, I.A., Paciuszkiewicz, K. and Belmer, N. (2018). 'Increased water pollution after closure of Australia's longest operating underground coal mine: a 13-month study of mine drainage, water chemistry and river ecology'. *Water Air Soil Pollution* 229: 55.

SM1 Subterranean tidal biome

Sac Actun cave system, Quintana Roo, Mexico.
Source: Alison Perkins

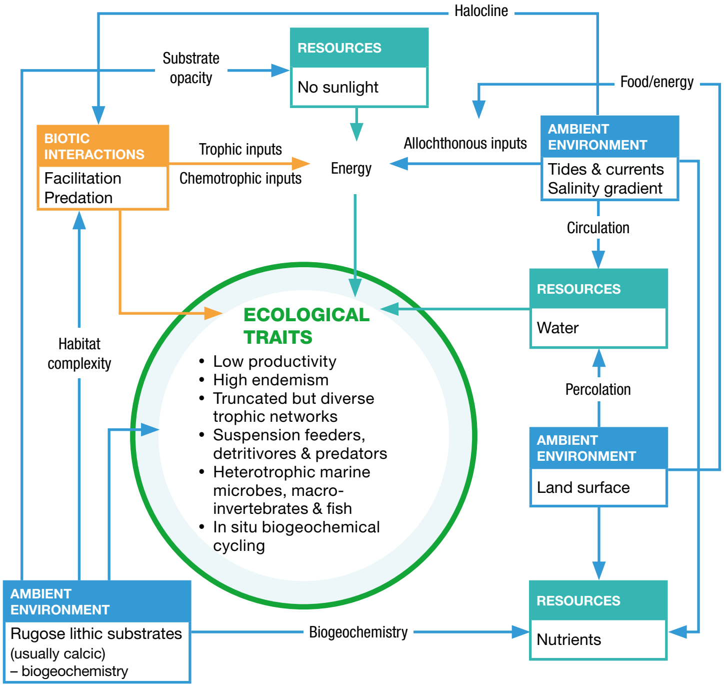
The subterranean tidal biome includes coastal pools and subterranean voids with a partially or entirely submerged connection to marine waters. Like all other subterranean ecosystems, sunlight is absent or too dim to sustain photosynthesis. Marine shelf ecosystems (M1), terrestrial aquifers (SF1) and surface coastal systems (T, MT) connected to these subterranean systems are their sources of allochthonous energy, nutrients and oxygenation. Food and energy availability are influenced by in situ microbial processing (biogeochemical transformation) of these allochthonous organic matter inputs. The marine interface, a typical feature of coastal aquifers and subterranean estuaries, also generates a marked salinity gradient is the primary zone of biogeochemical cycling. In carbonate and volcanic geologies, the salinity gradient can often be observed in the flooded pools, voids, and caves as a halocline (a sharp salinity gradient in the water column), which is not present in other subterranean environments. In comparison to other subterranean ecosystems, diverse assemblages of chemoautotrophic and heterotrophic microbes, as well as scavengers, filter feeders and predators. Physiological traits enabling osmotic regulation allow some species to transit across haloclines between the fresh- and saline waters. In dark sections of the subterranean marine systems where photoautotrophs are absent, trophic webs are truncated. Some of the subterranean marine biota belong to lineages otherwise restricted to the deep sea floor (M3), and share traits with those in other low-productivity, dark biomes, including depigmentation, reduced visual organs, increased tactile and chemical sensitivity, low fecundity, long lifespans, and slow metabolism and growth rates. Tides are an important means of hydrological mixing, resource flux, biotic dispersal and perturbation. In subterranean tidal systems with more direct connections to the sea, marine suspension feeders, particularly sponges and other sessile invertebrates, are dominant. Farther into marine and anchialine caves, where tidal flushing and water exchange diminishes or disappears, the fauna consists of stygobitic crustaceans, annelids and several other faunal groups (i.e. strictly subterranean aquatic fauna that complete their entire life in this environment).

SM1.1 Anchialine caves

BIOME: SM1 SUBTERRANEAN TIDAL SYSTEMS
REALM: TRANSITIONAL SUBTERRANEAN-MARINE

Contributors: T.M. Iliffe, D. Brankovits, V. Gerovasileiou, B. Gonzalez, A. Martínez, D.A. Keith

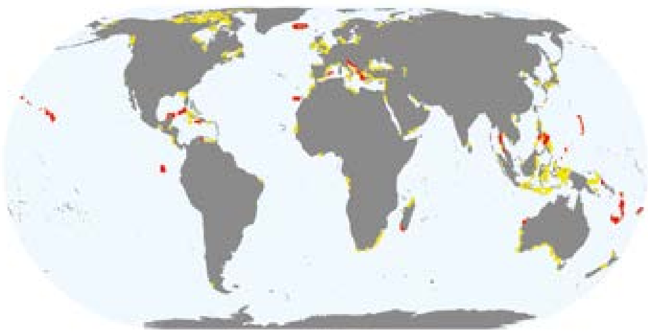
Deep Blue Cave, Bermuda.
Source: Tom Iliffe and Deron Long (2003)



ECOLOGICAL TRAITS: Anchialine caves contain bodies of saline or brackish waters with subterranean connections to the sea. Since virtually all anchialine biota are marine in origin, these caves have a larger and more diverse species pool than underground freshwaters. The trophic network is truncated and dominated by heterotrophs (scavenging and filter-feeding detritivores and their predators), with photosynthetic primary producers and herbivores only present where sinkholes connect caves to the surface and sunlight. Productivity is limited by the scarcity of light and food, but less so than in insular freshwater subterranean systems (SF1.1) due to influx of marine detritus and biota. The dominant fauna includes planktonic bacteria, protozoans, annelids, crustaceans and fish. Anchialine obligates that inhabit locations deep within the caves, with marine biota increasing in frequency with proximity to the sea. Caves closely connected with the ocean tend to have stronger tidal currents and biota, such as sponges and hydroids commonly associated with sea caves (SM1.3). Distinctive traits of cave obligates that reflect selection under darkness and food scarcity include varying degrees of eye loss and depigmentation, increased tactile and chemical sensitivity, reproduction with few large eggs, long lifespans, and slow metabolism and growth rates. Some anchialine biota are related to in deep sea species, including shrimps that retain red pigmentation, while others include relict taxa inhabiting anchialine caves on opposite sides of ocean basins. Characteristic anchialine taxa also occur in isolated water bodies, far within extensive seafloor cave systems.

KEY ECOLOGICAL DRIVERS: Anchialine caves originate from seawater penetration into faults, fractures, and lava tubes as well as sea-level rise into limestone caves formed by solution. Cave waters are characterised by an absence or scarcity of light, low food abundance and strong salinity gradients. Sharp haloclines, which fluctuate with tides and rainfall percolation, occur at deeper depths with increasing distance inland. Tidal connections result in suck and blow phases of water movement that diminish with increasing distance from the sea. In karst terrain with no surface runoff, anchialine caves are closely linked via hydrology to overlying subaerial coastal systems and can serve as subterranean rivers with haloclines separating seaward flowing freshwater from underlying saltwater. Temperatures are moderate, increasing at the halocline, then stabilise with depth. Dissolved oxygen declines with depth.

DISTRIBUTION: Scattered worldwide, mostly in the Northern Hemisphere in limestone, basalt flows, and more rarely other lithic substrates.



Reference:

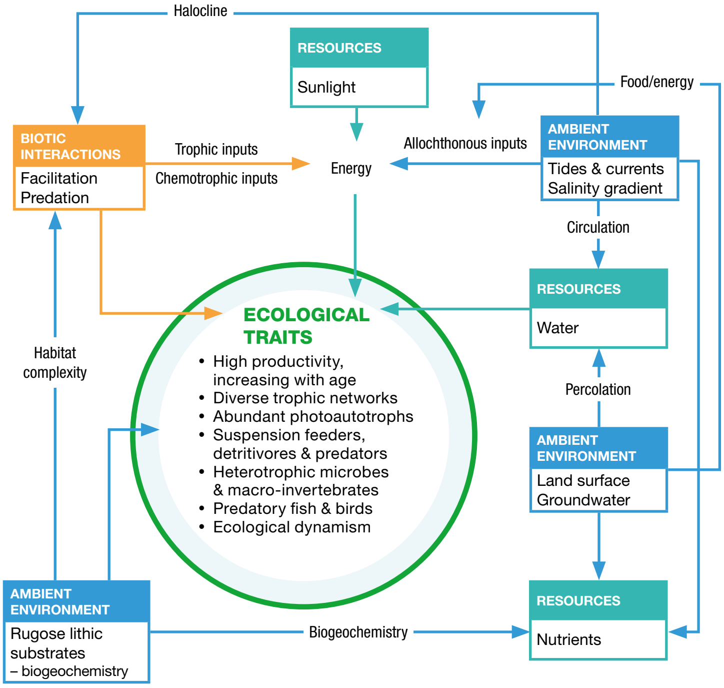
Iliffe, T.M. (2000). 'Ancialine cave ecology'. In: H. Wilkens, D.C. Culver, W.F. Humphreys (eds.), *Subterranean ecosystems. Ecosystems of the World. Vol. 30*, pp. 59–76. Amsterdam, The Netherlands: Elsevier.

SM1.2 Anchialine pools

BIOME: SM1 SUBTERRANEAN TIDAL SYSTEMS
REALM: TRANSITIONAL SUBTERRANEAN-MARINE

Contributors: T.S. Sakihara, M. Lamson, B. Seidel, D.M. Sedar, S. Santos, J. Havird, T.M. Iliffe, D.A. Keith

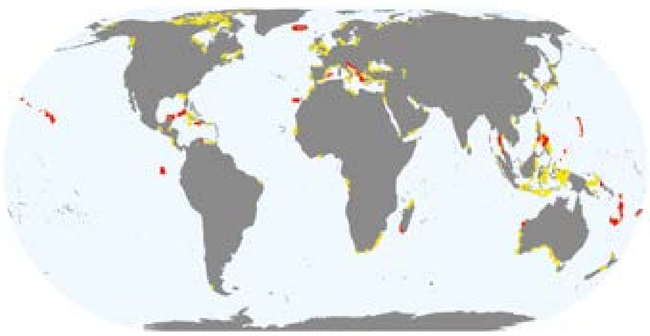
Anchialine pond with a subterranenan connection to the Pacific Ocean, Ahihi Kinau Natural Reserve, Maui, Hawaii, USA.
Source: Design Pics Inc/Alamy Stock Photo.



ECOLOGICAL TRAITS: Anchialine pools, like anchialine caves (SM1.1), are tidally influenced bodies of brackish water with subterranean connections to the sea and groundwater, but with significant or full exposure to open air and sunlight. They have no surface connection to the ocean or freshwater ecosystems. Younger anchialine pools are exposed to abundant sunlight, characterised by relatively low productivity, and tend to support only benthic microalgae, cyanobacteria and primary consumers. Older pools with more established biological communities have higher productivity with a wider range of autotrophs, including macroalgae, aquatic monocots, established riparian and canopy vegetation, and primary and secondary consumers. High productivity is attributed to a combination of sunlight exposure, rugose substrates and relatively high natural concentrations of inorganic nutrients from groundwater. Anchialine pools may support complex benthic microbial communities, primary consumers, filter-feeders, detritivores, scavengers and secondary consumers. These consumers are primarily molluscs and crustaceans, several of which are anchialine obligates. Due to connections with deeper hypogeal habitats, obligate species may display physical and physiological traits similar to anchialine cave species. However, larger predatory fish and birds also utilize anchialine pools for food and habitat. Anchialine pools are ecologically dynamic systems due to their openness, connections with surrounding terrestrial habitats and subterranean hydrologic connections. Consequently, they are inherently sensitive to ecological phase shifts throughout their relatively ephemeral existence, with senescence initiating in as little as 100 years. However, new anchialine pools may form within a few months after basaltic lava flows.

KEY ECOLOGICAL DRIVERS: Anchialine pools form from subterranean mixing of seawater and groundwater, primarily through porous basalt or limestone substrates, and more rarely other lithic substrates. Tidal influences can drive large fluctuations in water level and salinity on a daily cycle, but are typically dampened with increased distance from the ocean. Sunlight, UV exposure and other environmental characteristics vary within anchialine pools and haloclines are common. The pools can also be connected to anchialine cave systems (SM1.1) through tension fissures in basalt flows, and collapsed openings in lava tubes.

DISTRIBUTION: Scattered worldwide, mostly in the Northern Hemisphere. Many well- known examples occur in Hawaii, Palau and Indonesia, volcanic cracks or grietas in the Galapagos Islands, and open-air entrance pools of anchialine caves (e.g. cenotes in Mexico's Yucatan Peninsula and blue holes in the Bahamas).



References:

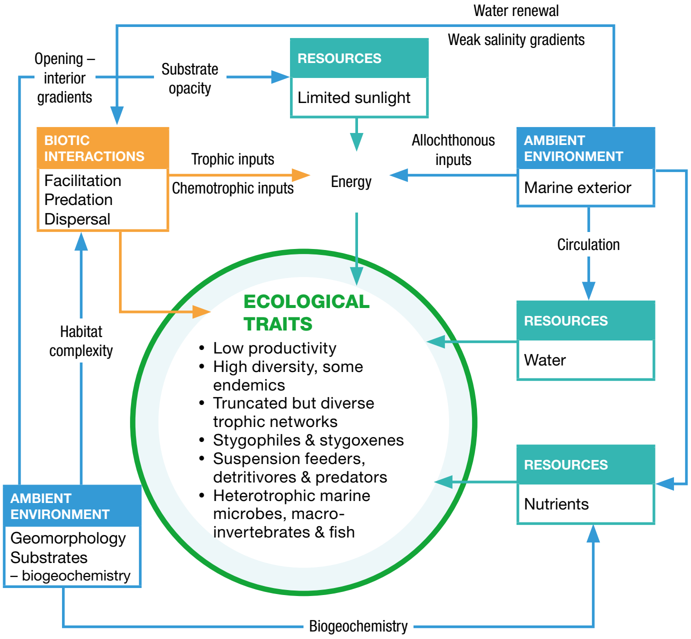
Becking, L.E., Renema, W., Santodomingo, N.K., Hoeksema, B.W., Tuti, Y. and de Voogd, N.J. (2011). 'Recently discovered landlocked basins in Indonesia reveal high habitat diversity in anchialine systems'. *Hydrobiologia* 677: 89–105.
Por, F.D. (1985). 'Anchialine pools—comparative hydrobiology'. In: G.M. Friedman, W.E. Krumbein (eds.), *Hypersaline Ecosystems. Ecological Studies (Analysis and Synthesis),* vol. 53, pp. 136–144. Berlin, Heidelberg, Germany: Springer.

SM1.3 Sea caves

BIOME: SM1 SUBTERRANEAN TIDAL SYSTEMS.
REALM: TRANSITIONAL SUBTERRANEAN-MARINE

Contributors: V. Gerovasileiou, T.M. Iliffe, B. Gonzalez,
D. Brankovits, A. Martínez, D.A. Keith

Sea cave on Aorangaia Island, New Zealand. Inset: Sponge assemblage on submerged semi-dark cave wall, Aegean Sea, Greece
Source: Pseudopanax. Inset: Vasilis Gerovasileiou (with permission)



ECOLOGICAL TRAITS: Sea caves (also known as marine or littoral caves) are usually formed by wave action abrasion in various rock types. In contrast to anchialine caves (SM1.1), sea caves are not isolated from the external marine environment. Thus, the biota in sea caves are mostly stygophiles (typical of dim-light cryptic and deep-water environments outside caves) or stygoxenes (species sheltering in caves during daytime but foraging outside at night). However, numerous taxa (mostly sessile invertebrates) have so far been reported only from sea caves, and thus can be considered as cave-exclusive *sensu lato*. Visitors often enter sea caves by chance (i.e. carried in by currents), and survive only for short periods. The diverse sea-cave biota is dominated by sessile (e.g. sponges, cnidarians, bryozoans) and mobile invertebrates (i.e. molluscs crustaceans, annelids) and fish. Photoautotrophs are restricted close to cave openings, while chemoautotrophic bacteria form extensive mats in sea caves with hydrothermal sulphur springs, similar to those in some terrestrial caves (SF1.1) and deep sea vents (M3.7). In semi-dark and dark cave sectors, the main trophic categories are filter-feeders (passive and active), detritivores, carnivores, and omnivores. Decomposers also play important roles. Filter-feeders consume plankton and suspended organic material delivered by tidal currents and waves. Other organisms either feed on organic material produced by filter-feeders or move outside caves in to find food. These “migrants”, especially swarm-forming crustaceans and schooling fish can be significant import pathways for organic matter, mitigating oligotrophy in confined cave sectors.

KEY ECOLOGICAL DRIVERS: Sea caves openings vary from fully submerged and never exposed to the atmosphere to partially submerged and exposed to waves and tides. Sea caves are generally shorter and receive less input of freshwater from terrestrial sources than anchialine caves (SM1.1). Sea caves thus lack haloclines, a defining feature of anchialine caves, and are influenced more strongly by marine waters and biota throughout their extent. While salinity gradients are weak, the decrease of light and sea water renewal from the opening to the cave interior drive marked zonation of biota by creating oligotrophic conditions and limiting larval supply. Submersion level, cave morphology and micro-topography play key roles in forming such gradients.

DISTRIBUTION: Globally distributed in coastal headlands, rocky reefs and in coral reefs.

References:
Cicogna, F., Bianchi, C.N., Ferrari, G., Forti, P. (2003). *Le grotte marine: cinquant’anni di ricerca in Italia* (Marine caves: 50 years of research in Italy). Rome, Italy: Ministero dell’Ambiente e della Tutela del Territorio.
Gerovasileiou, V., Martínez, A., Álvarez, F., Boxshall, G., Humphreys, W., Jaume, D., Becking, L., Muricy, G., van Hengstum, P., Dekeyzer, S. et al. (2016). ‘World Register of marine Cave Species (WoRCS): a new thematic species database for marine and anchialine cave biodiversity’. *Research Ideas and Outcomes* 2: e10451.
Riedl, R. (1966). *Biologie der Meereshöhlen: Topographie, Faunistik und Ökologie eines unterseeischen Lebensraumes. Eine Monographie* (Biology of seacaves: topography, fauna and ecology of an underwater habitat. A monograph). Hamburg and Berlin, Germany: Paul Parey.
Gerovasileiou ,V., Bianchi, C.N. (In press). ‘Mediterranean marine caves: a synthesis of current knowledge’. *Oceanography and Marine Biology: An Annual Review* 59.

TF1 Palustrine wetlands biome

Okavango Delta, Botswana.
Source: Richard Kingsford (with permission)

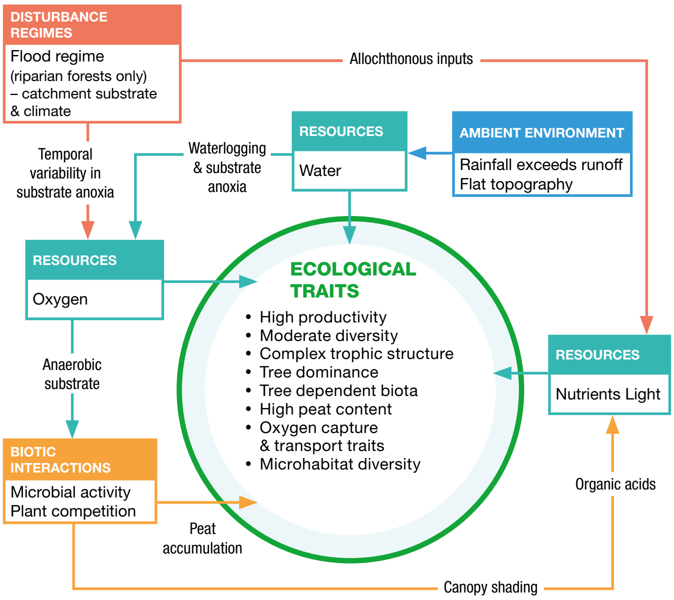
At the interface of terrestrial and freshwater realms, the Palustrine wetlands biome includes vegetated floodplains, groundwater seeps, and mires with permanent or intermittent surface water. Although water and light are abundant at least periodically, saturation of the soil may result in oxygen deprivation below the ground. This suppresses microbial activity and, in many systems, production exceeds decomposition, resulting in peat accumulation. The water regime influences resource availability and productivity and thus regulates these ecosystems from the bottom-up. Interactions among catchment precipitation, local evapotranspiration, and substrate and surface morphology regulate run-on, runoff, infiltration, and percolation. This results in water regimes that vary from permanent shallow standing water or near-surface water tables to seasonally high water tables to episodic inundation with long inter-annual dry phases. As a consequence of their indirect relationships with climate, wetland biomes are traditionally classified as ‘azonal’. Spatial heterogeneity is a key feature of palustrine wetlands. At landscape scales, they function as resource sinks and refuges with substantially higher productivity than the surrounding matrix. Fine-scale spatial variation in the water regime often produces restricted hydrological niches and intricate mosaics of patch types with contrasting structure and biotic composition. Autotrophs dominate complex trophic webs. Amphibious macrophytes are the dominant autotrophs, although epibenthic algae are important in some systems. Amphibious plants have specialised traits enabling growth and survival in low-oxygen substrates and often engineer habitats for heterotrophs. Microbial decomposers and invertebrate detritivores are most abundant in surface soils. A range of microscopic and macroinvertebrates with sedentary adult phases (i.e. crustaceans) have obligate associations with Palustrine wetlands, which also provide important foraging and breeding sites for macroinvertebrate and vertebrate herbivores and predators that disperse more widely across the landscape, including waterbirds.

TF1.1 Tropical flooded forests and peat forests

BIOME: TF1 PALUSTRINE WETLANDS
REALM: TRANSITIONAL FRESHWATER-TERRESTRIAL

Contributors: D.A. Keith, R.T. Kingsford, R. Mac Nally, K.M. Rodriguez-Clark, A. Etter

Left: White water riparian forest, Rio Carrao, Venezuela.
Source: David Keith (2012)
Right: Black water peat swamp forest, Gunung Mulu National Park, Sarawak, Malaysia.
Source: JeremiahsCPs (2007)



ECOLOGICAL TRAITS: Closed-canopy forests in tropical swamps and riparian zones have high biomass and LAI, with unseasonal growth and reproductive phenology. The canopy foliage is evergreen, varying in size from mesophyll to notophyll with moderate SLA. Productivity differs markedly between high-nutrient 'white water' riparian systems and low-nutrient 'black water' systems. In the latter, most of the nutrient capital is sequestered in plant biomass, litter, or peat, whereas in white water systems, soil nutrients are replenished continually by fluvial subsidies. Some trees have specialised traits conferring tolerance to low-oxygen substrates, such as surface root mats, pneumatophores and stilt roots. Palms (sometimes in pure stands), hydrophytes, pitcher plants, epiphytic mosses, and ferns may be abundant, but lianas and grasses are rare or absent. The recent origin of these forests has allowed limited time for evolutionary divergence from nearby lowland rainforests (T1.1), but strong filtering by saturated soils has resulted in low diversity and some endemism. The biota is spatially structured by local hydrological gradients. Riparian galleries of floodplain forests also occur within savanna matrices. Trophic networks are complex but with less diverse representation of vertebrate consumers and predators than T1.1, although avian frugivores, primates, amphibians, macroinvertebrates, and crocodilian predators are prominent. Plant propagules are dispersed mostly by surface water or vertebrates. Seed dormancy and seedbanks are rare. Gap-phase dynamics are driven by individual tree-fall, storm events, or floods in riparian forests, but many plants exhibit leaf-form plasticity and can recruit in the shade.

KEY ECOLOGICAL DRIVERS: High rainfall, overbank flows or high water tables maintain an abundant water supply. Continual soil profile saturation leads to anaerobic black water conditions and peat accumulation. In contrast, white water riparian zones undergo frequent fluvial disturbance and drain rapidly. Peat forests often develop behind lake shore vegetation or mangroves, which block lateral drainage. Black water peatlands may become domed, ombrogenous (i.e. rain-dependent), highly acidic, and nutrient-poor, with peat accumulating to depths of 20 m. In contrast, white water riparian forests are less permanently inundated and floods continually replenish nutrients, disturb vegetation, and rework sediments. Hummock-hollow micro-topography is characteristic of all forested wetlands and contributes to niche diversity. Light may be limited by dense tree canopies. There is low diurnal, intra- and inter-annual variability in rainfall and temperature, with the latter rarely <10°C, which promotes microbial activity when oxygen is available.

DISTRIBUTION: Flat equatorial lowlands of Southeast Asia, South America, and Central and West Africa, notably in Borneo and the Amazonian lowlands.

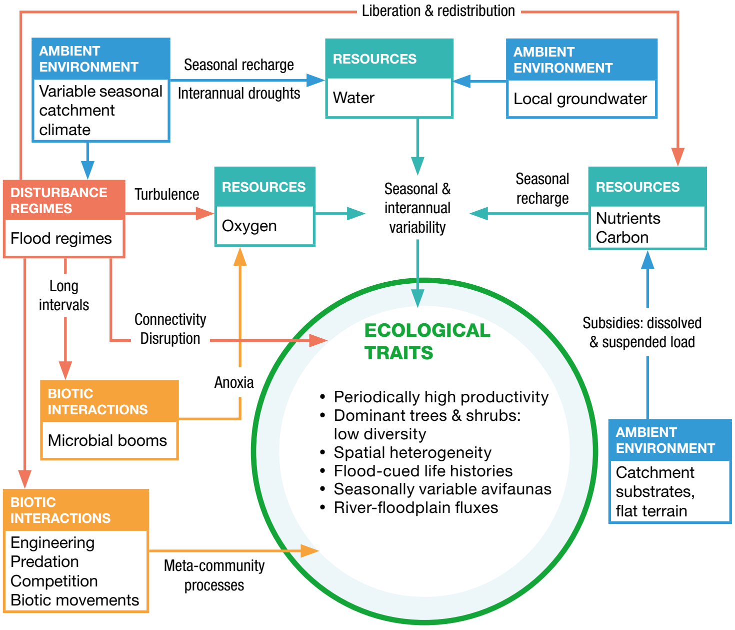
Reference:
Page, S.E., Rieley, J.O., Wüst, R. (2006). 'Lowland tropical peatlands of Southeast Asia'. In: I.P. Martini, A. Martínez Cortizas, W. Chesworth (eds.), *Peatlands: Evolution and Records of Environmental and Climate Changes*, pp. 145–172. Amsterdam, The Netherlands: Elsevier.

River Red Gum forest in flood, Campaspe River, Echuca, Australia.
Source: David Keith (2010)

TF1.2 Subtropical-temperate forested wetlands

BIOME: TF1 PALUSTRINE WETLANDS
REALM: TRANSITIONAL FRESHWATER-TERRESTRIAL

Contributors: R. Mac Nally, R.T. Kingsford, J.A. Catford, B.J. Robson, D.A. Keith



ECOLOGICAL TRAITS: These hydrophilic forests and thickets have an open to closed tree or shrub canopy, 2–40 m tall, dependent on flood regimes or groundwater lenses. Unlike tropical forests (TF1.1), they typically are dominated by one or very few woody species. Trees engineer fine-scale spatial heterogeneity in resource availability (water, nutrients, and light) and ecosystem structure, which affects the composition, form, and functional traits of understorey plants and fauna. Engineering processes include the alteration of sediments, (i.e. surface micro-topography by the growth of large roots), the deposition of leaf litter and woody debris, canopy shading, creation of desiccation refuges for fauna and the development of foraging or nesting substrates (i.e. tree hollows). Forest understories vary from diverse herbaceous assemblages to simple aquatic macrophyte communities in response to spatial and temporal hydrological gradients, which influence the density and relative abundance of algae, hydrophytes and dryland plants. Primary production varies seasonally and inter-annually and can be periodically high due to the mobilisation of nutrients on floodplains during inundation. Nutrients accumulate on floodplains during low flows, and may drive microbial blooms, leading to aquatic anoxia, and fish kills, which may be extensive when flushing occurs. Plant and animal life histories are closely connected to inundation (e.g. seed-fall, germination fish-spawning and bird breeding are stimulated by flooding). Inundation-phase aquatic food webs are moderately complex. Turtles, frogs, birds and sometimes fish exploit the alternation between aquatic and terrestrial phases. Waterbirds forage extensively on secondary production, stranded as floodplains recede, and breed in the canopies of trees or mid-storey. Forested wetlands are refuges for many vertebrates during droughts. Itinerant mammalian herbivores (e.g. deer and kangaroos) may have locally important impacts on vegetation structure and recruitment.

KEY ECOLOGICAL DRIVERS: These forests occur on floodplains, riparian corridors, and disconnected lowland flats. Seasonally and inter-annually variable water supply influences ecosystem dynamics. Allochthonous water and nutrient subsidies from upstream catchments supplement local resources and promote the extension of floodplain forests and their biota into arid regions ('green tongues'). Water movement is critical for the connectivity and movement of biota, while some groundwater-dependent forests are disconnected. High-energy floods in riparian corridors displace standing vegetation and woody debris, redistribute nutrients, and create opportunities for dispersal and recruitment. Low-energy environments with slow drainage promote peat accumulation. Extreme drying and heat events may generate episodes of tree dieback and mortality. Fires may occur depending on the frequency of fire weather, ignition sources, and landscape context.

DISTRIBUTION: Temperate and subtropical floodplains. riparian zones and lowland flats worldwide.

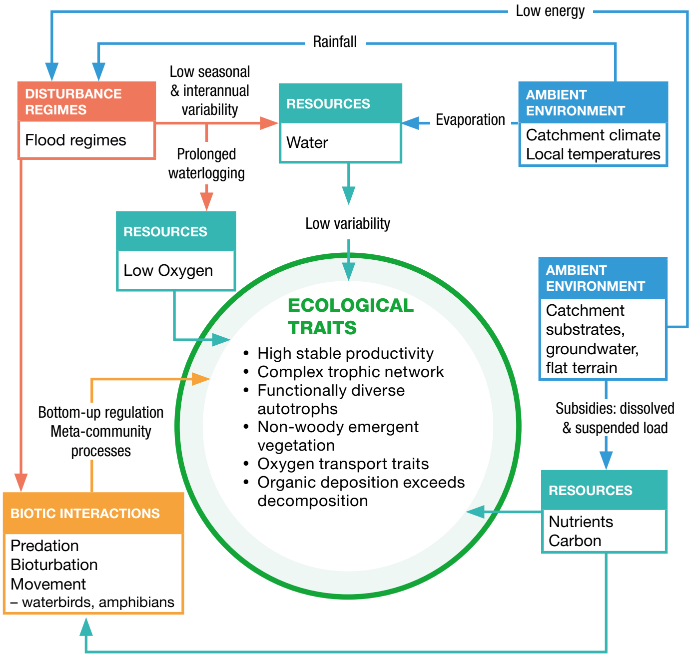
Reference:
Mac Nally, R., Cunningham, S.C., Baker, P.J., Horner, G.J., Thomson, J.R. (2011). 'Dynamics of Murray-Darling floodplain forests under multiple stressors: The past, present, and future of an Australian icon'. *Water Resources Research* 47(12): W00g05.

Everlasting Swamp, Clarence River floodplain, Australia.
Source: John Spencer/OEH

TF1.3 Permanent marshes

BIOME: TF1 PALUSTRINE WETLANDS
REALM: TRANSITIONAL FRESHWATER-TERRESTRIAL

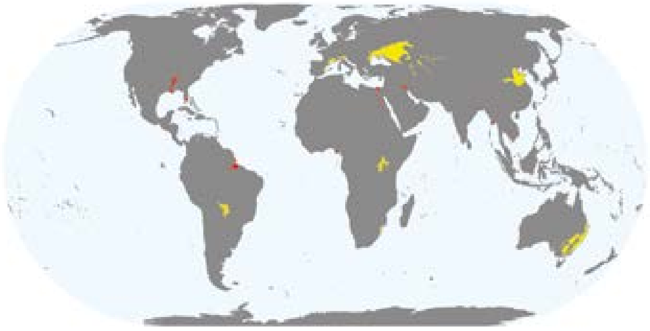
Contributors: R.T. Kingsford, J.A. Catford, M.C. Rains, B.J. Robson, D.A. Keith



ECOLOGICAL TRAITS: These shallow, permanently inundated freshwater wetlands lack woody vegetation but are dominated instead by emergent macrophytes growing in extensive, often monospecific groves of rhizomatous grasses, sedges, rushes, or reeds in mosaics with patches of open water. These plants, together with phytoplankton, algal mats, epiphytes, floating, and amphibious herbs, sustain high primary productivity and strong bottom-up regulation. Although most of the energy comes from these functionally diverse autotrophs, inflow and seepage from catchments may contribute allochthonous energy and nutrients. Plant traits, including aerenchymatous stems and leaf tissues (i.e. with air spaces), enable oxygen transport to roots and rhizomes and into the substrate. Invertebrate and microbial detritivores and decomposers inhabit the water column and substrate. Air-breathing invertebrates are more common than gill-breathers, due to low dissolved oxygen. The activity of microbial decomposers is also limited by low oxygen levels and organic deposition continually exceeds decomposition. Their aquatic predators include invertebrates, turtles, snakes and sometimes small fish. The emergent vegetation supports a complex trophic web, including insects with winged adult phases, waterbirds, reptiles, and mammals, which feed in the vegetation and also use it for nesting (e.g. herons, muskrat, and alligators). Waterbirds include herbivores, detritivores, and predators. Many plants and animals disperse widely beyond the marsh through the air, water and zoochory (e.g. birds, mammals). Reproduction and recruitment coincide with resource availability and may be cued to floods. Most macrophytes spread vegetatively with long rhizomes but also produce an abundance of wind- and water-dispersed seeds.

KEY ECOLOGICAL DRIVERS: These systems occur in several geomorphic settings, including lake shores, groundwater seeps, river floodplains and deltas, always in low-energy depositional environments. Shallow but perennial inundation and low variability are maintained by frequent floods and lake waters, sometimes independently of local climate. This sustains high levels of water and nutrients, but also generates substrate anoxia. Substrates are typically organic. Their texture varies, but silt and clay substrates are associated with high levels of P and N. Salinity is low but may be transitional where wetlands connect with brackish lagoons (FM1.2, FM1.3). Surface fires may burn vegetation in some permanent marshes, but rarely burn the saturated substrate, and are less pervasive drivers of these ecosystems than seasonal floodplain marshes (TF1.4).

DISTRIBUTION: Scattered throughout the tropical and temperate regions worldwide.



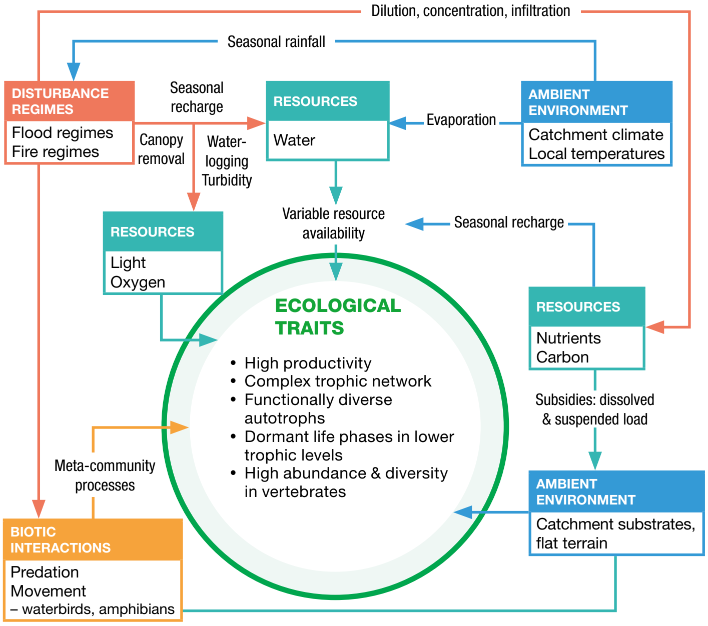
Reference:
Grace, J.B., Wetzel, R.G. (1981). 'Habitat Partitioning and Competitive Displacement in Cattails (Typha): Experimental Field Studies'. *The American Naturalist* 118(4): 463–474.

TF1.4 Seasonal floodplain marshes

BIOME: TF1 PALUSTRINE WETLANDS
REALM: TRANSITIONAL FRESHWATER-TERRESTRIAL

Contributors: D.A. Keith, R.T. Kingsford, R. Mac Nally, B.J. Robson, J.A. Catford, M.C. Rains, K. Irvine, K.M. Rodriguez-Clark, A. Etter

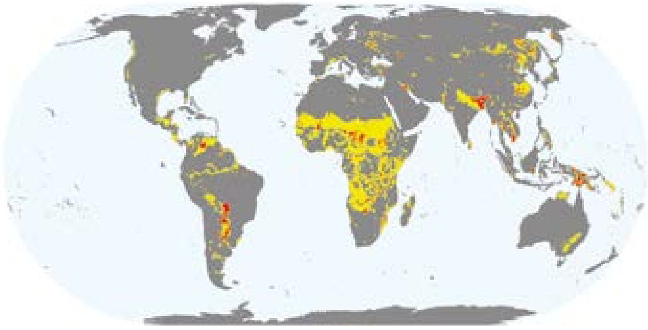
The Pantanal, Brazil.
Source: Richard Kingsford



ECOLOGICAL TRAITS: This group includes high-productivity floodplain wetlands fed regularly by large inputs of allochthonous resources that drive strong bottom-up regulation, and smaller areas of disconnected oligotrophic wetlands. Functionally diverse autotrophs include phytoplankton, algal mats and epiphytes, floating and amphibious herbs and graminoids, and semi-terrestrial woody plants. Interactions of fine-scale spatial gradients in anoxia and desiccation are related to differential flooding. These gradients shape ecosystem assembly by enabling species with diverse life-history traits to exploit different niches, resulting in strong local zonation of vegetation and high patch-level diversity of habitats for consumers. Wetland mosaics include very productive and often extensive grasses, sedges and forbs (sedges dominate oligotrophic systems) that persist through dry seasons largely as dormant seeds or subterranean organs as well as groves of woody perennials that are less tolerant of prolonged anoxia but access ground water or arrest growth during dry phases. Productive and functionally diverse autotrophs support complex trophic networks with zooplankton, aquatic invertebrates, fish, amphibians, reptiles, aquatic mammals, waterbirds, and terrestrial animals with diverse dietary and foraging strategies. During dry phases, obligate aquatic organisms are confined to wet refugia. Others, including many invertebrates, have dormancy traits allowing persistence during dry phases. Very high abundances and diversities of invertebrates, waterbirds, reptiles, and mammals exploit resource availability, particularly when prey are concentrated during drawdown phases of floods. Reproduction and recruitment, especially of fish, coincide with food availability cued by flood regimes.

KEY ECOLOGICAL DRIVERS: Regular seasonal flooding and drying is driven by river flow regimes, reflecting seasonal precipitation or melt patterns in catchments. Salinity gradients and tides influence these marshes where they adjoin estuaries, with brackish marshes on transitions to TF1.2, TF1.3 and MFT1.3. Disconnected oligotrophic systems rely on rainfall and low substrate permeability for seasonal waterlogging. Seasonal flood extent and duration vary inter-annually, especially in temperate zones. Geomorphic heterogeneity in the depositional floodplains promote spatial and temporal variability in moisture status, creating contrasting patches, including perennially inundated refuges and dry 'islands' that seldom flood and dry rapidly. Substrates are fertile alluvia or infertile white sands with variable grain sizes, moisture, and organic content that reflect fine-scale depositional patterns and hydrological gradients. Fires may occur in dry seasons, releasing resources, changing vegetation structure and composition, consuming organic substrates and lowering the wetland surface.

DISTRIBUTION: Throughout the seasonal tropics and subhumid temperate regions of the world.



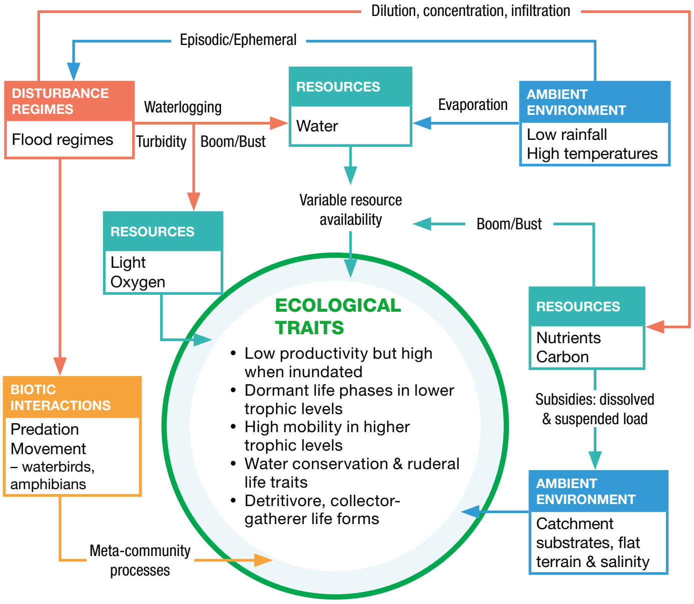
Reference:
Damasceno-Junior, G.A., Semir, J., Dos Santos, F.A.M., de Freitas Leitão-Filho, H. (2005). 'Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil'. *Flora-Morphology, Distribution, Functional Ecology of Plants* 200(2): 119–135.

TF1.5 Episodic arid floodplains

BIOME: TF1 PALUSTRINE WETLANDS
REALM: TRANSITIONAL FRESHWATER-TERRESTRIAL

Contributors: R.T. Kingsford, R. Mac Nally, A.H. Arthington, J.A. Catford, B.J. Robson, D.A. Keith

Episodic Eyre Creek arid floodplain, Queensland, Australia.
Source: Richard Kingsford (2004)



ECOLOGICAL TRAITS: Highly episodic freshwater floodplains are distinct from, but associated with, adjacent river channels, which provide water and sediment during flooding. These are low-productivity systems during long, dry periods (maybe years), with periodic spikes of very high productivity when first inundated. These floodplains have a high diversity of aquatic and terrestrial biota in complex trophic networks, with ruderal life-history traits enabling the exploitation of transient water and nutrient availability. Primary producers include flood-dependent macrophytes and algae with physiological traits for water conservation or drought avoidance. Lower trophic levels (e.g. algae, invertebrate consumers) avoid desiccation with traits, such as dormant life-cycle phases, deposition of resting eggs (e.g. crustaceans and rotifers) and burial in sediments banks (i.e. larvae of cyclopoid copepods). Higher trophic levels (e.g. fish, amphibians, reptiles and waterbirds) are highly mobile in large numbers or with resting strategies (i.e. burrowing frogs). These taxa can be important mobile links for the movement of biota and resources, but floods are the primary allochthonous sources of energy and nutrients. Floods are important triggers for life-history processes, such as seed germination, emergence from larval stages, dispersal and reproduction. Common lifeforms include detritus-feeding invertebrate collector-gatherers, indicating a reliance on heterotrophic energy pathways.

KEY ECOLOGICAL DRIVERS: Multi-year dry periods are punctuated by brief intervals of shallow inundation caused by the overspill from flooding river channels. These boom-bust systems have temporarily high productivity driven by water and partly by elevated levels of dissolved Carbon and nutrients (notably N and P) released from leaf litter, oxygen, and organic matter in newly inundated, shallow areas. High temperatures promote productivity and rapid drying in arid environments. Water may be turbid or clear, which affects light environments and may limit benthic algal production to the shallow littoral margins of small channels. This in turn affects aquatic food webs and Carbon dynamics. Drainage is predominantly horizontal and bidirectional (i.e. in and out of the river), but infiltration and evapotranspiration can be significant in the flat terrain and may influence salinity if there are sources of salt in the catchment or ground water.

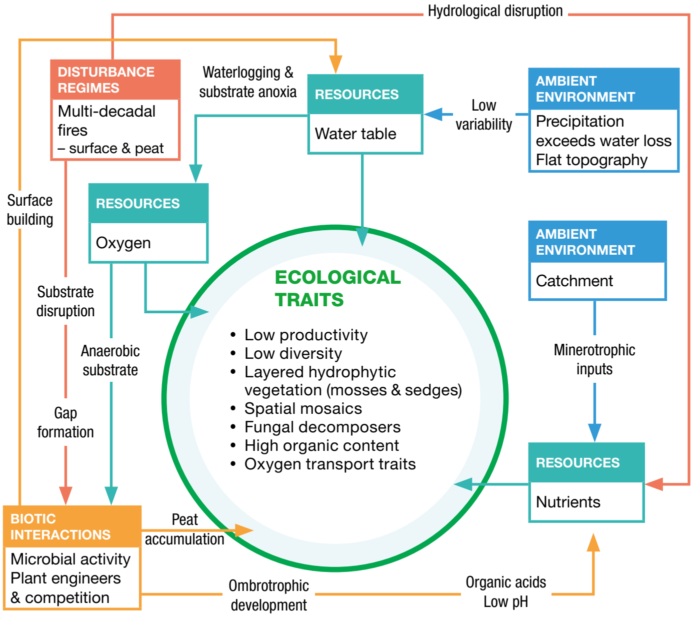
DISTRIBUTION: Connected to ephemeral rivers in semi-arid and arid regions of all continents.

