

## **F1.1 Permanent upland streams**

Belongs to biome F1. Rivers and streams biome, part of the Freshwater realm.

### **Short description**

These small rivers or streams in mountainous or hilly areas are characterised by steep gradients and fast flow. They flow all year, increasing in wet periods, in humid tropical and temperate zones. Stones are common along their rapids and pools, turning over and oxygenating the water. Dependent organisms are specialised for these high flow-velocity environments, with resources for food webs derived mainly from the stream and inputs from adjacent and upstream vegetation.

### **Key Features**

High-medium velocity, low-medium volume perennial flows with abundant benthic filter feeders, algal biofilms & small fish.

### **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 (e.g. 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..

## **F1.2 Permanent lowland rivers**

Belongs to biome F1. Rivers and streams biome, part of the Freshwater realm.

## Short description

Lowland rivers with slow continuous flows up to 10,000m<sup>3</sup>/s are common at low elevations throughout tropical and temperate parts of the world. These are productive ecosystems with major energy and fine sediment inputs from floodplains and upper catchments. Zooplankton can be abundant, along with aquatic plants and diverse communities of fish able to tolerate a range of temperatures and oxygen concentrations, as well as reptiles, birds, and mammals that depend wholly or partly on lowland lotic aquatic habitats.

## Key Features

Low-medium velocity, high volume, perennial flows with abundant zooplankton, fish, macrophytes, macroinvertebrates & piscivores.

## 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 (e.g. mussels) and scavenging (e.g. 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 (e.g. sturgeons), smaller predators of invertebrates, herbivores, and detritivores. The feeding activities and movement of piscivorous birds (e.g. cormorants), diadromous fish (seawater-freshwater migrants), mammals (e.g. otters), and reptiles (e.g. 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 (<10,000m<sup>3</sup>/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..

## F1.3 Freeze-thaw rivers and streams

Belongs to biome F1. Rivers and streams biome, part of the Freshwater realm.

## **Short description**

In cold climates at high latitudes or altitudes, the surfaces of both small streams and large rivers freeze in winter. In winter, the layer of surface ice reduces nutrient inputs and light penetration, limiting the productivity of these ecosystems and the diversity of their biota. In spring, meltwaters transport increased organic matter and nutrients, producing seasonal peaks in abundance of algae and phytoplankton. Animals, such as fish and beavers, tolerate near-freezing water temperatures, while a range of invertebrates and other vertebrates come to forage from spring to autumn.

## **Key Features**

Cold-climate streams with seasonally frozen surface water and variable melt flows and aquatic biota with cold-resistance and/or seasonal dormancy.

## **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 (e.g. 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, 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..

## **F1.4 Seasonal upland streams**

Belongs to biome F1. Rivers and streams biome, part of the Freshwater realm.

### **Short description**

Seasonal rainfall patterns in large parts of the tropics and temperate regions generate flows that are hugely variable in narrow and steep upland streams. Globally, these streams account for the greatest stream length of any flowing ecosystem. During the dry season, flows in some streams are reduced to very levels, while in others flow ceases altogether and water persists only in isolated stagnant pools. Algae and leaf fall support moderate productivity, with seasonal floods sending organic matter downstream. The diversity of organisms fluctuates seasonally, with many localised (endemic) species, and specialised adaptations that enable animals to survive both flooding and dry conditions.

### **Key Features**

High-medium velocity, low-medium volume, highly seasonal flows with abundant benthic filter feeders, algal biofilms & small fish.

### **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 (e.g. dippers). Diversity and abundance of invertebrates and their predators (e.g. 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, 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 allochthonous subsidies and downstream exports of organic matter and nutrients..

### **Distribution**

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

## **F1.5 Seasonal lowland rivers**

Belongs to biome F1. Rivers and streams biome, part of the Freshwater realm.

### **Short description**

These medium to large rivers in tropical, subtropical and temperate lowlands have markedly seasonal flows due to seasonal water supply in the catchments. Their single or multi-channelled forms link to floodplain wetlands, and transport large floods during wet seasons: summer in the tropics or winter-spring in temperate latitudes. Productivity is high, both within channels and on connected floodplains, with algae and aquatic plants supporting complex food webs, and providing seasonal nurseries for breeding animals.

