

## Freshwater Ecosystems and Biodiversity

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# Freshwater Ecosystems and Biodiversity

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## Abstract

Freshwater ecosystems are important for many reasons, including their ecosystem services to humans. This module serves to help introduce students to thinking critically about the ecological structure, function, and distribution of freshwater systems. Freshwater ecosystems are driven by physical habitat, energy sources, water quality biotic interactions, hydrology and connectivity. Variations in these factors result in significantly different environments, including upland streams and rivers, large lakes, floodplain rivers and wetlands, and xeric freshwaters.

## INTRODUCTION

### Module Format

This module provides instructors with resources to teach a 45-minute lecture and 3-hour laboratory exercise on freshwater ecosystems and biodiversity. This module material should be appropriate in introductory college-level courses for either science majors or non-majors. The components of this module are designed to be used together: the lecture introduces basic concepts that students subsequently explore in laboratory exercises. This module should also fit well with other NCEP modules and resources, such as *A Comprehensive Simulation of the Colorado River Basin: An Interactive Exercise*; we specifically recommend that this lecture and laboratory follow the NCEP module *Why is Biodiversity Important?* (All available at [ncep.amnh.org](http://ncep.amnh.org)). We hope that this module provides the basis for useful class and laboratory learning and we encourage instructors to adapt our template as necessary to suit their specific needs.

### Module Scope

This module examines freshwater ecosystems from a global perspective, focusing on streams, rivers, lakes, and wetlands and their associated biota. Our intent is to help students develop mastery of four primary content areas. First, we provide a brief discussion of the hydrological cycle and fresh water availability, highlighting the global scarcity of useable freshwater. Second, we provide an overview of global biodiversity patterns in fresh water, highlighting the ideas of species richness and endemism. Third, we present a conceptual

framework to understand how environmental factors influence freshwater biodiversity. Fourth, we apply this conceptual framework in a global survey of freshwater ecosystems.

Freshwater ecosystems are valued for many reasons, as they provide vital ecosystem services for humans (e.g., drinking water, flood control, climate regulation, food production) but such services are not the primary focus of this module. Likewise, specific conservation threats and strategies are also not the focus of this module. Instead, our goal is to help students develop a framework for critical thinking about the ecological structure, function, and distribution of freshwater ecosystems. We believe that such a framework is a prerequisite for further studies in freshwater conservation biology.

## THE HYDROLOGICAL CYCLE AND FRESHWATER AVAILABILITY

### Hydrological Cycle

All freshwater ecosystems are regulated by the hydrological cycle, the continuous process of water movement between states. This process can be viewed as steps of water storage and transport (Figure 1). Evaporation and evapotranspiration (i.e., water produced from vegetative respiration) move liquid water to atmospheric gas, then precipitation moves atmospheric water into liquid form and into streams, rivers, and lakes. Downstream flow then moves the liquid water into “storage” areas including groundwater, lakes, or the ocean. The length of time water remains