Raised peat bog with Sphagnum, scattered trees and flark pools, Kemeri Bog, Latvia.
Source: David Keith (2019)

TF1.6 Boreal, temperate and montane peat bogs

BIOME: TF1 PALUSTRINE WETLANDS
REALM: TRANSITIONAL FRESHWATER-TERRESTRIAL

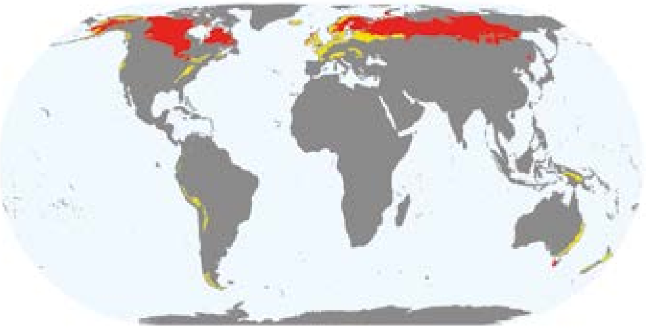
Contributors: D.A. Keith, R.T. Kingsford, F. Essl, L.J. Jackson, R.M. Kelly-Quinn, K.R. Young, T. Tahvanainen



ECOLOGICAL TRAITS: These patterned peatlands account for up to 40% of global soil carbon are dominated by a dense cover (high LAI) of hydrophytic mosses, graminoids, and shrubs, sometimes with scattered trees. Positive feedbacks between dense ground vegetation, hydrology, and substrate chemistry promote peat formation. through water retention and inhibition of microbial decomposition. Moderate to low primary production is partially broken down at the soil surface by anamorphic fungi and aerobic bacteria. Burial by overgrowth and saturation by the water table promotes anaerobic conditions, limiting subsurface microbial activity, while acidity, nutrient scarcity, and low temperatures enhance the excess of organic deposition over decomposition. Plant diversity is low but fine-scale hydrological gradients structure vegetation mosaics, which may include fens (TF1.7). Mosses (notably *Sphagnum spp*.) and graminoids with layering growth forms promote peat formation. Their relative abundance influences microbial communities and peat biochemistry. Plant traits, such as lacunate stem tissues, aerenchyma and surface root mats, promote oxygen transport into the anaerobic substrate. Woody plant foliage is small (leptophyll-microphyll) and sclerophyllous, reflecting excess carbohydrate production in low-nutrient conditions. Plants and fungi reproduce primarily by cloning, except where disturbances (i.e. fires) initiate gaps enabling recruitment. Pools within the bogs have specialised aquatic food webs underpinned by algal production and allochthonous carbon. Invertebrate larvae are prominent consumers in the trophic network of bog pools, and as adults they are important pollinators and predators. Assemblages of flies, dragonflies, damselflies, caddisflies and other invertebrates vary with the number, size and stability of pools. Carnivorous plants (i.e. sundews) support N cycling. Vertebrates are mostly itinerant but include specialised resident amphibians, reptiles, rodents, and birds. Some regions are rich in locally endemic flora and fauna, particularly in the Southern Hemisphere.

KEY ECOLOGICAL DRIVERS: Bogs are restricted to cool humid climates where moisture inputs (e.g. precipitation, seepage, and surface inflow) exceed outputs (e.g. evapotranspiration, percolation and runoff) for extended periods, enabling these systems to function as landscape sponges. Seasonally low temperatures and/or frequent cloud cover limit evapotranspiration. Substrates are waterlogged, anaerobic, highly organic (usually >30% dry weight), acidic (pH 3.5–6), and nutrient-poor. Peat growth may produce raised ombrotrophic bogs entirely fed by rain, but if minerotrophic inflows from catchments occur, they provide limited nutrient subsidies (cf. TF1.6). Fires may occur in dry summers, sometimes igniting peat with long-term consequences for ecosystem function and stability.

DISTRIBUTION: Extensive across boreal-subarctic latitudes, with small areas on tropical mountains of South America, New Guinea, and Central Africa and at cool, temperate southern latitudes in Patagonia and Australasia.



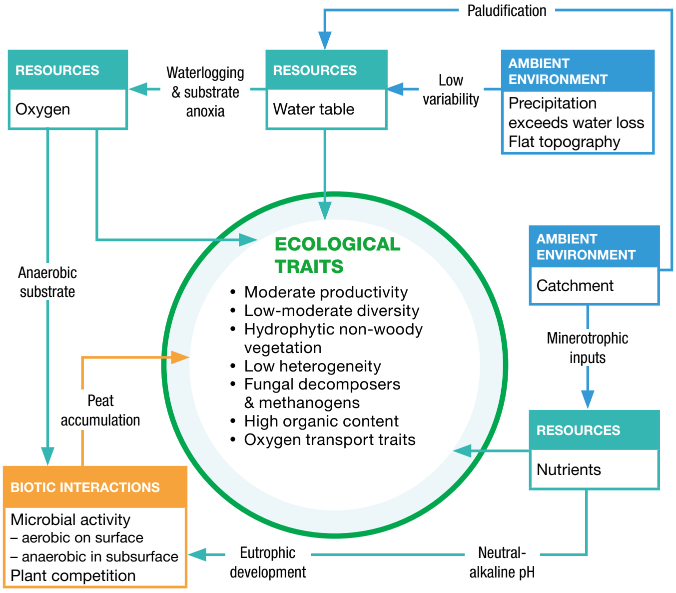
References:
Palozzi, J.E., Lindo, Z. (2017). 'Boreal peat properties link to plant functional traits of ecosystem engineers'. *Plant and Soil* 418: 277–291.
Wieder, R.K., Vitt, D.H. (eds.) (2006). 'Boreal Peatland Ecosystems'. *Ecological studies* 188. Berlin, Germany: Springer-Verlag.

TF1.7 Boreal and temperate fens

BIOME: TF1 PALUSTRINE WETLANDS
REALM: TRANSITIONAL FRESHWATER-TERRESTRIAL

Contributors: D.A. Keith, R.T. Kingsford, F. Essl, L.J. Jackson, M. Kelly-Quinn, K.R. Young, T. Tahvanainen

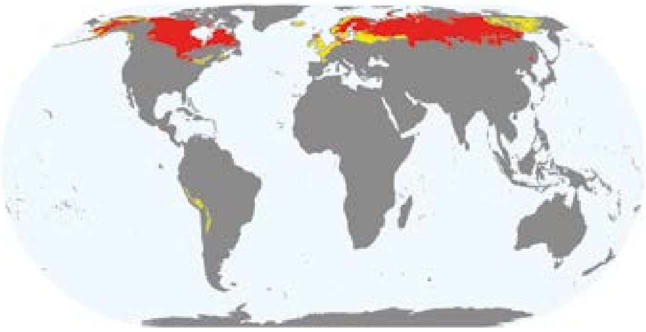
A mesotrophic flark fen within an aapa mire complex, Muonio, Finland.
Source: Hannu Nousiainen (with permission)



ECOLOGICAL TRAITS: Fens are peatland ecosystems dominated by hydrophytic grasses, sedges, or forbs. Fens have higher productivity but lower functional diversity than bogs (TF1.6). Productivity is subsidised by inflow of minerotrophic waters and limited by anoxic substrates. Plant diversity is very low where surface hydrology varies temporally from complete saturation to desiccation but can be high in mineral-rich fens with stable near-surface water tables. Some regions are rich in locally endemic flora and fauna. Woody plants are typically scarce or absent, though some boreal forests (T2.1) develop on minerotrophic peats. Sphagnum mosses and hummock-forming sedges are absent from rich fens but ‘brown mosses’ are common. Primary production is partly broken down on soil-surface layers by anamorphic fungi and aerobic bacteria. Anaerobic conditions due to high water tables limit subsurface microbial activity so that organic deposition exceeds decomposition and peat accumulates. Plant traits, such as lacunate stem tissues, aerenchyma and surface root mats, promote oxygen transport into the anaerobic substrate. Methanogenic archaea and anaerobic bacteria may occur in the subsoil if N, Fe and S are sufficient to sustain them. Fens may be spatially homogeneous or form string mosaics with bogs (i.e. aapa mires of Finland) but often display zonation reflecting differences in water chemistry (notably pH) or saturation. Patches of fen and bogs may be juxtaposed within peatland mosaics. Ongoing peat build-up may lead to transition from fen to bog systems. Plants and fungi reproduce locally by cloning, but seed and spore production enables dispersal and the colonisation of new sites. Invertebrates are dominant consumers in the trophic network, including dragonflies, caddisflies, flies, as well as calcareous specialists such as snails. Vertebrates are mostly itinerant but include specialised resident amphibians and birds.

KEY ECOLOGICAL DRIVERS: Moisture inputs (e.g. precipitation, seepage, and surface inflow) exceed outputs (e.g. evapotranspiration, percolation and runoff) for extended periods, enabling these systems to function as landscape sponges. Seasonally low temperatures and/or frequent cloud cover limit evapotranspiration. Fens typically develop through the paludification (i.e. peat accumulation) of shallow lakes or around springs, and thus shallow standing water is present frequently as flark pools. Such lakes may be abundant in post-glacial landscapes. Substrates are waterlogged, anaerobic, highly organic (usually >30% dry weight), slightly acidic or alkaline, and rich in mineral nutrients. Minerotrophic water (i.e. inflow from catchments) provides significant nutrient subsidies that vary with catchment geology. Fens on the Arctic Circle (palsa mires) have subsurface permafrost. Fires may occur in dry summers, rarely consuming peat, lowering the surface and degrading permafrost.

DISTRIBUTION: Extensive across boreal-subarctic latitudes and cool temperate regions, especially mountains. Very restricted in the Southern Hemisphere. Fens may also occur in tropical mountains (i.e. Andes), but are poorly known there.



References:
Godwin, K.S., Shallenberger, J.P., Leopold, D.J., Bedford, B.L. (2002). ‘Linking landscape properties to local hydrogeologic gradients and plant species occurrence in New York fens: A hydrogeologic setting (HGS) framework’. *Wetlands* 22(4): 722–737.
Wieder, R.K., Vitt, D.H. (eds.) (2006). ‘Boreal Peatland Ecosystems’. *Ecological studies* 188. Berlin, Germany: Springer-Verlag.

F1 Rivers and streams biome

Zambezi River, Zimbabwe.
Source: Richard Kingsford (2019)

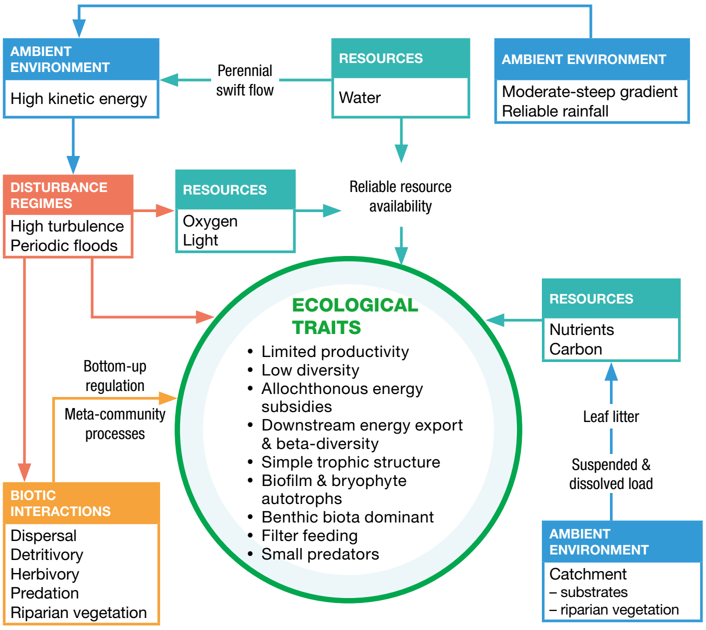
Rivers and streams include lotic (running water) ecosystems, flowing from elevated uplands or underground springs to deltas, estuaries, and lakes. They are defined primarily by their linear structure, unidirectional flow regimes, and close interaction with the surrounding landscape. Individual rivers drain catchments separated by watersheds. Channels that make up a river system can be classified into stream orders, with 1st order streams having no tributaries, 2nd order streams having 1st order tributaries, 3rd order having 2nd order tributaries and so on. The world's largest rivers are 10th-12th order. Flow regimes depend on stream order and rainfall patterns in the catchment (except in regulated rivers and spring-fed streams), which vary from year-round to seasonal to episodic. Stream gradients determine flow velocity and turbulence, bank and substrate structure, and habitat variability, but flow variability depends on regional climate and local weather. River systems in arid zones may remain dry for several years. These factors act as selection filters, differentiating lotic ecosystems and their species' traits amongst flow regimes, and between uplands and lowlands. Productivity tends to increase from uplands to lowlands and is driven both by allochthonous energy sources that contribute coarse organic matter from terrestrial ecosystems in adjacent riparian zones and upper catchments, and by autochthonous energy synthesis by biofilms or phytoplankton. Phytoplankton is important downstream in larger, slower rivers that carry smaller organic particles and more dissolved organic matter. Erosion and depositional processes depend on the gradient and position of a stream reach within a catchment, and are fundamental to downstream passage of nutrients and organic matter and exchange between river ecosystems and surrounding land. Anthropogenic nutrient inputs increase downstream and vary with land use. Rivers with extensive peatlands in their catchments are rich in tannins, which reduce light penetration through the water column, increase acidity, promote microbial activity that thrives on dissolved organic carbon, and thereby reduce oxygen levels, productivity and biotic diversity, although endemism may be high. Streams in cold climates freeze over in winter, imposing seasonal constraints on productivity and the movement of organisms. Much of the biotic diversity resides in or on the stream benthos. Trophic webs are more complex in large rivers due to greater resource availability and niche diversity, and species-catchment area relationships. Invertebrate detritivores consume fragments of organic matter, providing resources for predatory macroinvertebrates and fish, which in turn support larger predatory fish, waterbirds, reptiles, and some mammals. Specialised species-level traits are associated with different flow regimes and life history strategies often align with patterns of resource availability. For example, suspension feeding is common in high flow velocities, cold tolerance and seasonal dormancy occur in freeze-thaw streams, life cycles are geared to autumnal leaf fall in temperate forested catchments, and desiccation tolerance and dormant life stages dominate in episodic rivers.

F1.1 Permanent upland streams

BIOME: F1 RIVERS AND STREAMS
REALM: FRESHWATER

Contributors: R.T. Kingsford, R. Mac Nally, P.S. Giller, M.C. Rains, M. Kelly-Quinn, A.H. Arthington, D.A. Keith

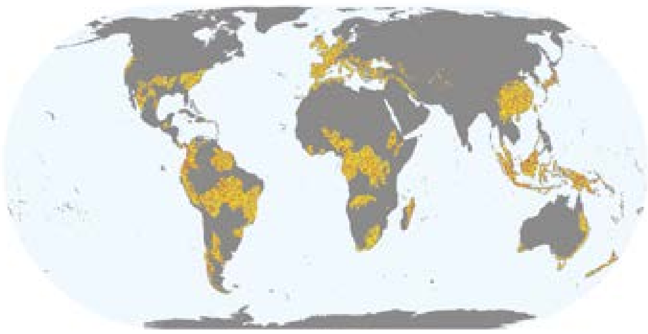
Appalachian Mountain stream, USA.
Source: Samuel H Austin, Virginia Water Science Center



ECOLOGICAL TRAITS: These 1st-3rd order streams generally have steep gradients, fast flows, coarse substrates, often with a riffle-pool (shallow and fast vs deeper and slow) sequence of habitats, and periodic (usually seasonal) high-flow events. Many organisms have specialised morphological and behavioural adaptations to high flow-velocity environments. Riparian trees produce copious leaf fall that provide allochthonous subsidies and support somewhat separate foodwebs to those based on in situ primary production by bryophytes and biofilms. Tree shade conversely light-limits productivity, a trade-off that relaxes seasonally where deciduous trees dominate. Microbes and detritivores (i.e. invertebrate shredders) break down leaf fall and other organic matter. Microbial biofilms comprising algae, fungi and bacteria establish on rocks and process dissolved organic matter. Invertebrates include shredders (consuming coarse particles), grazers (consuming biofilm), collectors and filter feeders (consuming benthic and suspended fine particles, respectively) and predators. Many benthic macroinvertebrates, mostly insects, have aquatic larvae and terrestrial adults. Filter feeders have traits adapted to swift flows, allowing them to hold fast to substrates while capturing resources, while benthic bryophytes provide shelter for other organisms. Fish are typically small predators of aquatic invertebrates and insects on the water surface. Birds typically have specialised foraging behaviours (e.g. dippers and kingfishers). Trophic cascades involving rapid algal growth, invertebrate grazers and fish are common.

KEY ECOLOGICAL DRIVERS: Upland streams have flash flow regimes with high velocity and relatively low, but variable perennial volume. Turbulence sustains highly oxygenation. Groundwater-delivered subsidies support streamflow, with up to 50% of summer flow and 100% of winter flow originating as groundwater. This modulates stream temperatures, keeping temperatures lower in summer and higher in winter; and deliver nutrients, especially if there are N-fixing plants along the groundwater flow path. They flow down moderate to steep slopes causing considerable erosion and sediment transport. These factors drive nutrient and organic matter transport downstream. Flow volume and variability, including periodic flood regimes, depend on rainfall seasonality, snowmelt from cold-climate catchments, as well as catchment size. Peat-rich catchments feed dark dystrophic waters to the streams.

DISTRIBUTION: High proportion of global stream length. In steep to moderate terrain throughout the humid tropical and temperate zones, rarely extending to boreal latitudes.



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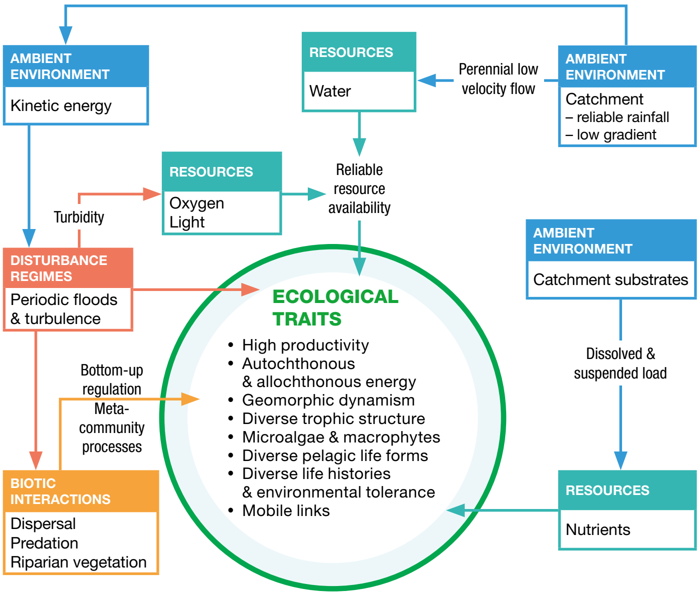
Giller, P.S. and Malmqvist, B. (1998). *The Biology of Streams and Rivers.* Oxford, UK: Oxford University Press.
Meyer, J.L., Wallace, J.B. (2001). 'Lost linkages and lotic ecology: Rediscovering small streams'. In: M.C. Press, N.J. Huntly, S. Levin (eds.), *Ecology: Achievement and Challenge*, pp. 295–317. Oxford, UK: Blackwell Scientific.
Meyer, J.L., Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S., Leonard, N.E. (2007). 'The Contribution of Headwater Streams to Biodiversity in River Networks'. *Journal of the American Water Resources Association* 43(1): 86–103.

F1.2 Permanent lowland rivers

BIOME: F1 RIVERS AND STREAMS
REALM: FRESHWATER

Contributors: R.T. Kingsford, R. Mac Nally, P.S. Giller, M.C. Rains, A.H. Arthington, D.A. Keith

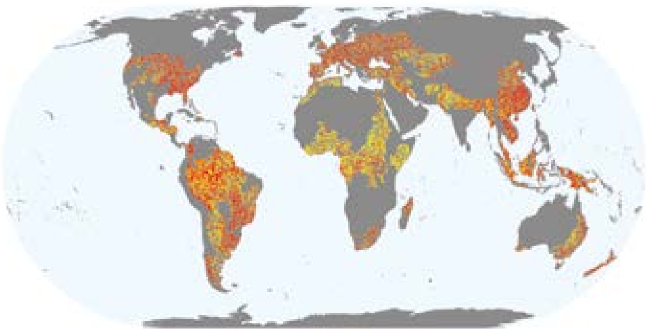
Rio Carrao, Venezuela.
Source: David Keith (2012)



ECOLOGICAL TRAITS: Small-medium lowland rivers (stream orders 4-9) are productive depositional ecosystems with trophic webs that are less diverse than large lowland rivers (F1.7). Macrophytes rooted in benthos or along the river margins contribute most primary production, but allochthonous inputs from floodplains and upper catchments generally dominate energy flow in the system. The biota tolerates a range of temperatures, which vary with catchment climate. Aquatic biota have physiological, morphological and even behavioural adaptations to lower oxygen concentrations, which may vary seasonally and diurnally. Zooplankton can be abundant in slower deeper rivers. Sessile (i.e. mussels) and scavenging (i.e. crayfish) macroinvertebrates are associated with the hyporheic zone and structurally complex microhabitats in moderate flow environments, including fine sediment and woody debris. Fish communities are diverse and may contribute to complex trophic networks. They include large predatory fish (i.e. sturgeons), smaller predators of invertebrates, herbivores, and detritivores. The feeding activities and movement of piscivorous birds (i.e. cormorants), diadromous fish (seawater-freshwater migrants), mammals (i.e. otters), and reptiles (i.e. turtles) extend trophic network beyond instream waters. Riparian zones vary in complexity from forested banks to shallow areas where emergent, floating and submerged macrophyte vegetation grows. Intermittently connected oxbow lakes or billabongs increase the complexity of associated habitats, providing more lentic waters for a range of aquatic fauna and flora.

KEY ECOLOGICAL DRIVERS: These rivers are distinguished by shallow gradients, low turbulence, low to moderate flow velocity and moderate flow volumes (<10,000m3/s). Flows are continuous but may vary seasonally depending on catchment precipitation. This combination of features is most common at low altitudes below 200 m and rarely occurs above 1,500 m. River channels are tens to a few hundred metres wide and up to tens of metres deep with mostly soft sediment substrates. They are dominated by depositional processes. Surface water and groundwater mix in the alluvium in the hyporheic zone, which plays an important role in nutrient cycling. Overbank flows increase turbulence and turbidity. Locally or temporally important erosional processes redistribute sediment and produce geomorphically dynamic depositional features (e.g. braided channels and point bars). Nutrient levels depend on riparian/floodplain inputs and vary with catchment geochemistry. Oxygen and temperatures also vary with climate and catchment features. For catchments with extensive peatlands, waters may be tannin-rich, poorly oxygenated, acidic and dark, thus reducing productivity and diversity.

DISTRIBUTION: Distributed throughout tropical and temperate lowlands but very uncommon in arid zones. They are absent from boreal zones, where they are replaced by F1.3.



Reference:

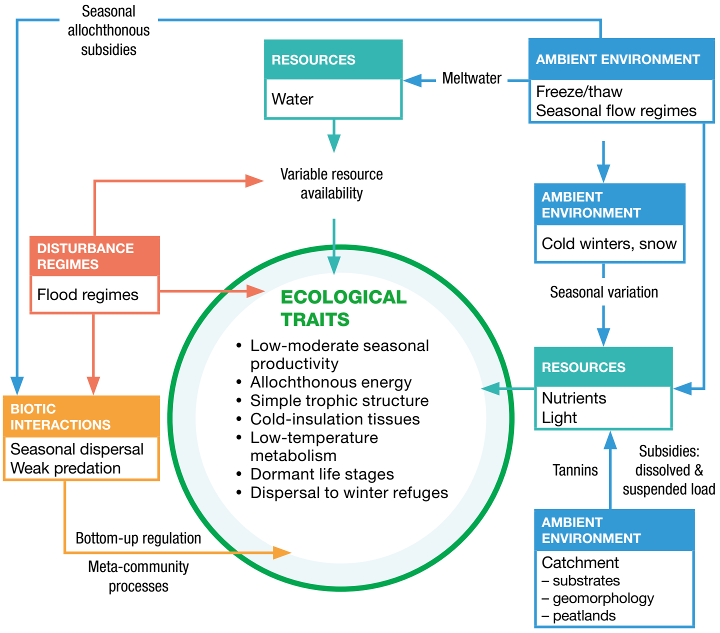
Tockner, K., Malard, F., Ward J.V. (2000). 'An extension of the flood pulse concept'. *Hydrological Processes* 14(16–17): 2861–2883.

F1.3 Freeze-thaw rivers and streams

BIOME: F1 RIVERS AND STREAMS
REALM: FRESHWATER

Contributors: R.T. Kingsford, P.S. Giller, D.A. Keith

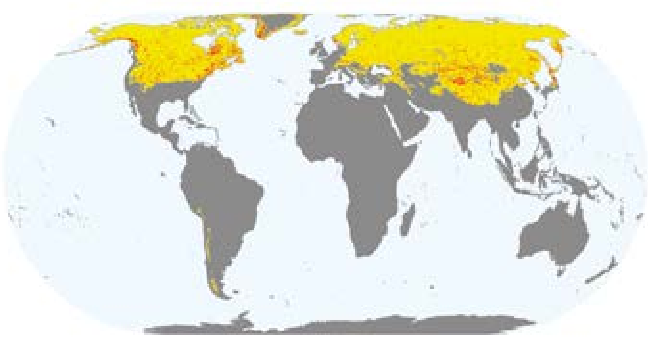
Zanskar River, 3,500 m above sea level, frozen in winter, near Leh, India
Source: Nitin Gupta on Unsplash



ECOLOGICAL TRAITS: In seasonally cold montane and boreal environments, the surfaces of both small streams and large rivers freeze in winter. These systems have relatively simple trophic networks with low functional and taxonomic diversity, but the biota may include local endemics. In small, shallow streams, substrate algae are the principal autotrophs, while phytoplankton occur in larger rivers and benthic macrophytes are rare. All are seasonally inactive or curtailed when temperatures are cold and surface ice reduces light penetration through the water. Bottom-up regulatory processes dominate, subsidies of dissolved organic carbon and nutrients from spring meltwaters and riparian vegetation along smaller streams are crucial to maintaining the detritivores that dominate the trophic network. Overall decomposition rates of coarse particles are low, but can exceed rates per degree day in warmer climates as the fauna are adapted to cold temperatures. Microbial decomposers often dominate small streams, but in larger rivers, the massive increase in fine organic particles in spring meltwaters can support abundant filter feeders which consume huge quantities of suspended particles and redeposit them within the river bed. Resident invertebrates survive cold temperatures, through dormant life stages extended life cycles and physiological adaptations. Vertebrate habitat specialists (e.g. dippers, small fish, beavers and otters) tolerate low temperatures with traits, such as subcuticular fat, thick hydrophobic and/or aerated fur or feathers. Many fish disperse from frozen habitat to deeper water refuges during the winter (i.e. deep pools) before foraging in the meltwater streams from spring to autumn. In the larger rivers, fish, and particularly migratory salmonids returning to their natal streams and rivers for breeding, Fish are a food source for itinerant terrestrial predators such as bears. When they die after reproduction, their decomposition in turn provides huge inputs of energy and nutrients to the system.

KEY ECOLOGICAL DRIVERS: These rivers experience low winter temperatures and seasonal freeze-thaw regimes. Winter freezing is generally limited to the surface but can extend to the substrate forming ‘anchor ice’. Flows may continue below the ice or may be intermittent in smaller streams or dry climates. Freezing reduces resource availability by reducing nutrient inputs, allochthonous organic matter and light penetration through the water. Light may also be attenuated at high latitudes and by high turbidity in erosional streams. Meltwaters drive increased flow and flooding in spring and summer. Carbon and nutrient concentrations are greatest during spring floods, and pH tends to decrease with flow during spring and autumn. When catchments include extensive peatlands, waters may be tannin-rich, acidic and dark, thereby reducing light penetration and productivity.

DISTRIBUTION: Restricted to boreal, subarctic, alpine and subalpine regions, with limited examples in the subantarctic and Antarctic.



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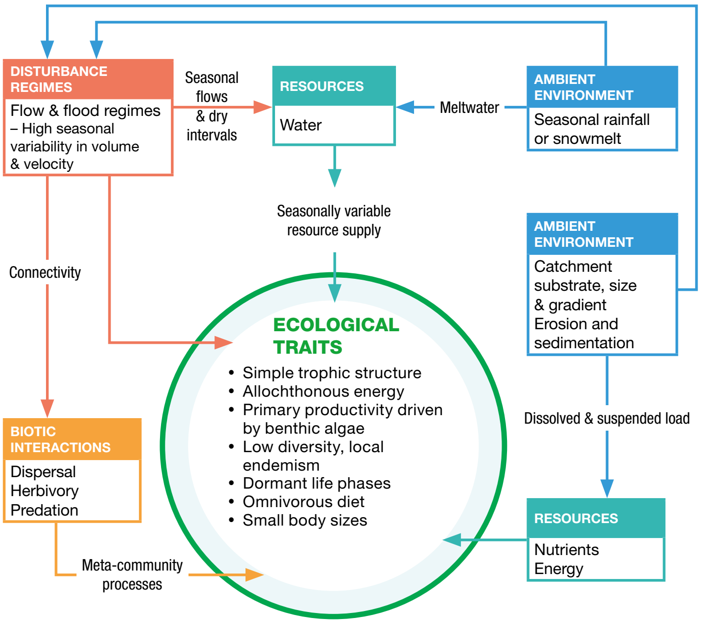
Guo, L.D., Cai, Y.H., Belzile, C., Macdonald, R.W. (2012). ‘Sources and export fluxes of inorganic and organic carbon and nutrient species from the seasonally ice-covered Yukon River’. *Biogeochemistry* 107(1/3): 187–206.
Olsson, T.I. (1981). ‘Overwintering of benthic macroinvertebrates in ice and frozen sediment in a North Swedish river’. *Holarctic Ecography* 4(3): 161–166.

Yamuna River near Mussoorie, India.
Source: Raanation (2016)

F1.4 Seasonal upland streams

BIOME: F1 RIVERS AND STREAMS
REALM: FRESHWATER

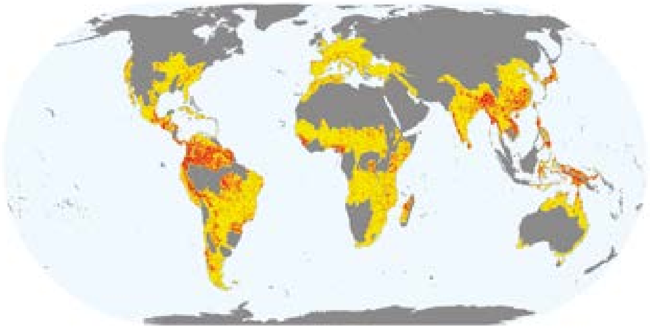
Contributors: R.T. Kingsford, B.J. Robson, P.S. Giller, A.H. Arthington, M. Kelly-Quinn, D.A. Keith



ECOLOGICAL TRAITS: Upland streams (orders 1-4) with highly seasonal flows generally have low to moderate productivity and a simpler trophic structure than lowland rivers. They tend to be shallow, hence benthic algae are major contributors to in-stream food webs and productivity, but riparian zones and catchments both contribute allochthonous energy and organic carbon through leaf fall, which may include an annual deciduous component. Primary production also varies with light availability and flow. Taxonomic diversity varies between streams, but can be lower than permanent streams and relatively high in endemism. Traits that enable biota to persist in narrow and shallow channels with large seasonal variations in flow velocity, episodes of torrential flow, and seasonal desiccation include small body sizes (especially in resident fish), dormant life phases and/or burrowing (crustaceans), omnivorous diets and high dispersal ability, including seasonal migration. Compared to lowland rivers, the trophic structure has a higher representation of algal and omnivorous feeders and low numbers of larger predators. Birds show specialist feeding strategies (i.e. dippers). Diversity and abundance of invertebrates and their predators (i.e. birds) fluctuate in response to seasonal flood regimes.

KEY ECOLOGICAL DRIVERS: Flow and flood regimes in these rivers are highly variable between marked wet and dry seasons, with associated changes in water quality as solute concentration varies with volume. They may be perennial, with flows much-reduced in the dry season, or seasonally intermittent with flows ceasing and water persisting in isolated stagnant pools. Channels are narrow with steep to moderate gradients and seasonally high velocity and sometimes large volumes of water, producing overbank flows. This results in considerable turbulence, turbidity, and erosion during the wet season and coarse substrates (cobbles and boulders). Seasonal floods are critical to allochtonous subsidies and downstream exports of organic matter and nutrients.

DISTRIBUTION: Elevated regions in seasonal tropical, subtropical and temperate climates worldwide.



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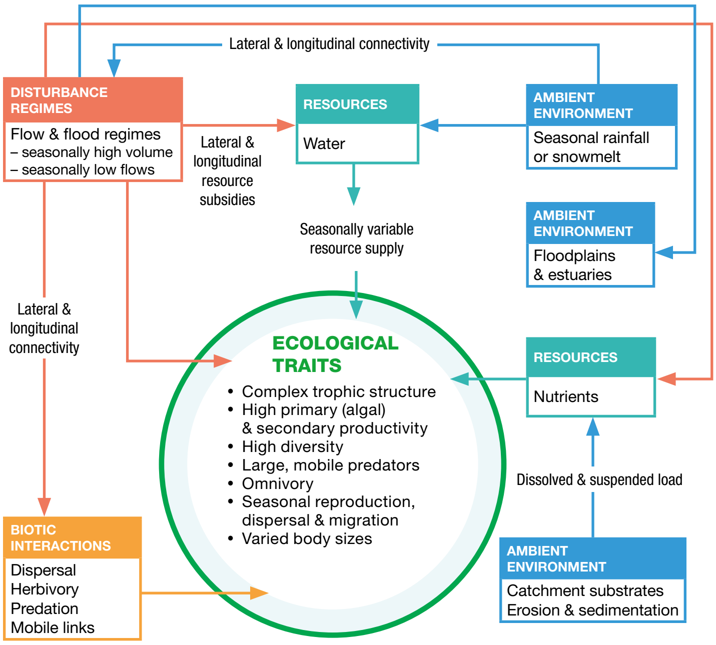
Datry, T., Bonada, N., Boulton, A. (eds.) (2017). *Intermittent Rivers and Ephemeral Streams. Ecology and Management.* Burlington, UK: Academic Press.
de Carvalho, R.A., Tejerina-Garro, F.L. (2018). 'Headwater-river gradient: trait-based approaches show functional dissimilarities among tropical fish assemblages'. *Marine and Freshwater Research* 69: 574–584.
Jardine, R.D., Bond, N.R., Burford, M.A., Kennard, M.J., Ward, D.P., Bayliss, P., Davies, P.M., Douglas, M.M., Hamilton, S.K., Melack, J.M. et al. (2015). 'Does flood rhythm drive ecosystem responses in tropical riverscapes?'. *Ecology* 96(3): 684–692.

F1.5 Seasonal lowland rivers

BIOME: F1 RIVERS AND STREAMS
REALM: FRESHWATER

Contributors: R.T. Kingsford, B.J. Robson, P.S. Giller, A.H. Arthington, D.A. Keith

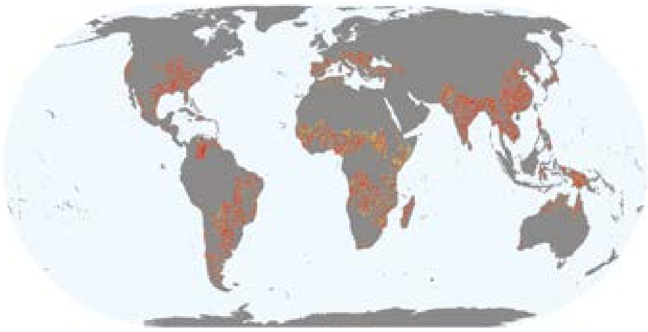
Patalon Chaung, upstream of Migyaungpon, Myanmar.
Source: David Keith (2018)



ECOLOGICAL TRAITS: These large riverine systems (stream orders 5–9) can be highly productive with trophic structures and processes shaped by seasonal hydrology and linkages to floodplain wetlands. In combination with biophysical heterogeneity, this temporal variability promotes functional diversity in the biota. Although trophic networks are complex due to the diversity of food sources and the extent of omnivory amongst consumers, food chains tend to be short and large mobile predator,s such as otters, large piscivorous waterbirds, sharks, dolphins and crocodilians (in the tropics), can have a major impact on the food webs. Benthic algae are key contributors to primary productivity, although macrophytes become more important during the peak and late wet season when they also provide substrate for epiphytic algae. Rivers receive very significant resource subsidies from both algae and macrophytes on adjacent floodplains when they are connected by flows. Enhanced longitudinal hydrological connectivity during the wet season enables fish and other large aquatic consumers to function as mobile links, extending floodplain and estuarine resource subsidies upstream. Life cycle processess, including reproduction, recruitment and dispersal in most biota, are tightly cued to seasonally high flow periods, often with floodplain nursery areas for river fish, amphibians and larger invertebrates.

KEY ECOLOGICAL DRIVERS: These rivers are driven by cyclical, seasonal flow regimes. High-volume flows and floods occur during summer in the tropics or winter-spring at temperate latitudes, with two peaks in some areas. A decline of flows and reduced flood residence times during the transition to the dry season is followed by low and disconnected flows during the dry season. Turbidity, light availability, erosion, sedimentation, lateral and longitudinal connectivity, biological activity, dissolved oxygen and solute concentrations all vary with this seasonal cycle. The inter-annual variability of this pattern depends on the catchment precipitation and sources of inflow that offset or mute the influences of rainfall seasonality (i.e. snow melt in South Asia). Streams may be single, multi-channelled or complex anabranching systems.

DISTRIBUTION: Tropical, subtropical and temperate lowlands with seasonal inflow patterns worldwide.



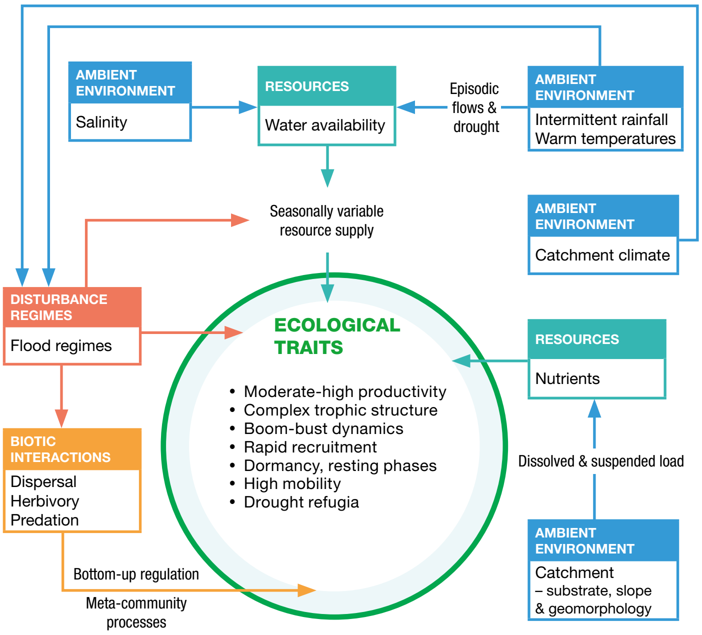
References:
Datry, T., Bonada, N., Boulton, A. (eds.) (2017). *Intermittent Rivers and Ephemeral Streams. Ecology and Management*. Burlington, UK: Academic Press.
Douglas, M.M., Bunn, S.E., Davies, P.M. (2005). 'River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management'. *Marine and Freshwater Research* 56(3): 329–342.

Cooper Creek in central Australia.
Source: Richard Kingsford (2015)

F1.6 Episodic arid rivers

BIOME: F1 RIVERS AND STREAMS
REALM: FRESHWATER

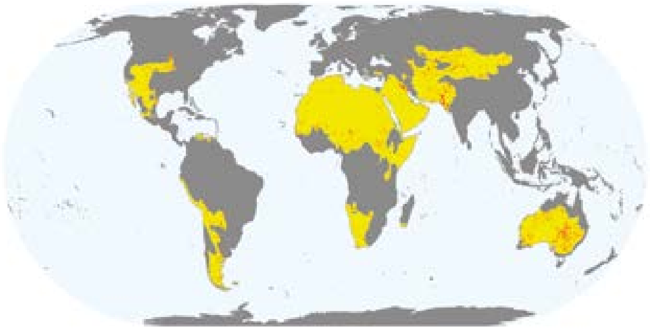
Contributors: J.L. Nell, R.T. Kingsford, R. Mac Nally, P.S. Giller, B.J. Robson, A.H. Arthington, D.A. Keith



ECOLOGICAL TRAITS: Episodic rivers have high temporal variability in flows and resource availability, shaping a low-diversity biota with periodically high abundance of some organisms. Productivity is episodically high and punctuated by longer periods of low productivity (i.e. boom-bust dynamics). The trophic structure can be complex and dominated by autochthonous primary production. Even though riparian vegetation is sparse, allochthonous inputs from connected floodplains may be important. Top-down control of ecosystem structure is evident in some desert streams. Episodic rivers are hotspots of biodiversity and ecological activity in arid landscapes, acting as both evolutionary and ecological refuges. Most biota have ruderal life cycles, dormancy phases, or high mobility enabling them to tolerate or avoid long, dry periods and to exploit short pulses of high resource availability during flooding. During dry periods, many organisms survive as dormant life phases (e.g. eggs or seeds), by reducing metabolism, or by persisting in perennial refugia (e.g. waterholes, shallow aquifers). They may rapidly recolonise the channel network during flow (networkers). Waterbirds survive dry phases by moving elsewhere, returning to breed during flows. The abundance of water, nutrients and food during flows and floods initiates rapid primary production (especially by algae), breeding and recruitment. Zooplankton are abundant in slower reaches during periods of flow. Macroinvertebrates, such as sessile filter-feeders (i.e. mussels) and scavengers (i.e. crayfish), may occur in moderate flow environments with complex microhabitats in fine sediment and amongst woody debris. Assemblages of fish and amphibians are dominated by small body sizes. Most fish species use inundated floodplains in larval, juvenile and mature life stages, and produce massive biomass after large floods. Organisms generally tolerate wide ranges of temperature, salinity and oxygen.

KEY ECOLOGICAL DRIVERS: These mostly lowland systems are distinguished by highly episodic flows and flood regimes that vary with catchment size and precipitation. High-volume, short duration flows (days to weeks, rarely months) punctuate long dry periods fill channels and flood wetlands. Low elevational gradients and shallow channels result in low turbulence and low to moderate flow velocity. Lowland stream channels are broad, flat, and often anastomising, with mostly soft sandy sediments. Groundwater is usually within rooting zones of perennial plants, which may establish in channels after flow events. Sediment loads drive periodically high turbidity. Locally or temporally important erosional processes have roles in geomorphic dynamism redistributing sediment in depositional features (e.g. braided channels and point bars). Upland streams are prone to erosive flash floods. High nutrient levels are due to large catchments and riparian inputs but depend on catchment geochemistry. These rivers often flow over naturally saline soils. Salinity can thus be high and increases in drying phases.

DISTRIBUTION: Arid and semi-arid mid-latitudes, in lowlands, and some uplands, but rarely above 1,500 m elevation.



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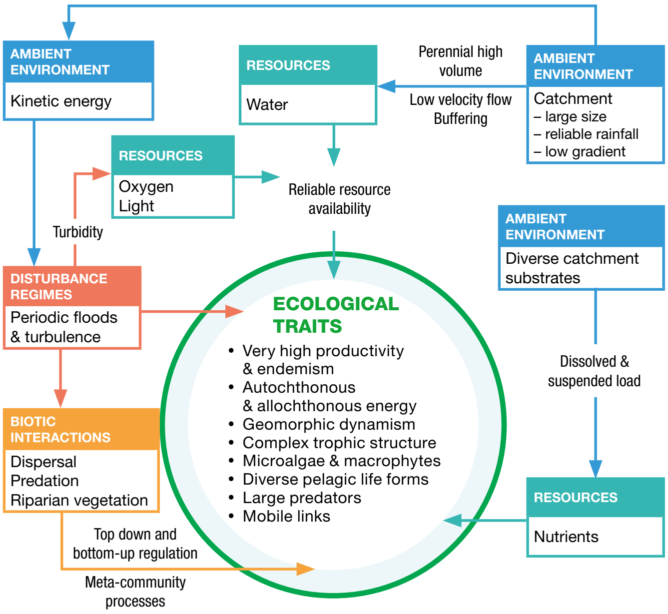
Kingsford, R.T. (2006). *Ecology of desert rivers*. Cambridge, UK: Cambridge University Press.
Sheldon, F., Bunn, S.E., Hughes, J.M., Arthington, A.H., Balcombe, S.R. and Fellows, C.S. (2010). 'Ecological roles and threats to aquatic refuges in arid landscapes: dryland river waterholes'. *Marine & Freshwater Research* 61(8): 885–895.

Amazon River near Iquitos, Peru.
Source: Amazon Images – Alamy Stock (2015)

F1.7 Large lowland rivers

BIOME: F1 RIVERS AND STREAMS
REALM: FRESHWATER

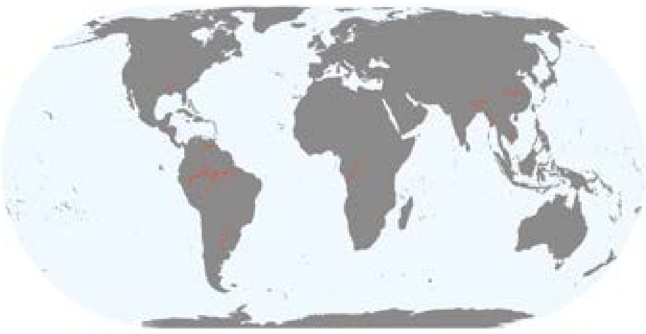
Contributors: R.T. Kingsford, P.S. Giller, R. Mac Nally, D.A. Keith



ECOLOGICAL TRAITS: Large lowland rivers (typically stream orders 8–12) are highly productive environments with complex trophic webs which are supported by very large flow volumes. Primary production is mostly from autochthonous phytoplankton and riparian macrophytes, with allochthonous inputs from floodplains and upper catchments generally dominating energy flow in the system. The fauna includes a significant diversity of pelagic organisms. Zooplankton are abundant, while sessile (i.e. mussels), burrowing (i.e. annelids) and scavenging (i.e. crustaceans) macroinvertebrates occur in the fine sediment and amongst woody debris. Fish communities are diverse and contribute to complex trophic networks. They include large predatory fish (e.g. freshwater sawfish, piranha, alligator gar) and in some rivers endemic river dolphins, smaller predators of invertebrates (benthic and pelagic feeders), phytoplankton herbivores, and detritivores. The feeding activities and movement of semi-aquatic piscivorous birds (i.e. cormorants), mammals (i.e. otters), and reptiles (e.g. turtles, crocodilians) connect the trophic network to other ecosystems beyond instream waters. Riparian and large floodplain zones vary in complexity from forested banks, to productive lentic oxbow lakes and extensive and complex flooded areas where emergent and floodplain vegetation grows (e.g. reeds and macrophytes, shrubs, trees). Riparian zones can be complex but have less direct influence on large rivers than smaller river ecosystems.

KEY ECOLOGICAL DRIVERS: These rivers have shallow gradients with low turbulence, low to moderate flow velocity and very high flow volumes (>10,000 m^3/s), which are continuous but may vary seasonally depending on catchment area and precipitation (e.g. Congo River up to 41,000 m^3/s, Amazon River up to 175,000 m^3/s). River channels are wide (i.e. Amazon River: 11 km in dry season, up to 25 km when flooded at its widest point) and deep (e.g. Congo River up to 200 m; Mississippi River up to 60 m) with mostly soft sediment substrates. They are dominated by depositional processes so turbidity may be high. Overbank flows increase turbulence and turbidity. Locally or temporally important erosional processes redistribute sediment and produce geomorphically dynamic depositional features (e.g. braided channels, islands and point bars). Nutrient levels are high due to large catchments and riparian/floodplain inputs but vary with catchment geochemistry. Moderate water temperatures are buffered due to large catchments.