## **Key Features**

Highly productive large rivers with seasonal hydrology large floodplain subsidies. Short food chains support large mobile predators.

## **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 predators 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 processes 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 (e.g. 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..

## **F1.6 Episodic arid rivers**

Belongs to biome F1. Rivers and streams biome, part of the Freshwater realm.

## **Short description**

These desert rivers occur mostly in flat areas of arid and semi-arid mid-latitudes. Channels are typically broad, flat, and often branching, with soft sandy sediments. They are dry most of the time, but punctuated by high-volume, short duration flows that transport nutrients and stimulate high productivity by algae and zooplankton. Plants and animals can either tolerate or avoid long, dry periods and then exploit short pulses of abundant resources, producing hotspots of biodiversity and ecological activity in arid landscapes.

## **Key Features**

Rivers with high temporal flow variability which determines periods of high and low productivity, supporting high levels of biodiversity and complex trophic networks during floods and simple trophic networks during dry periods.

## **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 (e.g. mussels) and scavengers (e.g. 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 anastomosing, 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..

## **F1.7 Large lowland rivers**

Belongs to biome F1. Rivers and streams biome, part of the Freshwater realm.

## **Short description**

These very large rivers transport massive volumes of freshwater ( $>10,000\text{m}^3/\text{s}$ ) through flat lowlands, mostly in tropical or subtropical regions. Their very large flow volumes, diverse habitats and slow to moderate flows make them highly productive. High nutrient levels come from upstream catchments and floodplains, with additional productivity contributed by in-channel algae and aquatic plants. Their food webs are complex, with a high diversity of plants and animals, including large-bodied fish, reptiles and mammals.

## **Key Features**

Large highly productive rivers with megaflow rates and complex food webs, reflecting the extent of habitat, connections with floodplains and available niches for plants, invertebrates and large vertebrates including

aquatic mammals..

### **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 (e.g. mussels), burrowing (e.g. annelids) and scavenging (e.g. 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, Pirhana, 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 (e.g. cormorants), mammals (e.g. 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 on smaller river ecosystems..

### **Key Ecological Drivers**

These rivers have shallow gradients with low turbulence, low to moderate flow velocity and very high flow volumes ( $>10,000\text{m}^3/\text{s}$ ), which are continuous but may vary seasonally depending on catchment area and precipitation (e.g. Congo up to  $41,000\text{ m}^3/\text{s}$ , Amazon up to  $175,000\text{ m}^3/\text{s}$ ). River channels are wide (e.g. Amazon River; 11 km in dry season, up to 25km when flooded at its widest point) and deep (e.g. Congo up to 200m; Mississippi up to 60m) 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..

## **F2.1 Large permanent freshwater lakes**

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

### **Short description**

Large volumes of permanent water in these lakes buffers water temperatures and effects of nutrient input on water quality. The spatial extent and range of habitats support very large numbers of species in some groups such as fish, some of which are unique to a single lake, often composed of closely related species, endemic to a lake. The high primary productivity from algae and aquatic plants lake supports diverse foodwebs. High numbers of plankton support large numbers of waterbugs, fish, frogs, reptiles, waterbirds, and mammals. Bacteria play key roles in cycling organic matter.

### **Key Features**

Large (usually  $>100\text{km}^2$ ) permanent freshwater lakes connected to rivers, with high spatial and bathymetric niche diversity supporting complex trophic networks supported by planktonic algae, high diversity and endemism.

## **Ecological traits**

Large permanent freshwater lakes, generally exceeding 100 km<sup>2</sup>, 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 (e.g. 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 (e.g. ~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..

## **F2.10 Subglacial lakes**

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

## **Short description**

These hidden lakes exist beneath permanent ice sheets, sometimes tens to thousands of metres below, mostly in Antarctica and Greenland. Bacteria and other microbes are the only forms of life, but there is a surprising diversity of them. Productivity is very low in the dark and freezing conditions, with species relying on metabolism of chemicals such as methane, iron and sulphur to support the simple foodweb.

