Lake and Pond Ecosystems

Angela L. Strecker[1], Alicia McGrew[2], Ariana Chiapella[3]

[1] Institute for Watershed Studies, Western Washington University, 516 High St., Bellingham, WA, USA, 98229, strecka2@wwu.edu

[2] Institute for Watershed Studies, Western Washington University, 516 High St., Bellingham, WA, USA, 98229, mcgrewa@wwu.edu

[3] Rubenstein School of Environment and Natural Resources, University of Vermont, 81 Carrigan Drive, Burlington, VT, USA, 05405, Ariana.Chiapella@uvm.edu

Key Points

- Lakes and ponds harbor diverse assemblages
- Freshwater biodiversity is shaped by processes acting from local to global scales
- Aquatic organisms and ecosystems are threatened by diverse human-mediated stressors

Abstract

Pond and lake ecosystems possess unique geophysical attributes that support diverse assemblages. Freshwater biota are among the most diverse, but also most threatened, taxa on the planet. Geological origins of waterbodies can play significant roles in structuring biodiversity, as can latitude, size (surface area, depth), shape, connectivity, and environmental conditions. Major threats to the biodiversity of freshwater ecosystems include habitat alteration, harvest, pollution, and the introduction of invasive species.

Keywords

Biogeographic Islands, Biota, Connectivity, Ecosystem Function, Environmental Stressors, Freshwater, Functional Diversity, Lake, Pond, Phylogenetic Diversity, Taxonomic Diversity

Glossary

pelagic: open-water habitat

littoral: well-lit, typically shallow habitat

benthic: bottom or sediment-associated habitat

lotic: flowing water

lentic: still water

Introduction

Freshwater lakes and ponds are found on all continents, and can be home to diverse communities of highly specialized taxa. Yet, due to the broad distribution of these waterbodies and challenges in sampling, knowledge of freshwater biodiversity is still incomplete, particularly for small-bodied taxa. Here, we consider overarching patterns of lake and pond biodiversity and how this biodiversity relates to ecosystem functioning by examining the roles of macroecological forces, environmental stressors, and geophysical structures unique to freshwater habitats. We note important knowledge gaps and future research needs to meet conservation goals for freshwater biodiversity.

1.0 Types of Waterbodies

Freshwater lakes and ponds are globally ubiquitous and can be found on all continents; however, they are proportionally rare, covering only 3% of the Earth's surface (Downing et al., 2006). Using a functional definition, ponds are small (surface area <5 ha), shallow (maximum depth <5 m), and have minimal emergent vegetation (<30%) (Richardson et al., 2022). Lakes are relatively large (surface area >5 ha), deep (maximum depth >5 m), and also typically have minimal emergent vegetation. Worldwide, ponds are incredibly numerous: there may be as many as 3.5 billion waterbodies <1 ha in size (Downing, 2010). By contrast, it's estimated that there are 1.4 million lakes >10 ha (Messager et al., 2016). Both lakes and ponds provide critical ecosystem functions and can support high biodiversity (e.g., Oertli et al., 2002).

1.1 Broad Characteristics of the Geography in Lakes and Ponds

Freshwater habitats are widely considered to be transient in geologic time and space in comparison with both terrestrial and marine habitats. This is true for many lakes and ponds; however, there can be great differences in the nature and the diversity of their biota depending on the origin and connectivity of the freshwater system. Several broad categories of waterbodies may be recognized, where biodiversity differences are driven primarily by lake or pond origin and frequency of connectivity to other aquatic systems.

1.1.1 Origin

The origin of lakes and ponds formed by natural geologic or anthropogenic processes can have important implications for their biodiversity. Both the length of time a basin takes to form (i.e., gradual vs. rapid processes), the time since formation, the permanence of the system, and the physical characteristics of each lake or pond govern both the physical and chemical structure of these waterbodies and the types of organisms that can be found there.