DISTRIBUTION: Tropical and subtropical lowlands, with a few extending to temperate zones. They are absent from arid regions, and in boreal zones are replaced by F1.3.



Reference:
Ashworth, P.J., Lewin, J. (2012). 'How do big rivers come to be different?'. *Earth-Science Reviews* 114(s 1–2): 84-107.
Best, J. (2019). 'Anthropogenic stresses on the world's big rivers'. *Nature Geoscience* 12: 7–21.

F2 Lakes biome

Andes Mountain Lake, Bolivia.
Source: Sylvain Didier/Alamy Stock Photo with permission

The Lakes biome includes lentic ecosystems defined by their still waters. They vary in area, depth, water regime and connectivity to other aquatic systems across a global distribution. Gradients in water regimes, temperature, lake size and salinity (and salt composition) exert critical influences on the function, productivity, diversity and trophic structure of lake ecosystems. Water regimes vary from permanent open waters to seasonal or episodic filling and drying on interannual time scales. Lakes span global climatic gradients, which influence their water regimes through catchment precipitation and evapotranspiration rates, as well as the seasonal freeze-thaw cycles of lake surfaces along latitudinal and altitudinal temperature gradients. The azonal character of the Lakes biome, however, is due to the buffering of climatic influences by groundwater, geomorphology, and substrate. This is most evident in the water regimes of artesian springs, oases and geothermal wetlands, as their water sources are largely independent of climate. Lake and catchment substrates influence nutrient stocks and salinity, but concentrations may vary temporally depending on water regimes and mixing. Deeper and freeze-thaw lakes are often characterised by stratification, producing depth gradients in nutrient and oxygen availability and temperatures. The deepest lakes extend to the aphotic zone. Productivity is determined by allochthonous inputs from the catchments and autochthonous inputs from phytoplankton, periphyton (i.e. biofilms), and submerged, floating and emergent macrophytes. Trophic webs tend to increase in size and complexity with lake size due to increased resource availability and niche diversity, but small shallow lakes have greater diversity than small deep lakes due to habitat heterogeneity and light penetration to the bottm allowing development of benthic macrophytes and associated biota. Salt lakes may have high productivity but simple trophic structures, with high abundances of few species. Invertebrate detritivores consume fragments of organic matter, providing resources for macroinvertebrates, fish, waterbirds, reptiles and mammals. Species traits appear to be strongly influenced by environmental filtering by the water regime (e.g. cold tolerance and seasonal dormancy occurs in freeze-thaw lakes and desiccation tolerance and dormant life stages dominate in ephemeral lakes) and water chemistry (i.e. tolerance to salinity in salt lakes).

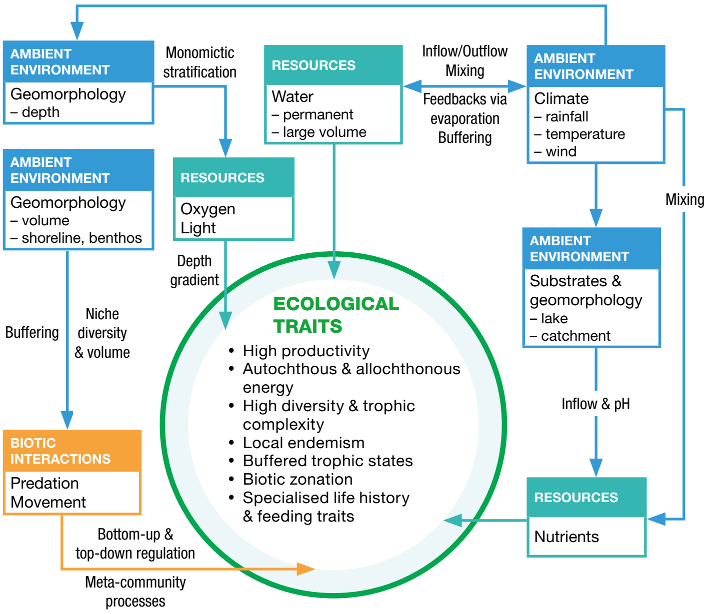
F2.1 Large permanent freshwater lakes

BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: R.T. Kingsford, R. Mac Nally, L.J. Jackson, F. Essl, K. Irvine, D.A. Keith

High cichlid fish diversity in Lake Malawi, Africa.
Source: Michel Roggo/roggo.ch

ECOLOGICAL TRAITS: Large permanent freshwater lakes, generally exceeding 100 km^2, are prominent landscape features connected to one or more rivers either terminally or as flow-through systems. Shoreline complexity, depth, bathymetric stratification, and benthic topography promote niche diversity and zonation. High niche diversity and large volumes of permanent water (extensive, stable, connected habitat) support complex trophic webs with high diversity and abundance. High primary productivity may vary seasonally, driving succession, depending on climate, light availability, and nutrient regimes. Autochthonous energy from abundant pelagic algae (mainly diatoms and cyanobacteria) and from benthic macrophytes and algal biofilms (in shallow areas) is supplemented by allochthonous inflows that depend on catchment characteristics, climate, season, and hydrological connectivity. Zooplankton, invertebrate consumers, and herbivorous fish sustain high planktonic turnover and support upper trophic levels with abundant and diverse predatory fish, amphibians, reptiles, waterbirds, and mammals. This bottom-up web is coupled to a microbial loop, which returns dissolved organic matter to the web (rapidly in warm temperatures) via heterotrophic bacteria. Obligate freshwater biota in large lakes, including aquatic macrophytes and macroinvertebrates (i.e. crustaceans) and fish, often display high catchment-level endemism, in part due to long histories of environmental variability in isolation. Marked niche differentiation in life history and behavioural feeding and reproductive traits enables sympatric speciation and characterises the most diverse assemblages of macroinvertebrates and fish (i.e. ~500 cichlid fish species in Lake Victoria). Large predators are critical in top-down regulation of lower trophic levels. Large lake volume buffers against nutrient-mediated change from oligotrophic to eutrophic states. Recruitment of many organisms is strongly influenced by physical processes such as large inflow events. Mobile birds and terrestrial mammals use the lakes as breeding sites and/or sources of drinking water and play key roles in the inter-catchment transfer of nutrients and organic matter and the dispersal of biota.



KEY ECOLOGICAL DRIVERS: Large water volumes influence resource availability, environmental stability (through thermal buffering), and niche diversity. Water is from catchment inflows, which may vary seasonally with climate. Large lakes influence regional climate through evaporation, cooling, and convection feedbacks. These processes also influence nutrient availability, along with catchment and lake substrates and vertical mixing. Mixing may be monomictic (i.e. annual) or meromictic (i.e. seldom), especially in large tropical lakes, depending on inflow, depth, wind regimes, and seasonal temperature variation. Light varies with lake depth, turbidity, cloud cover, and latitude.

DISTRIBUTION: Humid temperate and tropical regions on large land masses.

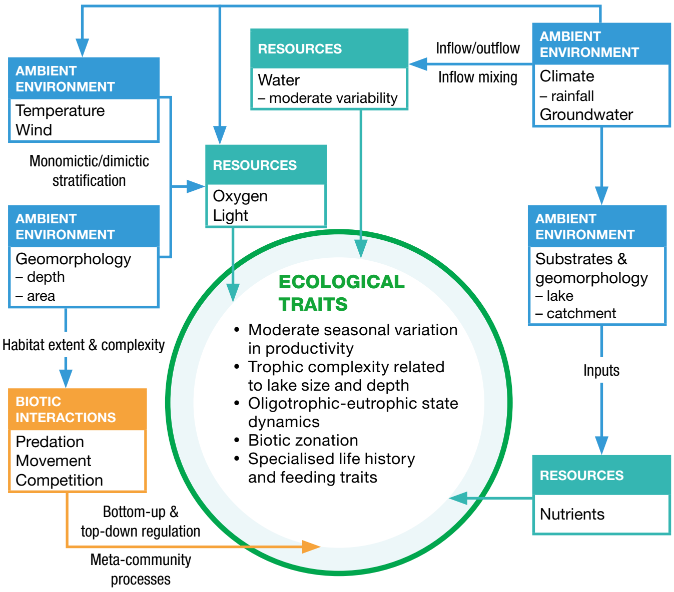
References:
Ludsin, S.A., DeVanna, K.M., Smith, R.E.H. (2014). 'Physical-biological coupling and the challenge of understanding fish recruitment in freshwater lakes'. *Canadian Journal of Fisheries and Aquatic Sciences* 71(5): 775–794.
Pennisi, E. (2018). 'Hybrids spawned Lake Victoria's rich fish diversity'. *Science* 361(6402): 539–539.

Lake Xinguti, Maputo Special Reserve, Mozambique.
Source: David Keith (2019)

F2.2 Small permanent freshwater lakes

BIOME: F2 LAKES
REALM: FRESHWATER

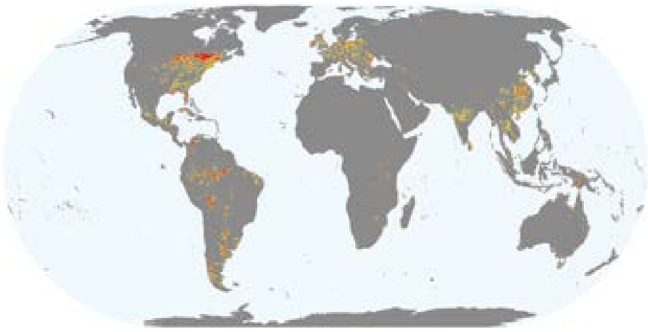
Contributors: R.T. Kingsford, B.J. Robson, R. Mac Nally, L. Jackson, F. Essl, M. Kelly-Quinn, K. Irvine, S. Bertilsson, D.A. Keith



ECOLOGICAL TRAITS: Small permanent freshwater lakes, pools or ponds are lentic environments with relatively high perimeter-to-surface area and surface-area-to-volume ratios. Most are <1 km^2 in area, but this functional group includes lakes of transitional sizes up to 100 km^2, while the largest lakes (>100 km^2) are classified in F2.1. Niche diversity increases with lake size. Although less diverse than larger lakes, these lakes may support phytoplankton, zooplankton, shallow-water macrophytes, invertebrates, sedentary and migratory fish, reptiles, waterbirds, and mammals. Primary productivity, dominated by cyanobacteria, algae, and macrophytes, arises from allochthonous and autochthonous energy sources, which vary with lake and catchment features, climate, and hydrological connectivity. Productivity can be highly seasonal, depending on climate, light, and nutrients. Permanent water and connectivity are critical to obligate freshwater biota, such as fish, invertebrates and aquatic macrophytes. Trophic structure and complexity depend on lake size, depth, location, and connectivity. Littoral zones and benthic pathways are integral to overall production and trophic interactions. Shallow lakes tend to be more productive (by volume and area) than deep lakes because light penetrates to the bottom, establishing competition between benthic macrophytes and phytoplankton, more complex trophic networks and stronger top-down regulation leading to alternative stable states and possible regime shifts between them. Clear lakes in macrophyte-dominated states support higher biodiversity than phytoplankton-dominated eutrophic lakes. Deep lakes are more dependent on planktonic primary production, which supports zooplankton, benthic microbial and invertebrate detritivores. Herbivorous fish and zooplankton regulate the main primary producers (biofilms and phytoplankton). The main predators are fish, macroinvertebrates, amphibians and birds, many of which have specialised feeding traits tied to different habitat niches (e.g. benthic or pelagic), but there are few filter-feeders. In many regions, shallow lakes provide critical breeding habitat for waterbirds, amphibians, and reptiles, while visiting mammals transfer nutrients, organic matter and biota.

KEY ECOLOGICAL DRIVERS: These lakes may be hydrologically isolated, groundwater-dependent or connected to rivers as terminal or flow-through systems. Nutrients depend on catchment size and substrates. Some lakes (e.g. on leached coastal sandplains or peaty landscapes) have dystrophic waters. The seasonality and amount of inflow, size, depth (mixing regime and light penetration), pH, nutrients, salinity and tanins shape lake ecology and biota. Seasonal cycles of temperature, inflow and wind (which drive vertical mixing) may generate monomictic or dimictic temperature stratification regimes in deeper lakes, while shallow lakes are polymicitic, sometimes with short periods of multiple stratification. Seasonal factors, such as light, increases in temperature and flows into lakes, can induce breeding and recruitment.

DISTRIBUTION: Mainly in humid temperate and tropical regions, rarely semi-arid or arid zones.



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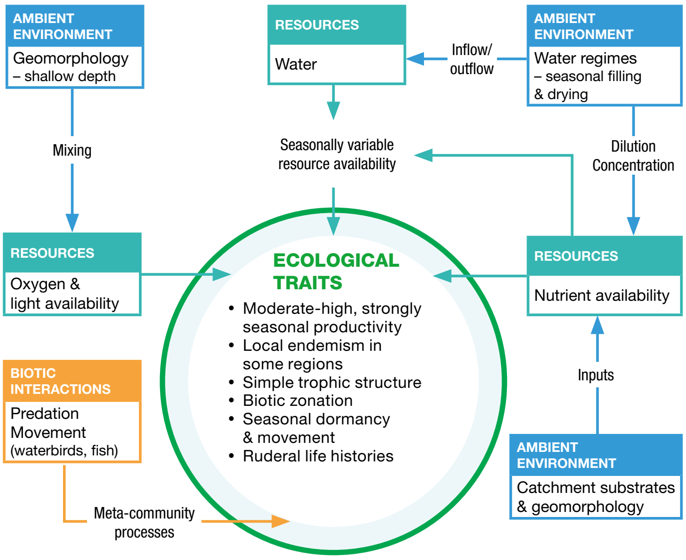
Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Pedersen, L.J., Jensen, L. (1997). 'Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth'. *Hydrobiologia* 342–343: 151–164.
_____ (1997). 'Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth'. In: L. Kufel, A. Prejs, J.I. Rybak (eds.), *Shallow Lakes '95. Developments in Hydrobiology* 119. Springer, Dordrecht.
Schindler, D.E., Scheuerell, M.D. (2002). 'Habitat coupling in lake ecosystems'. *Oikos* 98(2): 177–189.

F2.3 Seasonal freshwater lakes

BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: R.T. Kingsford, R. Mac Nally, M.C. Rains, B.J. Robson, K. Irvine, D.A. Keith

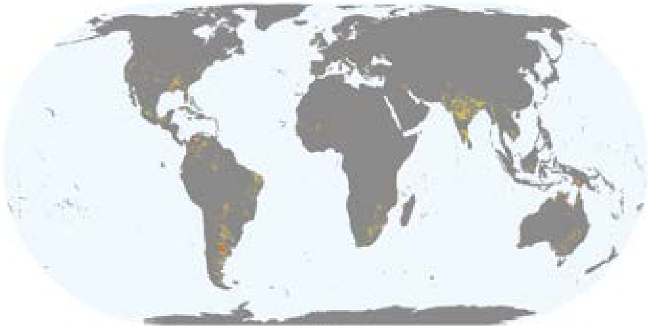
Vernal pool, Mather field, Sacramento Valley, California, USA.
Source: Jamie Kneitel



ECOLOGICAL TRAITS: These small (mostly <5 km^2 in area) and shallow (<2 m deep) seasonal freshwater lakes, vernal pools, turloughs, or gnammas (panholes, rock pools), are characterised by a seasonal aquatic biota. Local endemism may be high in lakes where hydrological isolation promotes biotic insularity, which occurs in some Mediterranean climate regions. Autochthonous energy sources are supplemented by limited allochthonous inputs from small catchments and groundwater. Seasonal variation in biota and productivity outweighs inter-annual variation, unlike in ephemeral lakes (F2.5 and F2.7). Filling induces microbial activity, the germination of seeds and algal spores, hatching and emergence of invertebrates, and growth and reproduction by specialists and opportunistic colonists. Wind-induced mixing oxygenates the water, but eutrophic or unmixed waters may become anoxic and dominated by air-breathers as peak productivity and biomass fuel high biological oxygen demand. Anoxia may be abated diurnally by photosynthetic activity. Resident biota persists through seasonal drying on lake margins or in sediments as desiccation-resistant dormant or quiescent life stages, for example, crayfish may retreat to burrows that extend to the water table, turtles may aestivate in sediments or fringing vegetation, amphibious perennial plants may persist on lake margins or in seedbanks. Trophic networks and niche diversity are driven by bottom-up processes, especially submerged and emergent macrophytes, and depend on productivity and lake size. Cyanobacteria, algae and macrophytes are the major primary producers, while annual grasses may colonise dry lake beds. The most diverse lakes exhibit zonation and support phytoplankton, zooplankton, macrophytes, macroinvertebrate consumers and seasonally resident amphibians (especially juvenile aquatic phases), waterbirds and mammals. Rock pools have simple trophic structure, based primarily on epilithic algae or macrophytes, and invertebrates, but no fish. Invertebrates and amphibians may reach high diversity and abundance in the absence of fish.

KEY ECOLOGICAL DRIVERS: Annual filling and drying are driven by seasonal rainfall, surface flows, groundwater fluctuation and seasonally high evapotranspiration. These lakes are polymicitc, mixing continuously when filled. Impermeable substrates (e.g. clay or bedrock) impede infiltration in some lakes; in others groundwater percolates up through sand, peat or fissures in karstic limestone (turloughs). Small catchments, low-relief terrain, high area-to-volume ratios and hydrological isolation promote seasonal fluctuation. Most lakes are hydrologically isolated, but some become connected seasonally by sheet flows or drainage lines. These hydrogeomorphic features also limit nutrient supply, in turn limiting pH buffering. High rates of organic decomposition, denitrification, and sediment retention are driven by water fluctuations. High alkalinity reflects high anaerobic respiration. Groundwater flows may ameliorate hydrological isolation. Seasonal filling and drying induce spatio-temporal variability in temperature, depth, pH, dissolved oxygen, salinity and nutrients, resulting in zonation within lakes and high variability among them.

DISTRIBUTION: Mainly subhumid temperate and wet-dry tropical regions in monsoonal and Mediterranean-type climates but usually not semi-arid or arid regions.



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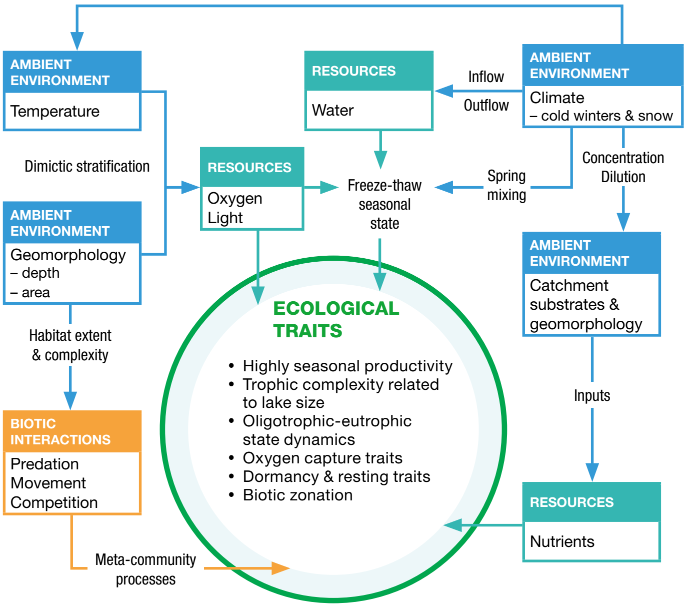
Pettit, N., Jardine, T. , Hamilton, S ., Sinnamon, V., Valdez, D., Davies, P., Douglas, M., Bunn, S. (2012). 'Seasonal changes in water quality and macrophytes and the impact of cattle on tropical floodplain waterholes'. *Marine and Freshwater Research* 63(9): 788–800.
Rains, M.C., Fogg, G.E., Harter, T., Dahlgren, R.A., Williamson, R.J. (2006). 'The role of perched aquifers in hydrological connectivity and biogeochemical processes in vernal pool landscapes, Central Valley, California'. *Hydrological Processes* 20(5): 1157–1175.

Frozen Lake Ulriken Bergen, Norway.
Source: Sveter (2009)

F2.4 Freeze-thaw freshwater lakes

BIOME: F2 LAKES
REALM: FRESHWATER

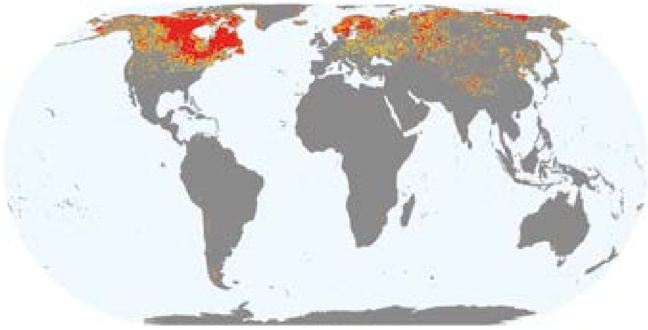
Contributors: R.T. Kingsford, S. Bertilsson, L. Jackson, B.J. Robson, D.A. Keith



ECOLOGICAL TRAITS: The majority of surface of these lakes is frozen for at least a month in most years. Their varied origins (tectonic, riverine, fluvioglacial), size and depth affect composition and function. Allochthonous and autochthonous energy sources vary with lake and catchment features. Productivity is highly seasonal, sustained in winter largely by the metabolism of microbial photoautotrophs, chemautotrophs and zooplankton that remain active under low light, nutrients, and temperatures. Spring thaw initiates a seasonal succession, increasing productivity and re-establishing complex trophic networks, depending on lake area, depth, connectivity, and nutrient availability. Diatoms are usually first to become photosynthetically active, followed by small and motile zooplankton, which respond to increased food availability, and cyanobacteria later in summer when grazing pressure is high. Large lakes with high habitat complexity (i.e. Lake Baikal) support phytoplankton, zooplankton, macrophytes (in shallow waters), invertebrate consumers, migratory fish (in connected lakes), waterbirds, and mammals. Their upper trophic levels are more abundant, diverse, and endemic than in smaller lakes. Herbivorous fish and zooplankton are significant top-down regulators of the main primary producers (i.e. biofilms and phytoplankton). These, in turn, are regulated by predatory fish, which may be limited by prey availability and competition. The biota is spatially structured by seasonally dynamic gradients in cold stratification, light, nutrient levels, and turbulence. Traits, such as resting stages, dormancy, freeze-cued spore production in phytoplankton and the ability of fish to access low oxygen exchange, enable persistence through cold winters under the ice and through seasonal patterns of nutrient availability.

KEY ECOLOGICAL DRIVERS: Seasonal freeze-thaw cycles typically generate dimictic temperature stratification regimes (i.e. mixing twice per year), where cold water lies above warm water in winter and vice versa in summer. Shallow lakes may mix continuously (polymicitic) during the summer and may freeze completely during winter. Mixing occurs in autumn and spring. Freezing reduces light penetration and turbulence, subduing summer depth gradients in temperature, oxygen, and nutrients. Ice also limits atmospheric inputs, including gas exchange. Very low temperatures reduce the growth rates, diversity, and abundance of fish. Many lakes are stream sources. Lake sizes vary from <1 ha to more than 30,000 km^2, profoundly affecting niche diversity and trophic complexity. Freezing varies with the area and depth of lakes. Thawing is often accompanied by flooding in spring, ameliorating light and temperature gradients, and increasing mixing. Dark-water inflows from peatlands in catchments influence water chemistry, light penetration, and productivity.

DISTRIBUTION: Predominantly across the high latitudes of the Northern Hemisphere and high altitudes of South America, New Zealand and Tasmania.



References:

Adrian, R., Walz, N., Hintze, T., Hoeg, S., Rusche, R. (1999). 'Effects of ice duration on plankton succession during spring in a shallow polymictic lake'. *Freshwater Biology* 41(3): 621–634.

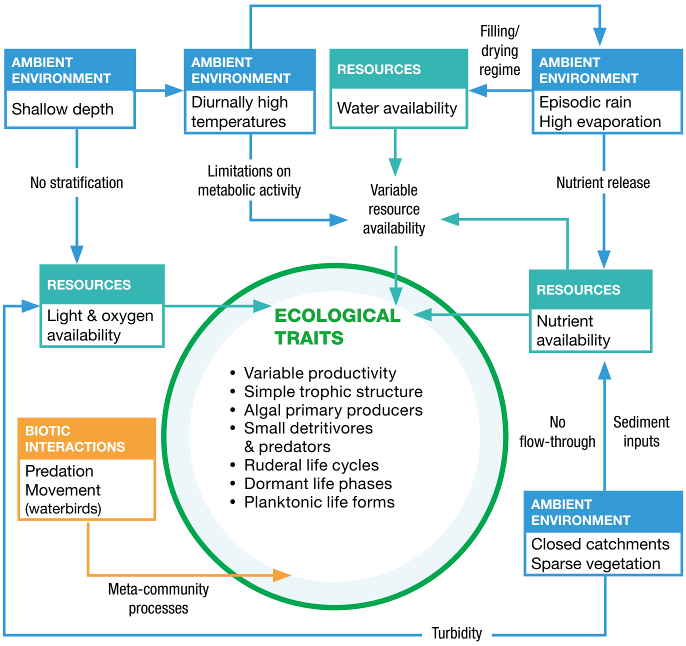
Bertilsson, S., Burgin, A., Carey, C.C., Fey, S.B., Grossart, H., Grubisic, L.M., Jones, I.D., Kirillin, G., Lennon J.T., Shade, A., Smyth, R.L. (2013). 'The under-ice microbiome of seasonally frozen lakes'. *Limnology Oceanography* 58(6): 1998–2012.

F2.5 Ephemeral freshwater lakes

BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: D.J. Roux, R. Mac Nally, R.T. Kingsford, J.T. Hollibaugh, D.A. Keith

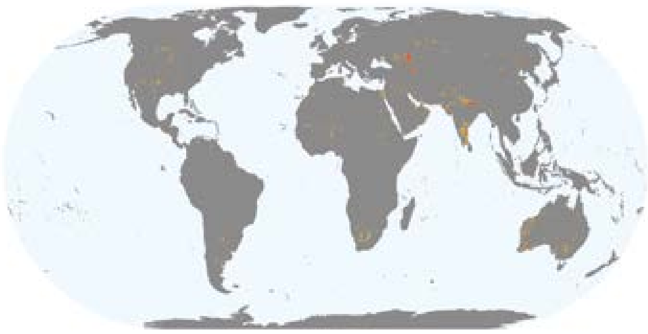
Small, episodic freshwater lake with inflow channel in the arid Tankwa-Karoo National Park, South Africa.
Source: Dirk Roux (2013)



ECOLOGICAL TRAITS: Shallow ephemeral freshwater bodies are also known as depressions, playas, clay pans or pans. Long periods of low productivity during dry phases are punctuated by episodes of high production after filling. Trophic structure is relatively simple with mostly benthic, filamentous and planktonic algae, detritivorous and predatory zooplankton (e.g. rotifers and Daphnia), crustaceans, insects, and in some lakes, molluscs. The often high invertebrate biomass provides food for amphibians and itinerant waterbirds. Terrestrial mammals use the lakes to drink and bathe and may transfer nutrients, organic matter and 'hitch-hiking' biota. Diversity may be high in boom phases but there are only a few local endemics (i.e. narrow-ranged charophytes). Specialised and opportunistic biota exploit boom-bust resource availability through life-cycle traits that confer tolerance to desiccation (i.e. desiccation-resistant eggs in crustaceans) and/or enable rapid hatching, development, breeding and recruitment when water arrives. Much of the biota (i.e. opportunistic insects) have widely dispersing adult phases enabling rapid colonisation and re-colonisation. Filling events initiate succession with spikes of primary production, allowing short temporal windows for consumers to grow and reproduce and for itinerant predators to aggregate. Drying initiates senescence, dispersal and dormancy until the next filling event.

KEY ECOLOGICAL DRIVERS: Arid climates have highly variable hydrology. Episodic inundation after rain is relatively short (days to months) due to high evaporation rates and infiltration. Drainage systems are closed or nearly so, with channels or sheet inflow from flat, sparsely vegetated catchments. Inflows bring allochthonous organic matter and nutrients and are typically turbid with fine particles. Clay-textured lake bottoms hold water by limiting percolation but may include sand particles. Bottom sediments release nutrients rapidly after filling and solute concentrations increase as drying progresses, placing these systems on a continuum with salt lakes. When filled, these lakes are shallow with small volumes, flat-bottomed and polymicitic, so light and oxygen are generally not limiting. Persistent turbidity may limit light but oxygen production by macrophytes and flocculation (i.e. clumping) from increasing salinity during drying reduce turbidity over time. Shallow depth promotes high daytime water temperatures (when filling in summer) and high diurnal temperature variability.

DISTRIBUTION: Semi-arid and arid regions at mid-latitudes of the Americas, Africa, Asia and Australia.



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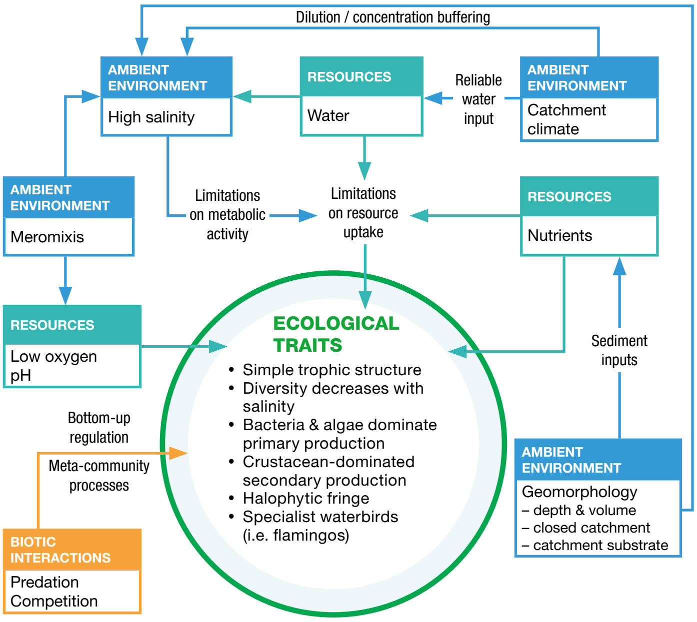
Hancock, M.A., Timms, B.V. (2002). 'Ecology of four turbid clay pans during a filling-drying cycle in the Paroo, semi-arid Australia'. *Hydrobiologia* 479: 95–107.
Meintjes, S. (1996). 'Seasonal changes in the invertebrate community of small shallow ephemeral pans at Bain's Vlei, South Africa '. *Hydrobiologia* 317: 51–64.
Williams, W.D. (2000). 'Biodiversity in temporary wetlands of dryland regions'. *SIL Proceedings, 1922–2010. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* 27(1): 141–144.

F2.6 Permanent salt and soda lakes

BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: R.T. Kingsford, J.T. Hollibaugh, B.J. Robson, R. Harper, D.A. Keith

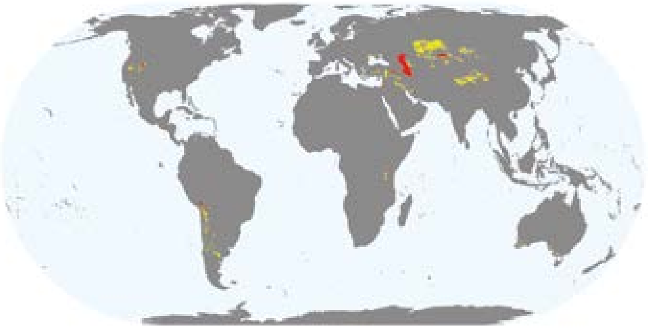
Flamingos on Lake Bogoria, a soda lake in Kenya.
Source: Richard Kingsford (2005)



ECOLOGICAL TRAITS: These lakes are united by relatively constant, high inorganic solute concentrations (notably sodium ions) and an associated specialist biota. Unlike hypersaline lakes (F2.7), productivity is not suppressed Autotrophs may be abundant, including phytoplankton, cyanobacteria, green algae and submerged and emergent macrophytes. These, supplemented by allochthonous energy and C inputs from lake catchments, support relatively simple trophic networks with few species in high abundance and some regional endemism. High biomass of archaeal and bacterial decomposers and phytoplankton in turn supports abundant consumers including brine shrimps, copepods, insects and other invertebrates, fish and waterbirds (i.e. flamingos). Predators and herbivores that become dominant at low salinity exert top-down control on algae and low-order consumers. Species niches are structured by spatial and temporal salinity gradients. Species in the most saline conditions tend to have broader ranges of salinity tolerance. Increasing salinity generally reduces diversity and the importance of top-down trophic regulation but not necessarily the abundance of organisms, except at hypersaline levels. Many organisms tolerate high salinity through osmotic regulation (at a high metabolic cost), limiting productivity and competitive ability.

KEY ECOLOGICAL DRIVERS: Lakes may be thousands of hectares in size and several metres deep. A few are larger and deeper (i.e. Caspian Sea), while some volcanic lakes are small and deep. Endorheic drainage promotes salt accumulation, but lake volume and reliable water inflows buffer salinity below extreme levels, despite high evaporation. Salt lakes are mostly legacies of marine incursions (since retreated) and dominated by sodium chloride (cf. seawater). Soda lakes derive more diverse solutes from catchment leachates, with sodium carbonate or sulphate dominant. Salinity varies temporally from 0.3% to rarely more than 10% depending on lake size, temperature, and the balance between freshwater inflows, precipitation, and evaporation. Ionic composition and concentration varies greatly among lakes due to differences in groundwater and inflow, with carbonate, sulphate, sulphide, ammonia and/or phosphorus sometimes reaching high levels, and pH varying from 3 to 11. Inflow is critical to ecosystem dynamics, partly by driving the indirect effects of salinity on trophic or engineering processes. Groundwater also contributes to water balance and chemistry. Ionic concentrations may be vertically stratified (i.e. meromictic), often seasonally, due to slow mixing after periodic inflows episodes of low-density freshwater. Dissolved oxygen is inversely related to salinity, so anoxia is common at depth in meromictic lakes.

DISTRIBUTION: Mostly in semi-arid regions of Africa, southern Australia, Eurasia, Europe, and western parts of North and South America.



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Boros, E., Kolpakova, M. (2018). 'A review of the defining chemical properties of soda lakes and pans: An assessment on a large geographic scale of Eurasian inland saline surface waters'. *PLoSONE* 13(8): e0202205.
Humayoun, S.B., Bano, N. and Hollibaugh, J.T. (2003). 'Depth distribution of microbial diversity in Mono Lake, a meromictic soda lake in California'. *Applied and Environmental Microbiology* 69(2): 1030–1042.
Williams, W.D. (1998). 'Salinity as a determinant of the structure of biological communities in salt lakes'. *Hydrobiologia* 381: 191–201

F2.7 Ephemeral salt lakes

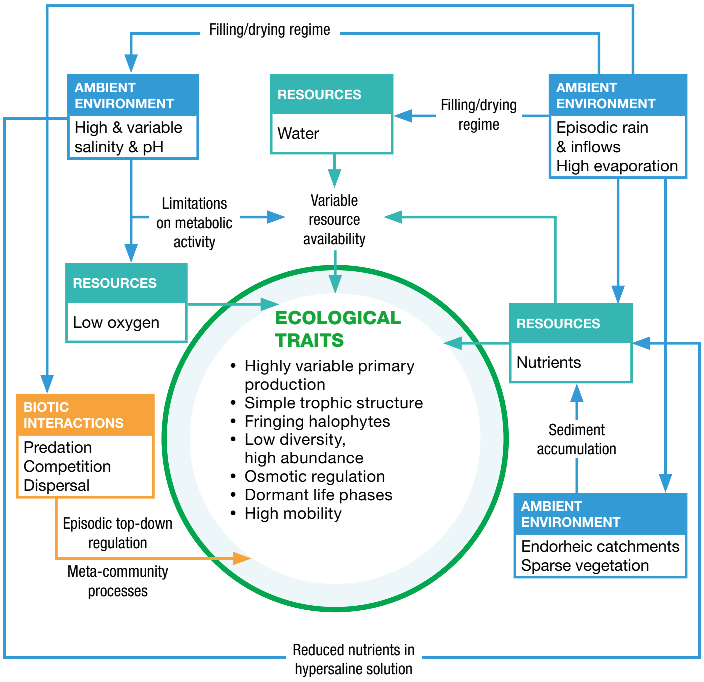
BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: R.T. Kingsford, J.T. Hollibaugh, K. Irvine, R. Harper, D.A. Keith

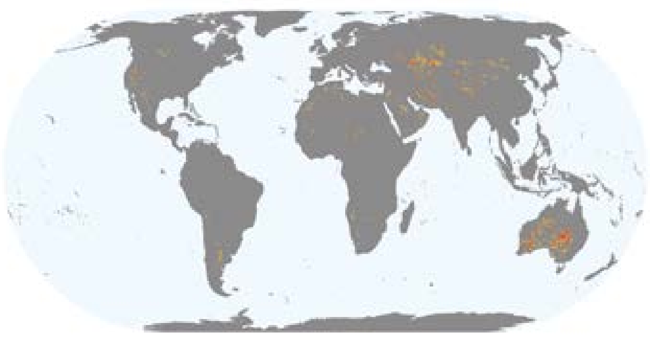
Hutt Lagoon a pink salt lake (coloured by the algae *Dunaliella salina*), Geraldton, Western Australia.
Source: David Keith (2007)

ECOLOGICAL TRAITS: Ephemeral salt lakes or playas have relatively short-lived wet phases and long dry periods of years to decades. During filling phases, inflow dilutes salinity to moderate levels, and allochthonous energy and carbon inputs from lake catchments supplement autochthonous energy produced by abundant phytoplankton, cyanobacteria, diatoms, green algae, submerged and emergent macrophytes, and fringing halophytes. In drying phases, increasing salinity generally reduces diversity and top-down trophic regulation, but not necessarily the abundance of organisms, except at hypersaline levels, which suppress productivity. Trophic networks are simple and characterised by few species that are often highly abundant during wet phases. The high biomass of archaeal and bacterial decomposers and phytoplankton in turn support abundant consumers, including crustaceans (i.e. brine shrimps and copepods), insects and other invertebrates, fish and specialist waterbirds (e.g. banded stilts, flamingos). Predators and herbivores that dominate at low salinity levels exert top-down control on algae and low-order consumers. Species niches are strongly structured by spatial and temporal salinity gradients and endorheic drainage promotes regional endemism. Species that persist in the most saline conditions tend to have broad salinity tolerance. Many organisms regulate salinity osmotically at a high metabolic cost, limiting productivity and competitive ability. Many specialised opportunists are able to exploit boom-bust resource cycles through life-cycle traits that promote persistence during dry periods (e.g. desiccation-resistant eggs in crustaceans and/or rapid hatching, development, breeding and recruitment). Much of the biota (e.g. insects and birds) have widely dispersed adult phases enabling rapid colonisation. Filling events drive specialised succession, with short windows of opportunity to grow and reproduce reset by drying until the next filling event.

KEY ECOLOGICAL DRIVERS: Up to 10,000 km^2 in area and usually less than a few metres deep, these lakes may be weakly stratified (i.e. meromictic) due to the slow mixing of freshwater inflow. Endorheic drainage promotes salt accumulation. Salinity varies from 0.3% up to 40% through wet-dry phases depending on lake size, depth, temperature, hydrochemistry, and the dynamic balance between freshwater inflow, groundwater, precipitation and evaporation. Inflow and groundwater are critical to ecosystem dynamics, mediate wet-dry phases, and drive the indirect effects of salinity on trophic and ecosystem processes. Dissolved oxygen is inversely related to salinity, hence anoxia is common in drying hypersaline lake states. Ionic composition varies, with carbonate, sulphate, sulphide, ammonia, arsenic, boron and/or phosphorus sometimes at high levels, and pH varying from 3 to 11.



DISTRIBUTION: Mostly in arid and semi-arid Africa, Eurasia, Australia, and North and South America.



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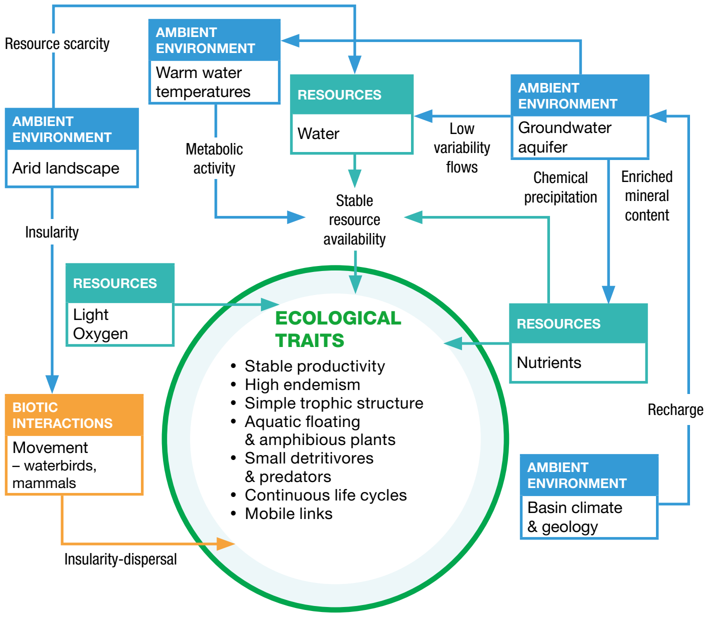
McCulloch, G., Aebischer, A. and Irvine, K. (2003). 'Satellite tracking of flamingos in southern Africa: the importance of small wetlands for management and conservation'. *Oryx* 7(4): 480–483.
Seaman, M.T., Ashton, P.J. and Williams, W.D. (1991). 'Inland salt waters of southern Africa'. *Hydrobiologia* 210: 75–91.
Williams, W.D. (1998). 'Salinity as a determinant of the structure of biological communities in salt lakes'. Hydrobiologia 381: 191–201.

F2.8 Artesian springs and oases

BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: D.J. Roux, R.T. Kingsford, A.H. Arthington, D.A. Keith

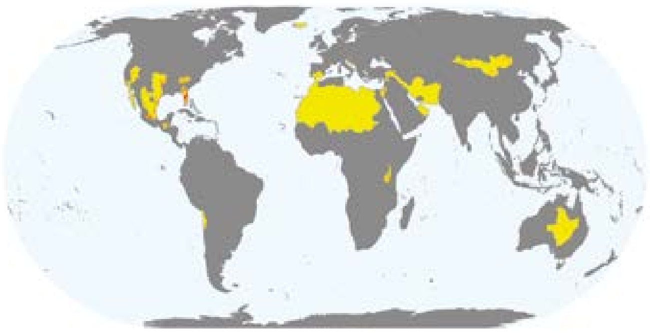
Ubari Oasis, Wadi Al Hayaa District, southwestern Libya.
Source: Sfivat on Wikimedia Commons



ECOLOGICAL TRAITS: These groundwater-dependent systems are fed by artesian waters that discharge to the surface. They are.surrounded by dry landscapes and receive little surface inflow, being predominantly disconnected from surface-stream networks. Insularity from the broader landscape results in high levels of endemism in sedentary aquatic biota, which are likely descendants of relic species from a wetter past. Springs may be spatially clustered due to their association with geological features such as faults or outcropping aquifers. Even springs in close proximity may have distinct physical and biological differences. Some springs have outflow streams, which may support different assemblages of plants and invertebrates to those in the spring orifice. Artesian springs and oases tend to have simple trophic structures. Autotrophs include aquatic algae and floating vascular plants, with emergent amphibious plants in shallow waters. Terrestrial plants around the perimeter contribute subsidies of organic matter and nutrients through litter fall. Consumers and predators include crustaceans, molluscs, arachnids, insects and small-bodied fish. Most biota are poorly dispersed and have continuous life cycles and other traits specialised for persistence in hydrologically stable, warm, or hot mineral-rich water. Springs and oases are reliable watering points for wide-ranging birds and mammals, which function as mobile links for resources and promote the dispersal of other biota between isolated wetlands in the dryland matrix.

KEY ECOLOGICAL DRIVERS: Flow of artesian water to the surface is critical to these wetlands, which receive little input from precipitation or runoff. Hydrological variability is low compared to other wetland types, but hydrological connections with deep regional aquifers, basin-fill sediments and local watershed recharge drive lagged flow dynamics. Flows vary over geological timeframes, with evidence of cyclic growth, waning and extinction. Discharge waters tend to have elevated temperatures, are polymicitic and enriched in minerals that reflect their geological origins. The precipitation of dissolved minerals (i.e. carbonates) and deposition by wind and water form characteristic cones or mounds known as "mound springs". Perennial flows and hydrological isolation from other spatially and temporally restricted surface waters make these wetlands important ecological refuges in arid landscapes.

DISTRIBUTION: Scattered throughout arid regions in southern Africa, the Sahara, the Middle East, central Eurasia, southwest of North America and Australia's Great Artesian Basin, but may also occur in humid landscapes.