## **Key Features**

Lakes beneath permanent ice sheets with a truncated microbial food web, including chemoautotrophic and heterotrophic of bacteria and archaea.



## Ecological traits

Remarkable lacustrine ecosystems occur beneath permanent ice sheets. They are placed within the Lakes biome (biome F2) due to their relationships with some Freeze-thaw lakes (F2.4), but they share several key features with the Subterranean freshwater biome (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 forms the base of the trophic web, chemolithoautotrophic species using reduced N, Fe and S and methane in energy-generating metabolic pathways. The abundance of micro-organisms is comparable to that in groundwater (SF1.2) (10<sup>4</sup> – 10<sup>5</sup> cells.ml<sup>-1</sup>), 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<sup>2</sup> to ~10,000 km<sup>2</sup>, 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..

## F2.2 Small permanent freshwater lakes

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

## Short description

With a surface area of up to 100 km<sup>2</sup>, the diversity of small permanent lakes, ponds and pools depends on their size, depth and connectivity. Littoral vegetation and benthic energy pathways are critical to productivity and food web complexity. Deep lakes have plankton, supporting fish, birds and frogs, in different habitats of the lake. Shallow lakes are often more productive, providing breeding habitat for birds, frogs and reptiles, but limited buffering against nutrient inputs may result in regime shifts between alternative stable states dominated either by large aquatic plants or phytoplankton.

## Key Features

Small permanent freshwater lakes or ponds with niche diversity strongly related to size and depth, and resource subsidies from catchments. Littoral zones and benthic macrophytes are important contributors to productivity.

## 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<sup>2</sup> in area, but this functional group includes lakes of transitional sizes up to 100 km<sup>2</sup>, while the largest lakes (>100 km<sup>2</sup>) 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 drives vertical mixing) may generate monomictic or dimictic temperature stratification regimes in deeper lakes, while shallow lakes are polymictic, 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..

## F2.3 Seasonal freshwater lakes

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

## Short description

Small seasonal lakes, pools and rock holes have plants and animals specialised to seasonally changing wet and dry conditions in temperate and wet-dry tropical regions. Their energy comes mostly from algae and plants. To survive the annual wet/dry cycles, the animals and plants have dormant life stages, such as eggs or seeds, within the lake sediments, or they shelter in damp burrows or other refuges. Plants and animals can build up high abundances during wet seasons, supporting plankton and waterbugs, frogs, birds and mammals but, in most cases, no fish.

## Key Features

Mostly small and shallow well mixed freshwater lakes with seasonal patterns of filling and seasonally variable abundance and composition of aquatic biota, including species with dormant life phases and some that retreat to refuges in dry seasons.

## Ecological traits

These small (mostly <5 km<sup>2</sup> in area) and shallow (<2 m deep) seasonal freshwater lakes, vernal pools, turloughs, or gnammas (panholes, rock pools), have a seasonal aquatic biota. Hydrological isolation promotes biotic insularity and local endemism, 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, e.g. 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

Seasonal rainfall, surface flows, groundwater fluctuation and seasonally high evapo-transpiration drive annual filling and drying. These lakes are polycyclic, 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. Water fluctuations drive high rates of organic decomposition, denitrification, and sediment retention. 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

Subhumid temperate and wet-dry tropical regions in monsoonal and Mediterranean-type climates but usually not semi-arid or arid regions..

## F2.4 Freeze-thaw freshwater lakes

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

## Short description

Many plants and animals survive surface freezing of freshwater lakes, in dormant life stages, by reducing activity beneath the ice, or by moving. Such freshwater lakes vary enormously in size and distribution,

providing a wide range of habitats for many organisms, which undergo a succession of emergence during lake thaw. The annual thaw triggers highly productive plant and animal activity, beginning with diatom algae and then zooplankton. Habitat diversity increases with lake size, increasing the variety of plankton, aquatic plants, waterbugs, birds, and sometimes fish.