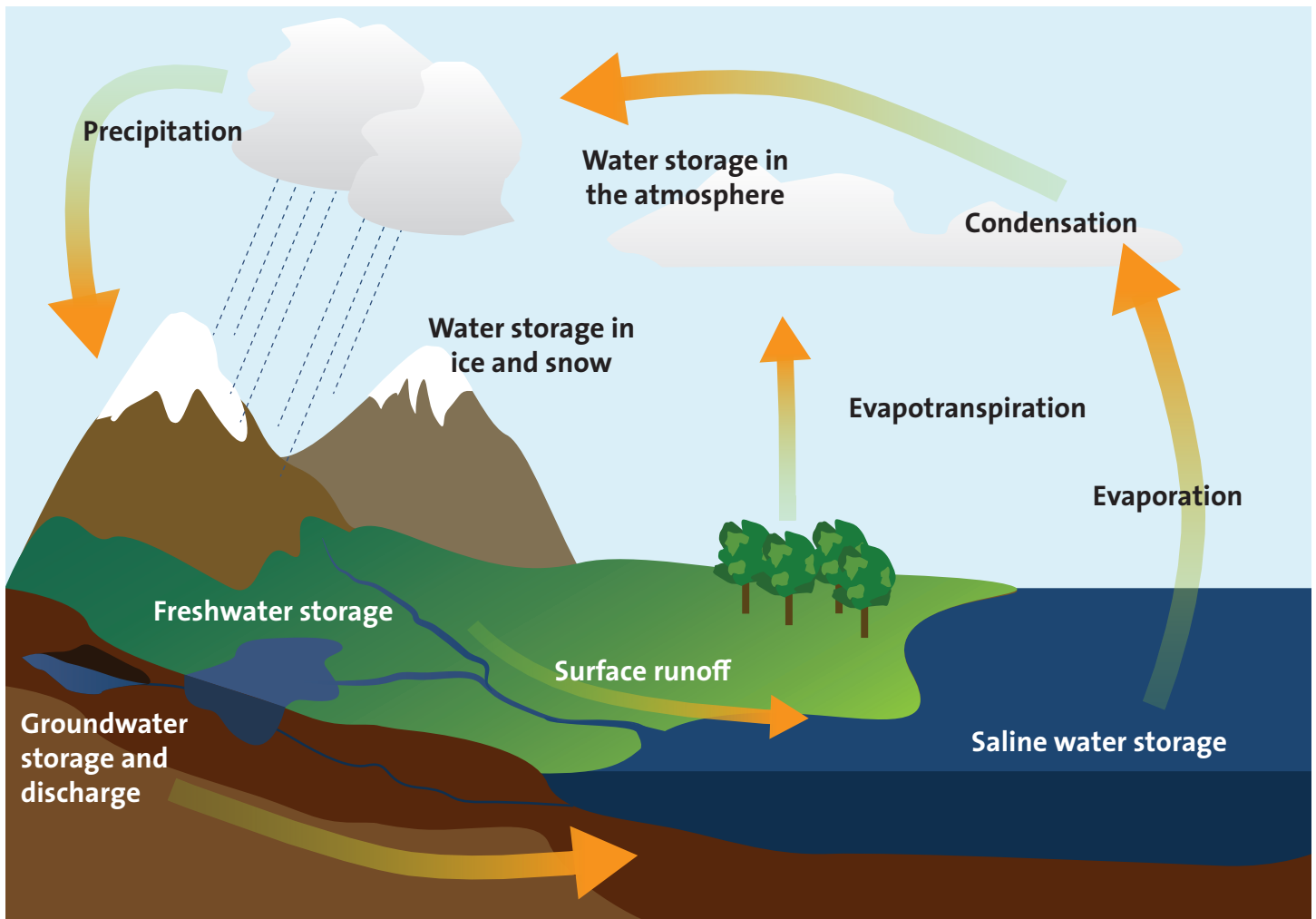


Figure 1. A simplistic model of the hydrological cycle. Illustration by Nadav Gazit.

in a particular place (i.e., retention time) varies based on several factors, including the size and shape of lakes, the connectivity to the groundwater (or water table, defined as the underground areas that are fully water-saturated), and the configuration of streams and rivers (e.g., flowing to oceans versus flowing to lakes). It is important to note that the hydrological cycle is ultimately driven by solar energy: without solar-driven evaporation, freshwater ecosystems as we know them would not exist.

Experimental research has demonstrated the importance of vegetation for stream flow. A classic example of this is from the Hubbard Brook Experimental Forest in New Hampshire, USA. After a deciduous forest was clear-cut (and regenerating vegetation was suppressed by herbicides), the annual volume of flow out of the watershed increased by 40% (and over

400% during the summer) (Allan 1995). This increased stream flow represents the volume of water moved by evapotranspiration through vegetation. Additional examples are provided in Likens and Bormann (1974).

### Total Fresh Water

Depending on where one lives, freshwater ecosystems may seem endless (e.g., Boundary Waters and Voyageurs National Park, North America or Lake Baikal, Russia) or limited and remote (e.g., Atacama Desert, South America). A global accounting is therefore necessary to comprehend the true abundance of fresh water. Of all the water on Earth, approximately 3% is considered “fresh water” (i.e., salinity < 0.5 parts per thousand) (Figure 2). Note that rivers and lakes are not visible on this pie chart because they comprise such a small proportion of the Earth’s total water (Figure 3).

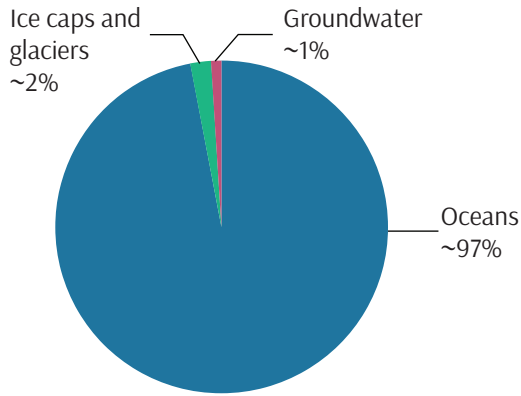


Figure 2. Global composition of fresh water

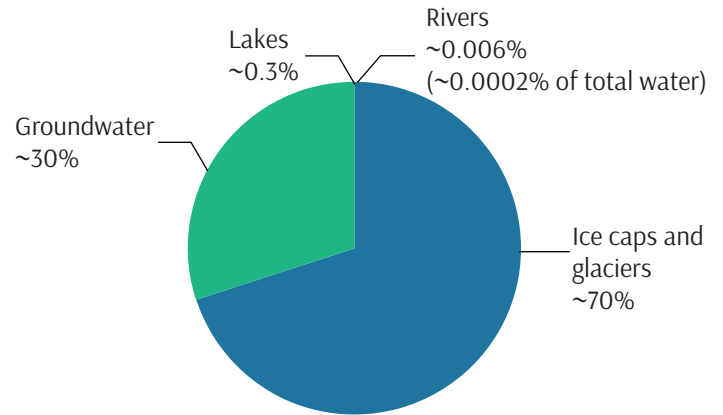


Figure 3. Global availability of fresh water

### Fresh water Available for Habitat

Of the 3% of global water that is fresh water, only an extremely small proportion is available as habitat for living organisms on the surface of the Earth (Figure 3). The largest portions of the Earth's fresh water are locked up as frozen water in the polar ice caps and glaciers (approximately 70%) or buried underground as groundwater (approximately 30%). Lakes and rivers comprise a tiny portion of the total fresh water