The majority of naturally formed lakes, ponds (and estuaries) result from a few main geologic processes: gradual tectonic activity, volcanism, and glacial activity. Tectonic activity drives basin formation along single ("rift") or multiple ("graben") fault-lines, often resulting in deep lakes with large surface areas (e.g., Lake Baikal). Uplift along fault-lines creates large, shallow lakes (e.g., Lake Okeechobee, Lake Chad). Volcanism can form small, deep crater lakes within volcanic cones ("calderas"), or indirectly through lava flow dams. Glacial retreat results in a variety of lake shapes, or morphometries, as glacial debris, chunks of ice, or physical basins by glacial scouring are left behind. These lakes range from small to large (e.g., "cirque", piedmont lakes) and shallow to deep (e.g., kettle lakes, *fjords*/estuaries). Glacial activity is ongoing under a warming climate, and new lakes are currently being formed at a rapid pace (Buckel, Otto, Prasicek, and Keuschnig, 2018). Other geophysical or biological processes related to the movement and composition of water can result in several natural lake types: solution or "karst" lakes, riverine floodplain "oxbow" lakes, and dammed lakes formed from sediment deposits or organisms (e.g., beavers). In contrast to relatively larger and deeper lakes, ponds are small and shallow systems, but can be formed by the same geophysical processes as lakes.

Human-made lakes (i.e., reservoirs) and ponds are constructed for purposes including energy generation, agricultural irrigation, wildlife habitat, stormwater management, or ecosystem restoration. Damming of small rivers is a millennia-old practice; however, construction of both large (>15 m height) and small dams and associated reservoirs over the past century has substantially altered lotic ecosystem hydrology (Carpenter, Stanley, and Vander Zanden, 2011). Reservoir size and shape depend on the stream or river size that is dammed, the surrounding geology, and each dam's management practices. Reservoirs have substantial impacts on both upstream and downstream hydrology, physical and chemical conditions, and impacts on biological communities both during formation, maintenance of the impoundment, and upon removal (Carpenter, Stanley, and Vander Zanden, 2011). Construction of human-made ponds comprises 42% of waterbodies in nine states of the United States (Smith, Renwick, Bartley, and Buddemeier, 2002), suggesting that they are a significant component of the aquatic landscape (Downing et al., 2006). Both human-made and natural ponds are fundamentally ecologically equivalent, in spite of differences in formation, acting as important local biodiversity hotspots and providing numerous ecosystem services (Céréghino et al., 2014).

In addition to permanent lakes and ponds listed above, some lentic waterbodies are temporary or ephemeral. These lakes or ponds are often isolated and shallow natural or human-made depressions that are alternatively present or absent during wet or dry periods.

1.1.2 Lake and Pond Connectivity

The spatial context of lakes and ponds may have significant effects on organisms (Olden, Jackson, and Peres-Neto, 2001; Zarnetske et al., 2017; King, Bremigan, Infante, and Cheruvelil, 2021). Using a landscape ecology lens, we can consider three main types of systems that vary across dimensions of spatial and temporal connectivity.

First we consider lakes and ponds that are permanently or frequently connected to river systems. This category includes river-connected lakes (e.g., Lake Geneva) or lakes that are part of a large floodplain system (Jones, 2010). In these lakes, exchanges of flora and fauna occur with the main river system so that their biota is usually greatly similar to the biota of the river system itself with the exception of a few species adapted to lentic waters.

Next, we consider isolated lakes and ponds with a limited drainage system. These could include headwater systems completely isolated from other surface water connections. Biota in these lakes have evolved in isolation from other species for a relatively long period of time, leading to speciation and endemicity over a sufficiently long time period. At higher latitudes and altitudes, Ice Age phenomena created most of the lakes in existence today. Therefore, the great majority of existing lakes are geologically very young and occupy basins formed by ice masses or glacial erosion after the retreat of continental ice sheets some 10,000 years ago. All such lakes are expected to fill slowly with sediment and to disappear in the future, along with any isolated and dispersal-limited biota.

In contrast with “young” lakes, which acquired their fauna and flora via aerial transport by wind, animal-mediated dispersal, and/or river-mediated dispersal (for more connected waterbodies), ancient lakes have been isolated for long time periods (i.e., >100,000 years), allowing speciation processes to occur. Only a few existing lakes are known to be much older, and most of them occupy basins formed by large-scale subsidence. They may date back to 20 million (Lake Tanganyika) or 30 million (Lake Baikal) years. These ancient lakes are of particular interest for biodiversity because they exhibit a rich endemic fauna and flora (e.g., Cristescu, Adamowicz, Vaillant, and Haffner, 2010).