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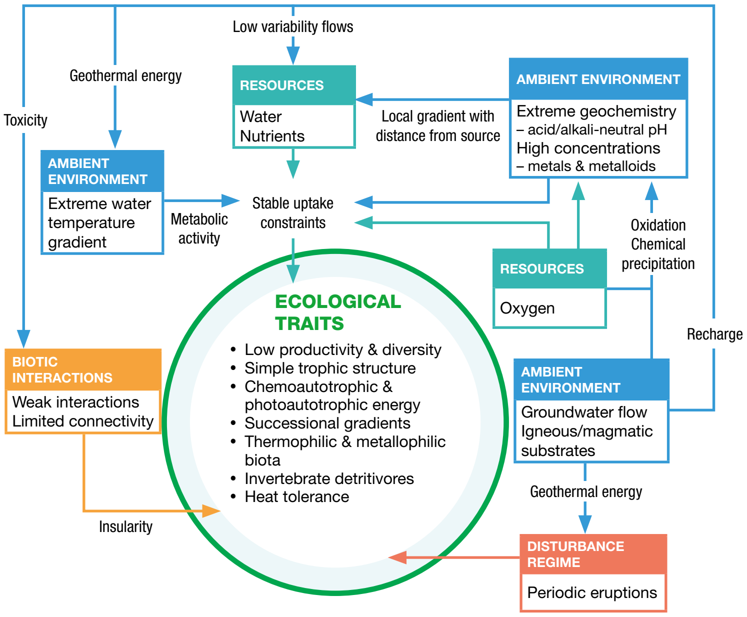
F2.9 Geothermal pools and wetlands

BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: D.A. Keith, A. Channing, P.S. Giller

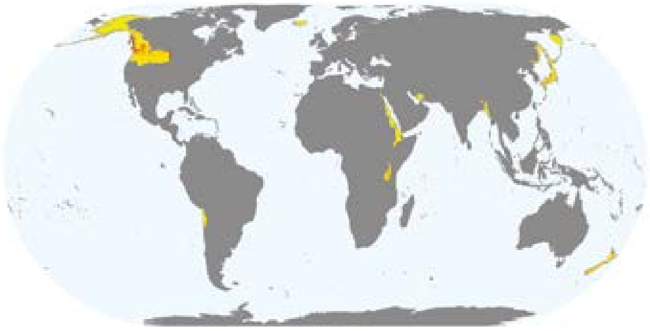
Cyanobacterial growth downstream of Waimangu Hot Springs, Taupo Volcanic Zone, New Zealand.
Source: Sylvia Hay

ECOLOGICAL TRAITS: These hot springs, geysers, mud pots and associated wetlands result from interactions of deeply circulating groundwater with magma and hot rocks that produce chemically precipitated substrates. They support a specialised but low-diversity biota structured by extreme thermal and geochemical gradients. Energy is almost entirely autochthonous, productivity is low and trophic networks are very simple. Primary producers include chemoautotrophic bacteria and archaea, as well as photoautotrophic cyanobacteria, diatoms, algae and macrophytes. Thermophilic and metallophilic microbes dominate the most extreme environments in vent pools, while mat-forming green algae and animal-protists occur in warm acidic waters. Thermophilic blue-green algae reach optimum growth above 45°C. Diatoms occur in less acidic warm waters. Aquatic macrophytes occur on sinter aprons and wetlands with temperatures below 35°C. Herbivores are scarce, allowing thick algal mats to develop. These are inhabited by invertebrate detritivores, notably dipterans and coleopterans, which may tolerate temperatures up to 55°C. Molluscs and crustaceans occupy less extreme microhabitats (notably in hard water hot springs), as do vertebrates, such as amphibians, fish, snakes and visiting birds. Microinvertebrates such as rotifers and ostracods are common. Invertebrates, snakes and fish exhibit some endemism due to habitat insularity. Specialised physiological traits enabling metabolic function in extreme temperatures include thermophilic proteins with short amino-acid lengths, chaperone molecules that assist protein folding, branched chain fatty acids and polyamines for membrane stabilisation, DNA repair systems and upregulated glycolysis providing energy to regulate heat stress. Three mechanisms enable metabolic function in extremely acidic (pH<3) geothermal waters: i) proton efflux via active transport pumps that counter proton influx; ii) decreased permeability of cell membranes to suppress proton entry into the cytoplasm; and iii) strong protein and DNA repair systems. Similar mechanisms enable metabolic function in waters with high concentrations of metal toxins. A succession of animal and plant communities occur with distance from the spring source as temperatures cool and minerals precipitate.



KEY ECOLOGICAL DRIVERS: Continual flows of geothermal groundwater sustain these polymicitic water bodies. Permanent surface waters may be clear or highly turbid with suspended solids as in 'mud volcanoes'. Water temperatures vary from hot (>44°C) to extreme (>80°C) on local gradients (e.g. vent pools, geysers, mounds, sinter aprons, terraces and outflow streams). The pH is either extremely acid (2–4) or neutral-alkaline (7–11). Mineral salts are concentrated, but composition varies greatly among sites with properties of the underlying bedrock. Dissolved and precipitated minerals include very high concentrations of silicon, calcium or iron, but also arsenic, antimony, copper, zinc, cadmium, lead, polonium or mercury, usually as oxides, sulphides or sulphates, but nutrients, such as nitrogen and phosphorus, may be scarce.

DISTRIBUTION: Tectonically or volcanically active areas from tropical to subpolar latitudes. Notable examples in Yellowstone (USA), Iceland, New Zealand, Atacama (Chile), Japan and east Africa.



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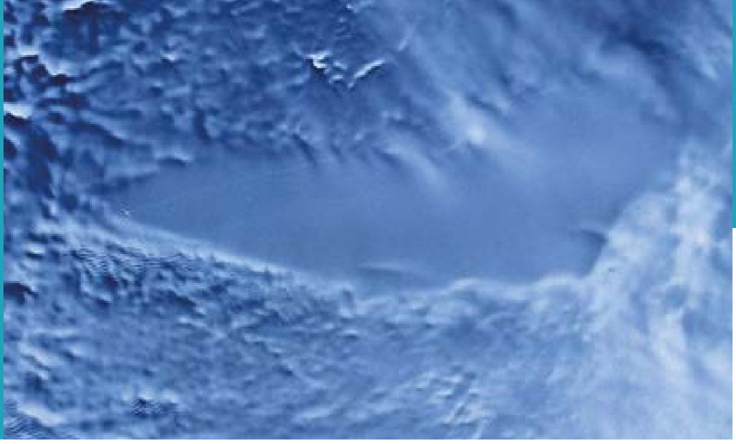
F2.10 Subglacial lakes

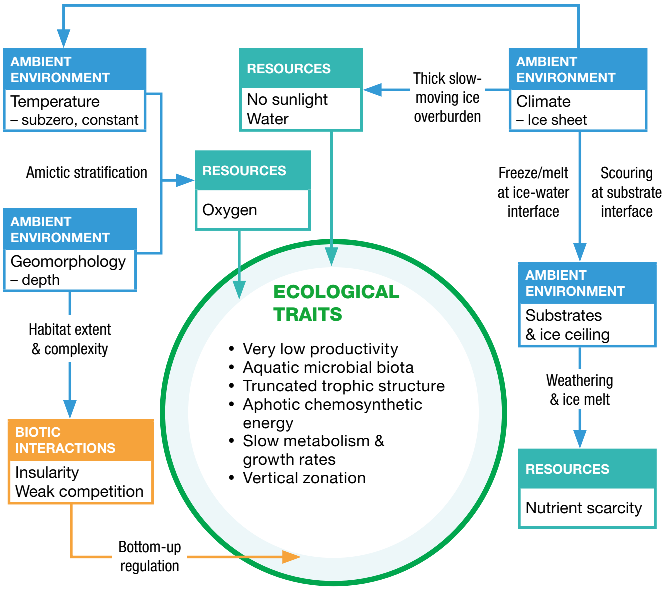
BIOME: F2 LAKES
REALM: FRESHWATER

Contributors: D.A. Keith, M.J. Siegert



Radar image of Lake Vostok ~4 km below the icesheet surface, East Antarctica.
Source: Goddard Space Flight Center - NASA, Public Domain,

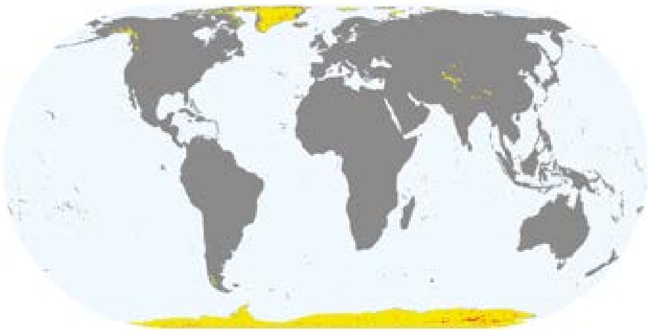
ECOLOGICAL TRAITS: Remarkable lacustrine ecosystems occur beneath permanent ice sheets. They are placed within the Lakes biome (F2) due to their relationships with some Freeze-thaw lakes (F2.4), but they share several key features with the Subterranean freshwater biome (SF1). Evidence of their existence first emerged in 1973 from airborne radar-echo sounding imagery, which penetrates the ice cover and shows lakes as uniformly flat structures with high basal reflectivity. The biota of these ecosystems is very poorly known due to technological limitations on access and concerns about the risk of contamination from coring. Only a few shallow lakes up to 1 km beneath ice have been surveyed (e.g. Lake Whillams in West Antarctica and Grímsvötn Lake in Iceland). The exclusively microbial trophic web is truncated, with no photoautotrophs and apparently few multi-cellular predators, but taxonomic diversity is high across bacteria and archaea, with some eukaryotes also represented. Chemosynthesis form the base of the trophic web, chemolithoautotrophic species using reduced Nitrogen, Iron and Sulphur and methane in energy-generating metabolic pathways. The abundance of micro-organisms is comparable to that in groundwater (SF1.2) ($10^4 – 10^5$ cells.ml^{-1}), with diverse morphotypes represented, including long and short filaments, thin and thick rods, spirals, vibrio, cocci and diplococci. Subglacial lakes share several biotic traits with extremophiles within ice (T6.1), subterranean waters (SF1.1, SF1.2) and deep oceans (e.g. M2.3, M2.4, M3.3), including very low productivity, slow growth rates, large cell sizes and aphotic energy synthesis. Although microbes of the few surveyed subglacial lakes, and from accreted ice which has refrozen from lake water, have DNA profiles similar to those of other contemporary microbes, the biota in deeper disconnected lake waters and associated lake-floor sediments could be highly relictual if it evolved in stable isolation over millions of years under extreme selection pressures.



KEY ECOLOGICAL DRIVERS: Subglacial lakes vary in size from less than 1 km^2 to ~10,000 km^2, and most are 10–20 m deep, but Lake Vostok (Antarctica) is at least 1,000 m deep.

The environment is characterised by high isostatic pressure (up to ~350 atmospheres), constant cold temperatures marginally below 0°C, low-nutrient levels, and an absence of sunlight. Oxygen concentrations can be high due to equilibration with gas hydrates from the melting ice sheet base ice, but declines with depth in amictic lakes due to limited mixing, depending on convection gradients generated by cold meltwater from the ice ceiling and geothermal heating from below. Chemical weathering of basal debris is the main source of nutrients supplemented by ice melt.

DISTRIBUTION: Some ~400 subglacial lakes in Antarctica, ~60 in Greenland and a few in Iceland and Canada have been identified from radar remote sensing and modelling.



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F3 Artificial wetlands biome

Hoover Dam, Nevada-Arizona, USA.
Source: Mario Roberto Durán Ortiz on Wikipedia, licensed under CC BY-SA 3.0 (2005)

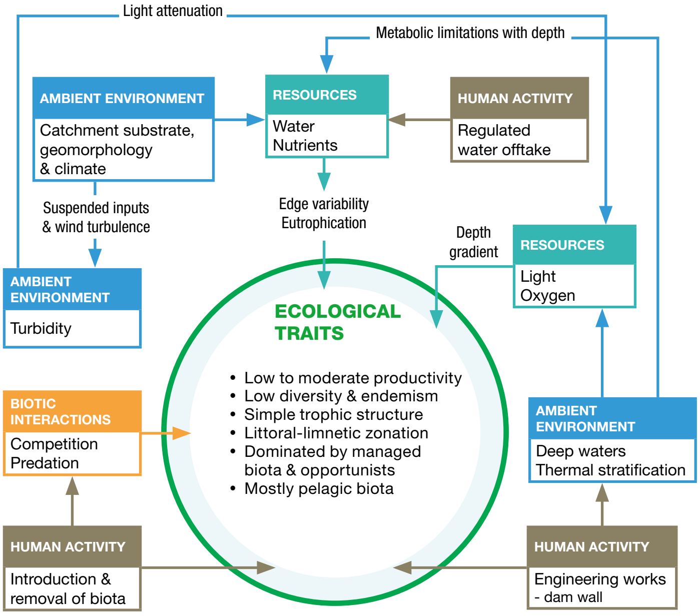
The Artificial wetlands biome includes built structures that hold or transfer water for human use, treatment, or disposal, including large storage reservoirs, farm dams or ponds, recreational and ornamental wetlands, rice paddies, freshwater aquafarms, wastewater storages and treatment ponds, and canals, ditches and drains. These are globally distributed but are most often found in humid and subhumid tropical and temperate environments where rural and urban developments are predominant. Most of these ecosystems contain standing water with the exception of canals and drains. For most of these ecosystems, energy, water and nutrients come primarily from allochthonous sources, either incidentally from runoff (e.g. farm dams, ditches and storm water canals) or groundwater, or deterministically by management (e.g. rice paddies, aquafarms, and wastewater ponds), but autochthonous energy sources (in situ algae and macrophytes) can be important in some artificial waterbodies. Water chemistry varies with human use, with some wastewater ponds accumulating toxins or eutrophic levels of nutrients, while large reservoirs with undisturbed catchments may be oligotrophic. Artificial wetlands are generally less temporally variable, more spatially homogeneous, and often support less biological diversity and trophic complexity of their natural analogues. Nonetheless, in some highly transformed landscapes, they may provide anthropogenic refuges and critical habitat for complementary suites of native biota to that remaining in depleted wetlands, including some biota that no longer occur in natural or semi-natural ecosystems, as well as a range of opportunistic colonists. Trophic webs vary with the connectivity and depth of the water body, temperature and substrate. The simplest artificial wetlands support only microbial biota, while the most diverse can include submerged or emergent plant communities, which promote complex habitats for invertebrates, fish, waterbirds, amphibians, reptiles and, sometimes, amphibious mammals.

F3.1 Large reservoirs

BIOME: F3 ARTIFICIAL WETLANDS
REALM: FRESHWATER

Contributors: D.J. Roux, R.T. Kingsford, C.A. Reidy Liermann, B.J. Robson, M. Kelly-Quinn, D.A. Keith

Gordon Dam, Tasmania, Australia.
Source: Dante Aguiar



ECOLOGICAL TRAITS: Rivers are impounded by the construction of dam walls, creating large freshwater reservoirs, mostly 15–250 m deep. Primary productivity is low to moderate and restricted to the euphotic zone (limnetic and littoral zones), varying with turbidity and associated light penetration, nutrient availability and water temperature. Trophic networks are simple with low species diversity and endemism. Shallow littoral zones have the highest species diversity, including benthic algae, macroinvertebrates, fish, waterbirds, aquatic reptiles, aquatic macrophytes and terrestrial or amphibious vertebrates. Phytoplankton and zooplankton occur through the littoral and limnetic zones. The profundal zone lacks primary producers and, if oxygenated, is dominated by benthic detritivores and microbial decomposers. Fish communities inhabit the limnetic and littoral zones and may be dominated by managed species and opportunists. Reservoirs may undergo eutrophic succession due to inflow from catchments with sustained fertiliser application or other nutrient inputs.

KEY ECOLOGICAL DRIVERS: Reservoirs receive water from the rivers they impound. Managed release or diversion of water alters natural variability. Large variations in water level produce wide margins that are intermittently inundated or dry, limiting productivity and the number of species able to persist there. Inflow volumes may be regulated. Inflows may contain high concentrations of phosphorus and/or nitrogen (e.g. from sewerage treatment effluents or fertilised farmland), leading to eutrophication. Reservoirs in upper catchments generally receive less nutrients and cooler water (due to altitude) than those located downstream. Geomorphology, substrate and land use of the river basin influence the amount of inflowing suspended sediment, and hence turbidity, light penetration and the productivity of planktonic and benthic algae, as well as rates of sediment build-up on the reservoir floor. Depth gradients in light and oxygen, as well as thermal stratification, strongly influence the structure of biotic communities and trophic interactions, as do human introductions of fish, aquatic plants and other alien species.

DISTRIBUTION: Large reservoirs are scattered across all continents with the greatest concentrations in Asia, Europe and North America. Globally, there are more than 3,000 reservoirs with a surface area ≥50 km^2.

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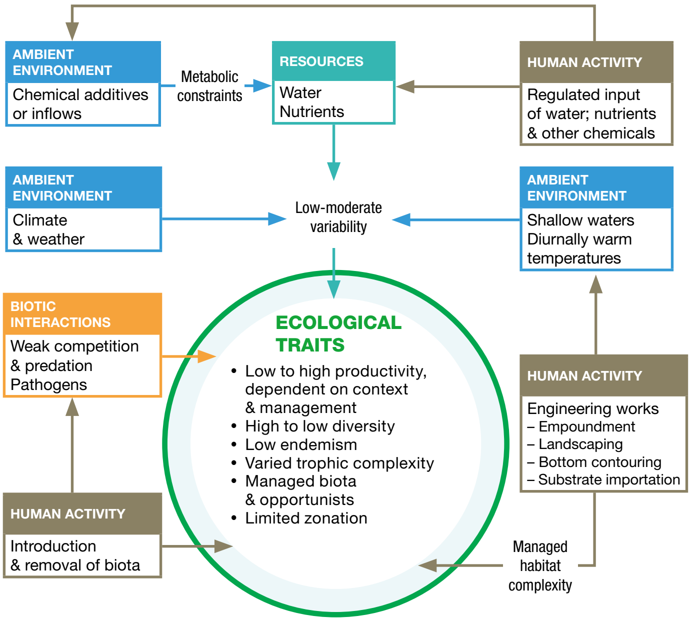
Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J. et al. (2011). 'High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management'. *Frontiers in Ecology and the Environment* 9(9): 494–502.

F3.2 Constructed lacustrine wetlands

BIOME: F3 ARTIFICIAL WETLANDS
REALM: FRESHWATER

Contributors: J.L. Nel, R.T. Kingsford, B.J. Robson, M. Kelly-Quinn, L.J. Jackson, R. Harper, D.A. Keith

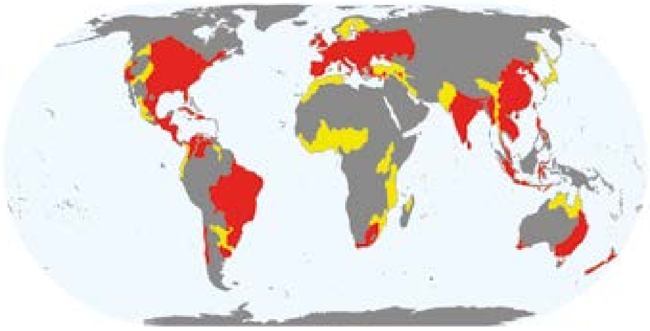
Farm pond, Washington County, Ohio, USA.
Source: Dianne Johnson, USDA



ECOLOGICAL TRAITS: Shallow, open water bodies have been constructed in diverse landscapes and climates. They may be fringed by amphibious vegetation, or else bedrock or bare soil maintained by earthworks or livestock trampling. Emergents rarely extend throughout the water body, but submerged macrophytes are often present. Productivity ranges from very high in wastewater ponds to low in mining and excavation pits, depending on depth, shape, history and management. Taxonomic and functional diversity range from levels comparable to natural lakes to much less, depending on productivity, complexity of aquatic or fringing vegetation, water quality, management and proximity to other waterbodies or vegetation. Trophic structure includes phytoplankton and microbial detritivores, with planktonic and invertebrate predators dominating limnetic zones. Macrophytes may occur in shallow littoral zones or submerged habitats, and some artificial water bodies include higher trophic levels, such as macroinvertebrates, amphibians, turtles, fish and waterbirds. Fish may be introduced by people or arrive by flows connected to source populations, where these exist. Endemism is generally low, but these waterbodies may be important refuges for some species now highly depleted in their natural habitats. Life histories often reflect those found in natural waterbodies nearby, but widely dispersed opportunists dominate where water quality is poor. Intermittent water bodies support biota with drought resistance or avoidance traits, while permanently inundated systems provide habitat for mobile species such as waterbirds.

KEY ECOLOGICAL DRIVERS: Water bodies are constructed for agriculture, mining, stormwater, ornamentation, wastewater, or other uses, or fill depressions left by earthworks, obstructing surface flow or headwater channels. Humans may directly or indirectly regulate inputs of water and chemicals (e.g. fertilisers, flocculants, herbicides), as well as water drawdown. Climate and weather also affect hydrology. Shallow depth and lack of shade may expose open water to rapid solar heating and hence diurnally warm temperatures. Substrates include silt, clay, sand, gravel, cobbles or bedrock, and fine sediments of organic material may build up over time. Nutrient levels are highest in wastewater or with runoff from fertilised agricultural land or urban surfaces. Some water bodies (e.g. mines and industrial wastewaters) have concentrated chemical toxins, extremes of pH or high salinities. Humans may actively introduce and remove the biota of various trophic levels (e.g. bacteria, algae, fish and macrophytes) for water quality management or human consumption.

DISTRIBUTION: Scattered across most regions of the world occupied by humans. Farm dams covered an estimated 77,000 km^2 globally in 2006.



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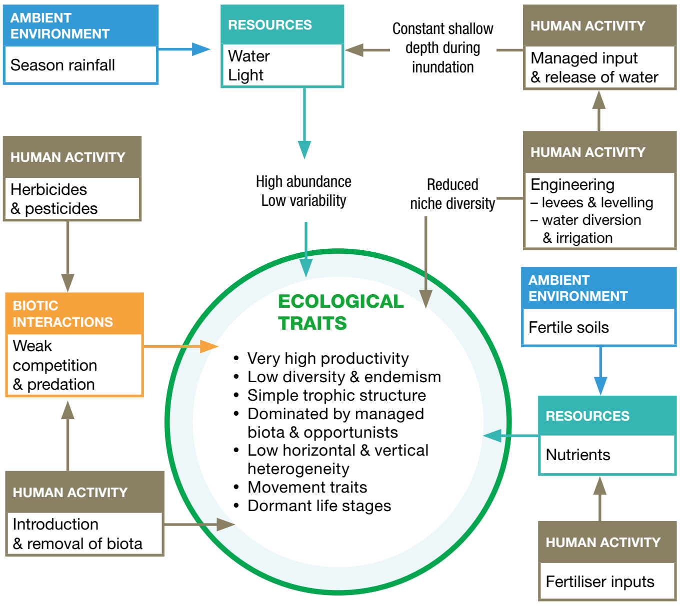
F3.3 Rice paddies

BIOME: F3 ARTIFICIAL WETLANDS
REALM: FRESHWATER

Contributors: R.T. Kingsford, D.A. Keith

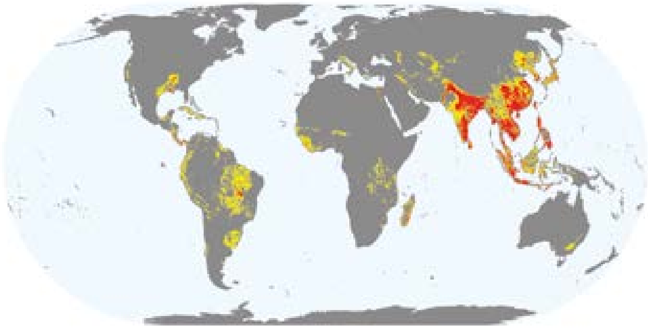

Rice paddies, Hai Duong, Vietnam.
Source: Eric Baker (2010) CC 2.0



ECOLOGICAL TRAITS: Rice paddies are artificial wetlands with low horizontal and vertical heterogeneity fed by rain or irrigation water diverted from rivers. They are predominantly temporary wetlands, regularly filled and dried, although some are permanently inundated, functioning as simplified marshes. Allochthonous inputs come from water inflow but also include the introduction of rice, other production organisms (e.g. fish and crustaceans), and fertilisers that promote rice growth. Simplified trophic networks are sustained by highly seasonal, deterministic flooding and drying regimes and the agricultural management of harvest crops, weeds and pests. Cultivated macrophytes dominate primary production, but other autotrophs, including archaea, cyanobacteria, phytoplankton and benthic or epiphytic algae, also contribute. During flooded periods, microbial changes produce anoxic soil conditions and emissions by methanogenic archaea. Opportunistic colonists include consumers, such as invertebrates, zooplankton, insects, fish, frogs and waterbirds, as well as other aquatic plants. Often they come from nearby natural wetlands or rivers and may breed within rice paddies. During dry phases, obligate aquatic organisms are confined to wet refugia away from rice paddies. These species possess traits that promote tolerance to low water quality and predator avoidance. Others organisms, including many invertebrates and plants, have rapid life cycles and dormancy traits allowing persistence as eggs or seeds during dry phases.

KEY ECOLOGICAL DRIVERS: Engineering of levees and channels enables the retention of standing water a few centimetres above the soil surface and rapid drying at harvest time. This requires reliable water supply either through summer rains in the seasonal tropics or irrigation in warm-temperate or semi-arid climates. The water has high oxygen content and usually warm temperatures. Deterministic water regimes and shallow depths limit niche diversity and have major influences on the physical, chemical, and biological properties of soils, which contain high nutrient levels. Rice paddies are often established on former floodplains but may also be created on terraced hillsides. Other human interventions include cultivation and harvest, aquaculture, and the addition of fertilisers, herbicides and pesticides.

DISTRIBUTION: More than a million square kilometres mostly in tropical and subtropical Southeast Asia with small areas in Africa, Europe, South America, North America and Australia.



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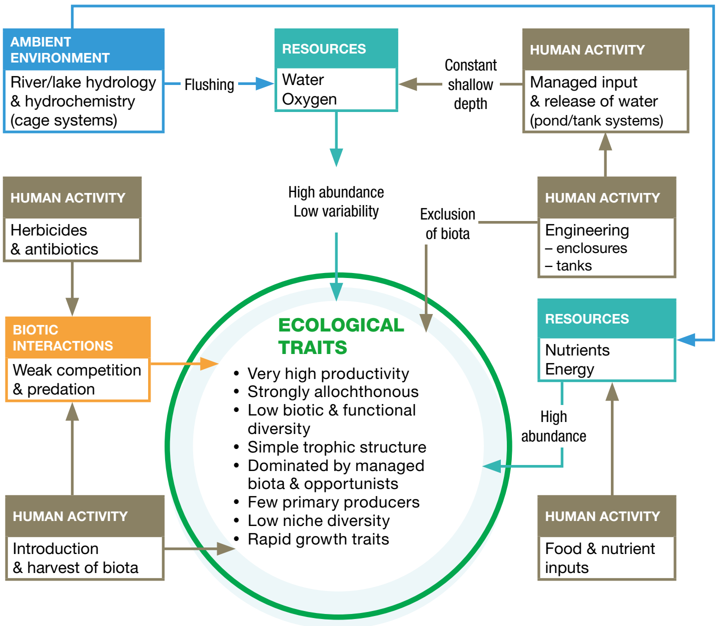
Fish farms, Rumpin, west Java, Indonesia.
Source: Tom Fisk

F3.4 Freshwater aquafarms

BIOME: F3 ARTIFICIAL WETLANDS
REALM: FRESHWATER

Contributors: R.T. Kingsford, M. Beveridge, D.A. Keith



ECOLOGICAL TRAITS: Freshwater aquaculture systems are mostly permanent water bodies in either purpose-built ponds, tanks, or enclosed cages within artificial reservoirs (F3.1), canals (F3.5), freshwater lakes (F2.1 and F2.2) or lowland rivers (F1.2). These systems are shaped by large allochthonous inputs of energy and nutrients to promote secondary productivity by one or a few target consumer species (mainly fish or crustaceans), which are harvested as adults and restocked as juveniles on a regular basis. Fish are sometimes raised in mixed production systems within rice paddies (F3.3), but aquaculture ponds may also be co-located with rice paddies, which are centrally located and elevated above the level of the ponds. The enclosed structures exclude predators of the target species, while intensive anthropogenic management of hydrology, oxygenation, toxins, competitors and pathogens maintains a simplified trophic structure and near-optimal survival and growth conditions for the target species. Intensive management and low niche diversity within the enclosures limit the functional diversity of biota within the system. However, biofilms and phytoplankton contribute low levels of primary production, sustaining zooplankton and other herbivores, while microbial and invertebrate detritivores break down particulate organic matter. Most of these organisms are opportunistic colonists, as are insects, fish, frogs and waterbirds, as well as aquatic macrophytes. Often these disperse from nearby natural wetlands, rivers and host waterbodies.

KEY ECOLOGICAL DRIVERS: Aquafarms are small artificial water bodies with low horizontal and vertical heterogeneity. Water regimes are mostly perennial but may be seasonal (i.e. when integrated with rice production). Engineering of tanks, channels and cages enables the intensive management of water, nutrients, oxygen levels, toxins, other aspects of water chemistry, as well as the introduction of target species and the exclusion of pest biota. Water lost through seepage and evaporation may be replenished by water from nearby lakes or streams. In more intensively managed pond systems, freshwater may also be added to improve water quality and dissolved oxygen, together with inputs of antibiotics and chemicals (e.g. pesticides and fertilisers). These additives influence the physical, chemical and biological properties of the water column and substrate. When located within cages in natural water bodies, freshwater aquafarms reflect the hydrological and hydrochemical properties of their host waterbody. Nutrient inputs drive the accumulation of ammonium and nitrite nitrogen, as well as phosphorus and declining oxygen levels, which may lead to eutrophication within aquaculture sites and receiving waters.

DISTRIBUTION: Concentrated in Asia but also in parts of northern and western Europe, North and West Africa, South America, North America, and small areas of southeast Australia and New Zealand.

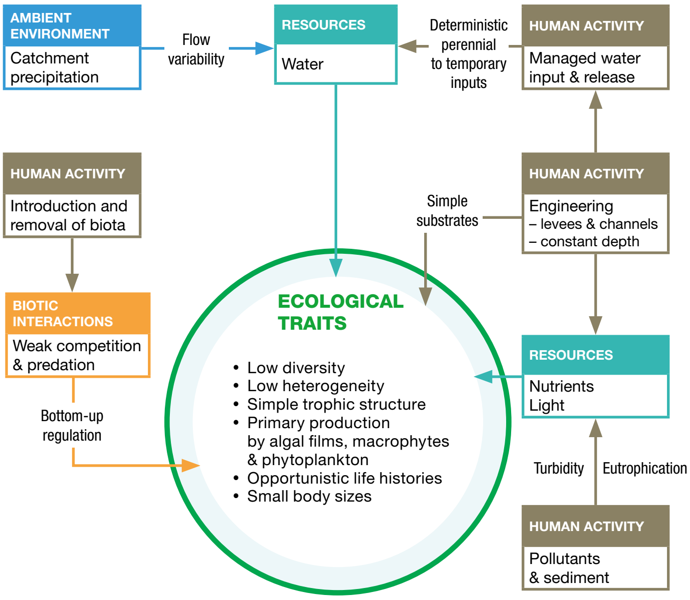
Reference:
Ottinger, M., Clauss, K., Kuenzer, C.J.O. (2016). 'Aquaculture: Relevance, distribution, impacts and spatial assessments – A review'. *Ocean & Coastal Management* 119: 244–266.

F3.5 Canals, ditches and drains

BIOME: F3 ARTIFICIAL WETLANDS
REALM: FRESHWATER

Contributors: R.T. Kingsford, B.J. Robson, M. Kelly-Quinn, D.A. Keith

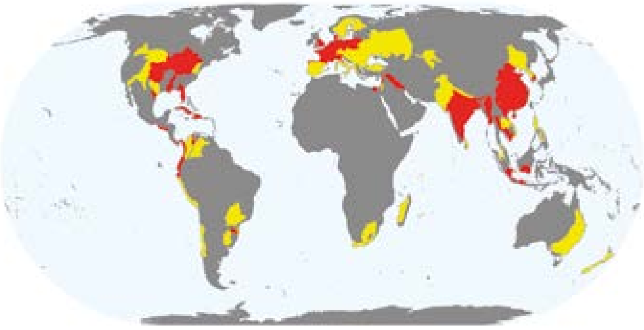
Irrigation canal and valve, California, USA.
Source: Richard Thornton



ECOLOGICAL TRAITS: Canals, ditches and storm water drains are artificial streams with low horizontal and vertical heterogeneity. They function as rivers or streams and may have simplified habitat structure and trophic networks, although some older ditches have fringing vegetation, which contributes to structural complexity. The main primary producers are filamentous algae and macrophytes that thrive on allochthonous subsidies of nutrients. Subsidies of organic carbon from urban or rural landscapes support microbial decomposers and mostly small invertebrate detritivores. While earthen banks and linings may support macrophytes and a rich associated fauna, sealed or otherwise uniform substrates limit the diversity and abundance of benthic biota. Fish and crustacean communities, when present, generally exhibit lower diversity and smaller body sizes compared to natural systems, and are often dominated by introduced or invasive species. Waterbirds, when present, typically include a low diversity and density of herbivorous and piscivorous species. Canals, ditches and drains may provide pathways for dispersal or colonisation of native and invasive biota.

KEY ECOLOGICAL DRIVERS: Engineered levees and channels enable managed water flow for human uses, including water delivery for irrigation or recreation, water removal from poorly drained sites or sealed surfaces (i.e. storm water drains), or routes for navigation. Deterministic water regimes and often shallow depths have major influences on the physical, chemical, and biological properties of the canals, ditches and drains. Flows in some ditches may be very slow, approaching lentic regimes. Flows in storm water drains they vary with rain or other inputs. Irrigation, transport or recreation canals, usually have steady perennial flows but may be seasonal for irrigation or intermittent where the water source is small. Turbidity varies but oxygen content is usually high. Substrates and banks vary from earthen material or hard surfaces (e.g. concrete, bricks), affecting suitability for macrophytes and niche diversity. The water may carry high levels of nutrients and pollutants due to inflow and sedimentation from sealed surfaces, sewerage, other waste sources, fertilised cropping, or pasture lands.

DISTRIBUTION: Urban landscapes and irrigation areas mostly in temperate and subtropical latitudes. Several hundred thousand kilometres of ditches and canals in Europe.



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Nunes, A.L., Tricarico, E., Panov, V.E., Cardoso, A.C., Katsanevakis, S. (2015). 'Pathways and gateways of freshwater invasions in Europe'. *Aquatic Invasions* 10(4), 359–370.
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FM1 Semi-confined transitional waters biome

Klamanth River estuary, CA, USA.
Source: U.S. Army Corps of Engineers

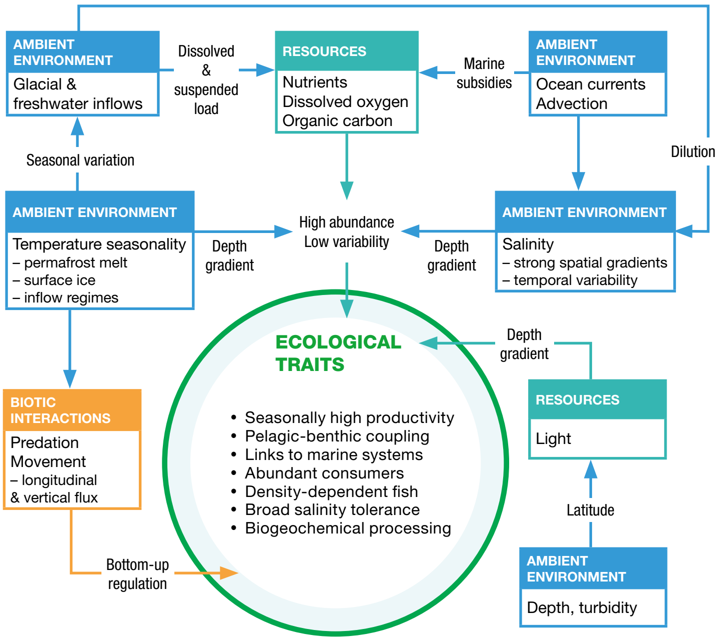
The Transitional waters biome includes coastal inlets that are influenced by inputs of both fresh and marine water from terrestrial catchments and ocean tides, waves and currents. They include deep-water coastal inlets or fjords mostly restricted to high latitudes, as well as estuaries, bays and lagoons, which are scattered around coastlines throughout the world. Gradients in water regimes, water chemistry, depth, temperature, size and salinity influence the function, productivity, diversity and trophic structure of these transitional ecosystems. The balance between marine or freshwater influences varies seasonally and inter-annually, depending on the climate and among inlets with differing geomorphology, catchment size, climate and exposure to waves and currents. In some cases, ecosystems characteristic of the marine shelf biome (i.e. M1.1 Seagrass meadows) may have significant occurrences within semi-confined transitional waters. Some inlets are permanently connected to the ocean, but others are only intermittently connected, influencing exchanges of water, nutrients and biota among ecosystems. The dynamics of connection and closure of shallow inlets are regulated by variations in steam flow inputs and wave activity. Strong horizontal and vertical salinity gradients (varying with freshwater and marine inputs) structure biotic communities and traits that equip species for occupying different salinity niches. Autochthonous energy generated by primary production from aquatic macrophytes, phytoplankton, macroalgae and diatoms is subsidised by allochthonous inputs from inlet shorelines, freshwater streams and marine incursion. These high levels of energy availability support complex trophic networks, including large populations of macroinvertebrates, fish, waterbirds, seabirds and some mammals and reptiles. Many inlets function as fish nurseries and bird breeding sites.

FM1.1 Deepwater coastal inlets

BIOME: FM1 TRANSITIONAL WATERS
REALM: TRANSITIONAL FRESHWATER-MARINE

Contributors: D.A. Keith, E.J. Gregr, A. Lindgaard, T.S. Bianchi

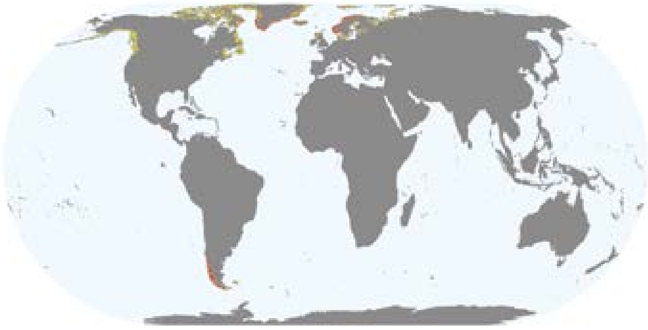
Sognefjord, Norway.
Source: Arild Lindgaard (2012)



ECOLOGICAL TRAITS: Deepwater coastal inlets (e.g. fjords, sea lochs) are semi-confined aquatic systems with many features of open oceans. Strong influences from adjacent freshwater and terrestrial systems produce striking environmental and biotic gradients. Autochthonous energy sources are dominant, but allochthonous sources (e.g. glacial ice discharge, freshwater streams and seasonal permafrost meltwater) may contribute 10% or more of particulate organic matter. Phytoplankton, notably diatoms, contribute most of the primary production, along with biofilms and macroalgae in the epibenthic layer. Seasonal variation in inflow, temperatures, ice cover and insolation drives pulses of in situ and imported productivity that generate blooms in diatoms, consumed in turn by jellyfish, micronekton, a hierarchy of fish predators and marine mammals. Fish are limited by food, density-dependent predation and cannibalism. As well as driving pelagic trophic networks, seasonal pulses of diatoms shape biogeochemical cycles and the distribution and biomass of benthic biota when they senesce and sink to the bottom, escaping herbivores, which are limited by predators. The vertical flux of diatoms, macrophytes and terrestrial detritus sustains a diversity and abundance of benthic filter-feeders (e.g. maldanids and oweniids). Environmental and biotic heterogeneity underpins functional and compositional contrasts between inlets and strong gradients within them. Zooplankton, fish and jellies distribute in response to resource heterogeneity, environmental cues and interactions with other organisms. Deep inlets sequester more organic carbon into sediments than other estuaries (FM1.2, FM1.3) because steep slopes enable efficient influx of terrestrial carbon and low-oxygen bottom waters abate decay rates. Inlets with warmer water have more complex trophic webs, stronger pelagic-benthic coupling, and utilise a greater fraction of organic carbon, sequestering it in sea-floor sediments at a slower rate than those with cold water.

KEY ECOLOGICAL DRIVERS: Deepwater coastal systems may exceed 300 km in length and 2 km in depth. Almost all have glacial origins and many are fed by active glaciers. The ocean interface at the mouth of the inlets, strongly influenced by regional currents, interacts with large seasonal inputs of freshwater to the inner inlet and wind-driven advection, to produce strong and dynamic spatial gradients in nutrients, salinity and organic carbon. Advection is critical to productivity and carrying capacity of the system. Advection drives water movement in the upper and lower layers of the water column in different directions, linking inlet waters with coastal water masses. Coastal currents also mediate upwelling and downwelling depending on the direction of flow. However, submerged glacial moraines or sills at the inlet mouth may limit marine mixing, which can be limited to seasonal episodes in spring and autumn. Depth gradients in light typically extend beyond the photic zone and are exacerbated at high latitudes by seasonal variation in insolation and surface ice. Vertical fluxes also create strong depth gradients in nutrients, oxygen, dissolved organic carbon, salinity and temperature.

DISTRIBUTION: Historically or currently glaciated coastlines at polar and cool-temperate latitudes.



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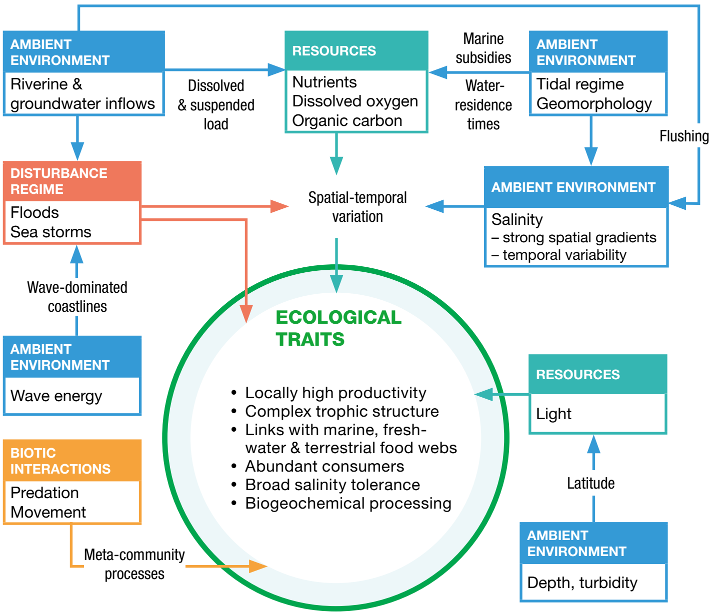
Bianchi, T.S., Arndt, S., Austin, W.E.N., Benn, D.I., Bertrand, S., Cui, X., Faust, J.C., Koziorowska-Makuch, K., Moy, C.M., Savage, C. et al. (2020). 'Fjords as Aquatic Critical Zones (ACZs)'. *Earth-Science Reviews* 203: 103145.
Zaborska, A., Włodarska-Kowalczuk, M., Legeżyńska, J., Jankowska, E., Winogradow, A., Deja, K. (2018). 'Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords — Signs of maturing of Arctic fjordic systems?'. *Journal of Marine Systems* 180: 112–123.

FM1.2 Permanently open riverine estuaries and bays

BIOME: FM1 TRANSITIONAL WATERS
REALM: TRANSITIONAL FRESHWATER-MARINE

Contributors: R. Mac Nally, R. Kingsford, M.J. Bishop, R.J. Woodland, K.A. Dafforn, D.A. Keith

Port Davey, with permanent opening to Southern Ocean, Tasmania, Australia.
Source: Jean-Paul Ferrero/AUSCAPE



ECOLOGICAL TRAITS: These coastal water bodies are mosaic systems characterised by high spatial and temporal variabilities in structure and function, which depend on coastal geomorphology, ratios of freshwater inflows to marine waters and tidal volume (hence residence time of saline water), and seasonality of climate. Fringing shoreline systems may include intertidal mangroves (MFT1.2), saltmarshes and reedbeds (MFT1.3), rocky (MT1.1), muddy (MT1.2) or sandy shores (MT1.3), while seagrasses and macrophytes (M1.1), shellfish beds (M1.4) or subtidal rocky reefs (M1.6) may occur in shallow intertidal and subtidal areas. Water-column productivity is typically higher than in nearby marine or freshwater systems due to substantial allochthonous energy and nutrient subsidies from shoreline vegetation and riverine and marine sources. This high productivity supports a complex trophic network with relatively high mosaic-level diversity and an abundance of aquatic organisms. Planktonic and benthic invertebrates (e.g. molluscs and crustaceans) often sustain large fish populations, with fish nursery grounds being a common feature. Waterbirds (i.e. cormorants), seabirds (i.e. gannets), top-order predatory fish, mammals (e.g. dolphins and dugongs) and reptiles (e.g. marine turtles and crocodilians) exploit these locally abundant food sources. Many of these organisms in upper trophic levels are highly mobile and move among different estuaries through connected ocean waters or by flying. Others migrate between different ecosystem types to complete their various life-history phases, although some may remain resident for long periods. Most biota tolerate a broad range of salinity or are spatially structured by gradients. The complex spatial mixes of physical and chemical characteristics, alongside seasonal, inter-annual, and sporadic variability in aquatic conditions, induce correspondingly large spatial-temporal variability in food webs. Low-salinity plumes, usually proportional to river size and discharge, may extend far from the shore, producing tongues of ecologically distinct conditions into the marine environment.

KEY ECOLOGICAL DRIVERS: Characteristics of these coastal systems are governed by the relative dominance of saline marine waters versus freshwater inflows (groundwater and riverine), the latter depending on the seasonality of precipitation and evaporative stress. Geomorphology ranges from wave-dominated estuaries to drowned river valleys, tiny inlets and enormous bays. These forms determine the residence time, proportion, and distribution of saline waters, which in turn affect salinity and thermal gradients and stratification, dissolved O_2 concentration, nutrients, and turbidity. The water column is closely linked to mudflats and sandflats, in which an array of biogeochemical processes occurs, including denitrification and N-fixation, and nutrient cycling.

DISTRIBUTION: Coastlines of most landmasses but rarely on arid or polar coasts.

Reference:

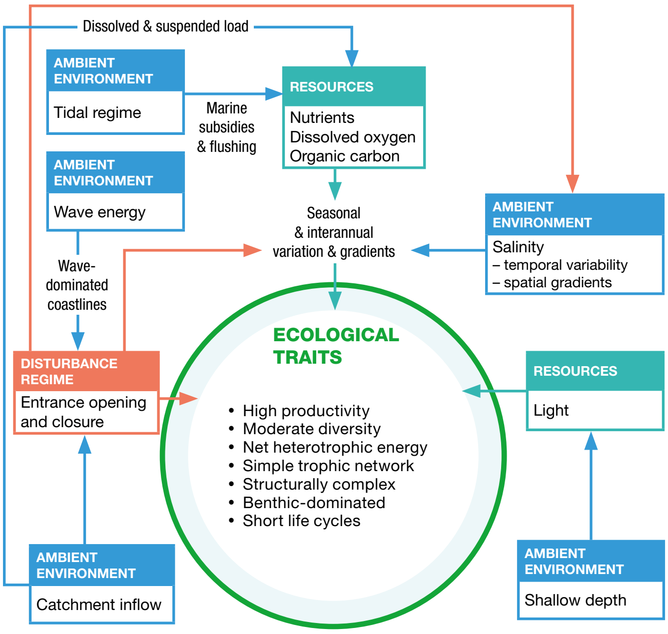
Gillanders, B.M. (2007). 'Linking terrestrial-freshwater and marine environments: An example from estuarine systems'. In: S.D. Connell, B.M. Gillanders (eds.), *Marine ecology*, pp. 252–278. Melbourne, Australia: Oxford University Press.