(approximately 0.3%). When compared to all water on Earth, rivers (including streams) comprise only 0.0002% of the total volume. In total, available freshwater ecosystems cover approximately 0.8% of the surface of the Earth. Interestingly, much of the Earth's aquatic biodiversity requires the freshwater flowing habitat found in these rare ecosystems. It is therefore not surprising that flowing-water habitats contain some of the most imperiled taxa on the planet (see Conservation section, below).

ECOSYSTEM TYPE	% EARTH AREA	% DESCRIBED SPECIES
Freshwater	0.8	2.4
Terrestrial	28.4	77.5
Marine	70.8	14.7

Table 1. Comparison of area and percent of described species for freshwater, terrestrial, and marine ecosystems. Note that the total percent of species described does not sum to 100 because symbiotic species are excluded. Data are from McAllister et al. (1997).

TAXONOMIC GROUP	APPROXIMATE NUMBER OF DESCRIBED FRESHWATER SPECIES
Insects (larval stage <sup>a</sup> )	20,000
Fishes	13,000 <sup>b</sup>
Amphibians	6,000
Snails	4,000
Mussels	1,000
Crayfishes	500

<sup>a</sup>Most freshwater insects emerge into a terrestrial adult stage, but egg deposition and juvenile development occurs in freshwater environments.

<sup>b</sup>Lévêque et al. (2008)

Table 2. Global freshwater species diversity. Note that data for small-bodied organisms (e.g., phytoplankton, zooplankton, amphipods, etc.) have not been well described and are not included here.



## GLOBAL PATTERNS OF FRESHWATER BIODIVERSITY

Species richness is defined as the number of species found within a given area. Although many organisms require fresh water for survival, in this module we define freshwater species as those which spend at least a portion of their lives in freshwater habitats. Given the relative rarity of freshwater habitat (i.e., 0.8% of the Earth's total surface area), one might predict that freshwater ecosystems would support 0.8% of the freshwater biodiversity. However, this estimate is extremely low (McAllister et al. 1997) (Table 1).

In fact, tens of thousands of freshwater species have been described, including insects, fishes, amphibians, snails, mussels, crayfishes, and others (Table 2). However, the list of known freshwater species is likely an underestimate due to a known bias for describing large-bodied organisms first (Gaston 2000). However, we can use the distribution of some well-studied taxonomic groups (i.e., fishes and amphibians) (Table 2) to provide insight into global patterns of freshwater biodiversity (Abell et al. 2008).

Similar to terrestrial organisms, the species richness of freshwater fishes follows a latitudinal pattern and tends to increase towards the equator (Figure 4), (Gaston 2000). Interestingly this pattern is not distributed evenly over the planet as some non-tropical regions have higher than expected richness (i.e., Southeastern North America, and Western China) while other areas have lower than expected richness (i.e., Western North America and Australia). Globally, the greatest concentrations of freshwater fish species are found in South America and Southeast Asia (Figure 4). In addition taxonomic patterns among fish species are also not homogenous around the globe. For example, fishes in the families *Centrarchidae* (sunfish) and *Ictaluridae* (bullhead catfish) are indigenous only to North America (Jenkins and Burkhead 1994).

Amphibian species also follow the same latitudinal trend (Figure 5), but the total number of species is generally lower (Table 1). When compared to the distribution of fish species, two distinct patterns are evident: (1) amphibian richness tends to be more evenly distributed across South America and Central Africa; and (2) Australia supports relatively more species of amphibians