Lastly, we can consider temporary lakes and ponds. Temporal connectivity is limited to wet periods in ephemeral or intermittent waterbodies. These temporary waterbodies (e.g., playas, vernal pools, tinajas) can host diverse assemblages, with fauna and flora that exhibit special biological adaptations to seasonal drying (Williams, 1997).

2.0 Origin and Diversity of Freshwater Biota

2.1 Major Groups

It is thought that the early evolution of all the major animal phyla took place in the ocean. Most phyla are predominantly marine and benthic: 32 phyla are found in the sea, 11 of which are exclusively marine, whereas 14 are represented in freshwater and 12 are found on land (May, 1994). Compared to the ocean, freshwater systems are deficient in major taxa and there are no uniquely freshwater metazoan phyla. The osmotic challenges of life in freshwaters probably discouraged invasion of the habitat by many marine invertebrates.

Major taxonomic groups in freshwater systems include: prokaryotes (Archaea and bacteria), protists (algae, protozoa), sponges, fungi, rotifers, annelids, microscopic and macroscopic crustaceans, insects, molluscs, fish and other vertebrates, and macrophytes. Some taxa only spend part of their life cycle in water (e.g., insects, amphibians), or move between freshwater and marine systems (e.g., Pacific salmon, eels) at some point in their life cycle.

2.2 Evaluating Biological Diversity

Freshwater ecosystems support significant biodiversity globally, containing about 10% of all animal species and 33% of vertebrate taxa (Dudgeon et al., 2006; Strayer and Dudgeon, 2010). In spite of rigorous efforts by taxonomists, a good estimation of the total number of species occurring in freshwater lakes and ponds does not exist. Recently, Balian et al. (2008) synthesized data from 163 experts on 59 different taxonomic groups of freshwater animals as part of the Freshwater Animal Diversity Assessment. They found ~126,000 species, representing nearly 10% of the total number of animal species globally (Table 1). Within the same assessment, Chambers et al. (2008) identified >2600 macrophyte species globally. However, the authors noted substantial geographic and taxonomic gaps. This is particularly true for microscopic organisms (e.g., algae, protists), with estimates of tens to hundreds of thousands of species many of which are not named yet (Sheath and Wehr, 2015). We shall provide here some additional recent findings about aquatic biodiversity.

<Table 1 near here>

2.2.1 Diversity of the Microbial Loop and Plankton

Plankton broadly consist of floating or weakly swimming organisms. The importance of bacteria and protozoa activities in the trophic structure of lacustrine food chains has been largely underestimated in the past. The major role played by microorganisms in controlling energy and nutrient fluxes is now better understood following the discovery of the microbial loop (Azam et al., 1983) and its role as a source or a sink for carbon and energy flow to higher trophic levels in pelagic systems. We know now that these microorganisms can control major fluxes of energy and nutrients. In some cases, 50% of the photosynthetic production does not pass directly to higher trophic level but is diverted into a microbial loop where nutrients are rapidly remineralized and fed back to the dissolved inorganic pools.

Several major size classes are usually recognized in pelagic, or open-water, plankton: picoplankton (0.2–2.0 μm), nanoplankton (2-20 μm), microplankton (20–200 μm), and macroscopic plankton (>200 μm; e.g., meso-, macro-, and megaplankton). In the late 1970s, phototrophic and heterotrophic picoplankton (e.g., bacteria, cyanobacteria) were discovered in great abundance in both marine and freshwater ecosystems. Among the nanoplankton are photosynthetic and heterotrophic protists (flagellates, ciliates, amoeba), small algae and diatoms. Grazing by heterotrophic organisms in this size class can assert strong top-down control over bacterial diversity and they are capable of consuming nearly the entire daily bacterial production (Yannarell and Kent, 2009). Nanoplankton also contribute substantially to primary production, regenerate significant amounts of nutrients, and serve as prey for micro- and mesoplankton.

Microplankton include the majority of phytoplankton taxa, large ciliate protozoans, rotifers, and juvenile, or “naupliar” life stages of copepods, while larger size classes include important detritivorous, herbivorous, and predatory crustaceans such as ostracods, cladocerans, and copepods.