### **Key Features**

Waterbodies with frozen surfaces for at least one month of the year, with spring thaw initiating trophic successional dynamics beginning with a flush of diatom productivity. Deeper lakes may be cold stratified and fish tolerate oxygen depletion in winter.

### **Ecological traits**

The majority of the 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 (e.g. 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 (polymictic) 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<sup>2</sup>, 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..

## **F2.5 Ephemeral freshwater lakes**

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

### **Short description**

These are shallow lakes that are mostly dry, and then fill for weeks or months, before drying again. During dry periods, many animals or plants survive as eggs, seeds or other dormant forms, while other species disperse. Floods, bring water from surrounding catchments and floodplains with organic matter, nutrients and fine sediments, and trigger movement of birds and mammals. Floods activate simple foodwebs, comprising abundant algae, zooplankton, waterbugs and crustaceans, which have rapid life-cycles able to exploit windows of productivity. This produces food for frogs and visiting waterbirds.

### **Key Features**

Shallow temporary lakes, depressions or pans with long dry periods of low productivity, punctuated by episodes of inflow that bring large resource subsidies from catchments, resulting in high productivity, population turnover and trophic connectivity.

### **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 (e.g. narrow-ranged charophytes). Specialised and opportunistic biota exploit boom-bust resource availability through life-cycle traits that confer tolerance to desiccation (e.g. desiccation-resistant eggs in crustaceans) and/or enable rapid hatching, development, breeding, and recruitment when water arrives. Much of the biota (e.g. 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. Lakes are shallow, flat-bottomed and polymictic when filled with small volumes, 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..

## **F2.6 Permanent salt and soda lakes**

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

### **Short description**

These lakes are usually large and shallow in semi-arid regions, with high concentrations of salts, mediated by inflows of water. Their productivity from growth of algae and plants can support large numbers, but

low diversity of organisms equipped with tolerance to high salinity and other solutes. They have relatively simple foodwebs, with high numbers of microbes and plankton, crustaceans, insect larvae, fish and specialised waterbirds such as flamingos.

### **Key Features**

Permanent waterbodies with high inorganic solute concentrations (particularly sodium), supporting simple trophic networks, including cyanobacteria and algae, invertebrates and specialist birds.

### **Ecological traits**

Permanent salt lakes have waters with periodically or permanently high sodium chloride concentrations. This group includes lakes with high concentrations of other ions (e.g. carbonate in soda lakes). Unlike in hypersaline lakes, productivity is not suppressed and 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 characterised by few species in high abundance and some regional endemism. The 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 (e.g. 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**

Permanent salt lakes tend to be large and restricted to semi-arid climates with high evaporation but with reliable inflow sources (e.g. snowmelt). They may be thousands of hectares in size and several metres deep. A few are much larger and deeper (e.g. Caspian Sea), while some volcanic lakes are small and deep. Endorheic drainage promotes salt accumulation, but lake volume and reliable water inflows are critical to buffering salinity below extreme levels. 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. Inflow is critical to ecosystem dynamics, partly by driving the indirect effects of salinity on trophic or engineering processes. Within lakes, salt concentrations may be vertically stratified (i.e. meromictic) due to the higher density of saltwater compared to freshwater inflow and slow mixing. Dissolved oxygen is inversely related to salinity, hence anoxia is common at depth in meromictic lakes. Ionic composition and concentration varies greatly among lakes due to differences in substrate and inflow, with carbonate, sulphate, sulphide, ammonia, and/or phosphorus sometimes reaching high levels, and pH varying from 3 to 11..

### **Distribution**

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

## **F2.7 Ephemeral salt lakes**

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

### **Short description**

Ephemeral salt lakes in semi-arid and arid regions are shallow, with extreme variation in salinity during wet-dry cycles that limits life to a low diversity of specialised salt-tolerant species. The lakes are dry and salt-encrusted most of the time, but episodic inundation dilutes salt, allowing high growth of algae and larger

plants which support crustaceans, insect larvae, fish and specialist waterbirds. These species use dormant life stages to survive drying, or disperse rapidly to other habitats when the lake dries.