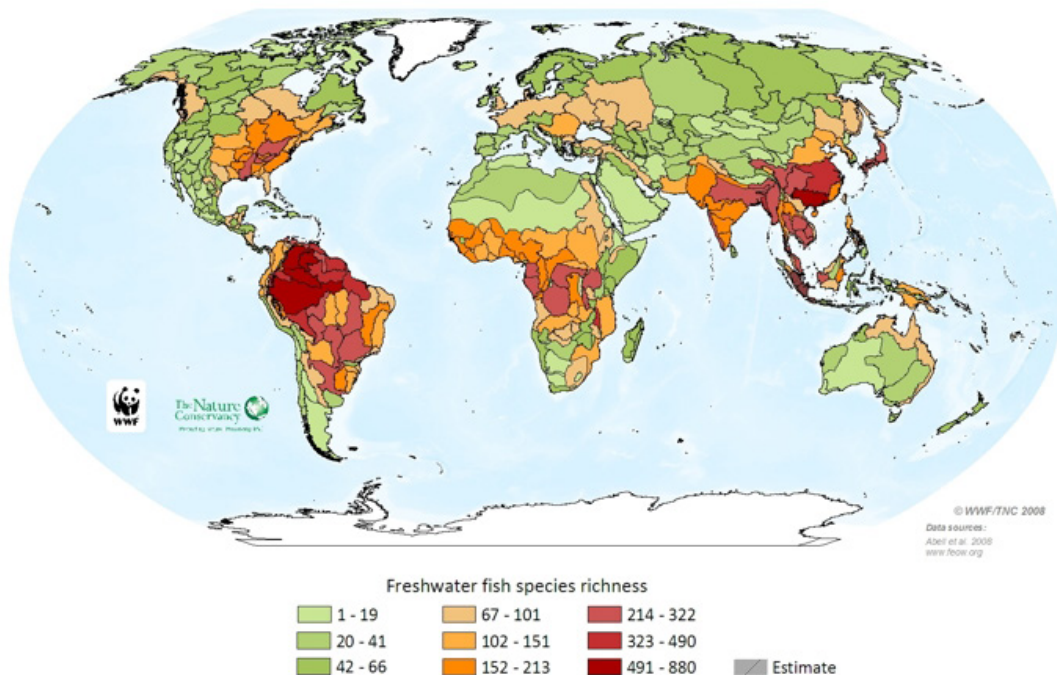


Figure 4. Freshwater fish species richness (from Freshwater Ecoregions of the World [FEOW] database, [www.feow.org](http://www.feow.org))

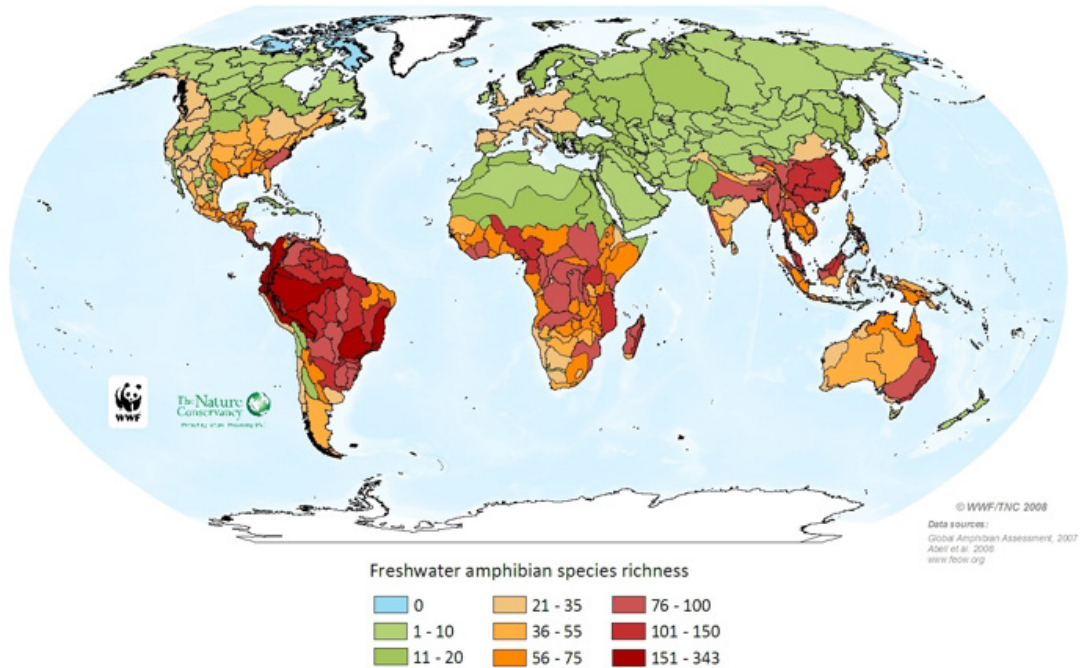


Figure 5. Freshwater amphibian species richness (from Freshwater Ecoregions of the World [FEOW] database, [www.feow.org](http://www.feow.org))

than fishes (Figure 5). However, when examining the distribution maps for fish and amphibian species (Figures 4 and 5), note that the numbers of species in each abundance category are different.

Another useful biodiversity measure is the idea of species endemism. Endemic species are ones whose global distribution is limited to a given area (i.e., they occur only within a particular ecoregion or watershed). Areas of high endemism often result from a combination of ecological forces including high biological productivity and geographic isolation. Patterns of endemism in freshwater fishes and amphibians generally follow species richness patterns. However, the southern hemisphere tends to support greater amphibian species endemism than the northern hemisphere (Abell et al. 2008). From a conservation perspective, endemic species are important because they contribute to global biodiversity and their extinction may be the result of small localized events.