FM1.3 Intermittently closed and open lakes and lagoons

BIOME: FM1 TRANSITIONAL WATERS
REALM: TRANSITIONAL FRESHWATER-MARINE

Contributors: M.J. Bishop, S.L. McSweeney, R.J. Woodland, K.A. Dafforn, D.A. Keith

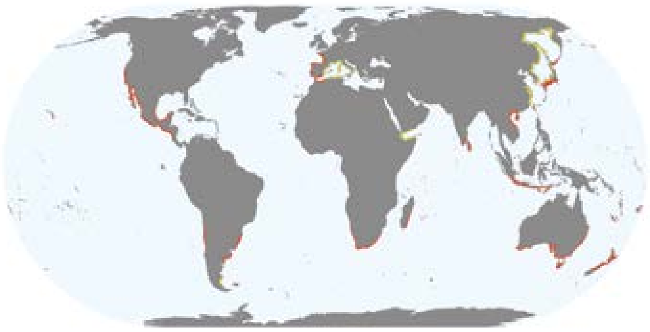
Waituna Lagoon, Southland, New Zealand.
Source: Phil Melgren/Department of Conservation (NZ)



ECOLOGICAL TRAITS: These coastal water bodies have high spatial and temporal variability in structure and function, which depends largely on the status of the lagoonal entrance (open or closed). Communities have low species richness compared to those of permanently open estuaries (FM1.2). Lagoonal entrance closure prevents the entry of marine organisms and resident biota must tolerate significant variation in salinity, inundation, dissolved oxygen and nutrient concentrations. Resident communities are dominated by opportunists with short lifecycles. Trophic networks are generally detritus-based, fuelled by substantial inputs of organic matter from the terrestrial environment and, to a lesser extent, from the sea. As net sinks of organic matter from the land, productivity is often high, and lagoons may serve as nursery habitats for fish. High concentrations of polyphenolic compounds (i.e. tannins) in the water and periods of low nutrient input limit phytoplankton populations. Benthic communities dominate with attached algae, microphytobenthos and micro- and macro-fauna being the dominant groups. The water column supports plankton and small-bodied fish. Emergent and fringing vegetation is key source of detrital carbon to the food webs, and also provides important structural habitats. Saltmarsh and reedbeds (MFT1.3) can adjoin lagoons while seagrasses (M1.1) occupy sandy bottoms of some lagoons, but mangroves (MFT1.2) are absent unless the waters are warm and the entrance opens frequently.

KEY ECOLOGICAL DRIVERS: These are shallow coastal water bodies that are intermittently connected with the ocean. Some lagoons are mostly open, closing only once every few decades. Some open and close frequently, and some are closed most of the time. The timing and frequency of entrance opening depend on the balance between onshore and offshore sedimentation processes (which close the entrance) and flushes of catchment inflow or erosive wave action (which open the entrance). Opening leads to changes in water level, tidal amplitude, salinity gradients, temperature, nutrients, dissolved oxygen and sources of organic carbon. Human-regulated opening influences many of these processes.

DISTRIBUTION: Wave-dominated coastlines worldwide, but prevalent along microtidal to low mesotidal mid-latitude coastlines with high inter-annual variability in rainfall and wave climate. Most prevalent in Australia (21% of global occurrences), South Africa (16%) and Mexico (16%).



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Maher, W., Mikac, K.M., Foster, S., Spooner, D., Williams, D. (2011). 'Form and functioning of micro size Intermittent Closed Open Lake Lagoons (ICOLLs) in NSW, Australia'. In: A.G. Friedman (ed.), *Lagoons: Biology, management and environmental impact*, pp. 119–151. New York, USA: Nova Science Publisher.
McSweeney, S.L., Kennedy, D.M., Rutherfurd, I.D., Stout, J.C. (2017). 'Intermittently Closed/Open Lakes and Lagoons: Their global distribution and boundary conditions'. *Geomorphology* 292: 142–152.

M1 Marine shelf biome

Black and white coral reef, Raja Ampat, West Papua.
Source: Tom Fisk public domain

The Marine shelf biome is distributed globally between the shoreline and deep sea-floor biomes and is dominated by benthic productivity. It includes ecosystems with biogenic substrates (such as seagrass meadows, kelp forests, oyster beds and coral reefs) and minerogenic substrates, including rocky reefs, sandy bottoms and muddy bottoms. The availability of light and nutrients are key structuring factors, influencing productivity and ecosystem structure and function. Turbidity and depth gradients influence light availability. Productivity depends on upwelling currents that deliver nutrients from the deep ocean floor, as well as the strength of nutrient inputs from the land, delivered largely by fluvial systems. Light is influenced by depth gradients, but also by water clarity (cf. turbidity), and determines whether macrophytes and animals dependent on photosynthetic symbionts are able to establish and persist. Additionally, whether the bottom type is hard or soft dictates whether sessile organisms can dominate, forming biogenic habitats that protrude into the water column. A shallow water biome, the marine shelf is shaped by kinetic wave energy and, in polar regions, also ice scour. Positive feedback loops, whereby the habitat structures formed by sessile organisms dampens kinetic energy, can enable ecotypes to persist under marginally suitable conditions. The strength of top-down control by consumers can be an important factor in determining community structure. Depending on the benthic biota, energy sources can vary from net autotrophic to net heterotrophic. Temperature and, to a lesser extent, salinity influence the presence and identity of dominant habitat-forming biota. Currents can influence ecotypes by determining patterns of larval dispersal and the flow of resources.

M1.1 Seagrass meadows

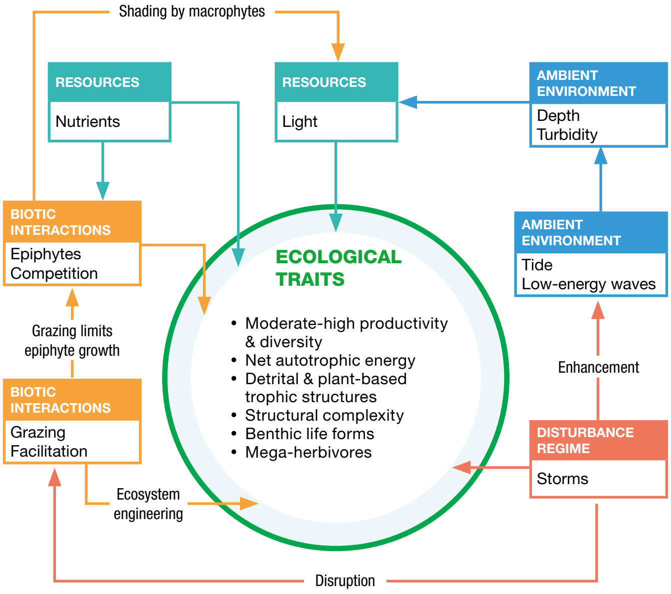
BIOME: M1 MARINE SHELFS
REALM: MARINE

Contributors: M.J. Bishop, A.H. Altieri, S.N. Porter, R.J. Orth, D.A. Keith

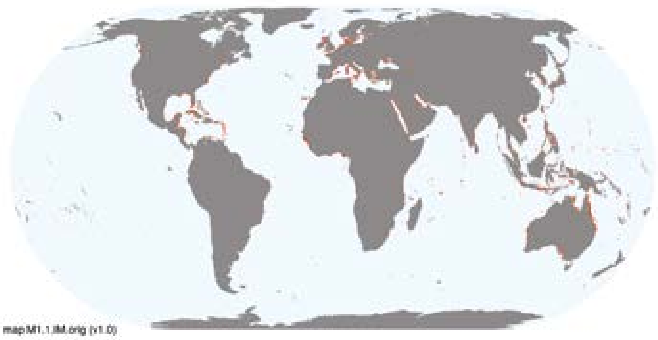
Seagrass meadows off the Florida coast, USA.
Source: U.S. Department of Agriculture (2015) CC

ECOLOGICAL TRAITS: Seagrass meadows are important sources of organic matter, much of which is retained by seagrass sediments. Seagrasses are the only subtidal marine flowering plants and underpin the high productivity of these systems. Macroalgae and epiphytic algae also contribute to productivity, supporting both detritus production and autochthonous trophic structures, but compete with seagrasses for light. The complex three-dimensional structure of the seagrass provides shelter and cover to juvenile fish and invertebrates, binds sediments and, at fine scales, dissipates waves and currents. Seagrass ecosystems support infauna living amongst their roots, epifauna, and epiflora living on their shoots and leaves, as well as nekton in the water column. They have a higher abundance and diversity of flora and fauna, compared to surrounding unvegetated soft sediments and comparable species richness and abundances to most other marine biogenic habitats. Mutualisms with lucinid molluscs may influence seagrass persistence. Mesograzers, such as amphipods and gastropods, play an important role in controlling epiphytic algal growth on seagrass. Grazing megafauna, such as dugongs, manatees and turtles, can contribute to patchy seagrass distributions, although they tend to 'garden' rather than deplete seagrass.

KEY ECOLOGICAL DRIVERS: Typically found in the subtidal zone on soft sedimentary substrates but also occasionally on rocky substrates on low- to moderate-energy coastlines with low turbidity and on intertidal shorelines. Minimum water depth is determined mainly by wave orbital velocity, tidal exposure and wave energy (i.e. waves disturb seagrass and mobilise sediment), while maximum depth is limited by the vertical diminution of light intensity in the water column. Seagrass growth can be limited by nitrogen and phosphorous availability, but in eutrophic waters, high nutrient availability can lead to the overgrowth of seagrasses by epiphytes and shading by algal blooms, leading to ecosystem collapse. Large storm events and associated wave action lead to seagrass loss.



DISTRIBUTION: Widely distributed along the temperate and tropical coastlines of the world.



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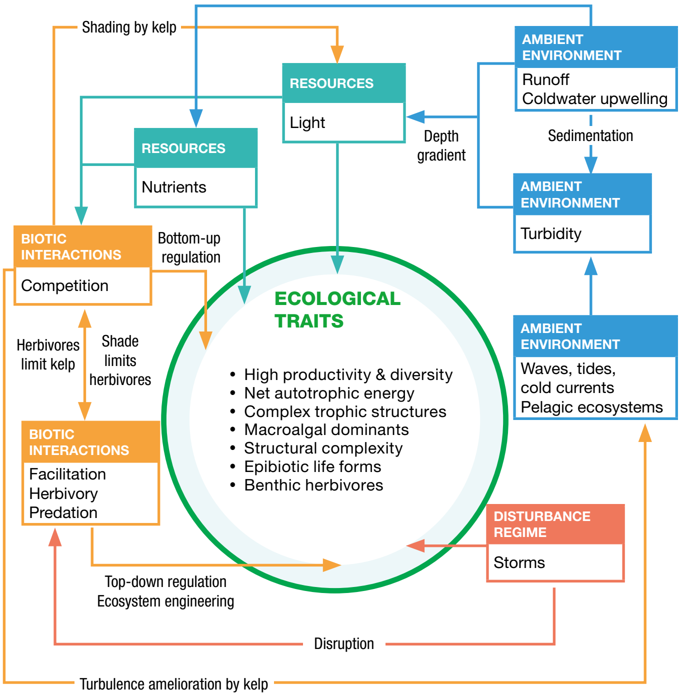
De Boer, W.F. (2007). 'Seagrass–sediment interactions, positive feedbacks and critical thresholds for occurrence: A review'. *Hydrobiologia* 591: 5–24.
Larkum, W.D., Orth, R.J., Duarte, C.M. (eds.) (2006). '*Seagrasses: Biology, Ecology and Conservation*'. The Netherlands: Springer.
Orth, R.J., Carruthers, T.J., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S. et al. (2006). 'A global crisis for seagrass ecosystems'. *BioScience* 56(12): 987–996.
Van der Heide, T., Govers, L.L., de Fouw, J., Olff, H., van der Geest, M., van Katwijk, M.M., Piersma, T., van de Koppel, J., Silliman, B.R., Smolders, A.J.P., van Gils, J.A. (2012). 'A three-stage symbiosis forms the foundation of seagrass ecosystems'. *Science* 336(6087): 1432–1434.

M1.2 Kelp forests

BIOME: M1 MARINE SHELFS
REALM: MARINE

Contributors: D.A. Keith, M.J. Bishop, S.N. Porter, E.J. Gregr

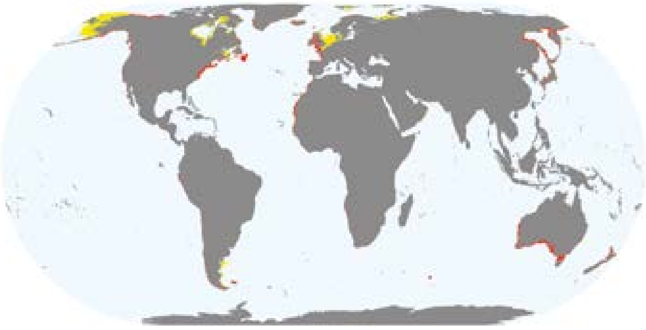
Giant kelp *(Macrocystis pyrifera)*, Channel Islands, California, USA.
Source: Brett Seymour, US Park Service



ECOLOGICAL TRAITS: Kelps are benthic brown macroalgae (Order Laminariales) forming canopies that shape the structure and function of these highly productive, diverse ecosystems. These large (up to 30 m in length), fast-growing (up to 0.5 m/day) autotrophs produce abundant consumable biomass, provide vertical habitat structure, promote niche diversity, alter light-depth gradients, dampen water turbulence and moderate water temperatures. Traits, such as large, flexible photosynthetic organs, rapid growth and strong benthic holdfasts enable kelps to persist on hard substrates in periodically turbulent waters. These kelps may occur as scattered individuals in other ecosystem types, but other macroalgae (e.g. green and coralline) rarely form canopies with similar function and typically form mixed communities with sessile invertebrates (see M1.5 and M1.6). Some kelps are fully submerged, while others form dense canopies on the water surface, which profoundly affect light, turbulence and temperature in the water column. Interactions among co-occurring kelps are generally positive or neutral, but competition for space and light is an important evolutionary driver. Kelp canopies host a diverse epiflora and epifauna, with some limpets having unique kelp hosts. Assemblages of benthic invertebrate herbivores and detritivores inhabit the forest floor, notably echinoderms and crustaceans. The structure and diversity of life in kelp canopies provide forage for seabirds and mammals, such as gulls and sea otters, while small fish find refuge from predators among the kelp fronds. Herbivores keep epiphytes in check, but kelp sensitivity to herbivores makes the forests prone to complex trophic cascades when declines in top predators release herbivore populations from top-down regulation. This may drastically reduce the abundance of kelps and dependent biota, and lead to replacement of the forests by urchin barrens, which persist as an alternative stable state.

KEY ECOLOGICAL DRIVERS: Kelp forests are limited by light, nutrients, salinity, temperature and herbivory. Growth rates are limited by light and proximity to sediment sources. High nutrient requirements are met by terrestrial runoff or upwelling currents, although eutrophication can lead to transition to turf beds. Truncated thermal niches limit the occurrence of kelps in warm waters. Herbivory on holdfasts influences recruitment and can constrain reversals of trophic cascades, even when propagules are abundant. Kelp forests occur on hard substrates in the upper photic zone and rely on wave action and currents for oxygen. Currents also play important roles in dispersing the propagules of kelps and associated organisms. Storms may dislodge kelps, creating gaps that may be maintained by herbivores or rapidly recolonized.

DISTRIBUTION: Nearshore rocky reefs to depths of 30 m in temperate and polar waters. Absent from warm tropical waters but present in upwelling zones off Oman, Namibia, Cape Verde, Peru and the Galapagos.



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Bennett, S., Wernberg, T., De Bettignies, T., Kendrick, G.A., Anderson, R.J., Bolton, J.J., Rodgers, K.L., Shears, N.T., Leclerc, J.C., Lévêque, L., Davoult, D. (2015). 'Canopy interactions and physical stress gradients in subtidal communities'. *Ecology Letters* 18(7): 677–686.
Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A., Tegner, M.J. (2002). 'Kelp forest ecosystem: biodiversity, stability, resilience and their future'. *Environmental Conservation* 29(4): 436–459.
Wernberg, T., Filbee-Dexter, K. (2019). 'Missing the marine forest for the trees'. *Marine Ecology Progress Series* 612: 209–215.

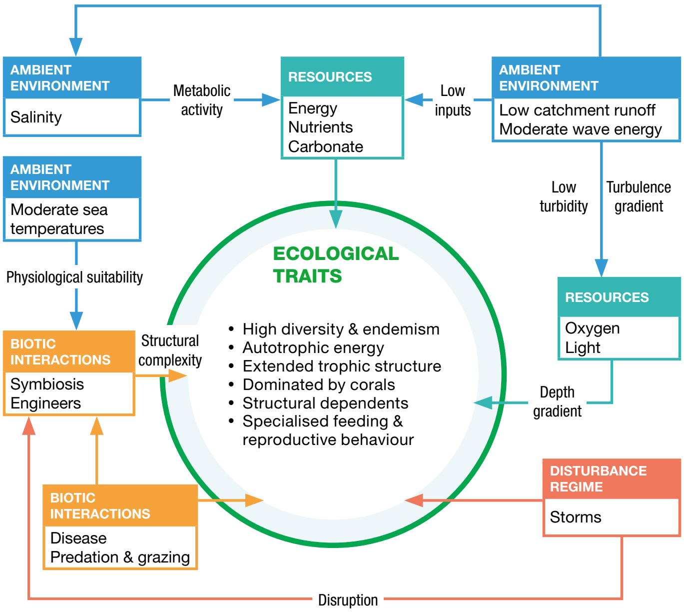
M1.3 Photic coral reefs

BIOME: M1 MARINE SHELFS
REALM: MARINE

Contributors: B.A. Polidoro, S. Rossi, C.R.C. Sheppard, S.N. Porter, D.A. Keith

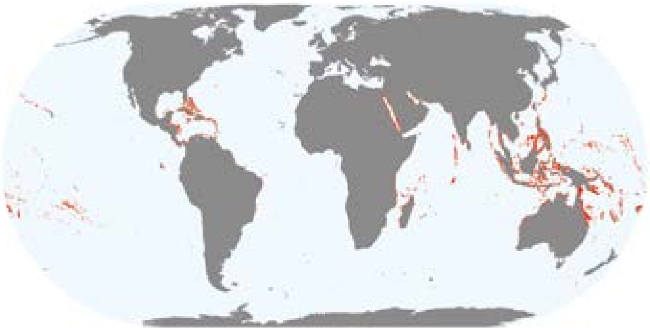
Coral reefs, structurally complex and harbouring diverse marine life, the Red Sea.
Source: Francesco Ungaro on Unsplash (free use)

ECOLOGICAL TRAITS: Coral reefs are biogenic structures that have been built up and continue to grow over decadal timescales as a result of the accumulation of calcium carbonate laid down by hermatypic (scleractinian) corals and other organisms. Reef-building corals are mixotrophic colonies of coral polyps in endosymbiotic relationships with photosynthesizing zooxanthellae that assimilate solar energy and nutrients, providing almost all of the metabolic requirements for their host. The corals develop skeletons by extracting dissolved carbonate from seawater and depositing it as aragonite crystals. Corals reproduce asexually, enabling the growth of colonial structures. They also reproduce sexually, with mostly synchronous spawning related to annual lunar cues. Other sessile organisms, including sponges, soft corals, gorgonians, coralline algae and other algae, add to the diversity and structural complexity of coral reef ecosystems. The complex three-dimensional structure provides a high diversity of habitat niches and resources that support a highly diverse and locally endemic marine biota, including crustaceans, polychaetes, holothurians, echinoderms and other groups, with one-quarter of marine life estimated to depend on reefs for food and/or shelter. Diversity is high at all taxonomic levels relative to all other ecosystems. The trophic network is highly complex, with functional diversity represented on the benthos and in the water column by primary producers, herbivores, detritivores, suspension-feeders, and multiple interacting levels of predators. Coral diseases also play a role in reef dynamics. The vertebrate biota includes fish, snakes, turtles and mammals. The fish fauna is highly diverse, with herbivores and piscivores displaying a wide diversity of generalist and specialist diets (including parrot fish that consume corals), feeding strategies, schooling and solitary behaviours and reproductive strategies. The largest vertebrates include marine turtles and sharks.



KEY ECOLOGICAL DRIVERS: Coral reefs are limited to warm, shallow (rarely >60 m deep), clear, relatively nutrient-poor, open coastal waters, where salinity is 3.0–3.8% and sea temperatures vary (17–34°C). Cooler temperatures are insufficient to support coral growth, while warmer temperatures cause coral symbiosis to break down (i.e. bleaching). Reef geomorphology varies from atolls, barrier reefs, fringing reefs and lagoons to patch reefs depending upon hydrological and geological conditions. Reef structure and composition vary with depth gradients, such as light intensity and turbulence, and exposure gradients, such as exposure itself and sedimentation. Storm regimes and marine heat waves (thermal anomalies) drive cycles of reef destruction and renewal.

DISTRIBUTION: Tropical and subtropical waters on continental and island shelves, mostly within latitudes of 30°N and 30°S.



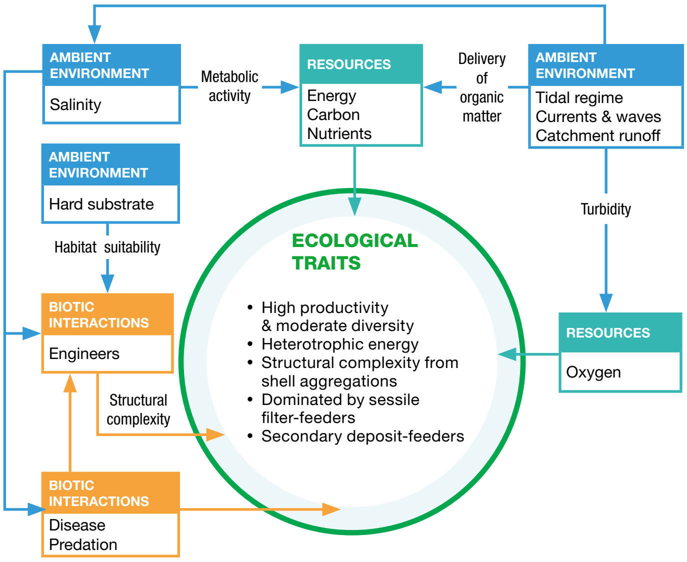
Reference:
Sheppard, C., Davy, S., Pilling, G. and Graham, N. (2018). *The Biology of Coral Reefs*. Second Edition. Oxford, UK: Oxford University Press.

M1.4 Shellfish beds and reefs

BIOME: M1 MARINE SHELFS
REALM: MARINE

Contributors: M.J. Bishop, S.E. Swearer, S.N. Porter, A.H. Altieri, D.A. Keith

Oyster reef, Georges Bay, Tasmania, Australia.
Source: Chris Gillies, The Nature Conservancy (with permission)



ECOLOGICAL TRAITS: These ecosystems are founded on intertidal or subtidal three-dimensional biogenic structures formed primarily by high densities of oysters and/or mussels, which provide habitat for a moderate diversity of algae, invertebrates and fishes, few of which are entirely restricted to oyster reefs. Structural profiles may be high (i.e. reefs) or low (i.e. beds). Shellfish reefs are usually situated on sedimentary or rocky substrates, but pen shells form high-density beds of vertically orientated non-gregarious animals in soft sediments. Sessile filter-feeders dominate these strongly heterotrophic but relatively high-productivity systems. Tides bring in food and carry away waste. Energy and matter in waste is processed by a subsystem of deposit-feeding invertebrates. Predators are a small component of the ecosystem biomass, but are nevertheless important in influencing the recruitment, biomass and diversity of prey organisms (i.e. seastar predation on mussels). Shellfish beds and reefs may influence adjoining estuaries and coastal waters physically and biologically. Physically, they modify patterns of currents, dampen wave energy and remove suspended particulate matter through filter-feeding. Biologically, they remove phytoplankton and produce abundant oyster biomass. They function in biogeochemical cycling as carbon sinks, by increasing denitrification rates, and through N burial/sequestration. Relatively (or entirely) immobile and thin-shelled juveniles are highly susceptible to benthic predators, such as crabs, fish and birds. Recruitment can depend on protective microhabitats provided either by abiogenic or biogenic structures. In intertidal environments, the survival of shellfish can increase with density due to self-shading and moisture retention.

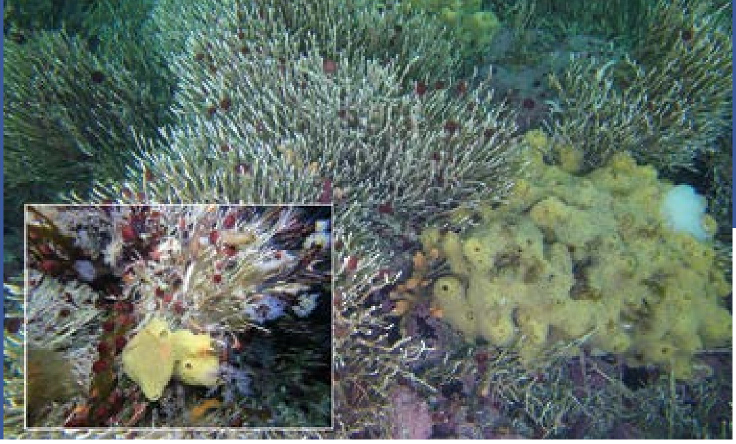
KEY ECOLOGICAL DRIVERS: The availability of hard substrate, including shells of live or dead conspecifics, can limit the establishment of reef-forming shellfish, though a few occur on soft substrates. Many shellfish are robust to changes in salinity, closing their valves for days to weeks to avoid adverse conditions, but salinity may indirectly influence survival by determining susceptibility to parasites. High suspended sediment loads caused by high energy tides, rainfall and runoff events, or the erosion of coastal catchments can smother larvae and impede filter-feeding. Most reef- or bed-building shellfish cannot survive prolonged periods of low dissolved oxygen. They are also sensitive to climate change stressors, such as temperature (and associated increased risk of desiccation for intertidal species), as well as lowered pH as they are calcifiers. In subtidal environments, the formation of reefs can help elevate animals above anoxic bottom waters.

DISTRIBUTION: Estuarine and coastal waters of temperate and tropical regions, extending from subtidal to intertidal zones. Present-day distributions are shaped by historic overharvest, which has removed 85% of reefs globally.

References:
Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C. et al. (2011). 'Oyster Reefs at Risk and Recommendations for Conservation, Restoration and Management'. *BioScience* 61(2): 107–116.
Dame, R.F. and Patten, B.C. (1981). 'Analysis of Energy Flows in an Intertidal Oyster Reef'. *Marine Ecology Progress Series* 5: 115–124.

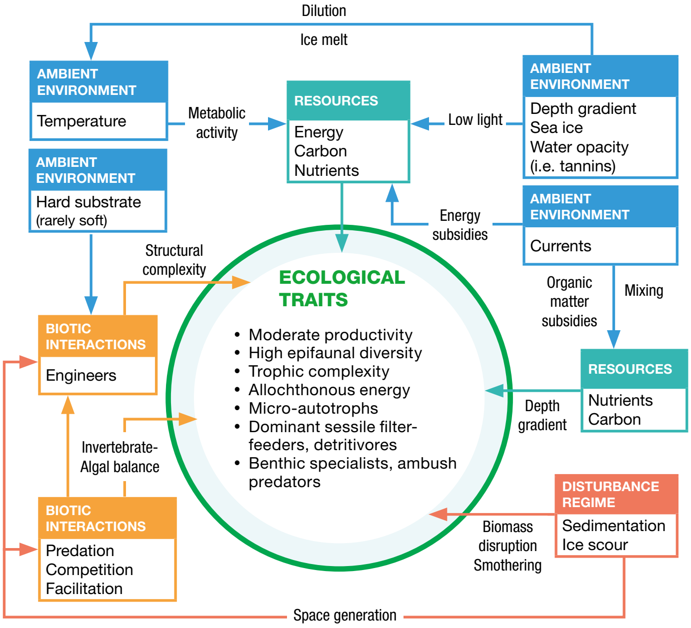
M1.5 Photo-limited marine animal forests

BIOME: M1 MARINE SHELFS
REALM: MARINE



Polychaete reef ~20 m deep, Ellis fjord, Antarctica.
Source: Jonathan Stark, Australian Antarctic Division

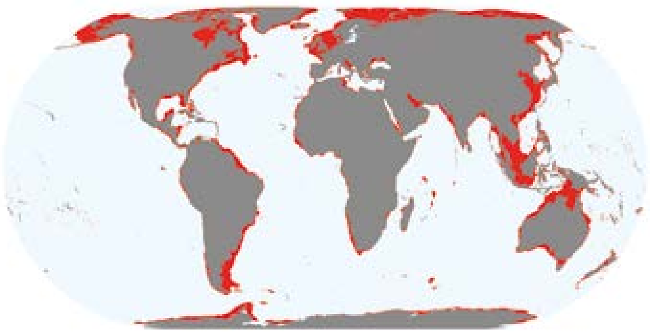
Contributors: J.S. Stark, E.J. Gregr, S. Rossi, S.N. Porter, A.H. Altieri, D.A. Keith



ECOLOGICAL TRAITS: These benthic systems are characterised by high densities of megabenthic, sessile heterotrophic suspension feeders that act as habitat engineers and dominate a subordinate autotrophic biota. Unlike coral reefs and shellfish beds (also animal forests), the major sessile animals include sponges, aphotic corals, hydroids, ascidians, hydrocorals, bryozoans, polychaetes and bivalves (the latter only dominate in M1.4). These engineer complex three-dimensional biogenic structures, sometimes of a single species or distinct phylogenetic groups. The structural complexity generates environmental heterogeneity and habitat, promoting a high diversity of invertebrate epifauna, with microphytobenthos and fish. Endemism may be high. Low light limits primary productivity especially by macroalgae, although microphytobenthos can be important. Energy flow and depth-related processes distinguish these systems from their deepwater aphotic counterparts (M3.7). Overall, however, these systems are strongly heterotrophic, relying on benthic-pelagic coupling processes. Consequently, these systems are generally of moderate productivity and are often found near shallower, less photo-limited, high-productivity areas. Complex biogeochemical cycles govern nutrient release, particle retention and carbon fixation. Biodiversity is enhanced by secondary consumers (i.e. deposit-feeding and filter-feeding invertebrates). Predators may influence the biomass and diversity of epifaunal prey organisms. Recruitment processes in benthic animals can be episodic and highly localised and, together with slow growth rates, limit recovery from disturbance.

KEY ECOLOGICAL DRIVERS: Light is generally insufficient to support abundant macroalgae but is above the photosynthetic threshold for coralline algae and cyanobacteria. Light is limited by diffusion through deepwater, surface ice cover, turbidity from river outflow, or tannins in terrestrial runoff. Low to moderate temperatures may further limit productivity. These systems are generally found on hard substrates but can occur on soft substrates. Currents or resuspension and lateral transport processes are important drivers of benthic-pelagic coupling, hence food and nutrient supply. Natural physical disturbances are generally of low severity and frequency, but ice scour can generate successional mosaics where animal forests occur on subpolar shelves.

DISTRIBUTION: Tropical to polar coastal waters extending from the shallow subtidal to the 'twilight' zone on the shelf. Present-day distributions are likely to have been modified by benthic trawling.



References:

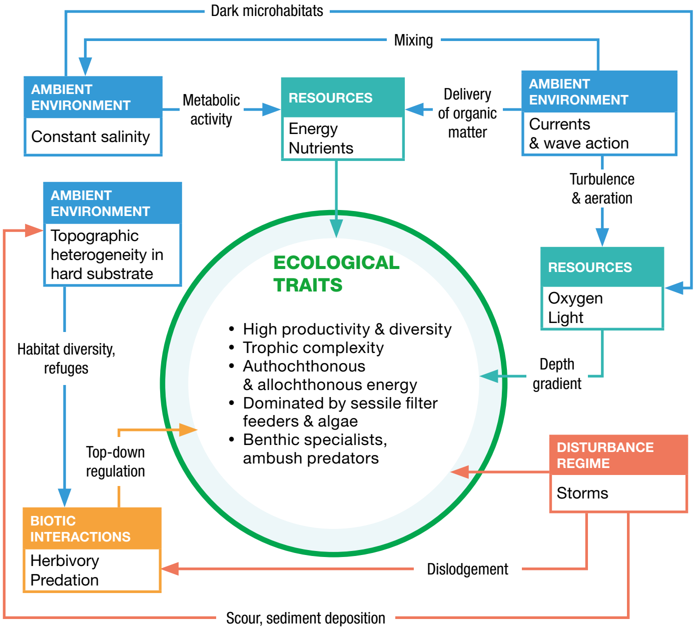
Baldwin, C., Tornabene, L., Robertson, D. (2018). 'Below the mesophotic'. *Scientific Reports* 8: 4920.
Rossi, S., Bramanti, L., Gori, A., Orejas, C. (eds.) (2017). *Marine Animal Forests: The Ecology of Benthic Diodiversity Hotspots*. Cham, Switzerland: Springer.
Rossi, S. (2013). 'The destruction of the 'animal forests' in the oceans: Towards an over-simplification of the benthic ecosystems'. *Ocean & Coastal Management* 84: 77–85.

M1.6 Subtidal rocky reefs

BIOME: M1 MARINE SHELFS
REALM: MARINE

Contributors: B.A. Polidoro, E.J. Gregr, S.E. Swearer, S.N. Porter, D.A. Keith

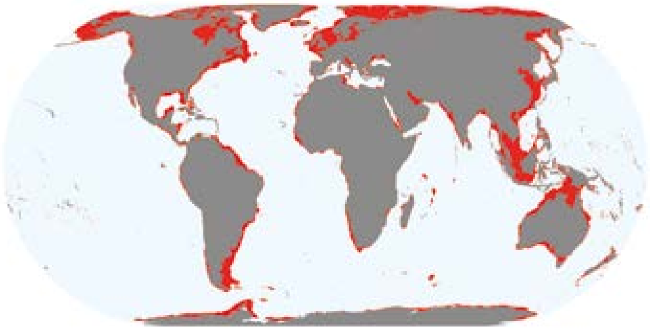
Starry rockfish and strawberry anemone on a rocky reef, Cordell Bank, USA
Source: Jodi Pirtle



ECOLOGICAL TRAITS: Submerged rocky reefs host trophically complex communities lacking a dense macroalgal canopy (cf. M1.2). Sessile primary producers and invertebrate filter-feeders assimilate autochthonous and allochthonous energy, respectively. Mobile biota occur in the water column. Reef-associated organisms have diverse dispersal modes. Some disperse widely as adults, some have non-dispersing larvae, others with sessile adult phases develop directly on substrates, or have larval stages or spores dispersed widely by currents or turbulence. Sessile plants include green, brown and red algae. To reduce dislodgement in storms, macroalgae have holdfasts, while smaller species have low-growing 'turf' life forms. Many have traits, such as air lacunae or bladders that promote buoyancy. Canopy algae are sparse at the depths or levels of wave exposure occupied by this functional group (cf. kelp forests in M1.2). Algal productivity and abundance decline with depth due to diminution of light and are also kept in check by periodic storms and a diversity of herbivorous fish, molluscs and echinoderms. The latter two groups and some fish are benthic and consume algae primarily in turf form or at its juvenile stage before stipes develop. Sessile invertebrates occur throughout. Some are high-turbulence specialists (e.g. barnacles, ascidians and anemones), while others become dominant at greater depths as the abundance of faster-growing algae diminishes (e.g. sponges and red algae). Fish include both herbivores and predators. Some are specialist bottom-dwellers, while others are more generalist pelagic species. Herbivores promote diversity through top-down regulation, influencing patch dynamics, trophic cascades and regime shifts involving kelp forests in temperate waters (M1.2). Mosaics of algal dominance, sessile invertebrate dominance and barrens may shift over time. Topographic variation in the rocky substrate promotes habitat diversity and spatial heterogeneity. This provides refuges from predators but also hiding places for ambush predators including crustaceans and fish.

KEY ECOLOGICAL DRIVERS: Minerogenic rocky substrates with variable topography and cobbles are foundational to the habitats of many plants and animals, influencing how they capture resources and avoid predation. A strong depth gradient and substrate structures (e.g. overhangs and caves) limit light availability, as does turbidity. Currents and river outflows are crucial to the delivery of resources, especially nutrients, and also play a key role in biotic dispersal. Animal waste is a key nutrient source sustaining algal productivity in more nutrient-limited systems. Salinity is relatively constant through time (3.5% on average). Turbulence from subsurface wave action promotes substrate instability and maintains high levels of dissolved oxygen. Episodic storms generating more extreme turbulence shift sand and dislodge larger sessile organisms, create gaps that may be maintained by herbivores or rapidly recolonized.

DISTRIBUTION: Widespread globally on rocky parts of continental and island shelves.



Reference:

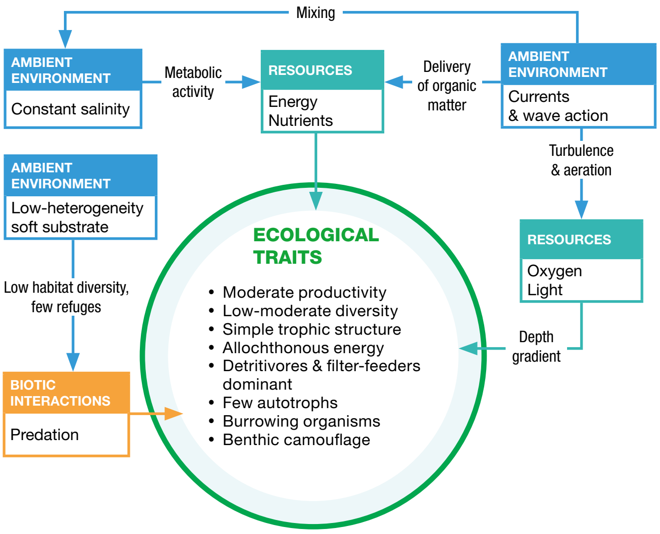
Witman, J.D., Genovese, S.J., Bruno, J,F, McLaughlin, J.W. and Pavlin, B,I, (2003). 'Massive prey recruitment and the control of rocky subtidal communities on large spatial scales'. *Ecological Monographs* 73(3): 441–462.

M1.7 Subtidal sand beds

BIOME: M1 MARINE SHELFS
REALM: MARINE

Contributors: B.A. Polidoro, S.E. Swearer, D.A. Keith

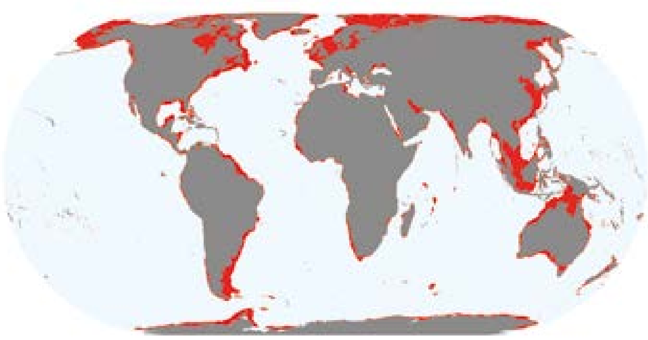
Left: Dover sole on sand, Cordell Bank National Marine Sanctuary, CA, USA. Right: Jawfish in sandy burrow.
Sources: Left, Rick Starr, NOAA/CBNMS; right: Andrew David, NOAA/NMFS



ECOLOGICAL TRAITS: Medium to coarse-grained, unvegetated and soft minerogenic sediments show moderate levels of biological diversity. The trophic network is dominated by consumers with very few in situ primary producers. Interstitial microalgae and planktonic algae are present, but larger benthic primary producers are limited either by substrate instability or light, which diminishes with depth. In shallow waters, where light is abundant and soft substrates are relatively stable, this group of systems is replaced by group M1.1, which is dominated by vascular marine plants. In contrast to those autochthonous systems, subtidal sand beds rely primarily on allochthonous energy, with currents generating strong bottom flows and a horizontal flux of food. Sandy substrates tend to have less organic matter content and lower microbial diversity and abundance than muddy substrates (M1.8). Soft sediments may be dominated by invertebrate detritivores and suspension-feeders, including burrowing polychaetes, crustaceans, echinoderms and molluscs. Suspension-feeders tend to be most abundant in high-energy environments where waves and currents move sandy sediments, detritus, and living organisms. The homogeneity and low structural complexity of the substrate exposes potential prey to predation, especially from pelagic fish. Large bioturbators, such as dugongs, stingrays and whales, may also be important predators. Consequently, many benthic animals possess specialised traits that enable other means of predator avoidance, such as burrowing, shells or camouflage.

KEY ECOLOGICAL DRIVERS: The substrate is soft, minerogenic, low in organic matter, relatively homogeneous, structurally simple and mobile. The pelagic waters are moderate to high-energy environments, with waves and currents promoting substrate instability. Nonetheless, depositional processes dominate over erosion, leading to net sediment accumulation. Fluvial inputs from land and the erosion of headlands and sea cliffs contribute sediment, nutrients and organic matter, although significant lateral movement is usually driven by longshore currents. Light availability diminishes with depth. Mixing is promoted by waves and currents, ensuring low temporal variability in salinity, which averages 3.5%.

DISTRIBUTION: Globally widespread around continental and island shelves.



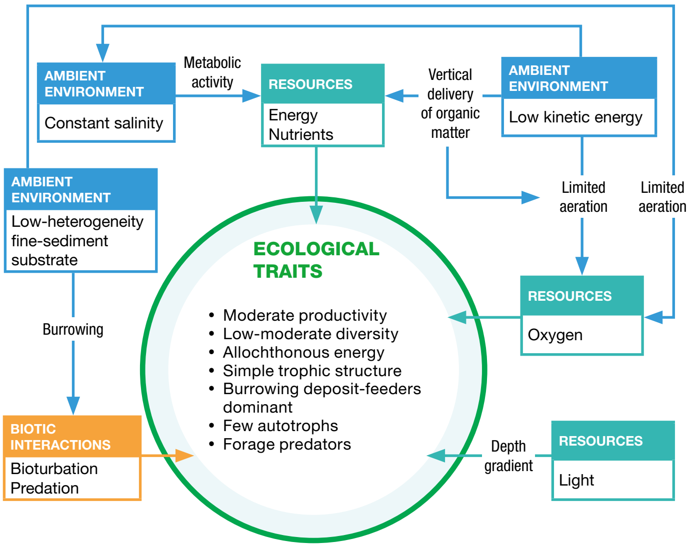
References:
Byers, J.E., Grabowski, J.H. (2014). 'Soft-sediment communities'. In: M.D. Bertness, J.F. Bruno, B.R. Silliman and J.J. Stachowicz (eds.), *Marine community ecology and conservation*, pp. 227–249. Oxford, UK: Oxford University Press.
Snelgrove, P.V.R. (1999). 'Getting to the Bottom of Marine Biodiversity: Sedimentary Habitats: Ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services'. *BioScience* 49(2): 129–138.

M1.8 Subtidal mud plains

BIOME: M1 MARINE SHELFS
REALM: MARINE

Contributors: B.A. Polidoro, S.E. Swearer, D.A. Keith

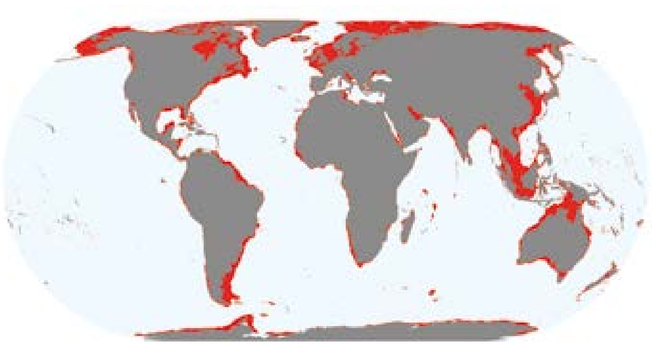
Polynoid worm on muddy sediments, near Puerto Rico and U.S. Virgin Islands.
Source: NOAA Ocean Exploration and Research



ECOLOGICAL TRAITS: The muddy substrates of continental and island shelves support moderately productive ecosystems based on net allochthonous energy sources. In situ primary production is contributed primarily by microphytobenthos, mainly benthic diatoms with green microalgae, as macrophytes are scarce or absent. Both decline with depth as light diminishes. Drift algae can be extensive over muddy sediments, particularly in sheltered waters. Abundant heterotrophic microbes process detritus. The microbial community mediates most of the biogeochemical cycles in muddy sediments, with features distinguishing these ecosystems from subtidal sand beds (M1.7). Deposit feeders (notably burrowing polychaetes, crustaceans, echinoderms and molluscs) are important components of the trophic network, as the low kinetic energy environment promotes vertical food fluxes, which they are able to exploit more effectively than suspension-feeders. The latter are less abundant on subtidal mud plains than on rocky reefs (M1.6) and Subtidal sand beds (M1.7), where waters are more turbulent and generate stronger lateral food fluxes. Deposit feeders may also constrain the abundance of co-occurring suspension-feeders by disturbing benthic sediment that resettles and smothers their larvae and clogs their filtering structures. Nonetheless, suspension-feeding tube worms may be common over muddy sediments when settlement substrates are available. Although such interference mechanisms may be important, competition is generally weak. In contrast, foraging predators, including demersal fish, may have a major structuring influence on these systems through impacts on the abundance of infauna, particularly on settling larvae and recently settled juveniles, but also adults. Burrowing is a key mechanism of predator avoidance, and the associated bioturbation is influential on microhabitat diversity and resource availability within the sediment.

KEY ECOLOGICAL DRIVERS: These depositional systems are characterised by low kinetic energy (weak turbulence and currents), which promotes the accumulation of fine-textured, stable sediments that are best developed on flat bottoms or gentle slopes. The benthic surface is relatively homogeneous, except where structure is engineered by burrowing organisms. The small particle size and poor interchange of interstitial water limit oxygen supply, and anaerobic conditions are especially promoted where abundant in-fall of organic matter supports higher bacterial activity that depletes dissolved oxygen. On the other hand, the stability of muddy substrates makes them more conducive to the establishment of permanent burrows. Bioturbation and bio-irrigation activities by a variety of benthic fauna in muddy substrates are important contributors to marine nutrient and biogeochemical cycling as well as the replenishment of oxygen.