### **Key Features**

Salt lakes with salt crusts in long dry phases and short productive wet phases. Trophic networks are simple but high productivity is driven by bacteria and phytoplankton, supporting specialist birds.

### **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 (e.g. 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**

Ephemeral salt lakes are up to 10,000 km<sup>2</sup> in area and usually less than a few metres deep. They may be weakly vertically stratified (i.e. meromictic) due to the slow mixing of freshwater inflow with higher density saltwater. Endorheic drainage promotes salt accumulation. Salinity varies temporally from 0.3% to over 26% depending on lake size, depth temperature, and the balance between freshwater inflows, precipitation, and evaporation. Inflow is critical to ecosystem dynamics, mediates wet-dry phases, and drives the indirect effects of salinity on trophic and ecosystem processes. Dissolved oxygen is inversely related to salinity, hence anoxia is common in hypersaline lake states. Ionic composition varies, with carbonate, sulphate, sulphide, ammonia, 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..

## **F2.8 Artesian springs and oases**

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

### **Short description**

Surface waterbodies fed by (often warm) groundwaters rising to the surface are scattered in dry landscapes of Africa, the Middle East, Eurasia, North America and Australia, but also occur in humid landscapes. Algae, floating plants and leaf fall support waterbugs, crustaceans and small fish making simple foodwebs with some locally restricted species found nowhere else. These ecosystems are sometimes important waterholes for birds and mammals, in otherwise dry landscapes.

## **Key Features**

Groundwater dependent ecosystems from artesian waters discharged to the surface, maintaining relatively stable water levels. Often insular systems with high endemism.

## **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 polymictic and enriched in minerals that reflect their geological origins. The precipitation of dissolved minerals (e.g. 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..

## **F2.9 Geothermal pools and wetlands**

Belongs to biome F2. Lakes biome, part of the Freshwater realm.

### **Short description**

Geothermal pools and associated wetlands are fed by deeply circulating groundwater that mixes with magma and hot rocks in volcanically active regions. Mineral concentrations are therefore high and produce chemically precipitated substrates as waters cool. The extreme temperatures and water chemistry limit life to a low diversity of specialised bacteria, extensive algal mats and insect larvae which can live in warm acid or alkaline water with high mineral content. Away from their hottest waters, aquatic plants, crustaceans, frogs, fish, snakes and birds can all occur.



## Key Features

Hot springs, geysers and mud pots dependent on groundwater interactions with magma and hot rocks, supporting highly specialised low diversity biota tolerate of high temperatures and high concentrations of inorganic salts.

## 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: proton efflux via active transport pumps that counter proton influx, decreased permeability of cell membranes to suppress proton entry into the cytoplasm, and 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 polymictic 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..

### F3.1 Large reservoirs

Belongs to biome F3. Artificial wetlands biome, part of the Freshwater realm.

#### Short description

Large dams or reservoirs occur in humid, populated areas of the world. Their biological productivity and diversity is generally limited due to their depth and frequent and large changes in water level. Shallow zones have the highest diversity, with simple food webs of algae, waterbugs, birds, frogs and aquatic plants, often

supporting introduced fish species. Plankton live at the surface, but life is scarce in the depths. Algal blooms may be common if there are high nutrient inputs from rivers.

### **Key Features**

Large, usually deep stratified waterbodies impounded by walls across outflow channels. Productivity and biotic diversity are lower than unregulated lakes of similar size and complexity. Trophic networks are simple.

### **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 3000 reservoirs with a surface area greater or equal 50km<sup>2</sup>. Spatial data are incomplete for some countries.

## **F3.2 Constructed lacustrine wetlands**

Belongs to biome F3. Artificial wetlands biome, part of the Freshwater realm.

### **Short description**

Small farm dams, wastewater ponds and mine pits generally form lake-like environments, common in humid and semi-arid climates world-wide. Nutrient inputs vary greatly depending on purpose and surrounding land uses. They are often warm and shallow, and biological productivity and diversity vary widely depending on the cover and state of fringing vegetation, with the most diverse examples rivalling equivalent natural wetlands. Aquatic plants, plankton, algae and waterbugs may dominate in the shallows, supporting amphibians, turtles, fish, and waterbirds.