## ECOSYSTEM DRIVERS OF FRESHWATER BIODIVERSITY

Many environmental factors affect freshwater biodiversity (Wetzel 2001). The purpose of this section is

to provide a systematic approach to understanding how environmental factors affect biota. We first describe each factor, and then return to these factors when examining the major types of freshwater ecosystem. Although each factor is presented separately, interactions among factors are important and commonplace (discussion questions are presented in this module's accompanying component "Presentation Notes and Discussion Questions" for students to explore how these factors are integrated in specific ecosystems, available at [ncep.amnh.org](http://ncep.amnh.org)).

### Physical Habitat

Classifying aquatic habitat is not always straightforward and simple. Numerous systems of aquatic classification have been developed around the world (Higgins et al. 2005). Most systems are hierarchical and fall into one of two categories: 'top-down' approaches or 'bottom-up' approaches. 'Top-down' approaches start from large, ecologically diverse areas, and divide these into lower more homogeneous levels. 'Bottom-up' approaches begin in a completely different manner with the lowest levels of the hierarchy and group them according to shared characteristics (Ricklefs and Miller, 2000). It is generally agreed that understanding processes



and patterns of freshwater systems at multiple scales is critical for conserving freshwater biodiversity, yet there is still much debate over which approach is best to classify these processes and patterns (Frissell et al. 1986; Fausch et al. 2002).

In a very general sense, aquatic physical habitat may include any submerged materials or structures. One of the more important of these for flowing water is the substrate size of the benthos. Small substrates (e.g., clays) have a high surface-to-volume ratio and are relatively easily transported, as compared to larger substrates (e.g., boulders). In addition, high surface-to-volume ratios on substrate particles tend to support robust microbial communities (and thus affect dissolved oxygen levels via microbial respiration). Also, large amounts of surface area provide binding sites for ionic compounds such as dissolved nutrients (i.e., nitrogen and phosphorous). In streams and rivers, substrate size combined with flow patterns affect the development of instream habitat such as pools and riffles (Frissell et al. 1986). Woody debris, undercut banks, and rooted plants also provide important physical habitats. For example, large woody debris (e.g., root wads, logs) can affect the formation of instream pools by altering the direction of water flow (Shields et al. 2003).

Instream habitat features also provide organisms with physical structures that can be used for feeding or reproduction, as well as refugia from predators or disturbance events. For example, anadromous fishes (i.e., ones that migrate between fresh and salt water) at higher latitudes may travel hundreds of kilometers to reach habitat that has the appropriate physical conditions for spawning (often clean gravel in small streams). In addition, benthic macroinvertebrates may cluster together on patches of substrate with low flow velocity (i.e., low shear stress) during high-flow events (Lancaster 2000). Because individual species need different types of physical habitat at different times, the spatial configuration of habitat patches may influence movement rates as well as population and community structure (Dunning et al. 1992).

The overall general importance of physical habitat may vary with the volume of water in an ecosystem. For example, in small streams or spring ecosystems, the

percent of water in contact with the substrate is much higher than in large rivers or lakes. In lakes, the most important physical habitats are likely to be in the shallow and near-shore environments (Wetzel 2001).

### Energy Sources

For our purposes, energy source refers to primary production or the basal level in the food web. Sunlight is the main factor regulating photosynthesis by green algae and some species of bacteria. Dissolved nutrients (particularly nitrogen and phosphorous) also promote algal growth and photosynthetic activity (Allan and Castillo 2007). In turn, the products of photosynthesis (carbohydrates and oxygen) are moved downstream and incorporated into biomass throughout the food web. In contrast, microbial respiration consumes dissolved oxygen and acts to somewhat counter-balance photosynthesis.

The River Continuum Concept is a general hypothesis about how rivers and streams are structured and suggests that the ratio of photosynthesis to respiration can be used as an index of energy transport in flowing water systems (Vannote et al. 1980). In small streams, overall instream photosynthesis may be limited either by riparian vegetative shading or the low concentration of dissolved nutrients. Most photosynthesis in small streams originates with attached tiny algae called periphyton. In contrast, most photosynthesis in large rivers originates with microscopic plants floating in the water column called phytoplankton. The volume and dynamics of water therefore have important consequences for freshwater energy sources.

Energy sources also influence the trophic structure of food webs at higher levels. Benthic (i.e., bottom-dwelling) macroinvertebrate (MI) communities tend to vary in relation to a stream's energy sources. For example, insects that shred coarse particulate organic matter tend to inhabit headwater streams where leaf-litter and coarse organic matter is abundant. Further downstream the abundance of collecting and grazing MI increases due to an abundance of fine particles of organic matter (Vannote 1980). In a similar manner, the abundance of insect eating fishes increases in downstream areas. However, food supply is not the only factor limiting



fish distributions as physical habitat and hydrological regimes also play a role (Hynes 1972).

### Water Quality

For our purposes, water quality refers primarily to the chemical attributes of water. Dissolved oxygen (DO), pH, dissolved nutrients, dissolved metals, and suspended solids are some of the major components of water quality. DO and pH influence organismal physiology (i.e., respiration and metabolism) and therefore can regulate where organisms survive and reproduce. Dissolved nutrients are believed to have a large effect on algal growth, and therefore have an indirect effect on MI and fishes. Dissolved metals may be important for organismal physiology, but can also cause toxic effects at high levels. Suspended solids may affect the optical properties of water, therefore influencing visual communication as well as vulnerability to predators.