DISTRIBUTION: Globally distributed in the low-energy waters of continental and island shelves.



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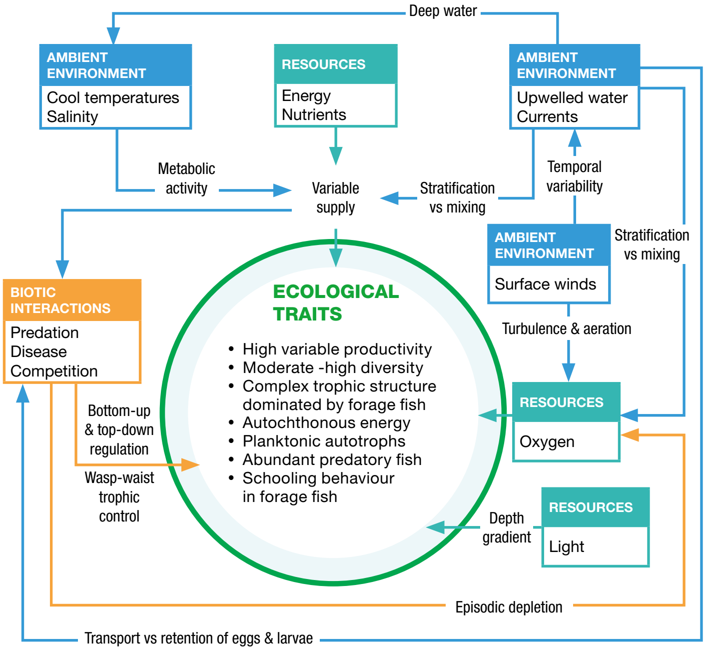
Byers, J.E., Grabowski, J.H. (2014). 'Soft-sediment communities'. In: M.D. Bertness, J.F. Bruno, B.R. Silliman and J.J. Stachowicz (eds.), *Marine community ecology and conservation,* pp. 227–249. Oxford, UK: Oxford University Press.
Snelgrove, P.V.R. (1999). 'Getting to the Bottom of Marine Biodiversity: Sedimentary Habitats: Ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services'. *BioScience* 49(2): 129–138.

M1.9 Upwelling zones

BIOME: M1 MARINE SHELFS/PELAGIC OCEAN WATERS
REALM: MARINE

Contributors: K.E. Watermeyer, E.J .Gregr, R.R. Rykaczewski, L.J. Shannon, I.M. Suthers, D.A. Keith

Sardine school in the upwelling zone, Mactan, Cebu, Philippines.
Source: Juuyoh Tanaka (2007) Wikimedia Commons



ECOLOGICAL TRAITS: Upwelled, nutrient-rich water supports very high net autochthonous primary production, usually through diatom blooms. These in turn support high biomass of copepods, euphausiids (i.e. krill), pelagic and demersal fish, marine mammals and birds. Fish biomass tends to be dominated by low- to mid-trophic level species, such as sardine, anchovy and herring. The abundance of these small pelagic fish has been hypothesised to drive ecosystem dynamics through 'wasp-waist' trophic control. Small pelagic fish exert top-down control on the copepod and euphausiid plankton groups they feed on and exert bottom-up control on predatory fish, although diel-migrant mesopelagic fish (M2.2) may have important regulatory roles. Abundant species of higher trophic levels include hake and horse mackerel, as well as pinnipeds and seabirds. Highly variable reproductive success of planktivorous fish reflects the fitness of spawners and suitable conditions for concentrating and retaining eggs and larvae inshore prior to maturity.

KEY ECOLOGICAL DRIVERS: Upwelling is a wind-driven process that draws cold, nutrient-rich water towards the surface, displacing warmer, nutrient-depleted waters. The strength of upwelling depends on interactions between local current systems and the Coriolis effect that causes divergence, generally on the eastern boundaries of oceans. The rate of upwelling, the offshore transportation of nutrients and the degree of stratification in the water column once upwelling has occurred all determine the availability of nutrients to plankton, and hence the size and structure of the community that develops after an event. The main upwelling systems around the world extend to depths of up to 500 m at the shelf break, although primary production is restricted to the epipelagic zone (<200 m). Upwelling zones are characterised by low sea-surface temperatures and high chlorophyll a concentrations, high variability due to large-scale interannual climate cycles (e.g El Niño Southern Oscillation), as well as the pulsed and seasonal nature of the driving winds, and periodic low-oxygen, low pH events due to high biological activity and die-offs.

DISTRIBUTION: The most productive upwelling zones are coastal, notably in four major eastern-boundary current systems (the Canary, Benguela, California and Humboldt). Weaker upwelling processes occurring in the open ocean are included in M2.1 (i.e. along the intertropical convergence zone).

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Demarcq, H. (2009). 'Trends in primary production, sea surface temperature and wind in upwelling systems (1998–2007)'. *Progress in Oceanography* 83(1–4): 376-385.
Hutchings, L., Pitcher, G.C., Probyn, T.A., Bailey, G.W. (1995). 'The chemical and biological consequences of coastal upwelling'. In: C.P. Summerhayes, K.C. Emeis, M.V. Angel, R.L. Smith, B. Zeitzschel (eds.), *Upwelling in the oceans: Modern processes and ancient records*, pp. 65–81. New York, USA: John Wiley.

M2 Pelagic ocean waters biome

Large school of pelagic ocean fishes.
Source: Hiroko Yoshii on Unsplash

The Pelagic ocean biome is the largest on earth, comprising the open-ocean water column across all latitudes. Diversity is highest in near-surface layers, particularly in niche habitats at water-mass boundaries where contrasting communities overlap. The depth gradient strongly structures the availability of light (and hence constraints on primary producers and visual predators), nutrients and organic carbon, and differentiates functional groups within the biome. Primary production is limited to the uppermost, euphotic, epipelagic zone, while deeper layers depend on allochthonous fluxes of carbon from above via sedimentation or vertically migrating organisms. This flux is diminished by consumers as it falls to deeper layers, resulting in low productivity and low diversity at the greatest depths. A consistent Redfield ratio (C:N:P) throughout the oceans marks feedbacks between planktonic biota and ocean chemistry, with deviations often attributable to nutrient deficiency. Iron and silica concentrations may also be limiting in some waters. Latitudinal variation in productivity relates to the local characteristics of the water column, such as temperature, mixing and availability of nutrients and light. Migration is a common characteristic in this biome, both horizontal between feeding and breeding areas, and diel or ontogenetic vertical migrations, such as that between the refuge provided by the low-light environment in the mesopelagic zone and the productive, upper epipelagic zone with its associated visual predators. Organisms in each depth zone display adaptations to the light environment. Bioluminescence is common in mesopelagic species, while species found at greater, aphotic depths may have enhanced sensory organs.

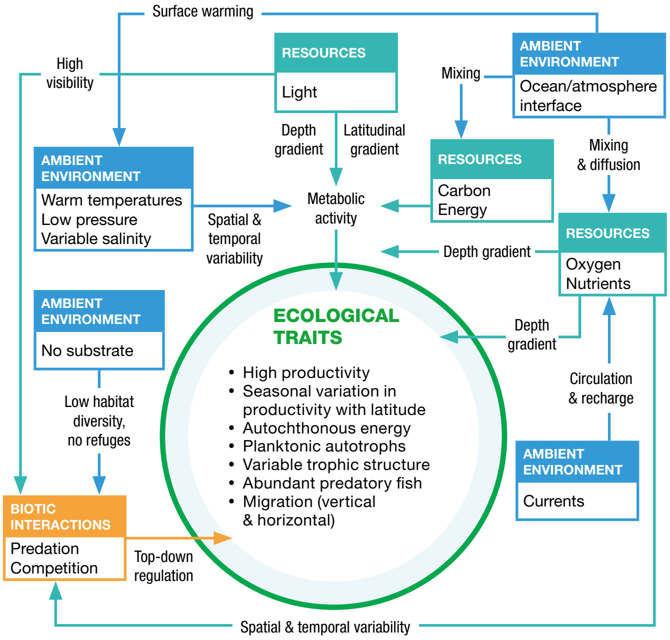
M2.1 Epipelagic ocean waters

BIOME: M2 PELAGIC OCEAN WATERS
REALM: MARINE

Contributors: K.E. Watermeyer, R.R. Rykaczewski, I.G. Priede, T.T. Sutton, D.A. Keith

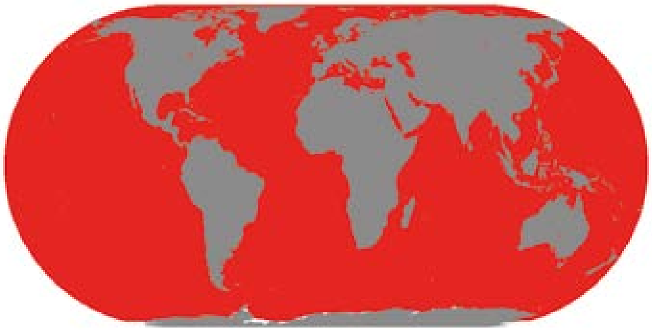
White-tipped Shark, an epipelagic visual predator, near Wake Island, North Pacific Ocean.
Source: NOAA Ocean Exploration and Research

ECOLOGICAL TRAITS: The epipelagic or euphotic zone of the open ocean is the uppermost layer that is penetrated by enough light to support photosynthesis. The vast area of the ocean means that autochthonous productivity in the epipelagic layer, largely by diatoms, accounts for around half of all global carbon fixation. This in turn supports a complex trophic network and high biomass of diatoms, copepods (resident and vertical migrants), fish, cephalopods, marine mammals and seabirds, including fast-swimming visual predators taking advantage of the high-light environment. The suitability of conditions for recruitment and reproduction depends on the characteristics of the water column, which vary spatially and impact productivity rates, species composition, and community size structure. Mid-ocean subtropical gyres, for example, are characteristically oligotrophic, with lower productivity than other parts of the ocean surface. In contrast to the rest of the epipelagic zone, upwelling zones are characterised by specific patterns of water movement that drive high nutrient levels, productivity and abundant forage fish, and are therefore included in a different functional group (M1.9). Seasonal variation in productivity is greater at high latitudes due to lower light penetration and duration in winter compared to summer. The habitat and lifecycle of some specialised pelagic species (e.g. herbivorous copepods, flying fish) are entirely contained within epipelagic ocean waters, but many commonly occurring crustaceans, fish and cephalopods undertake either diel or ontogenetic vertical migration between the epipelagic and deeper oceanic layers. These organisms exploit the food available in the productive epipelagic zone either at night (when predation risk is lower) or for the entirety of their less mobile, juvenile life stages. Horizontal migration is also common and some species (e.g. tuna and migratory whales) swim long distances to feed and reproduce. Other species use horizontal currents for passive migration, particularly smaller planktonic organisms or life stages (e.g. copepods and small pelagic fish larvae) moving between spawning and feeding grounds. Unconsumed plankton and dead organisms sink from this upper oceanic zone, providing an important particulate source of nutrients to deeper, aphotic zones.



KEY ECOLOGICAL DRIVERS: The epipelagic zone is structured by a strong depth gradient in light, which varies seasonally at high latitudes. Light also varies with local turbidity, but at lower latitudes may extend to ~200 m where light attenuates to 1% of surface levels. Interaction at the surface between the ocean and atmosphere leads to increased seasonality, mixing and warming, and makes this the most biologically and physicochemically variable ocean layer. Nutrient levels are spatially variable as a result. Salinity varies with terrestrial freshwater inputs, evaporation and mixing, with greater variation in semi-enclosed areas (i.e. the Mediterranean Sea) than the open ocean.

DISTRIBUTION: The surface layer of the entire open ocean beyond the near-shore zone.



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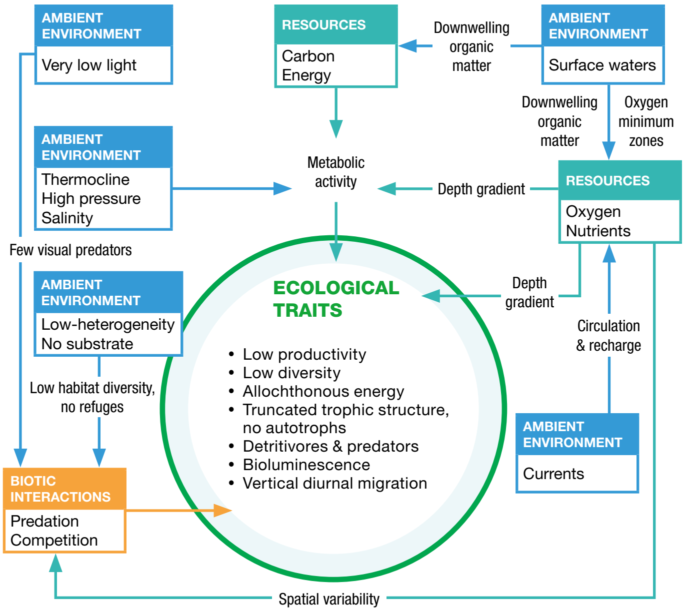
Sutton, T.T. (2013). 'Vertical ecology of the pelagic ocean: Classical patterns and new perspectives'. *Journal of Fish Biology* 83(6): 1508–1527

Sunfish in the mesopelagic zone at ~350 m depth above Pourtalès Terrace, near Florida Keys, USA.
Source: NOAA Ocean Exploration and Research

M2.2 Mesopelagic ocean waters

BIOME: M2 PELAGIC OCEAN WATERS
REALM: MARINE

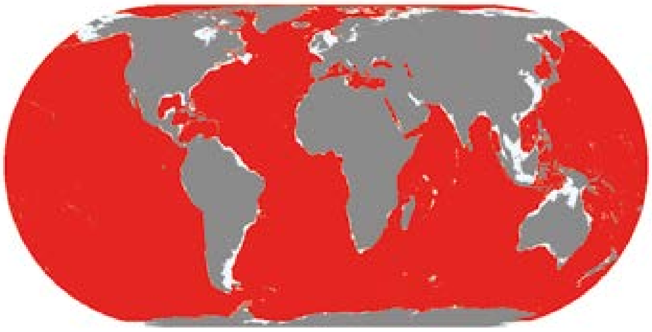
Contributors: K.E. Watermeyer, E.J. Gregr, R.R. Rykaczewski, I.G. Priede, T.T. Sutton, D.A. Keith



ECOLOGICAL TRAITS: The mesopelagic, dysphotic, or 'twilight' zone, begins below the epipelagic layer and receives enough light to discern diurnal cycles but too little for photosynthesis. The trophic network is therefore dominated by detritivores and predators. The diverse organisms within this layer consume and reprocess allochthonous organic material sinking from the upper, photosynthetic layer. Hence, upper mesopelagic waters include layers of concentrated plankton, bacteria and other organic matter sinking from the heterogeneous epipelagic zone (M2.1). Consumers of this material, including detritivorous copepods, deplete oxygen levels in the mesopelagic zone more so than in other layers where oxygen can be replenished via diffusion and mixing at the surface or photosynthesis (as in the epipelagic zone), or where lower particulate nutrient levels limit biological processes (as in the deeper layers). Many species undertake diel vertical migration into the epipelagic zone during the night to feed when predation risk is lower. These organisms use the mesopelagic zone as a refuge during the day and increase the flow of carbon between ocean layers. Bioluminescence is a common trait present in more than 90% of mesopelagic organisms often with silvery reflective skin (i.e. lantern fish). Fish in the lower mesopelagic zone (>700 m) are less reflective and mobile due to reduced selection pressure from visual predators in low light conditions. These systems are difficult to sample, but advances in estimating fish abundances indicate that biomass is very high, possibly two orders of magnitude larger than global fisheries landings (1×10^{10} t).

KEY ECOLOGICAL DRIVERS: Nutrient and energy availability depend on allochthonous fluxes of carbon from the upper ocean. Energy assimilation from sunlight is negligible. This is characteristically episodic and linked to events in the epipelagic zone. Buffered from surface forcing by epipelagic waters, the mesopelagic zone is less spatially and temporally variable, but the interface between the two zones is characterised by heterogeneous regions with greater biotic diversity. Areas of physicochemical discontinuity (e.g. current and water-mass boundaries and eddies) also result in niche habitats with increased local diversity. Oxygen minimum zones are formed in mesopelagic waters when biological activity reduces oxygen levels in a water mass that is then restricted from mixing by physical processes or features. Oxygen minimum zones support specialised biota and have high levels of biological activity around their borders.

DISTRIBUTION: Global oceans from a depth of ~200 m or where <1% of light penetrates, down to 1,000 m.



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Robinson, C., Steinberg, D.K., Anderson, T.R., Aristegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.F., Hernández-León, S., Jackson, G.A., Koppelmann, R. et al. (2010). 'Mesopelagic zone ecology and biogeochemistry – a synthesis'. *Deep-Sea Research II* 57(16): 1504–1518.
Sutton, T.T. (2013). 'Vertical ecology of the pelagic ocean: classical patterns and new perspectives'. *Journal of Fish Biology* 83(6): 1508–1527.

M2.3 Bathypelagic ocean waters

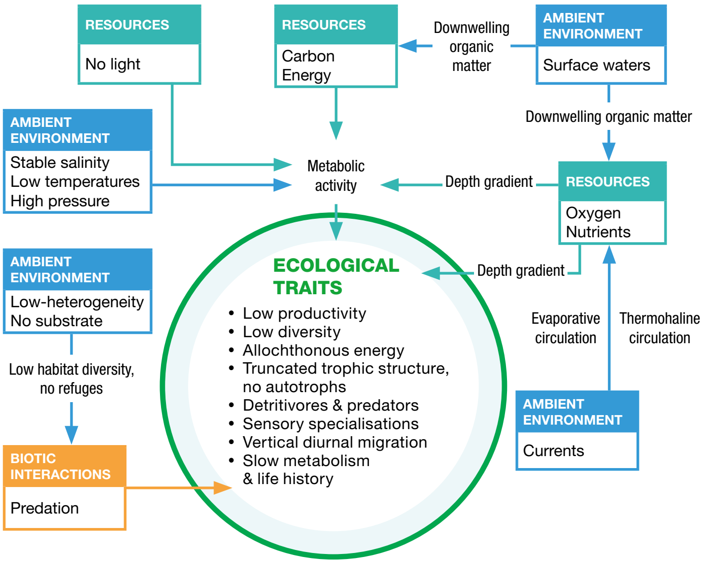
BIOME: M2 PELAGIC OCEAN WATERS
REALM: MARINE

Contributors: C. Linardich, T.T. Sutton, I.G. Priede, D.A. Keith

Dark ctenophore with tentacles extended at 1,460 m depth in the Gulf of Mexico, USA.
Source: NOAA Ocean Exploration and Research

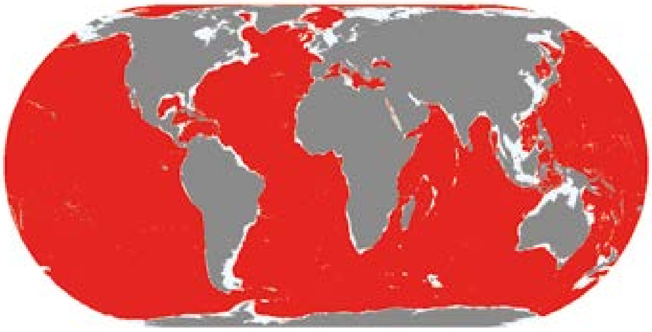
ECOLOGICAL TRAITS: These are deep, open-ocean ecosystems in the water column, generally between 1,000–3,000 m in depth. Energy sources are allochthonous, derived mainly from the fallout of particulate organic matter from the epipelagic horizon (M2.1). Total biomass declines exponentially from an average of 1.45 $mg.C.m^{-3}$ at 1,000 m deep to 0.16 $mg.C.m^{-3}$ at 3,000 m. Trophic structure is truncated, with no primary producers. Instead, the major components are zooplankton, micro-crustaceans (i.e. shrimps), medusozoans (i.e. jellyfish), cephalopods and four main guilds of fish (gelativores, zooplanktivores, micronektivores and generalists). These organisms generally do not migrate vertically, in contrast to those in the mesopelagic zone (M2.2). Larvae often hatch from buoyant egg masses at the surface to take advantage of food sources. Long generation lengths (>20 years in most fish) and low fecundity reflect low energy availability. Fauna typically have low metabolic rates, with bathypelagic fish having rates of oxygen consumption ~10% of that of epipelagic fish. Fish are consequently slow swimmers with high water content in muscles and relatively low red-to-white muscle tissue ratios. They also have low-density bodies, reduced skeletons and/or specialised buoyancy organs to achieve neutral buoyancy for specific depth ranges. Traits related to the lack of light include reduced eyes, lack of pigmentation, and enhanced vibratory and chemosensory organs. Some planktonic forms, medusas and fish have internal light organs that produce intrinsic or bacterial bioluminescence to attract prey items or mates or to defend themselves. Most of the biota possess cell membranes with specialised phospholipid composition, intrinsic protein modifications and protective osmolytes (i.e. organic compounds that influence the properties of biological fluids) to optimise protein function at high pressure.

KEY ECOLOGICAL DRIVERS: No light penetrates from the ocean surface to bathypelagic waters. Oxygen concentrations are not limiting to aerobic respiration (mostly 3–7 $mL.L^{-1}$) and are recharged through thermohaline circulation by cooling.



Oxygenated water is circulated globally from two zones (the Weddell Sea and the far North Atlantic Ocean) where ice formation and surface cooling create high-salinity, oxygenated water that sinks and is subsequently circulated globally via the 'great ocean conveyor'. Re-oxygenation frequency varies from 300 to 1,000 years, depending on the circulation route. More local thermohaline circulation occurs by evaporation in the Mediterranean and Red Seas, resulting in warm temperatures (13–15°C) at great depths. Otherwise, bathypelagic temperatures vary from –1°C in polar waters to 2–4°C in tropical and temperate waters. Nutrient levels are low and derive from the fall of organic remains from surface horizons. Pressure varies with depth from 100 to 300 atmospheres.

DISTRIBUTION: All oceans and deep seas beyond the continental slope and deeper than 1,000 m.

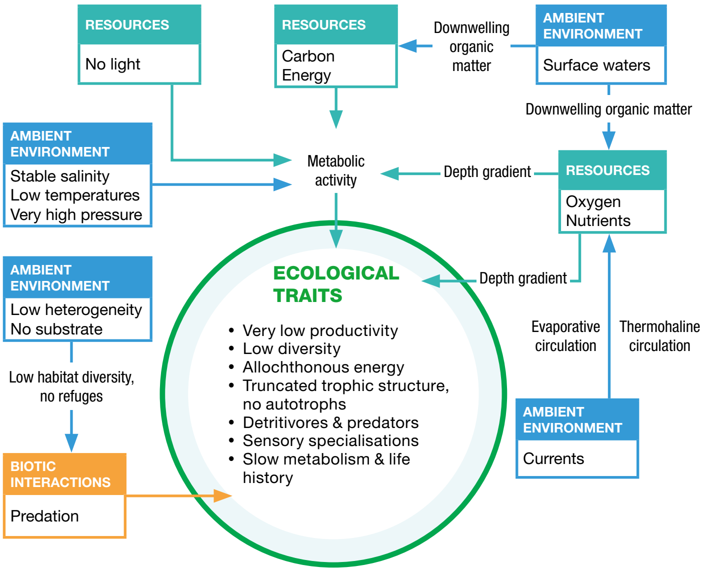


Reference:
Priede, I.G. (2017). *Deep-sea fishes: Biology, diversity, ecology and fisheries*. Cambridge, UK: Cambridge University Press.

M2.4 Abyssopelagic ocean waters

BIOME: M2 PELAGIC OCEAN WATERS
REALM: MARINE

Contributors: C. Linardich, D.A. Keith

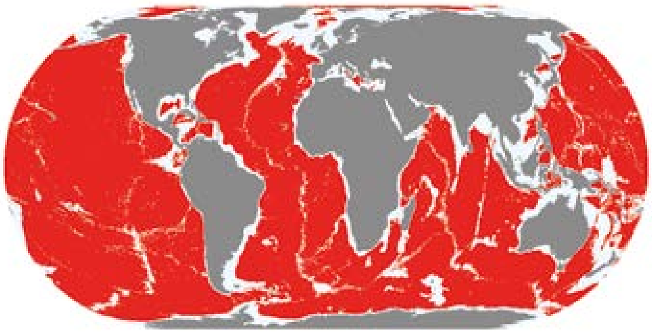


Abyssopelagic anglerfish (*Himantolophus sp.* female) with bioluminescent lure, Atlantic Ocean.
Source: Bluegreen Pictures/Alamy Stock Photo

ECOLOGICAL TRAITS: These deep, open-ocean ecosystems span depths from 3,000 to 6,000 m. Autotrophs are absent and energy sources are entirely allochthonous. Particulate organic debris is imported principally from epipelagic horizons (M2.1) and the flux of matter diminishing through the mesopelagic zone (M2.2) and bathypelagic zone (M2.3). Food for heterotrophs is therefore very scarce. Due to extreme conditions and limited resources, biodiversity is very low. Total biomass declines exponentially from an average of 0.16 mg.C.m^{-3} at 3,000 m deep to 0.0058 mg.C.m^{-3} at 6,000 m. However, there is an order of magnitude variation around the mean due to regional differences in the productivity of surface waters. Truncated trophic networks are dominated by planktonic detritivores, with low densities of gelatinous invertebrates and scavenging and predatory fish. Fauna typically have low metabolic rates and some have internal light organs that produce bioluminescence to attract prey or mates or to defend themselves. Vertebrates typically have reduced skeletons and watery tissues to maintain buoyancy. Most of the biota possesses cell membranes with specialised phospholipid composition, intrinsic protein modifications and protective osmolytes (i.e. organic compounds that influence the properties of biological fluids) to optimise protein function at high pressure.

KEY ECOLOGICAL DRIVERS: No light penetrates from the ocean surface to abyssopelagic waters. Nutrient concentrations are very low and recharge is dependent on organic flux and detrital fall from the epipelagic zone. Oxygen concentrations, however, are not limiting to aerobic respiration (mostly 3–7mL.L^{-1}) and are generally recharged through global thermohaline circulation driven by cooling in polar regions. Water temperatures vary from below zero in polar waters up to 3°C in parts of the Atlantic. Hydrostatic pressure is extremely high (300–600 atmospheres). Currents are weak, salinity is stable and there is little spatial heterogeneity in the water column.

DISTRIBUTION: All oceans and the deepest parts of the Mediterranean Sea beyond the continental slope, mid-ocean ridges, and plateaus at depths of 3,000–6,000 m.



Reference:

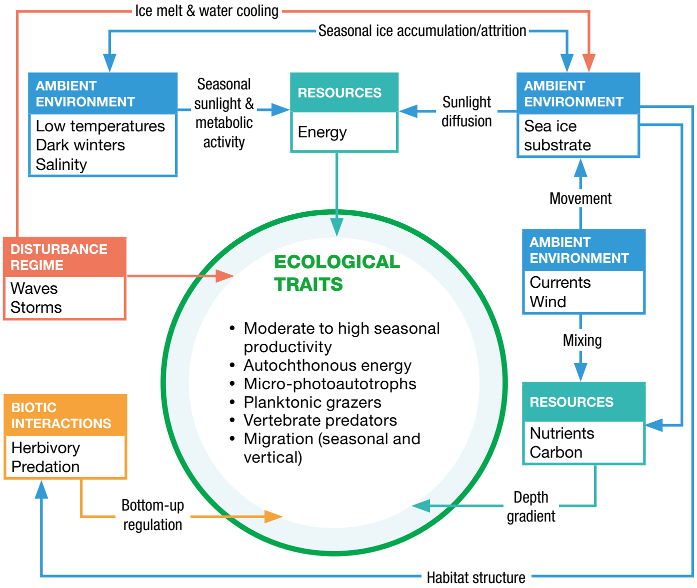
Priede, I.G. (2017). *Deep-sea fishes: Biology, diversity, ecology and fisheries.* Cambridge, UK: Cambridge University Press.

M2.5 Sea ice

BIOME: M2 PELAGIC OCEAN WATERS
REALM: MARINE

Contributors: J.S. Stark, D.A. Keith

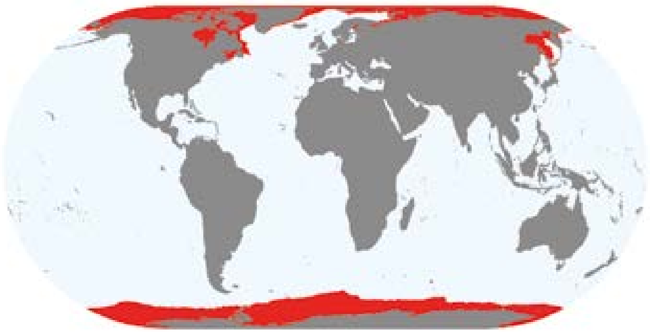
Top: Leopard seal on ice floe. Below left: Krill aggregation under sea ice. Below right: Sea-ice microbes and algae within the pack-ice substratum. Antarctica.
Sources: ACE/CRC/Australian Antarctic Division.



ECOLOGICAL TRAITS: The seasonally frozen surface of polar oceans (1–2 m thick in the Antarctic and 2–3 m thick in the Arctic) may be connected to land or permanent ice shelves and is one of the most dynamic ecosystems on earth. Sympagic (i.e. ice-associated) organisms occur in all physical components of the sea-ice system, including the surface, the internal matrix and brine channel system, the underside and nearby waters modified by sea-ice presence. Primary production by microalgal and microbial communities beneath and within sea ice form the base of the food web, and waters beneath sea ice develop standing stocks significantly higher than in ice free areas, despite shading by the ice. These are grazed by diverse zooplankton, including krill. The sea ice underside provides refuge from surface predators and is an important nursery for juvenile krill and fish. Deepwater fish migrate vertically to feed on zooplankton beneath the sea ice. High secondary production (particularly of krill) in sea ice and around its edges supports seals, seabirds, penguins (in the Antarctic) and baleen whales. The highest trophic levels include vertebrate predators, such as polar bears (in the Arctic), leopard seals and toothed whales. Sea ice also provides resting and/or breeding habitats for pinnipeds (seals), polar bears and penguins. As the sea ice decays annually, it releases biogenic material consumed by grazers and particulate, and dissolved organic matter, nutrients, freshwater and iron, which stimulate phytoplankton growth and have important roles in biogeochemical cycling.

KEY ECOLOGICAL DRIVERS: Sea ice is integral to the global climate system and has a crucial influence on pelagic marine ecosystems and biogeochemical processes. Sea ice limits atmosphere-ocean gas and momentum exchanges, regulates sea temperature, reflects solar radiation, acquires snow cover and redistributes freshwater to lower latitudes. The annual retreat of sea ice during spring and summer initiates high phytoplankton productivity at the marginal ice zone and provides a major resource for grazing zooplankton, including krill. Polynyas, where areas of low ice concentration are bounded by high ice concentrations, have very high productivity levels. Most sea ice is pack-ice transported by wind and currents. Fast ice forms a stationary substrate anchored to the coast, icebergs, glaciers and ice shelves and can persist for decades.

DISTRIBUTION: Arctic Ocean 0–45°N (Japan) or only to 80°N (Spitsbergen). Southern Ocean 55–70°S. At maximum extent, sea ice covers ~5% of the Northern Hemisphere and 8% of the Southern Hemisphere.



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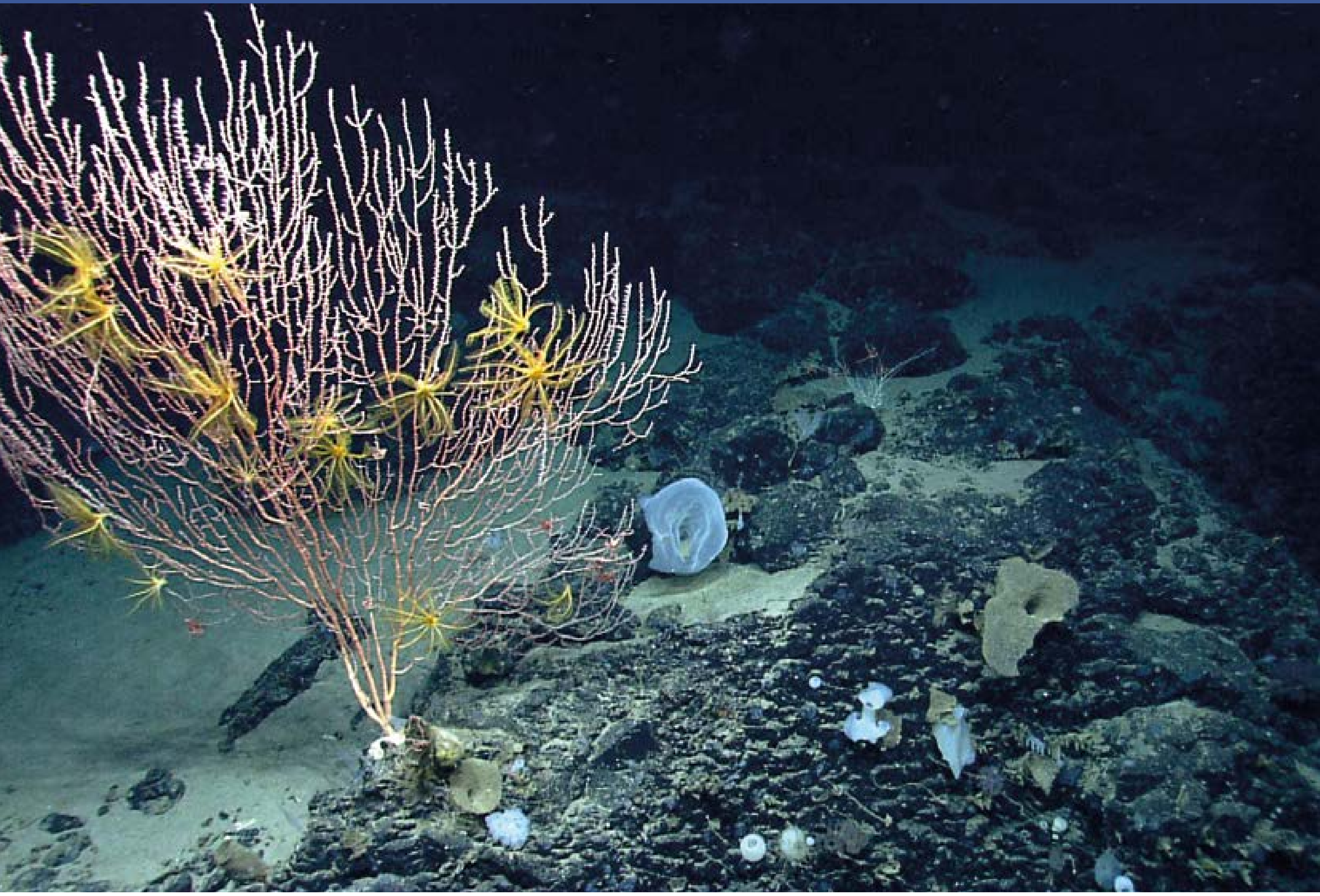
Arrigo, K.R., Thomas, D.N. (2004). 'Large scale importance of sea ice biology in the Southern Ocean'. *Antarctic Science* 16(4): 471–486.
Brierley, A.S., Thomas, D.N. (2002). 'Ecology of Southern Ocean pack ice'. *Advances in Marine Biology* 43: 171–276.
Horner, R., Ackley, S.F., Dieckmann, G.S., Gulliksen, B., Hoshiai, T., Legendre, L., Melnikov, I.A., Reeburgh, W.S., Spindler, M., Sullivan, C.W. (1992). 'Ecology of sea ice biota'. *Polar Biology* 12: 417–427.

M3 Deep sea floors biome



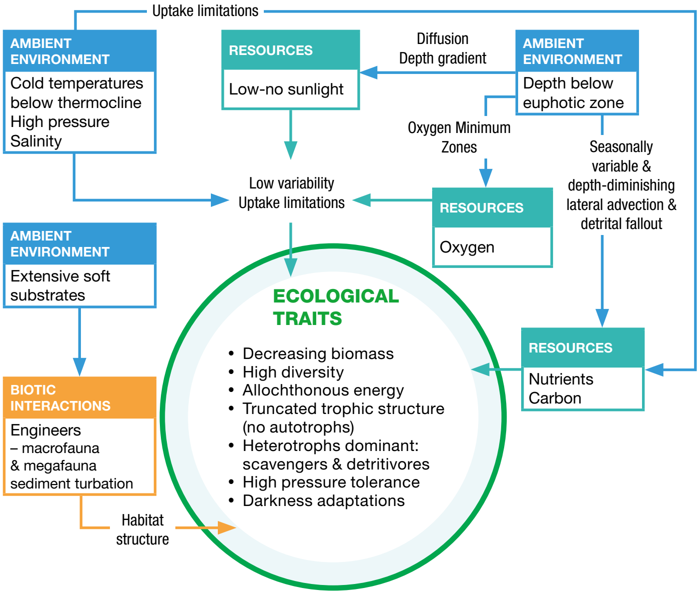
Colony of Jasonisis, a bamboo coral, with crinoid associates, Mytilus seamount.
Source: National Oceanic and Atmospheric Administration (NOAA), public domain.

The Deep-sea floor covers the entire oceanic benthos below ~250 m deep, where there is not enough light to support primary productivity through photosynthesis. It extends from the upper bathyal seafloor to the deepest parts of the ocean, at just under 11 km in the Mariana Trench. Most deep-sea communities are therefore heterotrophic, depending ultimately on allochthonous energy and nutrients from the vertical flux and/or advection down-slopes of organic matter produced in the upper photic layers of ocean waters. Chemosynthetically-based ecosystems, such as those found at hydrothermal vents and cold seeps, are an exception, as chemoautotrophic microorganisms synthesise reduced compounds (i.e. hydrogen sulphide and methane) in hydrothermal and cold-seep fluids as autochthonous source of energy. Oxygen is not limiting due to global-scale thermohaline circulation via deep ocean currents, except in bathyal (200 m–1,000 m) areas along the eastern Pacific, southwestern Africa, the Arabian Sea and the Bay of Bengal, where physical and biological processes result in the formation of oxygen-minimum zones. Depth generates a strong gradient in hydrostatic pressure, increasing one atmosphere with every 10 m in depth, excluding fish from depths >8.5 km. Currents, geomorphology and substrate type also influence ecosystem function. Geomorphology differentiates several functional groups of ecosystems within the deep seafloor biome because of its influence on both the movement of currents and the vertical flux of resources, with marine canyons, seamounts and trenches creating resource-rich hotspots. Extensive soft sediments on the abyssal plains support burrowing detritivores and predators, whereas sessile suspension feeders dominate hard substrates. Deep-sea benthic biodiversity is usually very high and mostly composed of meio-fauna and macro-fauna, with high abundances of microbes. Chemosynthetically-based ecosystems are exceptional again, as their biota is characterised by high biomass, low diversity and high endemism. Organisms are equipped with traits that enable survival in the absence of light, high hydrostatic pressure, and low levels of nutrients and carbon.

M3.1 Continental and island slopes

BIOME: M3 DEEP SEA FLOORS
REALM: MARINE

Contributors: E. Ramirez-Llodra, U.C. Fernandez-Arcaya, I.G. Priede, D.A. Keith

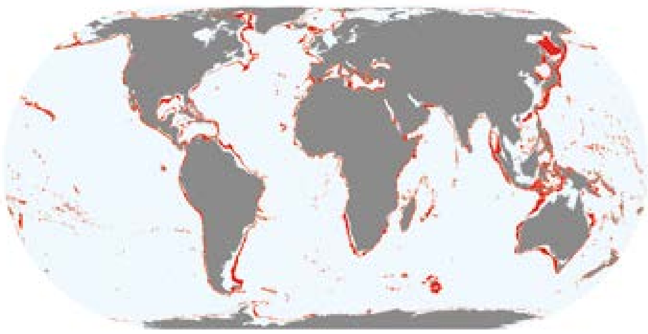


Holothurian feeding on detritus in sediments on the Celebes Sea island continental slope, Indian Ocean.
Source: Verena Tunnicliffe (UBC, Canada)

ECOLOGICAL TRAITS: These aphotic heterotrophic ecosystems fringe the margins of continental plates and islands, extending from the shelf break (~250 m deep) to the abyssal basins (4,000 m). These large sedimentary slopes with localised rocky outcrops are characterised by strong depth gradients in the biota and may be juxtaposed with specialised ecosystems, such as submarine canyons (M3.2), deep-water biogenic systems (M3.6) and chemosynthetic seeps (M3.7), as well as landslides and oxygen-minimum zones. Energy sources are derived mostly from lateral advection from the shelf and vertical fallout of organic matter particles through the water column and pelagic fauna impinging on the slopes, which varies seasonally with the productivity of the euphotic layers. Other inputs of organic matter include sporadic pulses of large falls (e.g. whale falls and wood falls). Photoautotrophs and resident herbivores are absent, and the trophic network is dominated by microbial decomposers, detritivores and their predators. Depth-related gradients result in a marked bathymetric zonation of faunal communities, and there is significant basin-scale endemism in many taxa. The taxonomic diversity of these heterotrophs is high and reaches a maximum at middle to lower depths. The biomass of megafauna decreases with depth and the meio-fauna and macro-fauna become relatively more important, but maximum biomass occurs on mid-slopes in some regions. The megafauna is often characterised by sparse populations of detritivores, including echinoderms, crustaceans and demersal fish, but sessile benthic organisms are scarce and the bottom is typically bare, unconsolidated sediments.

KEY ECOLOGICAL DRIVERS: The continental slopes are characterised by strong environmental depth gradients in pressure, temperature, light and food. Limited sunlight penetration permits some visual predation but no photosynthesis below 250 m and rapidly diminishes with depth, with total darkness (excluding bioluminescence) below 1,000 m. Hydrostatic pressure increases with depth (one atmosphere every 10 m). Temperature drastically shifts below the thermocline from warmer surface waters to cold, deep water (1–3°C), except in the Mediterranean Sea (13°C) and the Red Sea (21°C). Food quantity and quality decrease with increasing depth, as heterotrophic zooplankton efficiently use the labile compounds of the descending particulate organic matter. Sediments on continental slopes provide important ecosystem services, including nutrient regeneration and carbon sequestration.

DISTRIBUTION: Fringing the margins of all ocean basins and oceanic islands. Extending beneath 11% of the ocean surface at depths of 250–4,000 m.



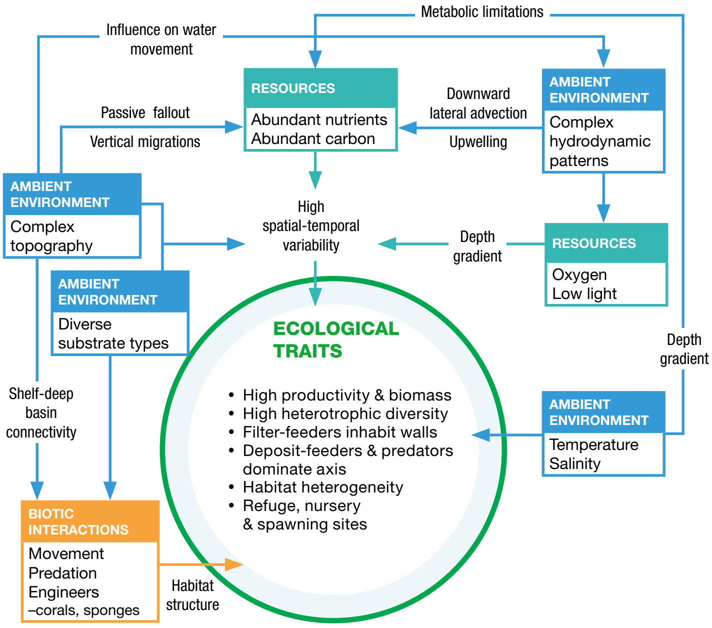
Reference:
Menot, L., Sibuet, M., Carney, R.S., Levin, L.A., Rowe, G.T., Billett, D.S.M., Poore, G., Kitazato, H., Vanreusel, A., Galéron, J. et al. (2010). New perceptions of continental margin biodiversity. In: A.D. McIntyre, *Life in the world's oceans: diversity, distribution and abundance*, Chapter 5, pp. 79–101. Chichester, UK: Blackwell.

M3.2 Submarine canyons

BIOME: M3 DEEP SEA FLOORS
REALM: MARINE

Contributors: U.C. Fernandez de Arcaya, E. Ramirez-Llodra, D.A. Keith

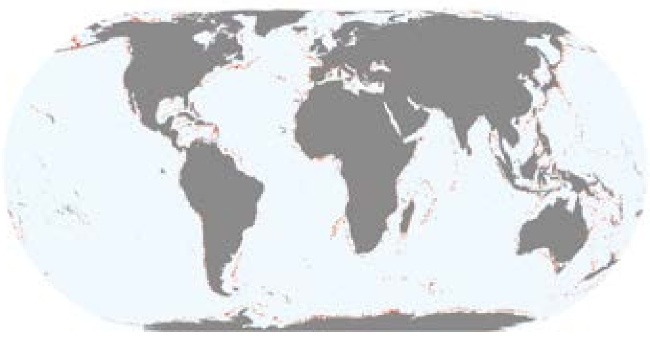
A) Wall of La Gaviera canyon, with cold-water corals, sponges, anemones and fish. B) Soft bottom in Lastres canyon, covered by pennatulids with fish and ophiura. Both locations ~850 m deep in the Cantabrian Sea.
Source: Francisco Sanchez (IEO)



ECOLOGICAL TRAITS: Submarine canyons are major geomorphic features that function as dynamic flux routes for resources between continental shelves and ocean basins. As a result, canyons are one of the most productive and biodiverse habitats in the deep sea. Habitat heterogeneity and temporal variability are key features of submarine canyons, with the diversity of topographic and hydrodynamic features and substrate types (e.g. mud, sand and rocky walls) within and among canyons contributing to their highly diverse heterotrophic faunal assemblages. Photoautotrophs are present only at the heads of some canyons. Canyons are characterised by meio-, macro-, and mega-fauna assemblages with greater abundances and/or biomass than adjacent continental slopes (M3.1) due mainly to the greater quality and quantity of food inside canyon systems. Habitat complexity and high resource availability make canyons important refuges, nurseries, spawning areas and regional source populations for fish, crustaceans and other benthic biota. Steep exposed rock and strong currents may facilitate the development of dense communities of sessile predators and filter-feeders, such as cold-water corals and sponges, engineering complex three-dimensional habitats. Soft substrates favour high densities of pennatulids and detritivores such as echinoderms. The role of canyons as centres of carbon deposition makes them an extraordinary habitat for deep-sea deposit-feeders, which represent the dominant mobile benthic trophic guild. The high productivity attracts pelagic-associated secondary and tertiary consumers, including cetaceans, which may visit canyons for feeding and breeding.

