



TF1.3 Permanent marshes

Kingsford, Richard; Catford, Jane; Rains, MC; et.al.

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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)



INTERNATIONAL UNION FOR CONSERVATION OF NATURE



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Content

List of figures	viii
List of tables	viii
Executive summary	ix
Authors and affiliations	x
Acknowledgements	xv
Glossary of selected terms and acronyms used in ecosystem descriptions	xvi
Introduction	1
Part I	2
1 Development of the typology	2
2 Design principles	3
3 Levels of classification within the Global Ecosystem Typology	5
3.1 Realms	5
3.2 Biomes	9
3.3 Ecosystem Functional Groups	10
3.4 Lower levels of classification	11
4 Reflections on the approach to typology development	18
4.1 Theoretical foundations	18
4.2 Top-down and bottom-up construction	18
4.3 Discrete representation of continuous patterns in nature	18
4.4 Classification and mapping	19
5 Descriptive profiles for Ecosystem Functional Groups	19
5.1 Nomenclature	19
5.2 Text descriptions	19
5.3 Exemplary photographs	19
5.4 Major ecosystem drivers	19
5.5 Diagrammatic assembly models	20
5.6 Indicative distribution maps	20
5.7 Use of references	21
5.8 Updates	21
References	28
Appendix 1. List of Ecosystem Functional Groups by realms and biomes	33

Part II	37
T1 Tropical-subtropical forests biome	38
T1.1 Tropical subtropical lowland rainforests	39
T1.2 Tropical subtropical dry forests and thickets	40
T1.3 Tropical-subtropical montane rainforests	41
T1.4 Tropical heath forests	42
T2 Temperate-boreal forests and woodlands biome	43
T2.1 Boreal and temperate high montane forests and woodlands	44
T2.2 Deciduous temperate forests	45
T2.3 Oceanic cool temperate rainforests	46
T2.4 Warm temperate laurophyll forests	47
T2.5 Temperate pyric humid forests	48
T2.6 Temperate pyric sclerophyll forests and woodlands	49
T3 Shrublands and shrubby woodlands biome	50
T3.1 Seasonally dry tropical shrublands	51
T3.2 Seasonally dry temperate heaths and shrublands	52
T3.3 Cool temperate heathlands	53
T3.4 Rocky pavements, lava flows and screes	54
T4 Savannas and grasslands biome	55
T4.1 Trophic savannas	56
T4.2 Pyric tussock savannas	57
T4.3 Hummock savannas	58
T4.4 Temperate woodlands	59
T4.5 Temperate subhumid grasslands	60
T5 Deserts and semi-deserts biome	61
T5.1 Semi-desert steppes	62
T5.2 Succulent or Thorny deserts and semi-deserts	63
T5.3 Sclerophyll hot deserts and semi-deserts	64
T5.4 Cool deserts and semi-deserts	65
T5.5 Hyper-arid deserts	66
T6 Polar-alpine (cryogenic) biome	67
T6.1 Ice sheets, glaciers and perennial snowfields	68
T6.2 Polar alpine rocky outcrops	69
T6.3 Polar tundra and deserts	70
T6.4 Temperate alpine grasslands and shrublands	71
T6.5 Tropical alpine grasslands and herbfields	72
T7 Intensive land-use biome	73
T7.1 Annual croplands	74
T7.2 Sown pastures and fields	75

T7.3 Plantations	76
T7.4 Urban and industrial ecosystems	77
T7.5 Derived semi-natural pastures and old fields	78
S1 Subterranean lithic biome	79
S1.1 Aerobic caves	80
S1.2 Endolithic systems	81
S2 Anthropogenic subterranean voids biome	82
S2.1 Anthropogenic subterranean voids	83
SF1 Subterranean freshwaters biome	84
SF1.1 Underground streams and pools	85
SF1.2 Groundwater ecosystems	86
SF2 Anthropogenic subterranean freshwaters biome	87
SF2.1 Water pipes and subterranean canals	88
SF2.2 Flooded mines and other voids	89
SM1 Subterranean tidal biome	90
SM1.1 Anchialine caves	91
SM1.2 Anchialine pools	92
SM1.3 Sea caves	93
TF1 Palustrine wetlands biome	94
TF1.1 Tropical flooded forests and peat forests	95
TF1.2 Subtropical-temperate forested wetlands	96
TF1.3 Permanent marshes	97
TF1.4 Seasonal floodplain marshes	98
TF1.5 Episodic arid floodplains	99
TF1.6 Boreal, temperate and montane peat bogs	100
TF1.7 Boreal and temperate fens	101
F1 Rivers and streams biome	102
F1.1 Permanent upland streams	103
F1.2 Permanent lowland rivers	104
F1.3 Freeze-thaw rivers and streams	105
F1.4 Seasonal upland streams	106
F1.5 Seasonal lowland rivers	107
F1.6 Episodic arid rivers	108
F1.7 Large lowland rivers	109
F2 Lakes biome	110
F2.1 Large permanent freshwater lakes	111
F2.2 Small permanent freshwater lakes	112
F2.3 Seasonal freshwater lakes	113
F2.4 Freeze-thaw freshwater lakes	114