### Biotic Interactions

Predation, competition, and hybridization are the major forms of biotic interactions. Predation rates can affect organismal behavior (i.e., predator avoidance) as well as population growth rates. In general, biotic interactions are considered to be density-dependent factors because the likelihood of biotic interactions will increase as the density of individuals increases (in contrast to density-independent factors that affect all individuals regardless of population numbers, e.g., a drought).

Anatomical features may provide clues about predator-prey relations. Among fishes, predators can often be identified by the size of their mouths (i.e., gape size). For example, bluegill sunfish (*Lepomis macrochirus*) and green sunfish (*L. cyanellus*) have a very similar body shape, but different gape sizes: fish-eating (piscivorous) green sunfish can be identified by their large mouths, when compared with insect-eating (insectivorous) bluegill with smaller mouths. Among benthic macroinvertebrates, mouth parts are also predictive of predatory behavior. For example, larval dragonflies (Odonata) have strong mandibles, which are used to pierce their prey.

Competition also may affect population growth rates

through density-dependent processes. Although inter-specific competition may be important in some cases, intra-specific competition is expected to have the greatest effects because members of the same species share traits and physiological requirements. Although dispersal processes are thought to diffuse competition pressures, organisms need to achieve a threshold of physiological capacity in order to be successful in dispersal. As a result, competition is thought to be greatest during the first year of life for fishes and amphibians (Hynes 1972).

Hybridization is a population-level phenomenon, resulting from breeding of individuals among gene pools. Hybridization may result in increased fitness (defined in terms of survival and reproduction), and this process is referred to as heterosis. Alternatively, hybridization may result in decreased fitness, and this process is referred to as outbreeding depression. Interspecific hybridization is more common in fishes than among other vertebrate groups due to the lack of isolating mechanisms in freshwater environments (Arnold 1992). Hybridization between native and introduced fishes presents a challenging problem for biological conservation (e.g., Hitt et al. 2003).

### Hydrology

Stream flow is thought to have five major defining features: magnitude, frequency, duration, predictability, and rate of change. These features have critical implications for freshwater ecosystems. When taken together, they define a particular stream's hydrological regime, which can affect aquatic organisms in direct and indirect ways. Direct effects can be through disturbances, such as floods that increase shear stress on benthic organisms, or droughts that increase physiological stress. Hydrological regimes also indirectly influence biota by regulating the availability of habitat (e.g., seasonal floodplains) and the development of habitat types (e.g., scouring of pools and riffles during high flows). It is no surprise, therefore, that species traits are often linked to a region's hydrological regime (Poff and Ward 1989, Lytle and Poff 2004). For these reasons, hydrology is sometimes considered a 'master variable' because it affects many other environmental influences in freshwater ecosystems.





## Connectivity

For our purposes, connectivity refers to the size and proximity of connected streams or lakes. As such, connectivity is not a feature of individual streams or lakes, but instead is an emergent property from the interactions of multiple freshwater habitats. In stream fishes, stream network connectivity affects seasonal movement to feeding and reproductive habitats (Osborne and Wiley 1992; Hitt and Angermeier 2008) as well as extinction probability (Campbell-Grant et al. 2007). Connectivity between lakes and rivers (i.e., lentic and lotic habitats, respectively) also helps predict the composition of the local community (Miranda 2005). As a result, the success of ecological restoration in freshwater ecosystems may be influenced by the degree of regional connectivity in addition to the restoration efforts themselves (Lake et al. 2007). Conversely, dams and culverts present major challenges for freshwater conservation at a landscape scale because they tend to block or restrict regional connectivity (Richter et al. 1997; Cumming 2004; Gibson et al. 2005).

## A GLOBAL SURVEY OF FRESHWATER ECOSYSTEMS AND BIOTA

This section provides a brief introduction to four common freshwater ecosystem types: upland streams and rivers, floodplain rivers and wetlands, large lakes, and xeric freshwaters. These categories are drawn from the Freshwater Ecoregions of the World database (Abell et al. 2008); however, for simplicity, we have collapsed two categories (montane freshwaters and upland streams) into a single category we call “upland streams and rivers.” We also combined temperate and tropical categories for upland streams and rivers, as well as floodplain rivers and wetlands. The purpose of this section is to provide an introduction to major ecological features of these habitat types, using the general framework provided above. Each of these habitat types is explored in more detail in the accompanying laboratory Exercise (online at [ncep.amnh.org](http://ncep.amnh.org)). Although our freshwater ecosystem classifications were developed for a global-scale analysis, we recognize that other classification schemes may be more appropriate for finer-scale assessments.<sup>1</sup>

<sup>1</sup>For a more comprehensive introduction to freshwater ecosystem types, see Silk and Ciruna (2004).