KEY ECOLOGICAL DRIVERS: Submarine canyons vary in their origin, length, depth range (mean: 2,000 m), hydrodynamics, sedimentation patterns and biota. Their complex topography modifies regional currents, inducing local upwelling, downwelling and other complex hydrodynamic processes (e.g. turbidity currents, dense shelf water cascading and internal waves). Through these processes, canyons act as geomorphic conduits of water masses, sediments and organic matter from the productive coastal shelf to deep basins. This is particularly evident in shelf-incising canyons directly affected by riverine inputs and other coastal processes. Complex hydrodynamic patterns enhance nutrient levels and food inputs mostly through downward lateral advection, but also by local upwelling, active biological transport by vertical migration of organisms and passive fall of organic flux of varied particles sizes. Differences among canyons are driven primarily by variation in the abundance and quality of food sources, as well as finer-scale drivers, including the variability of water mass structure (i.e. turbidity, temperature, salinity and oxygen gradients), seabed geomorphology, depth and substratum.

DISTRIBUTION: Submarine canyons cover 11.2% of continental slopes, with 9,000 large canyons recorded globally. Most of their extent is distributed below 200 m, with a mean depth of 2,000 m.

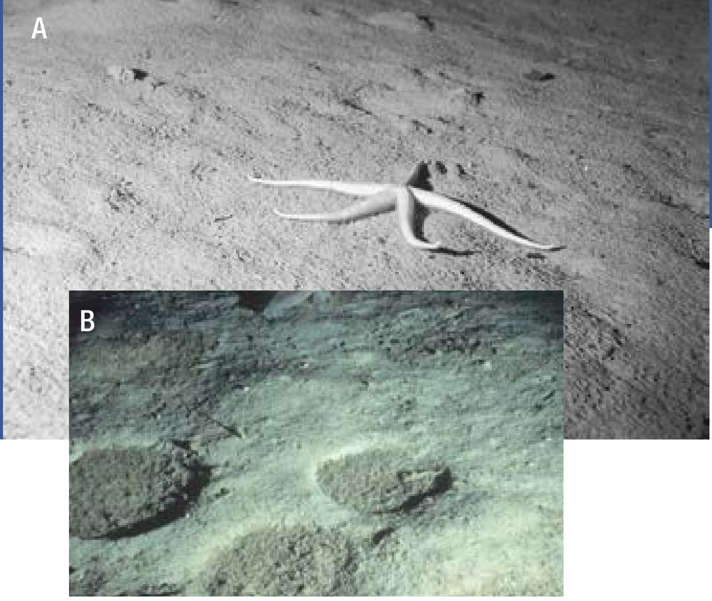


Reference:
Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J., Allcock, A.L., Davies, J.S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V.A., Macmillan-Lawler, M., Martín, J. (2017). 'Ecological Role of Submarine Canyons and Need for Canyon Conservation: A Review'. *Frontiers in Marine Science* 4: 5.

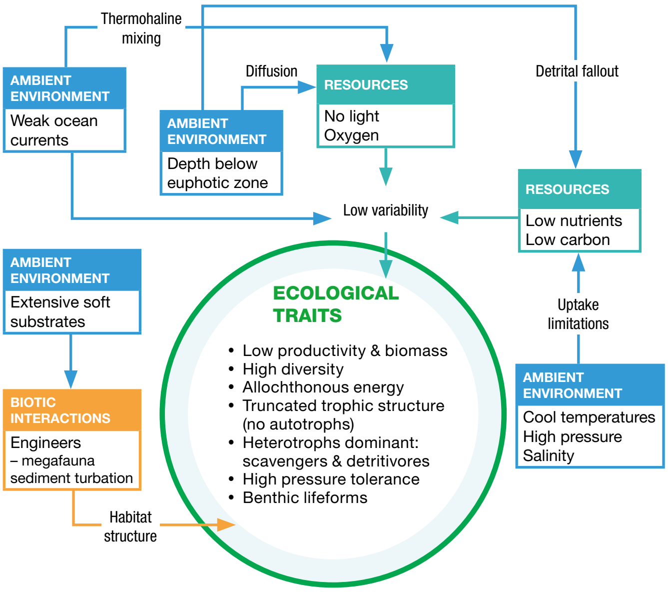
M3.3 Abyssal plains

BIOME: M3 DEEP SEA FLOORS
REALM: MARINE

Contributors: E. Ramirez-Llodra, I.G. Priede, D.A. Keith



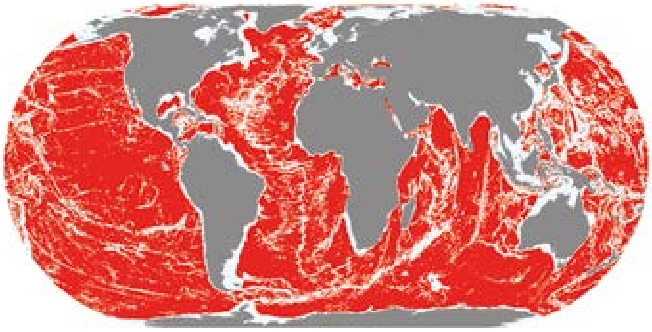
The Porcupine Abyssal Plain, Atlantic Ocean, showing **(A)** a Zoraster sea star and **(B)** patchy photo-detritus accumulations on seabed hollows with an Amperima holothurian in the background.
Source: D. Billett (NOCS, UK)



ECOLOGICAL TRAITS: This is the largest group of benthic marine ecosystems, extending between 3,000 and 6,000 m deep and covered by thick layers (up to thousands of metres) of fine sediment. Less than 1% of the seafloor has been investigated biologically. Tests of giant protozoans and the lebensspuren (i.e. tracks, borrows and mounds) made by megafauna structure the habitats of smaller organisms. Ecosystem engineering aside, other biotic interactions among large fauna are weak due to the low densities of organisms. Abyssal communities are heterotrophic, with energy sources derived mostly from the fallout of organic matter particles through the water column. Large carrion falls are major local inputs of organic matter and can later become important chemosynthetic environments (M3.7). Seasonal variation in particulate organic matter flux reflects temporal patterns in the productivity of euphotic layers. Input of organic matter can also be through sporadic pulses of large falls (e.g. whale falls and wood falls). Most abyssal plains are food-limited and the quantity and quality of food input to the abyssal seafloor are strong drivers shaping the structure and function of abyssal communities. Abyssal biomass is very low and dominated by meio-fauna and microorganisms that play key roles in the function of benthic communities below 3,000 m deep. The abyssal biota, however, is highly diverse, mostly composed of macro- and meio-fauna with large numbers of species new to science (up to 80% in some regions). Many species have so far been sampled only as singletons (only one specimen per species) or as a few specimens. The megafauna is often characterised by sparse populations of detritivores, notably echinoderms, crustaceans and demersal fish. Species distribution and major functions, such as community respiration and bioturbation, are linked to particulate organic carbon flux. These functions modulate the important ecosystem services provided by abyssal plains, including nutrient regeneration and carbon sequestration.

KEY ECOLOGICAL DRIVERS: No light penetrates to abyssal depths. Hydrostatic pressure is very high (300–600 atmospheres). Water masses above abyssal plains are well oxygenated and characterised by low temperatures -0.5–3°C), except in the Mediterranean Sea (13°C) and the Red Sea (21°C). The main driver of most abyssal communities is food, which mostly arrives to the seafloor as particulate organic carbon or ‘marine snow’. Only 0.5–2% of the primary production in the euphotic zone reaches the abyssal seafloor, with the quantity decreasing with increasing depth.

DISTRIBUTION: Seafloor of all oceans between 3,000 and 6,000 m deep, accounting for 76% of the total seafloor area, segmented by mid-ocean ridges, island arcs and trenches.

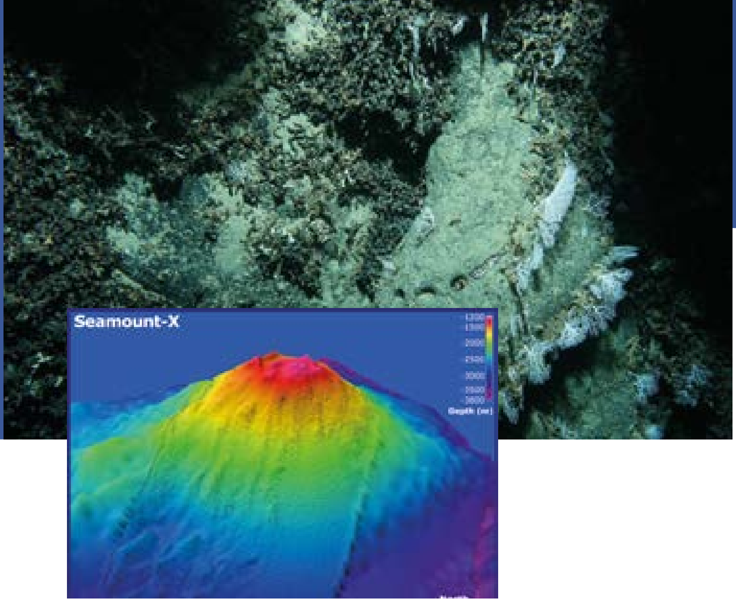


Reference:
Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Martinez Arbizu, P. (2008). ‘Abyssal food limitation, ecosystem structure and climate change’. *Trends in Ecology and Evolution* 23(9): 518–528.

M3.4 Seamounts, ridges and plateaus

BIOME: M3 DEEP SEA FLOORS
REALM: MARINE

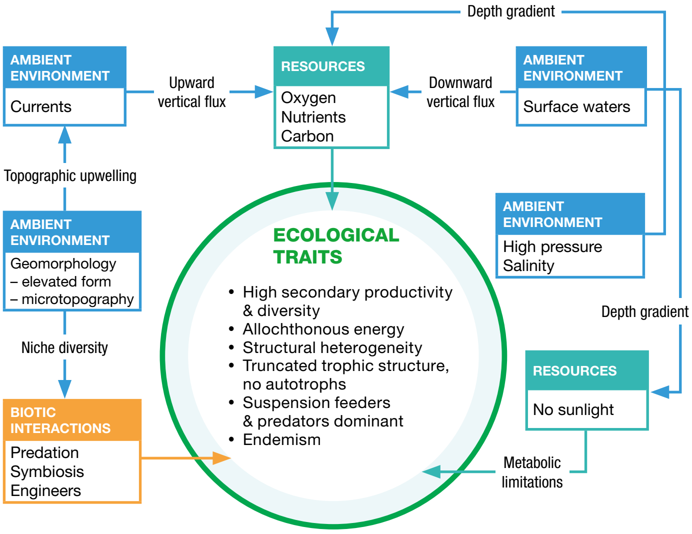
Contributors: E. Ramirez-Llodra, A.A. Rowden, I.G. Priede, D.A. Keith



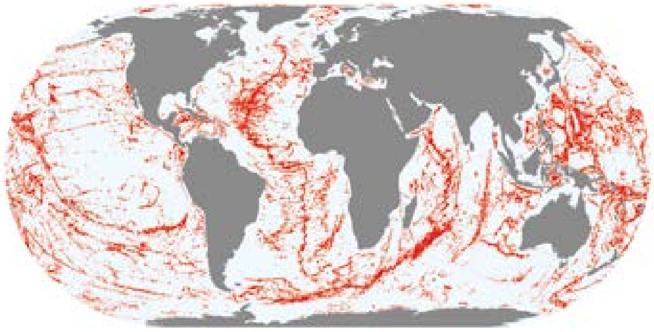
Corals on hard substratum on a seamount and bathymetric model of an insular seamount.
Sources: Main: NIWA, NZ. Inset: NOAA Vents Program

ECOLOGICAL TRAITS: Seamounts, plateaus and ridges are major geomorphic features of the deep oceanic seafloor, characterised by hard substrates, elevated topography and often higher productivity than surrounding waters. Topographically modified currents affect geochemical cycles, nutrient mixing processes and detrital fallout from the euphotic zone that deliver allochthonous energy and nutrients to these heterotroph-dominated systems. Suspension-feeders and their dependents and predators dominate the trophic web, whereas deposit-feeders and mixed-feeders are less abundant than in other deep-sea systems. Autotrophs are generally absent. Summits that reach the euphotic zone are included within functional groups of the Marine shelf biome. Bathymetric gradients and local substrate heterogeneity support marked variation in diversity, composition and abundance. Rocky walls, for example, may be dominated by sessile suspension-feeders, including cnidarians (especially corals), sponges, crinoids and ascidians. High densities of sessile animals may form deep-water biogenic beds (M3.5), but those systems are not limited to seamounts or ridges. Among the mobile benthic fauna, molluscs and echinoderms can be abundant. Seamounts also support dense aggregations of large fish, attracted by the high secondary productivity of lower trophic levels in the system, as well as spawning and/or nursery habitats. Elevated topography affects the distribution of both benthic and pelagic fauna. Seamounts and ridges tend to act both as stepping stones for the dispersal of slope-dwelling biota and as dispersal barriers between adjacent basins, while insular seamounts may have high endemism.

KEY ECOLOGICAL DRIVERS: Seamounts, rising more than 1,000 m above the sediment-covered seabed, and smaller peaks, knobs and hills are topographically isolated features, ostly of volcanic origin. Mid-ocean ridges are semi-continuous mountain chains that mark the spreading margins of adjacent tectonic plates. These prominent topographic formations interact with water masses and currents, increasing turbulence, mixing, particle retention, and the upward movement of nutrients from large areas of the seafloor. This enhances productivity on the seamounts and ridges themselves and also in the euphotic zone above, some of which returns to the system through detrital fallout. A diversity of topographic, bathymetric, and hydrodynamic features and substrate types (e.g. steep rocky walls, flat muddy areas and biogenic habitats at varied depths) contribute to niche diversity and biodiversity. Major bathymetric clines associated with elevated topography produce gradients that shape ecological traits, including species richness, community structure, abundance, biomass and trophic modes.



DISTRIBUTION: About 171,000 seamounts, knolls and hills documented so far worldwide, covering ~2.6% of the sea floor. Ridges cover ~9.2% of the sea floor along a semi-continuous, 55,000-km long system.



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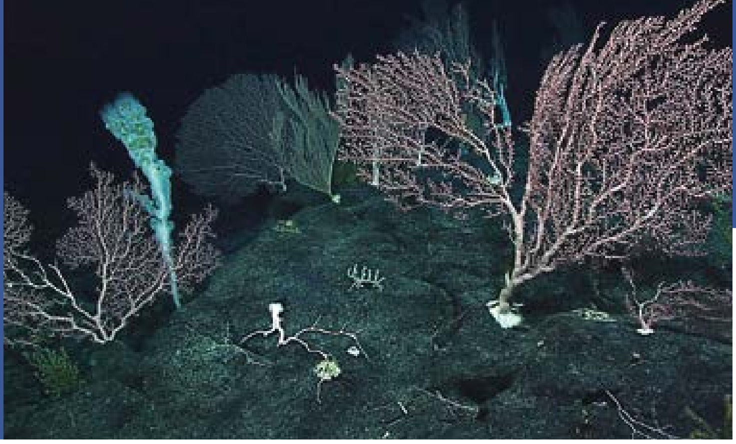
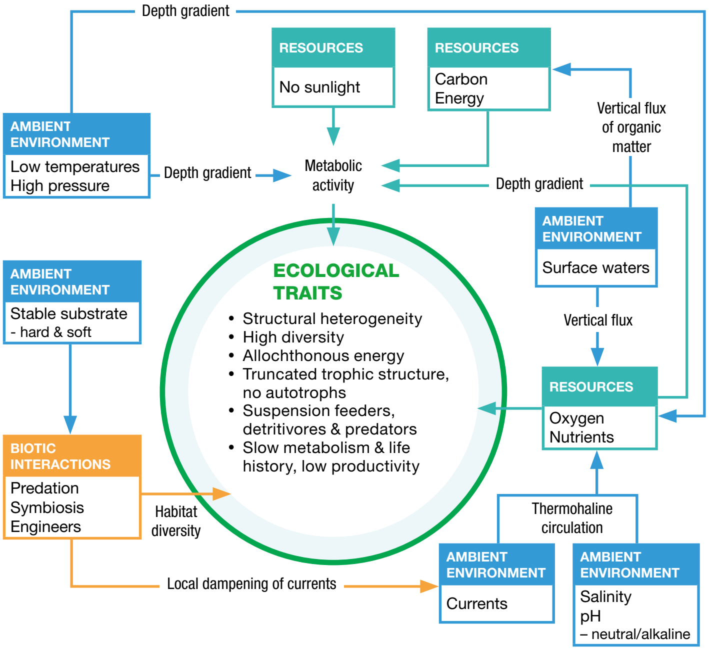
M3.5 Deepwater biogenic beds



Large deepwater corals dominate a biogenic bed community near Wake Island, Pacific Ocean.
Source: NOAA Ocean Exploration and Research

BIOME: M3 DEEP SEA FLOORS
REALM: MARINE

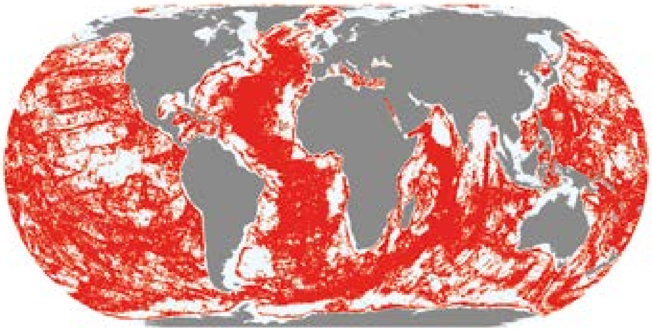
Contributors: E. Ramirez-Llodra, U.C. Fernandez-Arcaya, S. Rossi, D.A. Keith



ECOLOGICAL TRAITS: Benthic, sessile suspension-feeders, such as aphotic corals, sponges and bivalves, form structurally complex, three-dimensional structures or 'animal forests' in the deep oceans. In contrast to their shallow-water counterparts in coastal and shelf systems (M1.5), these ecosystems are aphotic and rely on allochthonous energy sources borne in currents and pelagic fallout. The trophic web is dominated by filter-feeders, decomposers, detritivores and predators. Primary producers and associated herbivores are only present at the interface with the photic zone (~250 m deep). The biogenic structures are slow growing but critical to local demersal biota in engineering shelter from predators and currents, particularly in shallower, more dynamic waters. They also provide stable substrates and enhance food availability. This habitat heterogeneity becomes more important with depth as stable, complex elevated substrate becomes increasingly limited. These structures and the microenvironments within them support a high diversity of associated species, including symbionts, microorganisms in coral biofilm, filter-feeding epifauna, biofilm grazers, mobile predators (e.g. polychaetes and crustaceans) and benthic demersal fish. Diversity is positively related to the size, flexibility and structural complexity of habitat-forming organisms. Their impact on hydrography and the flow of local currents increases retention of particulate matter, zooplankton, eggs and larvae from the water column. This creates positive conditions for suspension-feeders, which engineer their environment and play important roles in benthic-pelagic coupling, increasing the flux of matter and energy from the water column to the benthic community.

KEY ECOLOGICAL DRIVERS: The productivity of surface water, the vertical flux of nutrients, water temperature and hydrography influence the availability of food, and hence the distribution and function of deep-water biogenic beds. Although these systems occur on both hard and soft substrates, the latter are less structurally complex and less diverse. Chemical processes are important and ocean acidity is limiting. The presence of cold-water corals, for example, has been linked to the depth of aragonite saturation. Habitat-forming species prefer regions characterised by oxygenation and currents or high flow, generally avoiding oxygen-minimum zones. Benthic biogenic structures and their dependents are highly dependent on low levels of physical disturbance due to slow growth rates and recovery times.

DISTRIBUTION: Patchy but widespread distribution across the deep sea floor below 250 m deep. Poorly explored and possibly less common on abyssal plains.



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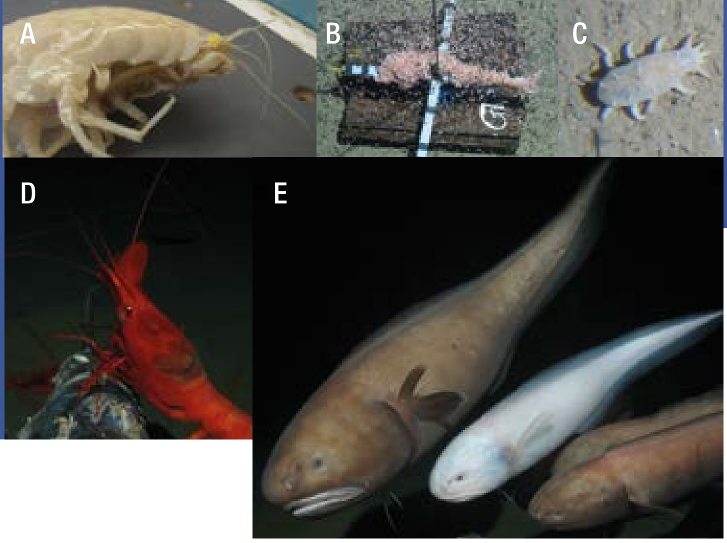
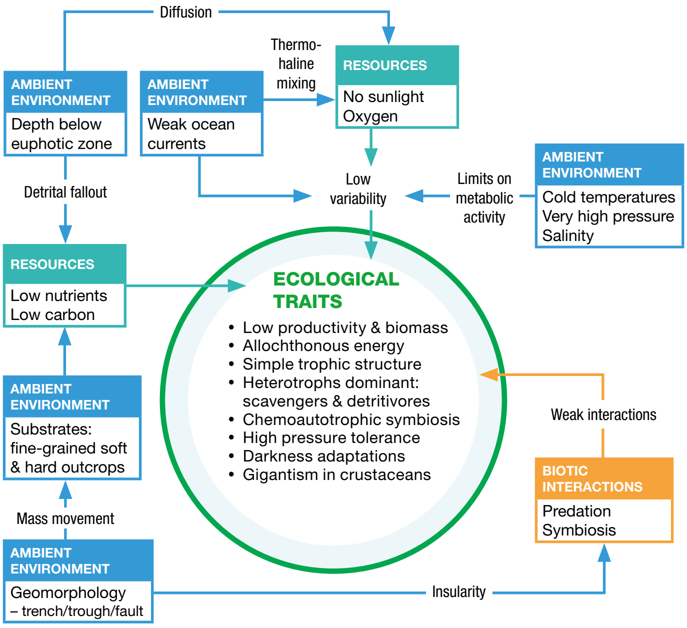
M3.6 Hadal trenches and troughs

BIOME: M3 DEEP SEA FLOORS
REALM: MARINE

Contributors: E. Ramirez-Llodra, A.A. Rowden, A.J. Jamieson, I.G. Priede, D.A. Keith



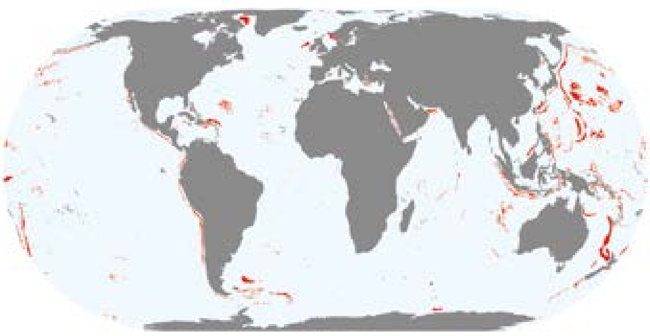
Typical hadal fauna: **A)** supergiant amphipod; **B)** dense clusters of scavenging amphipods; **C)** deposit-feeding holothurians; **D)** predatory decapods; and **E)** predatory fish.
Source: Alan Jamieson (with permission)



ECOLOGICAL TRAITS: Hadal zones are the deepest ocean systems on earth and among the least explored. They are heterotrophic, with energy derived from the fallout of particulate organic matter through the water column, which varies seasonally and geographically and accumulates in the deepest axes of the trenches. Most organic matter reaching hadal depths is nutrient-poor because pelagic organisms use the labile compounds from the particulate organic matter during fallout. Hadal systems are therefore food-limited, but particulate organic matter flux may be boosted by sporadic pulses (e.g. whale falls and wood falls) and sediment transported by advection and seismically induced submarine landslides. Additional energy is contributed by chemosynthetic bacteria that can establish symbiotic relationships with specialised fauna. These are poorly known but more are expected to be discovered in the future. Hadal trophic networks are dominated by scavengers and detritivores, although predators (including through cannibalism) are also represented. Over 400 species are currently known from hadal ecosystems, with most metazoan taxa represented, including amphipods, polychaetes, gastropods, bivalves, holothurians and fish. These species possess physiological adaptations to high hydrostatic pressure, darkness, low temperature, and low food supply. These environmental filters, together with habitat isolation, result in high levels of endemism. Gigantism in amphipods, mysids and isopods contrasts with the dwarfism in meio-fauna (e.g. nematodes, copepods and kinorhynchs).

KEY ECOLOGICAL DRIVERS: The hadal benthic zone extends from 6,000 to 11,000 m deep and includes 27 disjoint deep-ocean trenches, 13 troughs and 7 faults. Sunlight is absent, nutrients and organic carbon are scarce, and hydrostatic pressure is extremely high (600–1,100 atmospheres). Water masses in trenches and troughs are well oxygenated by deep currents and experience constant, low temperatures (1.5–2.5°C). Rocky substrates outcrop on steep slopes of trenches and faults, while the floors comprise large accumulations of fine sediment deposited by mass movement, including drift and landslides, which are important sources of organic matter. Sediment, organic matter and pollutants tend to be 'funnelled' and concentrated in the axis of the trenches.

DISTRIBUTION: A cluster of isolated trenches in subduction zones, faults, and troughs or basins, mostly in the Pacific Ocean, as well as the Indian and Southern Oceans, accounting for 1–2% of the total global benthic area.



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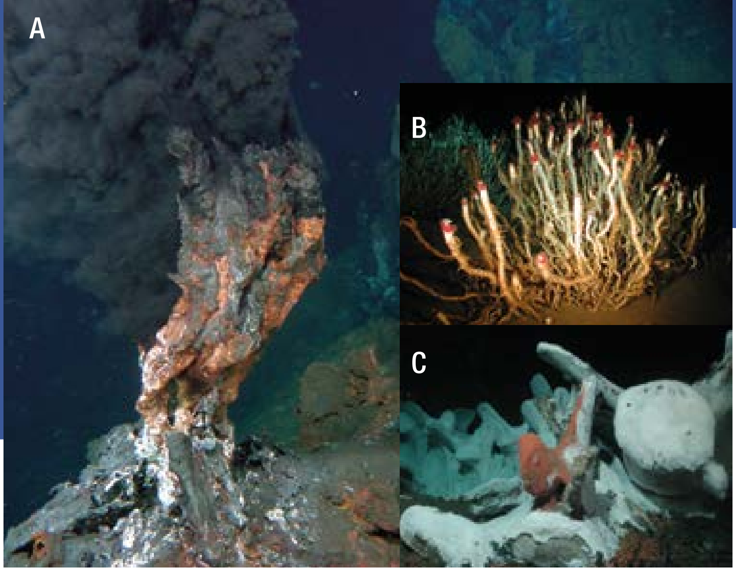
Jamieson, A., Fujii, T., Mayor, D.J., Solan, M., Priede, I.G. (2010). 'Hadal trenches: The ecology of the deepest places on Earth'. *Trends in Ecology and Evolution* 25(3): 190–197.
Stewart, H.A., Jamieson, A.J. (2018). 'Habitat heterogeneity of hadal trenches: Considerations and implications for future studies'. *Progress in Oceanography* 161: 47–65.

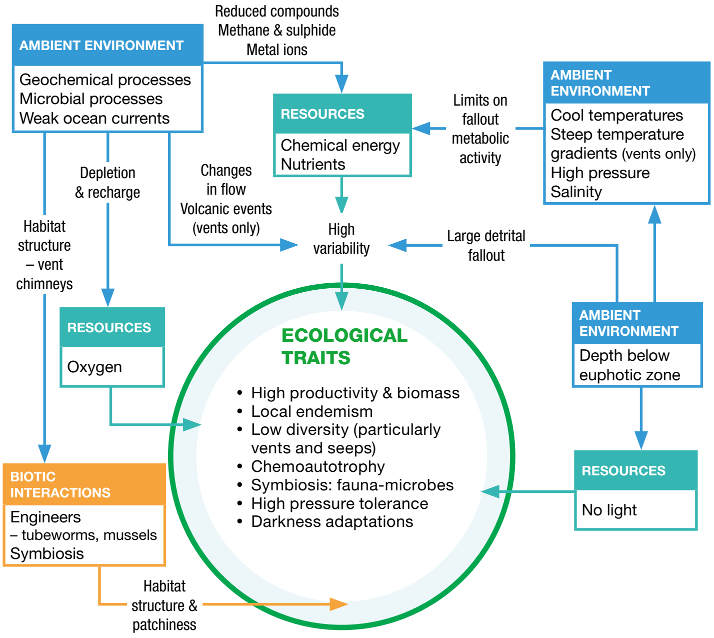
M3.7 Chemosynthetic-based ecosystems (CBEs)

BIOME: M3 DEEP SEA FLOORS
REALM: MARINE

Contributors: E. Ramirez-Llodra, D.A. Keith



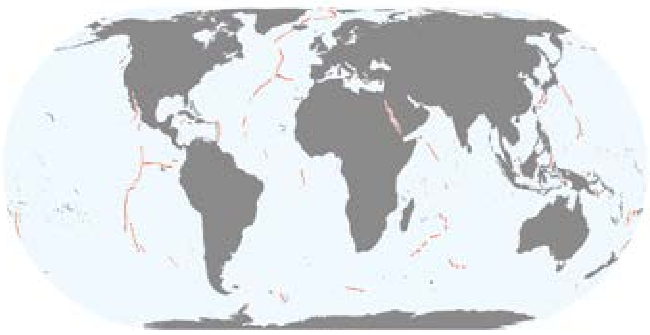
A) A hydrothermal vent chimney, Mid-Atlantic Ridge. Source: U. Azores with permission. **B)** Cold seep with Lamellibrachia tubeworms in the Gulf of Mexico. Source: C. Fisher, PSU with permission. **C)** Whale fall. Source: C. Smith, Uni. Hawaii, USA, with permission



ECOLOGICAL TRAITS: Chemosynthetic-based ecosystems (CBEs) include three major types of habitats between bathyal and abyssal depths: 1) hydrothermal vents on mid-ocean ridges, back-arc basins, and active seamounts; 2) cold seeps on active and passive continental margins; and 3) large organic falls of whales or wood. All these systems are characterised by microbial primary productivity through chemoautotrophy, which uses reduced compounds (such as H_2S and CH_4) as energy sources instead of light. Microbes form bacterial mats and occur in trophic symbiosis with most megafauna. The continuous sources of energy and microbial symbiosis fuel high faunal biomass. However, specific environmental factors (e.g. high temperature gradients at vents, chemical toxicity and symbiosis dependence) result in a low diversity and high endemism of highly specialised fauna. Habitat structure comprises hard substrate on vent chimneys and mostly biogenic substrate at seeps and food-falls. Most fauna is sessile or with low motility and depends on the fluids emanating at vents and seeps or chemicals produced by microbes on food-falls, and thus is spatially limited. Large tubeworms, shrimps, crabs, bivalves and gastropods dominate many hydrothermal vents, with marked biogeographic provinces. Tubeworms, mussels and decapod crustaceans often dominate cold seeps with demersal fish. These are patchy ecosystems where connectivity relies on the dispersal of planktonic larvae.

KEY ECOLOGICAL DRIVERS: No light penetrates to deep-sea CBEs. Hydrostatic pressure is very high (30–600 atmospheres). At hydrothermal vents, very hot fluids (up to 400°C) emanate from chimneys charged with metals and chemicals that provide energy to chemoautotrophic microbes. At cold seeps, the fluids are cold and reduced chemicals originate both biogenically and abiotically. At food-falls, reduced chemicals are produced by microorganisms degrading the organic matter of the fall. The main drivers of CBEs are the chemosynthetically based primary productivity and the symbiotic relationships between microorganisms and fauna.

DISTRIBUTION: Seafloor of all oceans. Vents (map) occur on mid-ocean ridges, back-arc basins and active seamounts. Cold seeps occur on active and passive continental margins. Food-falls occur mostly along cetacean migration routes (whale falls).



Reference:
Tunnicliffe, V., Juniper, K.S., Sibuet, M. (2003). 'Reducing environments of the deep-sea floor'. In: P.A. Tyler (ed.), *Ecosystems of the deep oceans'. Ecosystems of the World.* Vol. 28, pp. 81–110. London, UK: Elsevier.

M4 Anthropogenic marine biome

Fishing boat wrecked in 1935 in the Aegean Sea.
Source: U/Jaykirsch on Reddit

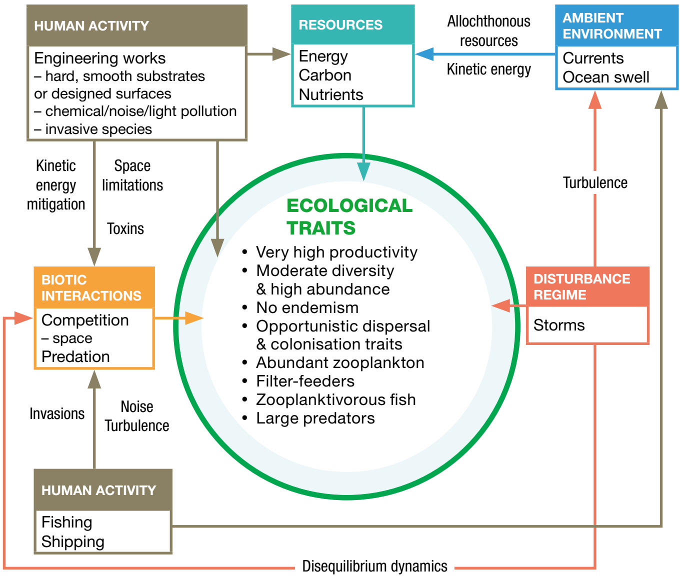
Humans have constructed, deposited or dumped artificial structures in the oceans that either confine managed marine organisms or attract marine biota that would not otherwise occupy such locations. These structures are distributed globally but are most common in regions of high-density occupation or transit. They include shipwrecks and mineral, gas, or energy infrastructure, pipelines, and rubble piles, as well as aquaculture infrastructure. These installations provide an epibenthic substrate for sessile benthic organisms, as well as a demersal or pelagic environment for mobile organisms. Diversity and biomass of the epibenthic biofouling community is positively related to substrate rugosity. Most energy is supplied to these ecosystems from allochthonous sources, either passively via currents or actively through addition by humans (as is the case in aquaculture). Epibenthic and planktonic marine algae, however, make a contribution to the energy budget through local primary production. Microbial decomposers and invertebrate detritivores in the sediments beneath and around the structures feed on particulate organic matter from the epibenthic biota (e.g. waste products and decaying bodies) or on unconsumed food delivered to managed species. The elevated productivity or visual features of artificial structures often attract larger pelagic predators, which forage in the vicinity.

M4.1 Submerged artificial structures

BIOME: M4 ANTHROPOGENIC MARINE SYSTEMS
REALM: MARINE

Contributors: I.M. Suthers, J.T. Claisse, T.P. Crowe, D.A. Keith

Wreck of the Amakasu Maru No. 1 sunk in 1942, Wake Island, North Pacific Ocean, provides habitat for anemones, glass sponges and anglerfish.
Source: NOAA Ocean Exploration and Research



ECOLOGICAL TRAITS: These deployments include submerged structures with high vertical relief including ship wrecks, oil and gas infrastructure, and designed artificial reefs, as well as some low-relief structures (i.e. rubble piles). The latter do not differ greatly from adjacent natural reefs, but structures with high vertical relief are distinguished by an abundance of zooplanktivorous fish, as well as reef-associated fishes. Macroalgae are sparse or absent as the ecosystem is fed by currents and ocean swell delivering phytoplankton to sessile invertebrates. Complex surfaces quickly thicken with a biofouling community characterised by an abundance of filter-feeding invertebrates (e.g. sponges, barnacles, bivalves and ascidians) and their predators (e.g. crabs and flatworms). Invertebrate diversity is high, with representatives from every living Phylum. Structures without complex surfaces, such as the smooth, wide expanse of a hull, may suffer the sporadic loss of all biofouling communities after storm events. This feeds the sandy bottom community, evident as a halo of benthic invertebrates (e.g. polychaetes and amphipods), which also benefit from the plume of waste and detritus drifting from the reef community. Artificial structures also provide a visual focus attracting pelagic fish and marine mammals, which respond similarly to fish-attraction devices and drift objects.

KEY ECOLOGICAL DRIVERS: The high vertical relief of many artificial structures enables biota to access plankton continuously transported by currents. They may be situated on otherwise flat, soft-bottom habitats and isolated to varying degrees from other hard substrates. High-energy waters experience low variation in temperature and salinity (except those near major river systems). Currents and associated eddies cause strong horizontal flow, while ocean swell creates orbital current velocities at least 10-fold greater than horizontal currents. Near large urban centres, fishing reduces populations of large predatory fish, resulting in a continuum across species and deployments from purely fish attraction to fish production (such as via the reef facilitating the planktivorous food chain).

The historical, opportunistic use of materials (e.g. rubber tyres, construction materials, or inadequately decommissioned vessels) has left legacies of pollutants. Compared to artificial reefs, oil and gas infrastructure is more exposed to light/noise/chemical pollution associated with operations as well the spread of invasive species.

DISTRIBUTION: Millions of artificial reefs and fish-attraction devices are deployed in coastal waters worldwide, including >10,000 oil and gas structures, mostly in tropical and temperate waters. More than 500 oil and gas platforms were decommissioned and left as artificial reefs in US waters since 1940. Many others are candidates for reefing after decommissioning in coming decades (>600 in the Asia-Pacific alone). Worldwide since 1984, over 130 ships and planes have purposely been sunk for recreational SCUBA-diving.

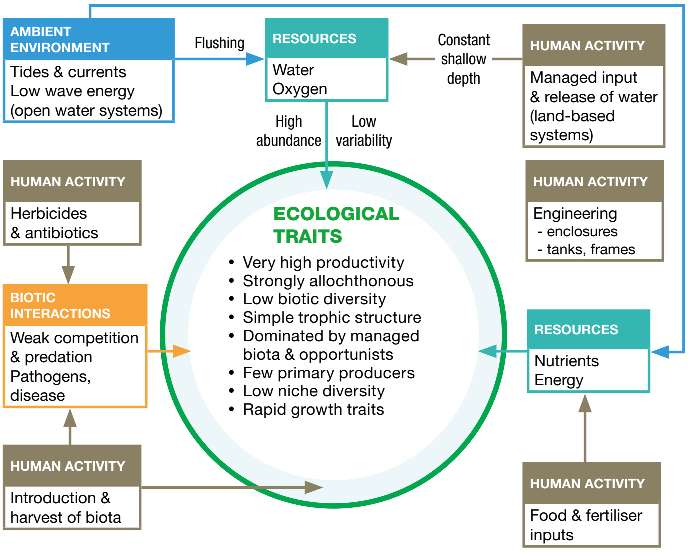
References:
Champion, C., Suthers, I.M., Smith, J.A. (2015). 'Zooplanktivory is a key process for fish production on a coastal artificial reef'. *Marine Ecology Progress Series* 541: 1–14.
Lima, J.S., Zalmo, R., Love, M. (2019). 'Overview and trends of ecological and socioeconomic research on artificial reefs'. *Marine Environmental Research* 145: 81–96.
Scarborough Bull, A., Love, M.S. (2020). 'Worldwide oil and gas platform decommissioning: A review of practices and reefing options'. *Ocean and Coastal Management* 168: 274–306.

M4.2 Marine aquafarms

BIOME: M4 ANTHROPOGENIC MARINE SYSTEMS
REALM: MARINE

Contributors: D.A. Keith, M. Beveridge, L.B. Firth

Salmon Farm, North-West Bay, Tasmania, Australia.
Source: Daniel Patman on Flickr, licensed under CC BY 3.0.



ECOLOGICAL TRAITS: Marine aquafarms (i.e. mariculture) are localised, high-productivity systems within and around enclosures constructed for the breeding, rearing and harvesting of marine plants and animals, including finfish, molluscs, crustaceans, algae and other marine plants. Allochthonous energy and nutrient inputs are delivered by humans and by diffusion from surrounding marine waters. Autochthonous inputs are small and produced by pelagic algae or biofilms on the infrastructure, unless the farmed species are aquatic macrophytes. More commonly, farmed species are consumers that belong to middle or upper trophic levels. Diversity is low across taxa, and the trophic web is dominated by a super-abundance of target species. Where multiple target species are cultivated, they are selected to ensure neutral or mutualistic interactions with one another (i.e. detritivores that consume the waste of a higher-level consumer). Farmed biota are harvested periodically to produce food, nutrient agar, horticultural products, jewellery and cosmetics. Their high population densities are maintained by continual inputs of food and regular re-stocking to compensate harvest. Farmed species may be 'genetically improved' for such traits as faster growth, greater yield, resistance to disease, etc., and are often bred selectively in hatcheries and then released into the enclosures. Inputs of food and nutrient may increase abundance of non-target species, including opportunistic microalgae, zooplankton, and pathogens and predators of the target species. These pest species or their impacts may be controlled by antibiotics or herbicides or by scaring or culling (e.g. pinnipeds around fish farms). The enclosures impose barriers to movement of larger organisms, but some cultivated stock may escape, while wild individuals from the surrounding waters may invade the enclosure. Escapees may interact with wild biota through completion, predation and genetic introgression. Enclosures are generally permeable to small organisms, propagules and waste products of larger organisms, nutrients and pathogens, enabling the farm ecosystem to extend beyond the confines of the infrastructure.

KEY ECOLOGICAL DRIVERS: Most marine farms are located in sheltered coastal waters but some are located in the open ocean or on land in tanks or ponds filled with seawater. Those in marine waters experience currents, tides, and flow-through of marine energy, matter and biota characteristic of the surrounding environment. Those on land are more insular, with intensively controlled light and temperature, recirculation systems that filter and recycle water and waste, and intensive anthropogenic inputs of food and nutrients, antibiotics and herbicides. Marine enclosures have netting and frames that provide substrates for biofilms and a limited array of benthic organisms (controlled with anti-fouling chemicals), but usually exclude the benthos. Land-based systems have smooth walls and floors that provide limited habitat heterogeneity for benthic biota.

DISTRIBUTION: Rapidly expanding around coastal Asia, Europe, North America and Mesoamerica, and southern temperate regions. Open-ocean facilities near Hawaii and Puerto Rico.

References:
Beveridge, M. (2004). *Cage Aquaculture.* Oxford, UK:. Blackwell Publishing Ltd.
Froehlich, H.E., Smith, A., Gentry, R.R., Halpern, B.S. (2017). 'Offshore aquaculture: I know it when I see it'. *Frontiers in Marine Science* 4(154): 154.

MT1 Shorelines biome

Twelve Apostles, Otway Coast, Victoria, Australia.
Source: Richard Mikalsen on Wikimedia commons

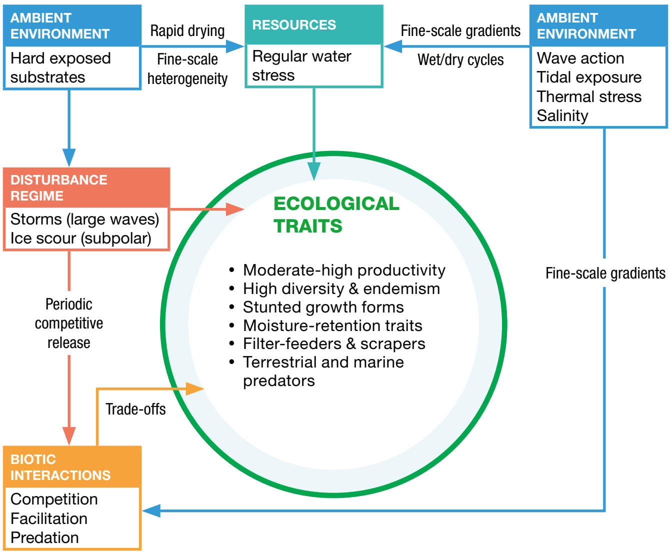
The Shoreline systems biome comprises naturally formed, intertidal abiogenic habitats situated at the interface between land and sea. The distribution of the biome spans all latitudes (temperate to polar) at which landmasses are present. Productivity ranges from high to low, is loosely proportional to the availability of stable hard substrate for macrophyte attachment and inversely proportional to the dependency on allochthonous energy sources derived from both land and sea. Productivity is also influenced by coastal upwelling and, for ecotypes of finer particle size, the nutrient content of adjacent terrestrial sediments. Within and across ecotypes, biotic communities are strongly structured by tides, waves and particle size, ranging from contiguous rock to fine silts and clays. Notably, some shorelines comprise mixed hard and soft substrates, with vertical zonation varying temporally in response to storm events and redeposition of soft sediments. Tides produce a vertical gradient of increasing aerial exposure across which desiccation and temperature stress increase, time available for filter-feeding decreases, and interactions with marine and terrestrial predators vary. Waves and particle size determine substrate stability and the physical disturbance regime. Wave action, diminishing from headlands to bays, produces horizontal gradients in community structure. Many organisms possess morphological and behavioural adaptations to prevent desiccation at low tide and dislodgement by wave forces. Burrowing animals are important in unconsolidated sediments. Competition (especially for space) is a major factor structuring communities, with its importance diminishing with decreasing particle size. Facilitative interactions (particularly those that protect organisms from desiccation stress or physical disturbance) can be important across ecosystems of all particle sizes. Biodiversity is generally high, with microscopic lifeforms dominating the biomass of systems of small particle size.