## **Key Features**

Small, shallow open waterbodies with high or low productivity depending on nutrient subsidies and complexity of littoral zones and benthos. Relatively simple trophic networks with algae, macrophytes, zooplankton, aquatic invertebrates and amphibians.

## **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 including 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 run-off 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 77,000km<sup>2</sup> globally in 2006..

## **F3.3 Rice paddies**

Belongs to biome F3. Artificial wetlands biome, part of the Freshwater realm.

### **Short description**

Rice paddies cover more than a million square kilometres mostly in tropical to warm temperate climates, especially Southeast Asia. They are filled by rainfall or river water diversions. Their levees and channels retain shallow water areas, with nutrients inputs from inflows and fertilisers. Planting and harvest establishes a regular cycle of disturbance, with many paddies also supporting production of fish and crustaceans. Their simple foodwebs are adapted to temporary flooding and the harvest cycle, including algae and plankton, waterbugs, frogs and waterbirds.

## **Key Features**

Artificial wetlands with limited horizontal and vertical heterogeneity, filled seasonally with water from rivers or rainfall and frequently disturbed by planting and harvest of rice. Simple trophic networks with colonists from rivers and wetlands that may also include managed fish populations.

## **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..

## **F3.4 Freshwater aquafarms**

Belongs to biome F3. Artificial wetlands biome, part of the Freshwater realm.

## **Short description**

Freshwater aquafarms are ponds constructed from earthworks or cages built within freshwater lakes, rivers and reservoirs. They are most common in Asia. and used to produce species. Their commercial production of fish and crustacean involves intensive interventions, including focussed inputs of food and nutrients, and control of competitors, predators and diseases that may limit production of target species. Consequently habitat diversity and primary production are low, and non-target biota is limited to opportunistic colonisers from adjacent water sources, including insects, fish, frogs, waterbirds and some aquatic plants.

## **Key Features**

Artificial mostly permanent waterbodies managed for production of fish or crustaceans with managed inputs of nutrients and energy. Simple trophic networks of opportunistic colonists supported mainly by algal productivity.

## **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 (e.g. 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. Removal of wastewater and replacement by freshwater from lakes or streams, together with inputs of antibiotics and chemicals (e.g. pesticides and fertilisers) 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..

## **F3.5 Canals, ditches and drains**

Belongs to biome F3. Artificial wetlands biome, part of the Freshwater realm.

## **Short description**

Canals, ditches and drains are associated with agriculture and cities throughout the world. They take freshwater to and from urban and rural areas, particularly in temperate and subtropical regions. They can carry high nutrient and pollutant loads. Diversity of organisms is generally low, but may be high where there are earthen banks and fringing vegetation. Algae and macrophytes (where present) support microbes and waterbugs and other invertebrates often small fish, amphibians and crustaceans. They are also important pathways for dispersal of some aquatic species.

## **Key Features**

Artificial streams often with low horizontal and vertical heterogeneity, but with productivity, diversity and trophic structure highly dependent on fringing vegetation and subsidies of nutrients and carbon from catchments.

## **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, though 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 (e.g. 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 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..

## **FM1.1 Deepwater coastal inlets**

Belongs to biome FM1. Semi-confined transitional waters biome, part of the Freshwater, Marine realm.

## **Short description**

Ecosystems in these deep, narrow inlets were mostly formed by glaciers and subsequently flooded (e.g. fjords). They have some features of open oceans, but are strongly influenced by freshwater inflows and the surrounding coast. Productivity by phytoplankton is seasonal and limited by cold, dark winters. Oxygen may be limited in the deepest parts of these systems. The diverse biota includes invertebrates and fish, such as jellyfish and salmon, and predatory marine mammals such as killer whales.

## **Key Features**

Strong gradients between adjacent terrestrial and freshwater systems, e.g. fjords. Seasonally abundant plankton, jellies, fish and mammals..

## 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. malidanids and owenids). 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..