## Upland Streams and Rivers

Upland stream and rivers occur in mountainous zones worldwide. Examples include the Himalayan mountains (Asia), the Amazon River uplands (South America), the Appalachian and Rocky Mountains (North America), and the Congo River uplands (Africa). Following the framework presented above, several environmental factors characterize upland streams and rivers:

- **Physical habitat:** Large substrate, copious woody debris
- **Energy sources:** Sunlight limited by riparian zone, energy mostly allochthonous (derived from outside the stream) in origin
- **Water quality:** High levels of dissolved oxygen and low levels of dissolved nutrients
- **Biotic interactions:** Weak biotic interactions (because large predators are generally excluded due to habitat limitations)
- **Hydrology:** Chaotic, non linear and disorganized flow
- **Connectivity:** High levels of connectivity among streams affects recolonization rates

Organisms and communities in upland streams and rivers must be able to cope with relatively harsh environmental conditions. Many larval insects are well-adapted in this regard. For example, black fly larvae (Simuliidae) use hooks and silk threads to attach themselves to substrate surfaces (Voshell 2002). Fishes tend to be benthically-oriented and often dorsoventrally (top to bottom) flattened (Poff and Ward 1989). Overall, species richness in upland streams and rivers tends to be relatively low, presumably due to the exclusion of biota in the harsh environmental conditions. Tropical upland systems tend to support a much greater diversity of aquatic organisms and have a higher degree of endemism than temperate regions (Gaston 2000). However, some upland streams and rivers in the Southern Appalachian mountains (North America) support levels of species richness comparable to tropical systems (e.g., Duck River and Clinch River, Tennessee, USA) (Benz and Collins 1997).

## Large Lakes

Large lakes are formed by geologic processes, including



tectonic, glacial, or volcanic activity (Table 3). Tectonic lakes, formed by the separation of continental plates, are the largest and deepest lakes on Earth (e.g., Lake Tanganyika in Africa, and Lake Baikal in Central Asia). Lake Baikal is the deepest lake on Earth, reaching approximately 1600 meters in depth (Wetzel 1983). In contrast glacial lakes are formed by the movement of glaciers across a landscape: advancing glaciers will carve geological basins and the retreating (melting) glaciers can fill these basins (e.g., Flathead Lake and the Laurentian Great Lakes in North America). Finally, volcanic lakes are formed by volcanic eruptions and magma flow and often tend to be smaller than tectonic or glacial lakes (Wetzel 1983) (Table 3).

Large lakes share several features that influence biotic composition:

- **Physical habitat:** Near-shore and shallow water habitat most important
- **Energy sources:** Energy mostly autochthonous (produced in place) by phytoplankton; highly productive in tropics
- **Water quality:** Oxygen varies with depth and season
- **Biotic interactions:** Predation important
- **Hydrology:** Stable systems often with seasonal pattern in turnover
- **Connectivity:** Isolation permits adaptive radiation (i.e., endemism)

Biota of large lakes are often distinct from those in upland rivers and streams in several ways. First, phytoplankton and zooplankton are generally more important in lake ecosystems than in upland rivers (phyto = “plants,” zoo = “animals,” plankton = “floating”). This is because turbulent flow and riparian cover in small streams is not conducive for plankton (although in very large rivers, plankton are often important in food webs). Insects in large lakes are generally limited to the lighted or photic

zone (and therefore water turbidity is important). Fishes in large lakes are typically segregated by near-shore and open-water habitats (and therefore lake morphology is important). Interestingly, fish diversity reaches its zenith in tropical rift valley lake ecosystems, such as Lake Malawi (Africa) where more than 850 species of cichlids have been described, which are thought to have diverged from a common ancestor (Moyle and Cech 2003).

### Floodplain Rivers and Wetlands

Floodplain rivers and wetlands are distributed worldwide. Notable examples include the Nile and Zambezi Rivers (Africa), the Mississippi River (North America), the Amazon River (South America), the Indus River (South Asia), and the Lower Mekong River (Southeast Asia). In each case, these ecosystems are characterized by hydrological connectivity to their floodplains and associated wetlands. Unlike upland streams and rivers, floodplain rivers occur in low-gradient terrain and exhibit a sinuous pattern across a landscape. Several environmental features typify floodplain rivers and wetlands:

- **Physical habitat:** Fine substrates in river; wetlands provide diverse physical habitats
- **Energy sources:** Highly productive autochthonous systems
- **Water quality:** Nutrients entrained from wetland soils; relatively low dissolved oxygen
- **Biotic interactions:** Competition/predation rates vary between wet and dry seasons
- **Hydrology:** Seasonal flooding
- **Connectivity:** Connectivity with floodplain provides breeding and feeding habitats

Floodplain rivers and wetlands are highly-productive systems, yielding some of the highest levels of fish biomass on Earth (Bayley 1995, Balcombe et al. 2007). Tropical systems are notable in this regard. For example,

LAKE TYPE	FORMATION PROCESS	EXAMPLES
<b>Tectonic</b>	Separation of continental plates	African Rift Valley lakes
<b>Glacial</b>	Glaciers advance and melt	North American Laurentian Great Lakes
<b>Volcanic</b>	Crater formation, magma flow	Crater Lake, Oregon, USA

Table 3. Lake types and formation processes



the Amazon River supports over 2500 species of fishes (Allan and Castillo 2007), whereas the Mississippi River supports approximately 433 fish species (Muneepeerakul et al. 2008). Hydrological connectivity to wetlands also increases predation of fishes by terrestrial predators. For example, floodplain wetlands characteristically support high levels of bird diversity (Bayley 1995).