F2.5 Ephemeral freshwater lakes	115
F2.6 Permanent salt and soda lakes	116
F2.7 Ephemeral salt lakes	117
F2.8 Artesian springs and oases	118
F2.9 Geothermal pools and wetlands	119
F2.10 Subglacial lakes	120
F3 Artificial wetlands biome	121
F3.1 Large reservoirs	122
F3.2 Constructed lacustrine wetlands	123
F3.3 Rice paddies	124
F3.4 Freshwater aquafarms	125
F3.5 Canals, ditches and drains	126
FM1 Semi-confined transitional waters biome	127
FM1.1 Deepwater coastal inlets	128
FM1.2 Permanently open riverine estuaries and bays	129
FM1.3 Intermittently closed and open lakes and lagoons	130
M1 Marine shelf biome	131
M1.1 Seagrass meadows	132
M1.2 Kelp forests	133
M1.3 Photic coral reefs	134
M1.4 Shellfish beds and reefs	135
M1.5 Photo-limited marine animal forests	136
M1.6 Subtidal rocky reefs	137
M1.7 Subtidal sand beds	138
M1.8 Subtidal mud plains	139
M1.9 Upwelling zones	140
M2 Pelagic ocean waters biome	141
M2.1 Epipelagic ocean waters	142
M2.2 Mesopelagic ocean waters	143
M2.3 Bathypelagic ocean waters	144
M2.4 Abyssopelagic ocean waters	145
M2.5 Sea ice	146
M3 Deep sea floors biome	147
M3.1 Continental and island slopes	148
M3.2 Submarine canyons	149
M3.3 Abyssal plains	150
M3.4 Seamounts, ridges and plateaus	151
M3.5 Deepwater biogenic beds	152

M3.6 Hadal trenches and troughs	153
M3.7 Chemosynthetic-based ecosystems (CBE)	154
M4 Anthropogenic marine biome	155
M4.1 Submerged artificial structures	156
M4.2 Marine aquafarms	157
MT1 Shorelines biome	158
MT1.1 Rocky shorelines	159
MT1.2 Muddy shorelines	160
MT1.3 Sandy shorelines	161
MT1.4 Boulder and cobble shores	162
MT2 Supralittoral coastal biome	163
MT2.1 Coastal shrublands and grasslands	164
MT3 Anthropogenic shorelines biome	165
MT3.1 Artificial shorelines	166
MFT1 Brackish tidal biome	167
MFT1.1 Coastal river deltas	168
MFT1.2 Intertidal forests and shrublands	169
MFT1.3 Coastal saltmarshes and reedbeds	170

List of figures

- Figure 1** Hierarchical structure of Global Ecosystem Typology
- Figure 2** Examples of major ecosystem assembly filters represented as gradients segregating functionally contrasting ecosystems
- 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.
- 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.

List of tables

- Table 1** Design principles for a global ecosystem typology
- Table 2** Definitions of hierarchical levels within the global ecosystem typology
- Table 3** Assembly filters and ecological traits distinguishing ecosystems within the five realms of the biosphere
- Table 4** Methods and source data for indicative maps of each Ecosystem Functional Group (EFG)

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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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).
C₃	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.
C₄	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-
Dimictic 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	<p>Terms describing leaf size follow Raunkiaer (1934) except 'Notophyll'.</p> <table> <tr> <th>Size class</th><th>Leaf area</th></tr> <tr> <td>Megaphyll</td><td>>164,025 mm²</td></tr> <tr> <td>Macrophyll</td><td>18,225–164,025 mm²</td></tr> <tr> <td>Mesophyll</td><td>2,025–18,225 mm²</td></tr> <tr> <td>[Notophyll]</td><td>2,025–4,500 mm²</td></tr> <tr> <td>Microphyll</td><td>225–2,025 mm²</td></tr> <tr> <td>Nanophyll</td><td>25–225 mm²</td></tr> <tr> <td>Leptophyll</td><td><25 mm²</td></tr> </table>	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
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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.																
Polymictic 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 plants) 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.

*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.

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 & Plischoff, 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 were 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 gazetteers (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).



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.



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

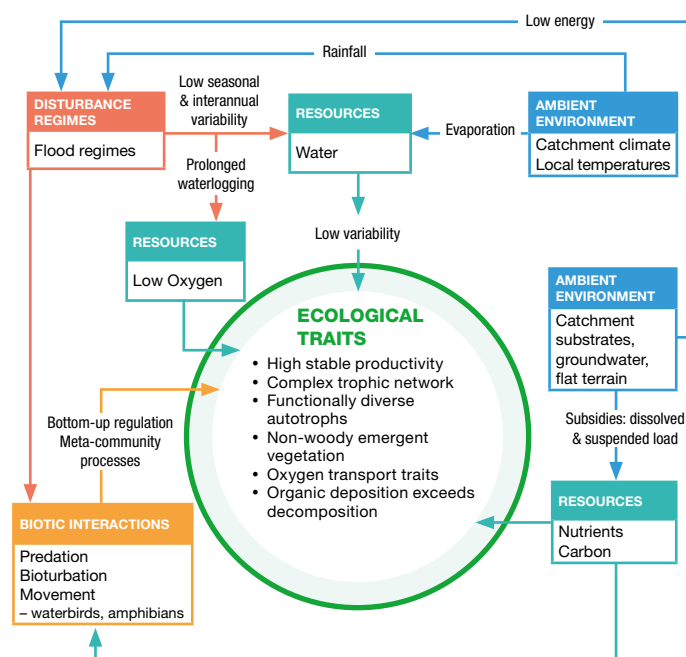
TF1.3 Permanent marshes

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.