MT1.1 Rocky shorelines

BIOME: MT1 SHORELINE SYSTEMS
REALM: TRANSITIONAL MARINE-TERRESTRIAL

Contributors: M.J. Bishop, L.B. Firth, S.L. McSweeney, T.P. Crowe, A.H. Altieri, D.A. Keith

Rocky shore with colonial ascidians, southeast Qld, Australia.
Source: Sven Lavender, Queensland Government



ECOLOGICAL TRAITS: These intertidal benthic systems, composed of sessile and mobile species, are highly structured by fine-scale resource and stress gradients, as well as trade-offs among competitive, facilitation and predatory interactions. Sessile algae and invertebrates form complex three-dimensional habitats that provide microhabitat refugia from desiccation and temperature stress for associated organisms; these weaken competitive interactions. The biota exhibit behavioural and morphological adaptions to minimise exposure to stressors, such as seeking shelter in protective microhabitats at low tide, possessing exoskeletons (i.e. shells), or producing mucous to reduce desiccation. In wave-swept environments, adaptations include morphologies, such as small body sizes and small cross-sectional areas to minimise drag. Key trophic groups include filter-feeders (which feed on phytoplankton and dissolved organic matter at high tide), grazers (which scrape microphytobenthos and macroalgal spores from rock or consume macroalgal thalli), and resident (e.g. starfish, whelks and crabs) and transient (e.g. birds and fish) marine and terrestrial predators. Rocky shores display high endemism relative to other coastal systems and frequently display high productivity due to the large amounts of light they receive, although this can vary according to nutrient availability from upwelling and terrestrial runoff.

KEY ECOLOGICAL DRIVERS: Tides and waves are the key ecological drivers, producing resource availability and physical disturbance gradients vertically and horizontally, respectively. Across the vertical gradient of increasing aerial exposure, desiccation and temperature stress increases, time available for filter-feeding decreases, and interactions with marine and terrestrial predators vary. Horizontal gradients of diminishing salinity and wave exposure from headlands to bays or inlets influences community composition and morphology. Many organisms rely on microhabitats formed from natural rock features (e.g. crevices, depressions and rock pools) or habitat-forming species (e.g. canopy-forming algae, mussels, oysters, and barnacles) to persist in an environment that would otherwise exceed their environmental tolerances. Rocky shores are open systems, so community structure can be influenced by larval supply, coastal upwelling and competition. Competition for space may limit the lower vertical distributions of some sessile species. The limited space available for the growth of marine primary producers can result in competition for food among grazers. Disturbances (i.e. storms, ice scour on subpolar shores) that free-up space can have a strong influence on community structure and diversity.

DISTRIBUTION: Found globally at the margins of oceans where waves are eroding rocks. They are the most common ecosystems on open, high-energy coasts and also occur on many sheltered and enclosed coastlines, such as sea lochs, fjords and rias.

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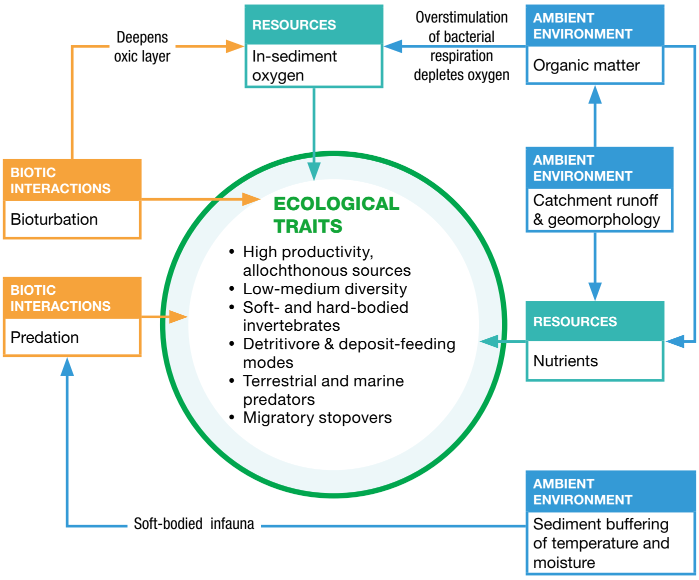
Connell, J.H. (1972). 'Community Interactions on Marine Rocky Intertidal Shores'. *Annual Review of Ecology and Systematics* 3: 169–192.
Thompson, R.C., Crowe, T.P. and Hawkins, S.J. (2002). 'Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years'. *Environmental Conservation* 29(2): 168–191.

MT1.2 Muddy shorelines

BIOME: MT1 SHORELINE SYSTEMS
REALM: TRANSITIONAL MARINE-TERRESTRIAL

Contributors: M.J. Bishop, N.J. Murray, S.E. Swearer, D.A. Keith

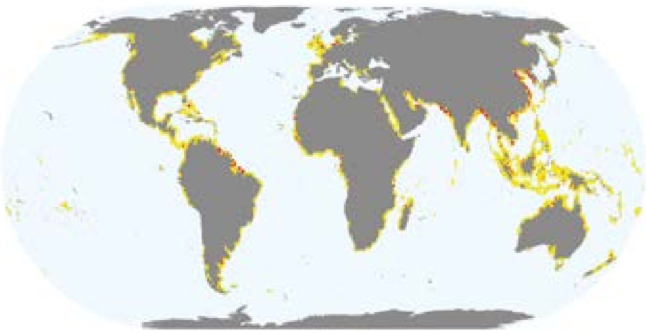
Muddy shore of the Wadden Sea, Germany.
Source: National Park Wattenmeer SH (CC)



ECOLOGICAL TRAITS: Highly productive intertidal environments are defined by their fine particle size (dominated by silts) and are fuelled largely by allochthonous production. Benthic diatoms are the key primary producer, although ephemeral intertidal seagrass may occur. Otherwise, macrophytes are generally absent unlike other ecosystems on intertidal mudfalts (MFT 1.2, MFT1.3). Fauna are dominated by deposit-feeding taxa (consuming organic matter that accumulates in the fine-grained sediments) and detritivores feeding on wrack (i.e. drift algae deposited at the high-water mark) and other sources of macro-detritus. Bioturbating and tube-dwelling taxa are key ecosystem engineers, the former oxygenating and mixing the sediments and the latter providing structure to an otherwise sedimentary habitat. Infauna residing within sediments are protected from high temperatures and desiccation by the surrounding matrix, and do not display the same marked patterns of zonation as rocky intertidal communities. Many infaunal taxa are soft-bodied. Nevertheless, competition for food resources carried by incoming tides can lead to intertidal gradients in fauna. Predators include the substantial shorebird populations that forage on infauna at low tide, including migratory species that depend on these systems as stopover sites. Fish, rays, crabs and resident whelks forage around lugworm bioturbation. Transitions to mangrove (MFT1.2), saltmarsh or reedbed (MFT1.3) ecosystems may occur in response to isostatic or sea level changes, freshwater inputs or changes in currents that promote macrophyte colonisation.

KEY ECOLOGICAL DRIVERS: These are depositional environments influenced by sediment supply and the balance of erosion and sedimentation. They occur on lower wave energy coastlines with lower slopes and larger intertidal ranges than sandy shorelines, resulting in lower levels of sediment transport and oxygenation by physical processes. In the absence of burrowing taxa, sediments may display low rates of turnover, which may result in an anoxic zone close to the sediment surface. Small particle sizes limit interstitial spaces, further reducing aeration. The depth of the anoxic zone can be a key structuring factor. In contrast to sandy shorelines, they are organically rich and consequently higher in nutrients. Generally, muddy shorelines are formed from sediments supplied by nearby rivers, often remobilised from the seafloor throughout the tidal cycle.

DISTRIBUTION: Muddy shorelines occur along low-energy coastlines, in estuaries and embayments where the velocity of water is so low that the finest particles can settle to the bottom.



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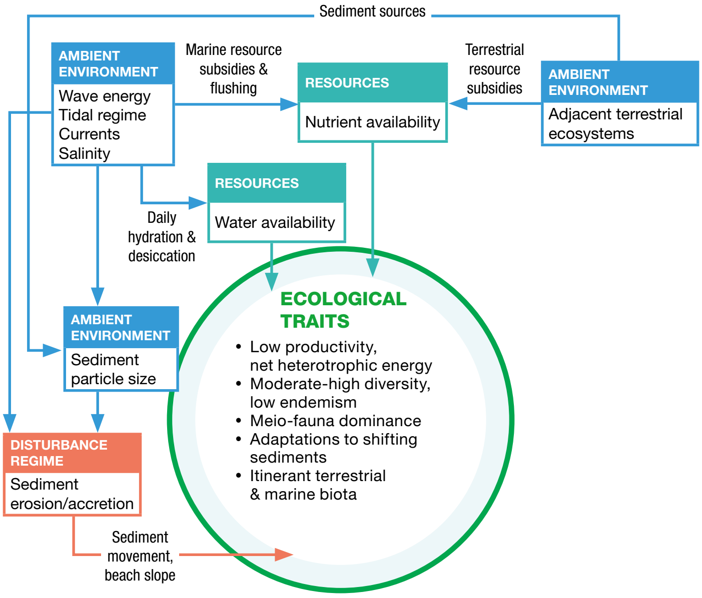
Peterson, C.H. (1991). 'Intertidal Zonation of Marine Invertebrates in Sand and Mud'. *American Scientist* 79(3): 236–249.
Wilson, W.H. (1990). 'Competition and Predation in Marine Soft-Sediment Communities'. *Annual Review of Ecology and Systematics* 21: 221–241.

MT1.3 Sandy Shorelines

BIOME: MT1 SHORELINE SYSTEMS
REALM: TRANSITIONAL MARINE-TERRESTRIAL

Contributors: M.J. Bishop, S.L. McSweeney, D.A. Keith

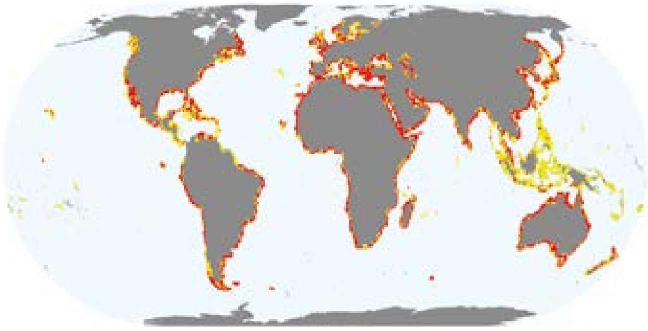
Shorebirds on intertidal beach sands, Shoalwater Bay, Australia.
Source: Roger Jaensch, Queensland Government



ECOLOGICAL TRAITS: Sandy shorelines include beaches, sand bars and spits. These intertidal systems typically lack macrophytes, with their low productivity largely underpinned by detrital subsidies dominated by wrack (i.e. drift seaweed accumulating at the high-water mark) and phytoplankton, particularly in the surf zone of dissipative beaches. Salt- and drought-tolerant primary producers dominate adjacent dune systems (MT2.1). Meio-faunal biomass in many instances exceeds macrofaunal biomass. In the intertidal zone, suspension-feeding is a more common foraging strategy among invertebrates than deposit-feeding, although detritivores may dominate higher on the shore where wrack accumulates. Invertebrate fauna are predominantly interstitial, with bacteria, protozoans and small metazoans contributing to the trophic network. Sediments are constantly shifting and thus invertebrate fauna are dominated by mobile taxa that display an ability to burrow and/or swash-ride up and down the beach face with the tides. The transitional character of these systems supports marine and terrestrial invertebrates and itinerant vertebrates from marine waters (i.e. egg-laying turtles) and from terrestrial or transitional habitats (i.e. shorebirds foraging on invertebrates or foxes foraging on carrion).

KEY ECOLOGICAL DRIVERS: Physical factors are generally more important ecological drivers than biological factors. Sand grain size (>85% grains 0.0625-2mm diam.), wave and tidal regimes, and their relative energy, determine beach morphology, all of which influence the spatial and temporal availability of resources and niche diversity. Particle size is influenced by sediment sources as well as physical conditions and affects interstitial habitat structure. Wave action maintains substrate instability and an abundant supply of oxygen through turbulence. Tides and currents influence the dispersal of biota and regulate daily cycles of desiccation and hydration as well as salinity. Beach morphology ranges from narrow and steep (i.e. reflective) to wide and flat (i.e. dissipative) as sand becomes finer and waves and tides larger. Reflective beaches are accretional and more prevalent in the tropics; dissipative beaches are erosional and more common in temperate regions. Sands filter large volumes of seawater, with the volume greater on reflective than dissipative beaches. Beaches are linked to nearshore surf zones and coastal dunes through the storage, transport, and exchange of sand. Sand transport is the highest in exposed surf zones and sand storage the greatest in well-developed dunes.

DISTRIBUTION: Sandy shores are most extensive at temperate latitudes, accounting for 31% of the ice-free global coastline, including 66% of the African coast and 23% of the European coast.



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Luijendijk, A., Hagenaars, G., Ranasinghe, R., Baart, F., Donchyts, G., Aarninkhof, S. (2018). 'The State of the World's Beaches'. *Scientific Reports* 8: 6641 (2018).
Schlacher, T.A., Schoeman, D.S., Dugan, J., Lastra, M., Jones, A., Scapini, .F, McLachlan, A. (2008). 'Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts'. *Marine Ecology* 29(s1): 70–90.

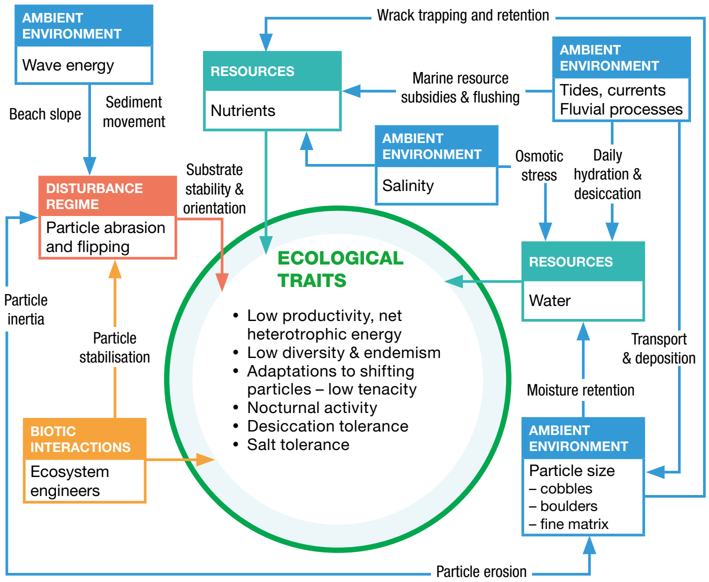
MT1.4 Boulder and cobble shores

BIOME: MT1 SHORELINE SYSTEMS
REALM: TRANSITIONAL MARINE-TERRESTRIAL

Contributors: M.J. Bishop, S.L. McSweeney, A.H. Altieri, D.A. Keith

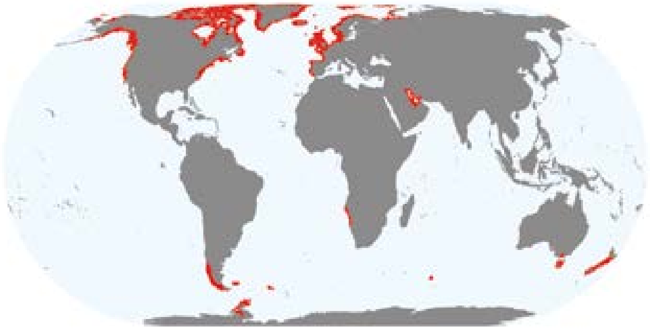
Cobble Beach, South Downes, England
Source: David Keith (2018)

ECOLOGICAL TRAITS: These low-productivity, net heterotrophic systems are founded on unstable rocky substrates and share some ecological features with sandy beaches (MT1.3) and rocky shores (MT1.1). Traits of the biota reflect responses to regular substrate disturbance by waves and exposure of particles to desiccation and high temperatures. For example, in the high intertidal zone of boulder shores (where temperature and desiccation stress is most pronounced), fauna may be predominantly nocturnal. On cobble beaches, fauna are more abundant on the sub-surface because waves cause cobbles to grind against each other, damaging or killing attached fauna. Conversely, on sandy beaches (MT1.3), most fauna occupy surface sediments. Intermediate frequencies of disturbance lead to the greatest biodiversity. Only species with low tenacity (i.e. top shells) are found in surface sediments because they can detach and temporarily inhabit deeper interstices during disturbance events. High-tenacity species (i.e. limpets) or sessile species (e.g. macroalgae and barnacles) are more readily damaged, hence rare on cobble shores. Large boulders, however, are only disturbed during large storms and have more stable temperatures, so more fauna can persist on their surface. Encrusting organisms may cement boulders on the low shore, further stabilising them in turbulent water. Allochthonous wrack is the major source of organic matter on cobble beaches, but in situ autotrophs include superficial algae and vascular vegetation dominated by halophytic forbs. On some cobble beaches of New England, USA, extensive intertidal beds of the cordgrass Spartina alterniflora stabilise cobbles and provide shade, facilitating establishment of mussels, barnacles, gastropods, amphipods, crabs and algae. In stabilising cobbles and buffering wave energy, cordgrass may also facilitate plants higher on the intertidal shore.



KEY ECOLOGICAL DRIVERS: Particle size (e.g. cobbles vs. boulders) and wave activity determine substrate mobility, hence the frequency of physical disturbance to biota. Ecosystem engineers modify these relationships by stabilising the substrate. Cobble beaches are typically steep because waves easily flow through large interstices between coarse beach particles, reducing the effects of backwash erosion. Hence swash and breaking zones tend to be similar widths. The permeability of cobble beaches leads to desiccation and heat stress at low tide along the beach surface gradient. Desiccation stress is extreme on boulder shores, playing a similar role in structuring communities as on rocky shores. The extent of the fine sediment matrix present amongst cobbles, water supply (i.e. rainfall) and the frequency of physical disturbance all influence beach vegetation. Alongshore grading of sediment by size could occur on long, drift dominated shorelines which may influence sediment calibre on the beach.

DISTRIBUTION: Cobble beaches occur where rivers or glaciers delivered cobbles to the coast or where they were eroded from nearby coastal cliffs. They are most common in Europe and also occur in Bahrain, North America, and New Zealand's South Island.



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Altieri, A.H., Silliman, B.R., Bertness, M.D. (2007). 'Hierarchical Organization via a Facilitation Cascade in Intertidal Cordgrass Bed Communities'. *The American Naturalist* 169(2): 195–206.
Gedan, K.B., Bernhardt, J., Bertness, M.D., Leslie, H.M. (2011). 'Substrate size mediates thermal stress in the rocky intertidal'. *Ecology* 92(1): 576–582.
Scott, G.A.M. (1963). 'The Ecology of Shingle Beach Plants'. *Journal of Ecology* 51(3): 517–527.

MT2 Supralittoral coastal biome

Auckland Islands sea cliff heath and rookery
Source: Jo Hiscock, New Zealand Department of Conservation

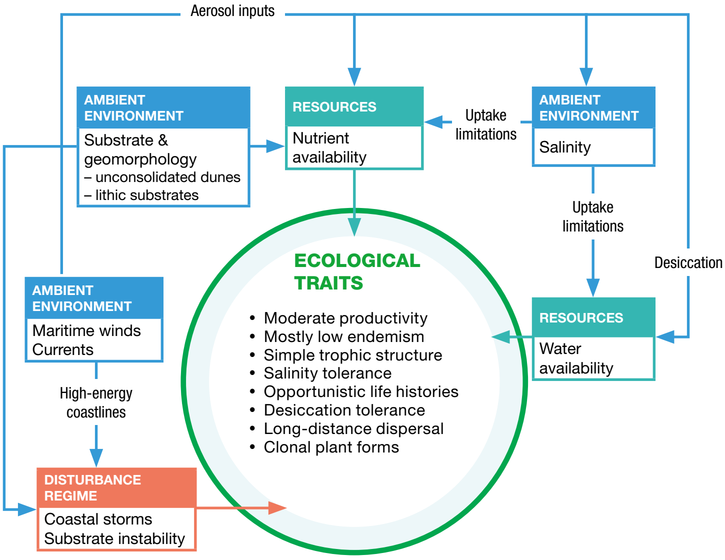
The Supralittoral coastal biome marks the landward extent of the transition from marine to terrestrial biomes. It is elevated above the direct influence of waves and tides (see MT1) and beyond the direct influence of freshwater seepage or rivers (see MFT1). Supratidal coastal ecosystems extend around all the world's land masses, occupying a fringe from tens of metres to a few kilometres wide and covering the entire extent of many small islands. Onshore winds, created by differences in air pressure related to the differing heat capacities of water and dry land, are a key driver of ecosystem function. These winds create desiccating conditions on elevated landforms, such as headlands and coastal dunes, as well as continual inputs of aerosol salts and salt spray. Even though the supralittoral zone is located above high spring tide, it is exposed to recurring disturbance from storms producing exceptional waves and tides that reduce standing biomass and destabilise substrates. These strong environmental gradients select for a specialised, low-diversity biota. Much of this biota is confined to supralittoral ecosystems and nowhere else, a key feature of these ecosystems, although it may be widely distributed behind shorelines on different land masses due to dispersal by coastal winds, oceanic currents, and/or migratory behaviour. Autochthonous energy is produced by wind-pruned vegetation with traits promoting tolerance to desiccation, high salinity and substrate instability (e.g. stomatal regulation, extensive rhizomes or root systems and succulence). The sea supplies allochthonous energy subsidies, such as wrack and guano, but also transports a portion of primary production to other ecosystems. Invertebrate detritivores and physical weathering contribute to rapid decay. Supralittoral ecosystems also provide nesting habitat for seabirds on the surface, in vegetation or in burrows, especially on islands free from terrestrial mammalian predators.

MT2.1 Coastal shrublands and grasslands

BIOME: MT2 COASTAL VEGETATION
REALM: TRANSITIONAL MARINE-TERRESTRIAL

Contributors: D.A. Keith, J. Loidi, A.T.R. Acosta

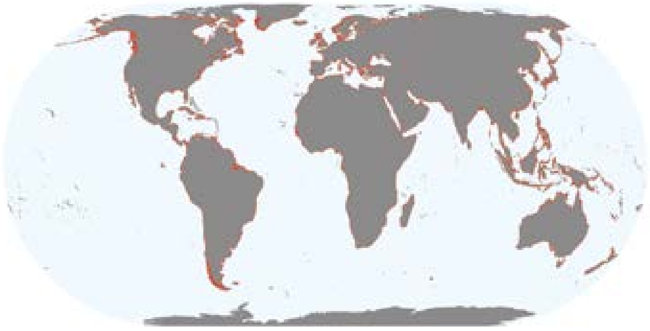
Littoral grassland and shrubland on the Atlantic coast of the Cape of Good Hope, South Africa.
Source: David Keith (2007)



ECOLOGICAL TRAITS: Relatively low productivity grasslands, shrublands and low forests on exposed coastlines are limited by salt influx, water deficit and recurring disturbances. Diversity is low across taxa and trophic networks are simple, but virtually all plants and animals have strong dispersal traits and most consumers move between adjacent terrestrial and marine ecosystems. Vegetation and substrates are characterised by strong gradients from sea to land, particularly related to aerosol salt inputs, substrate instability and disturbance associated with sea storms and wave action. Plant traits conferring salt tolerance (e.g. succulent and sub-succulent leaves and salt-excretion organs) are commonly represented. Woody plants with ramulose and/or decumbent growth forms and small (microphyll-nanophyll) leaves reflect mechanisms of persistence under exposure to strong salt-laden winds, while modular and rhizomatous growth forms of woody and non-woody plants promote persistence, regeneration and expansion under regimes of substrate instability and recurring disturbance. These strong environmental filters promote local adaptation, with specialised genotypes and phenotypes of more widespread taxa commonly represented on the strandline. Fauna are highly mobile, although some taxa, such as ground-nesting seabirds, may be sedentary for some parts of their lifecycles. Ecosystem dynamics are characterised by disturbance-driven cycles of disruption and renewal, with early phases dominated by colonists and in situ regenerators that often persist during the short intervals between successive disturbances.

KEY ECOLOGICAL DRIVERS: Desiccating winds promote an overall water deficit and appreciable exposure to salinity due to aerosol influx and salt spray. Warm to mild temperatures across the tropics to temperate zones and cold temperatures in the cool temperate to boreal zones are moderated by direct maritime influence. Above the regular intertidal zone, these systems are exposed to periodic disturbance from exceptional tides, coastal storm events, wind shear, bioturbation and aeolian substrate mobility. Consolidated substrates (headlands, cliffs) may differ from unconsolidated dunes in their influence on function and biota. Geomorphological depositional and erosional processes influence substrate stability and local vegetation succession.

DISTRIBUTION: Coastal dunes and cliffs throughout tropical, temperate, and boreal latitudes.



Reference:

van der Maarel, E. (1997). 'Dry Coastal Ecosystems: General Aspects'. In: *Ecosystems of the World 2C*. Vol. 2. Amsterdam, The Netherlands: Elsevier.

MT3 Anthropogenic shorelines biome

Exmouth Marina, Devon, England.
Source: Red Zeppelin on Unsplash, (licensed for use & modification)

The Anthropogenic shorelines biome is distributed globally where urbanised and industrial areas adjoin the coast, and includes some more remote structures such as artificial islands. It includes marine interfaces constructed from hard, smooth surfaces, including concrete, timber, lithic blocks and earthen fill, adjoining, extending or replacing natural shores, or floating in proximity to them. These relatively homogeneous substrates support an opportunistic, cosmopolitan biota with limited diversity and simplified trophic structure compared to other shoreline systems. Vertical surfaces are inhabited by algae and biofouling species but are exposed to strong tidal desiccation regimes that strongly filter potential colonists. Floating structures have downward-facing, usually smooth, surfaces, unlike almost anything in nature, which may be colonised by opportunists.

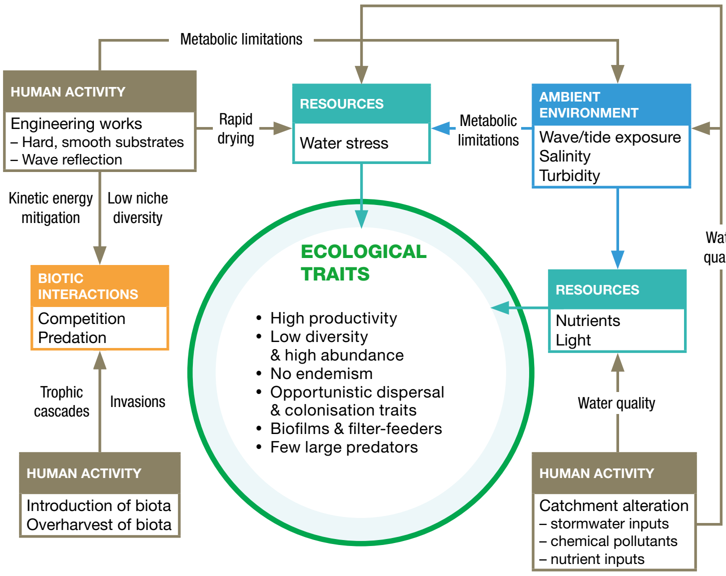
Influx of storm water and effluent enhances nutrient levels and eutrophic algae, which contribute autochthonous energy. Outflows from developed areas are also major sources of allochthonous energy. Strong bottom-up regulation stems from these resource inputs and from low populations of predators, which are depleted or deterred by human activity.

MT3.1 Artificial shorelines

BIOME: MT3 ARTIFICIAL MARINE SYSTEMS
REALM: TRANSITIONAL MARINE-TERRESTRIAL

Contributors: I.M. Suthers, M.J. Bishop, L.B. Firth, K.A. Dafforn. D.A. Keith

Cape Town Harbour, South Africa.
Source: SkyPixels (CC BY-SA 4.0)



ECOLOGICAL TRAITS: Constructed sea walls, breakwaters, piers, docks, tidal canals, islands and other coastal infrastructure create substrates inhabited by intertidal and subtidal, benthic and demersal marine biota around ports, harbours, and other intensively settled coastal areas. Structurally simple, spatially homogeneous substrates support a cosmopolitan biota, with no endemism and generally lower taxonomic and functional diversity than rocky shores (MT1.1). Trophic networks are simple and dominated by filter-feeders (e.g. sea squirts and barnacles) and biofilms of benthic algae and bacteria. Low habitat heterogeneity and the small surface area for attachment that the often vertical substrate provides regulate community structure by promoting competition and limiting specialised niches (e.g. crevices or pools) and restricting refuges from predators. Small planktivorous fish may dominate temperate harbours and ports. These can provide a trophic link, but overharvest of predatory fish and sharks may destabilise food webs and cause trophic cascades. Much of the biota possess traits that promote opportunistic colonisation, including highly dispersive life stages (e.g. larvae, eggs and spores), high fecundity, generalist settlement niches and diet, wide ranges of salinity tolerance, and rapid population turnover. These structures typically contain a higher proportion of non-native species than the natural substrates they replace.

KEY ECOLOGICAL DRIVERS: The substrate material influences the texture, chemistry, and thermal properties of the surface. Artificial structures of wood, concrete, rock, or steel have flat, uniform, and vertical surfaces that limit niche diversity and exacerbate inter-tidal gradients in desiccation and temperature. Floating structures have downward-facing surfaces, rare in nature. Some structures are ecologically engineered (designed for nature) to provide more complex surfaces and ponds to enhance biodiversity and ecosystem function. Structures may be located in high (i.e. breakwaters) or low (i.e. harbours) energy waters. Tides and waves are key drivers of onshore resource and kinetic energy gradients. Brackish water plumes from polluted storm water and sewage overflows add allochthonous nutrients, organic carbon, and open ecological space exploited by invasive species introduced by shipping and ballast water. The structures are often located close to vectors for invasive species (i.e. transport hubs). Boat traffic and storm water outflows cause erosion and bank instability and maintain high turbidity in the water column. This limits photosynthesis by primary producers, but nutrient runoff may increase planktonic productivity. Maintenance regimes (i.e. scraping) reduce biomass and reset succession.

DISTRIBUTION: Urbanised coasts through tropical and temperate latitudes, especially in North and Central America, Europe, and North and South Asia.

Reference:
Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L. (2015). 'Marine urbanization: an ecological framework for designing multifunctional artificial structures'. *Frontiers in Ecology and the Environment* 13(2): 82–90.

MFT1 Brackish tidal biome

Mangrove forest in the Saloum Delta National Park, Senegal.
Source: Curioso Photography on Unsplash

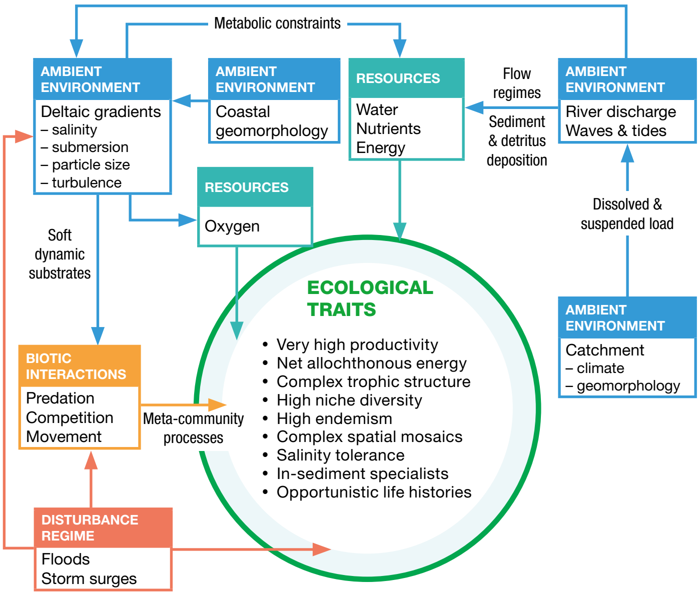
The Brackish tidal systems biome is associated with prograding depositional shorelines at the interface of terrestrial, freshwater, and marine realms. The relative influences of marine, freshwater, and terrestrial processes vary from strongly fluvial deltas to marine-dominated intertidal forests and terrestrial-dominated coastal saltmarsh. Autochthonous sources of energy, contributed by flowering plants and algae, are supplemented by allochthonous sources delivered by rivers, currents, and tides. These sources support high productivity and complex trophic webs that include highly mobile fish and birds that rely on brackish tidal systems to complete their lifecycles. Standing plants assimilate energy and engineer habitat structure for epifauna and epiflora as well as juvenile fish nurseries. They also promote sediment deposition by dampening wave and tidal energy. While terrestrial systems are the ultimate source of most sediment, fluvial and marine processes redistribute it and drive patch dynamics across temporal and spatial scales. Brackish tidal systems are structured by steep local gradients in salinity and tidal exposure. Physiological traits that confer differential fitness and competitive abilities, together with differential predation pressure, mediate species turnover along gradients. Brackish tidal systems are distributed on depositional coastlines throughout the world.

Sundarbans, Ganges Delta, India & Bangladesh.
Source: NASA Earth Observatory, Wikimedia Commons CC4.0

MFT1.1 Coastal river deltas

BIOME: MFT1 BRACKISH TIDAL SYSTEMS
REALM: TRANSITIONAL TERRESTRIAL-FRESHWATER-MARINE

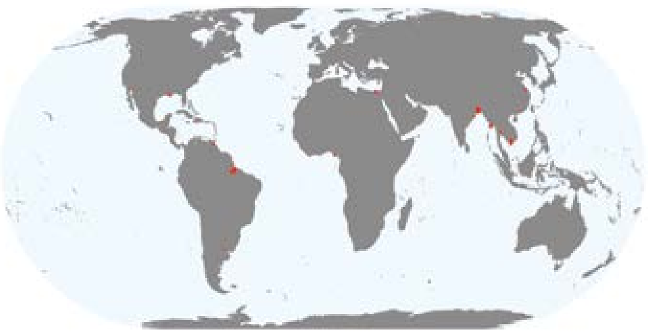
Contributors: D.A. Keith, R.T. Kingsford



ECOLOGICAL TRAITS: Coastal river deltas are prograding depositional systems, shaped by freshwater flows and influenced by wave and tidal flow regimes and substrate composition. The biota of these ecosystems reflects strong relationships with terrestrial, freshwater, and marine realms at different spatial scales. Consequently, they typically occur as multi-scale mosaics comprised of unique elements juxtaposed with other functional groups that extend far beyond the deltaic influence, such as floodplain marshes (TF1.4), mangroves (MFT1.2), sandy shorelines (MT1.3) and subtidal muddy plains (M1.8). Gradients of water submergence and salinity structure these mosaics. Allochthonous subsidies from riverine discharge and marine currents supplement autochthonous sources of energy and carbon and contribute to high productivity. Complex, multi-faceted trophic relationships reflect the convergence and integration of three contrasting realms and the resulting niche diversity. Autotrophs include planktonic algae and emergent and submerged aquatic plants, which contribute to trophic networks mostly through organic detritus (rather than herbivory). Soft sediments and flowing water are critical to in-sediment fauna dominated by polychaetes and molluscs. Freshwater, estuarine, and marine fish and zooplankton are diverse and abundant in the water column. These provide food for diverse communities of wading and fishing birds, itinerant marine predators and terrestrial scavengers and predators (e.g. mammals and reptiles). Virtually all biota have life-history and/or movement traits enabling them to exploit highly dynamic ecosystem structures and disturbance regimes. High rates of turnover in habitat and biota are expressed spatially by large fluctuations in the mosaic of patch types that make up deltaic ecosystems.

KEY ECOLOGICAL DRIVERS: River inflows structure the dynamic mosaics of coastal river deltas. Inflows depend on catchment geomorphology and climate and influence water levels, nutrient input, turbidity (hence light penetration), tidal amplitude, salinity gradients, temperature, dissolved oxygen and organic carbon. Rates of delta aggradation depend on interactions among riverine sedimentation and ocean currents, tides and wave action, which disperse sediment loads. Coastal geomorphology influences depth gradients. These processes result in complex, spatio-temporally variable mosaics of distributary channels, islands, floodplains, mangroves, subtidal mud plains and sand beds. Regimes of floods and storm surges driven by weather in the river catchment and ocean, respectively, have a profound impact on patch dynamics.

DISTRIBUTION: Continental margins where rivers connect the coast to high-rainfall catchments, usually with high mountains in their headwaters.



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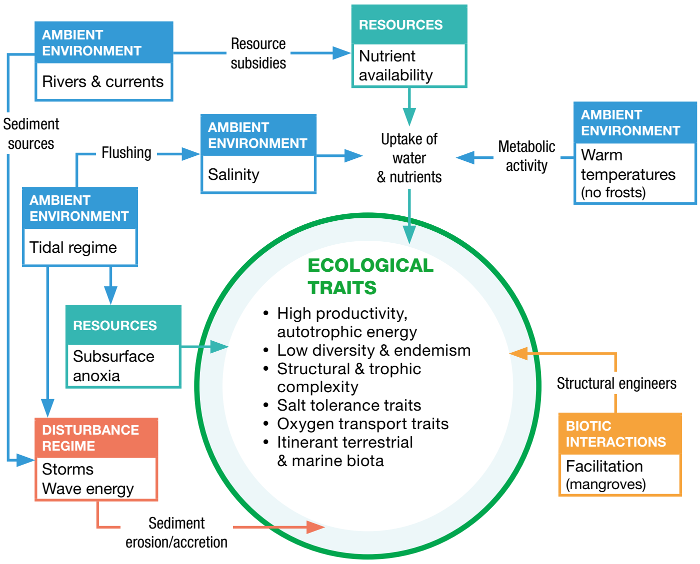
Bianchi, T.S. and Allison, M.A. (2009). 'Large-river delta-front estuaries as natural "recorders'' of global environmental change'. *PNAS* 106(20): 8085–8092.
Orton, G.J., Reading, G. (1993). 'Variability of deltaic processes in terms of sediment supply, with particular emphasis on grain-size'. *Sedimentology* 40(3): 475–512.

MFT1.2 Intertidal forests and shrublands

BIOME: MFT1 BRACKISH TIDAL SYSTEMS
REALM: TRANSITIONAL TERRESTRIAL-FRESHWATER-MARINE

Contributors: M.J. Bishop, A.H. Altieri, T.S. Bianchi, D.A. Keith

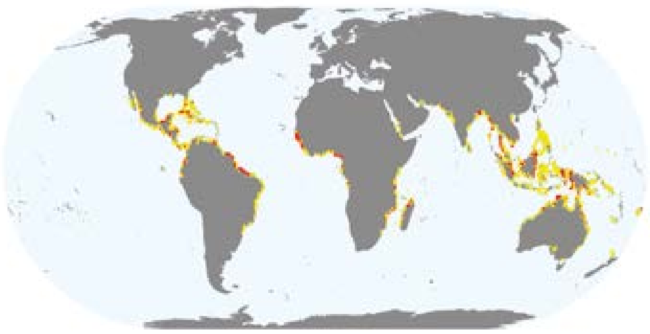
Red mangrove forest with stilt roots , Los Haitses National Park, Dominican Republic.
Source: Anton Bielousov



ECOLOGICAL TRAITS: Mangroves are structural engineers and possess traits, including pneumatophores, salt excretion glands, vivipary and propagule buoyancy, that promote survival and recruitment in poorly aerated, saline, mobile and tidally inundated substrates. They are highly efficient in nitrogen use efficiency and nutrient resorption. These systems are among the most productive coastal environments. They produce large amounts of detritus (e.g. leaves, twigs and bark), which is either buried in waterlogged sediments, consumed by crabs, or more commonly decomposed by fungi and bacteria, mobilising carbon and nutrients to higher trophic levels. These ecosystems are also major blue carbon sinks, incorporating organic matter into sediments and living biomass. Although highly productive, these ecosystems are less speciose than other coastal biogenic systems. Crabs are among the most abundant and important invertebrates. Their burrows oxygenate sediments, enhance groundwater penetration, and provide habitat for other invertebrates such as molluscs and worms. Specialised roots (pneumatophores and stilt roots) provide a complex habitat structure that protects juvenile fish from predators and serves as hard substrate for the attachment of algae as well as sessile and mobile invertebrates (e.g. oysters, mussels, sponges and gastropods). Mangrove canopies support invertebrate herbivores and other terrestrial biota, including invertebrates, reptiles, small mammals and extensive bird communities. These are highly dynamic systems, with species distributions adjusting to local changes in sediment distribution, tidal regimes, and local inundation and salinity gradients.

KEY ECOLOGICAL DRIVERS: Mangroves are physiologically intolerant of low temperatures, which excludes them from regions where mean air temperature during the coldest months is -20°C, where the seasonal temperature range exceeds 10°C, or where ground frost occurs. Many mangrove soils are low in nutrients, especially nitrogen and phosphorus. Limited availability of nitrogen and phosphorus Regional distributions are influenced by interactions among landscape position, rainfall, hydrology, sea level, sediment dynamics, subsidence, storm-driven processes and disturbance by pests and predators. Rainfall and sediment supply from rivers and currents promote mangrove establishment and persistence, while waves and large tidal currents destabilise and erode mangrove substrates, mediating local-scale dynamics in ecosystem distributions. High rainfall reduces salinity stress and increases nutrient loading from adjacent catchments, while tidal flushing also regulates salinity.

DISTRIBUTION: Widely distributed along tropical and warm temperate coastlines of the world. Large-scale currents may prevent buoyant seeds from reaching some areas.



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Krauss, K.W., Lovelock, C.E., McKee, K.L., López-Hoffman, L., Ewe, S.M., Sousa, W.P. (2008). 'Environmental drivers in mangrove establishment and early development: A review'. *Aquatic Botany* 89(2): 105–127.
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MFT1.3 Coastal saltmarshes and reedbeds

BIOME: MFT1 BRACKISH TIDAL SYSTEMS
REALM: TRANSITIONAL TERRESTRIAL-FRESHWATER-MARINE

Saltmarsh in tidal creeks near Al Thakira, Qatar.
Source: Alexey Sergeev

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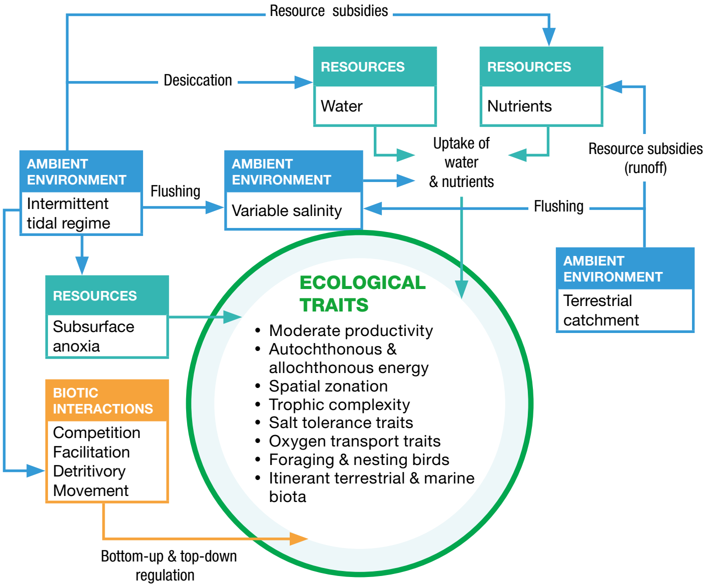
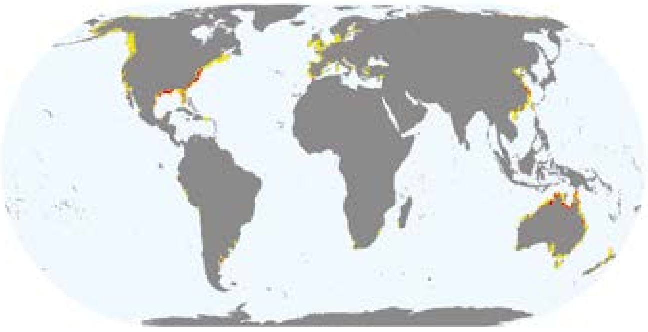


ECOLOGICAL TRAITS: Coastal saltmarshes are vegetated by salt-tolerant forbs, grasses and shrubs, with fine-scale mosaics related to strong local hydrological and salinity gradients, as well as competition and facilitation. Plant traits, such as succulence, salt excretion, osmotic regulation, reduced transpiration, C_4 photosynthesis (among grasses), modular growth forms and aerenchymatous tissues, confer varied degrees of tolerance to salinity, desiccation and substrate anoxia. Adjacent marine and terrestrial ecosystems influence the complexity and function of the trophic network, while freshwater inputs mediate resource availability and physiological stress. Angiosperms are structurally dominant autotrophs, but algal mats and phytoplankton imported by tidal waters contribute to primary production. Cyanobacteria and rhizobial bacteria are important N-fixers. Tides and runoff bring subsidies of organic detritus and nutrients (including nitrates) from marine and terrestrial sources, respectively. Nitrogen is imported into saltmarshes mainly as inorganic forms and exported largely as organic forms, providing important subsidies to the trophic networks of adjacent estuarine fish nurseries (FM1.2). Fungi and bacteria decompose dissolved and particulate organic matter, while sulphate-reducing bacteria are important in the decay of substantial biomass in the anaerobic subsoil. Protozoans consume microbial decomposers, while in situ detritivores and herbivores include a range of crustaceans, polychaetes and molluscs. Many of these ingest a mixture of organic material and sediment, structuring, aerating, and increasing the micro-scale heterogeneity of the substrate with burrows and faecal pellets. Fish move through saltmarsh vegetation at high tide, feeding mainly on algae. They include small-bodied residents and juveniles of larger species that then move offshore. Itinerant terrestrial mammals consume higher plants, regulating competition and vegetation structure. Colonial and solitary shorebirds breed and/or forage in saltmarsh. Migratory species that play important roles in the dispersal of plants, invertebrates and microbes, while abundant foragers may force top-down transformational change.

KEY ECOLOGICAL DRIVERS: High and variable salt concentration is driven by alternating episodes of soil desiccation and flushing, associated with cycles of tidal inundation and drying combined with freshwater seepage, rainfall and runoff in the upper intertidal zone. These interacting processes produce dynamic fine-scale hydrological and salinity gradients, which may drive transformation to intertidal forests (MFT1.2). Marshes are associated with low-energy depositional coasts but may occur on sea cliffs and headlands where wind deposits salt from wave splash (i.e. salt spray) and aerosol inputs. Salt approaches hypersaline levels where flushing events are infrequent. Other nutrients make up a low proportion of the total ionic content. Subsoils are generally anaerobic, but this varies depending on seepage water and the frequency of tidal inundation. Tidal cycles also influence temperature extremes, irregularities in photoperiod, physical disturbance and deposition of sediment.

DISTRIBUTION: Widely distributed, mostly on low-energy coasts from arctic to tropical and subantarctic latitudes.



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