### Xeric Freshwaters

Xeric<sup>2</sup> freshwaters occur in dry climates. There are two primary types of xeric freshwaters: endorheic basins and isolated springs. Here, we focus on endorheic basins, watersheds that flow inland instead of to an ocean outlet. This type of system occurs in arid regions worldwide, including, for example, the Sahel and Sahara deserts (Africa), the Tibetan plateau (Asia), Lake Eyre (Australia), the Sonoran and Gila deserts (North America), and Mar Chiquita (South America). These ecosystems provide important freshwater habitats in arid regions, but are subject to several important ecological constraints:

- **Physical habitat:** Sandy substrate, low physical habitat diversity
- **Energysources:** Low productivity (phytoplankton exclusion due to salinity)
- **Water quality:** High salinity from evaporation
- **Biotic interactions:** Weak biotic interactions (because harsh environmental conditions exclude potential predators and competitors)
- **Hydrology:** Ephemeral and unpredictable water levels
- **Connectivity:** Isolation yields high levels of endemism

Biota of xeric freshwaters are characterized by low diversity (species richness) but high endemism. Endemism is particularly high for turtle and amphibian species (Abell et al. 2008). Given the temporal variability in flows, organisms inhabiting xeric freshwaters commonly exhibit estivation (i.e., dormancy during dry periods) or diapause (e.g., delayed development of fertilized eggs). For example, the four species of African lungfishes can burrow into the substrate and estivate during the long dry season, only to recover and swim

away when the waters return (Moyle and Cech 2003). In general, large-bodied fishes are often absent from these freshwater habitats (Skelton 2001).

### CONSERVATION

As explained above, rather than specifically focusing on conservation of freshwater ecosystems, this module attempts to provide an ecological framework as a precursor for further studies in freshwater conservation biology. However, information on conservation status, trends, and threats will be useful for instructors to introduce the lecture and/or laboratory exercise. We therefore provide a brief summary of these issues here. (For more information on conservation and freshwater ecosystems, please see the relevant NCEP case studies and modules in this issue and *A Comprehensive Simulation of the Colorado River Basin: An Interactive Exercise*.)

Extinction rates for freshwater species are higher than for terrestrial species (Ricciardi and Rasmussen 1999). Of the more than 5,000 freshwater fish species assessed by the World Conservation Union (IUCN), over 40% are classified as threatened with extinction (Reid et al. 2013). Moreover, Jelks et al. (2008) estimated that over 120 freshwater species have gone extinct in North America since 1900. In addition, approximately 32% of the 338 crayfish species in North America are considered to be threatened or endangered (Taylor et al. 1996). Likewise, approximately 72% of mussel species in Canada and the United States are endangered, threatened, or of special concern (Williams et al. 1993). The American Fisheries Society Endangered Species Committee is currently in the process of revising the status list for mussel species of North America (USGS 2013).

Five major causes of freshwater ecosystem degradation are widely recognized:

1. Habitat loss and degradation: land use practices, water abstraction, impoundments (e.g., Moyle and Leidy 1992; Richter et al. 1997; Dudgeon et al. 2006);
2. Overexploitation: unsustainable fisheries harvest (e.g., Dudgeon et al. 2006);
3. Invasive species: evolutionarily-novel competition, predation, and hybridization (e.g.,

<sup>2</sup>Xeric = a dry habitat.



Moyle and Cech 2003; Light and Marchetti 2007);

4. Fragmentation: impassible dams and culverts (e.g., Wang et al. 2006); and
5. Climate change: synergistic effects with all of the above (e.g., Aston 2007).

However, the relative importance of these influences will vary among locations. For example, Richter et al. (1997) conclude that Eastern North America is primarily affected by altered sediment loads from agricultural activities, whereas Western North America is primarily affected by exotic species, altered hydrologic regimes, and drought (For example, see NCEP case study *How the West Was Watered: A Case Study of the Colorado River* available in this issue and online at [ncep.amnh.org](http://ncep.amnh.org)).

Angermeier (2007) argues that society needs to acknowledge three fundamental facts regarding freshwater conservation: (1) freshwater biota are critically imperiled; (2) human actions are causing this imperilment; and (3) current conservation efforts are not sufficient. He argues that the role of the freshwater biologist is not only to conduct ecological investigations, but also to educate the public and policy-makers about the role of freshwater ecosystems for biodiversity and human quality of life. We hope that the module provided here will contribute in this regard.

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