Traditional taxonomic identification of plankton via microscopy is challenging, particularly for the smallest size classes. Indeed, a recent comparison of light microscopy and DNA metabarcoding techniques found that diversity of cyanobacteria in the picoplankton size range were vastly underestimated using microscopy across a range of lake types (MacKeigan et al., 2022). With recent advances in molecular techniques, it is becoming apparent that the taxonomic diversity among picoplankton, as well as larger size classes of plankton, is much wider than that among the animals and plants.

2.2.2 Diversity of Invertebrates

Freshwater invertebrates include rotifers, nematodes and annelids, various micro- and macro-crustaceans, larval and adult insects, and molluscs, and encompass a broad array of morphological, trophic, life history, behavioral, and physiological traits. The global diversity of invertebrates is estimated to exceed >125,000 species (Table 1), though this is certainly an underestimate (Balian, Segers, Lévèque, and Martens, 2008). Although some invertebrate groups are relatively well-described (crustaceans, molluscs), others are poorly studied (nematodes, turbellarians) (Balian, Segers, Lévèque, and Martens, 2008). For example, it is estimated that 97% of nematodes are undescribed across all realms (Hugot, Baujard, and Morand, 2001).

As a result of this diversity, invertebrates are critical to lake and pond functioning, often acting as a trophic intermediary between primary producers and higher trophic levels, like fishes and other vertebrates. Many invertebrate taxa (e.g., insects, molluscs) act as important indicator species, where their presence and abundance reflects broader ecosystem health. Key differences in invertebrate diversity are driven by habitat types, both across and within waterbodies. For example, permanent waterbodies were observed to have higher invertebrate diversity compared to temporary waterbodies in a global meta-analysis (Anton-Pardo, Ortega, Melo, and Bini, 2019). Further, diversity of invertebrates is thought to be far greater in benthic, or bottom, habitats within waterbodies compared to open-water habitats, with benthic habitats supporting up to 50x more species compared to pelagic zones (Vander Zanden and Vadeboncoeur, 2020). Though freshwater invertebrates have comparable numbers of described species to freshwater fishes, they are far less studied (Strayer, 2006), with consequences for our understanding of their role in freshwaters.

2.2.3 Diversity in Freshwater Sediments

About 175,000 species of organisms associated with freshwater sediments have been described, including bacteria, protozoans, microcrustaceans, molluscs, insects, algae, and plants, but the true number is likely much higher than this (Palmer et al., 1997). Species living in the upper layers of sediments are critical in mediating biogeochemical processes, including decomposition of organic matter, chemical or photosynthetic production, and the movement of contaminants, gases, and other materials. The number of species associated with sediments can scarcely be estimated. For example, rotifer diversity is poorly understood for freshwater sediments, but it is estimated that there are thousands of undescribed species.

Most freshwater sediment species are small and concentrated in the upper sediment layers. In sufficiently deep lake or pond systems, the availability of light limits the development of plants and photosynthetic organisms in benthic zones, which may therefore be scarce or absent in most sediments. Moreover, oxygen level may influence species richness and the number of species is low in anoxic, or low-oxygen, waters.

2.2.4 Diversity of Vertebrates

Presently, 25,000 fish species have been described. Some 12,000 species are found only in freshwaters (Balian, Segers, Lévèque, and Martens, 2008), a large proportion of which occur in lakes and ponds. The freshwaters are therefore disproportionately rich in species of fishes on the basis of area when compared to oceans. That could be viewed as the result of the patchy nature of inland waters, which can lead to speciation and high endemicity of the biota. Fish live in almost every conceivable type of aquatic habitat; therefore, they exhibit enormous diversity in morphological, trophic, behavioral, and other life history strategies.

Other vertebrate species occur in or adjacent to freshwaters: a few mammals, several reptiles, and many birds and amphibians. Quantitative estimates of the total number of vertebrates whose life cycles include lakes or pond habitats suggest that there are >18,000 species globally that rely on these systems (Table 1).

2.3 Diversity Lens

Taxonomic diversity is but one lens to examine biodiversity. Lake and pond ecosystems also support broad functional, phylogenetic, genetic, and intraspecific diversity. Management and conservation decisions for lake and pond ecosystems may greatly depend on which diversity lens is used, and recent research in other ecosystems suggests that exploring communities from a combined perspective of traits and functions, evolutionary history, and genetic diversity can support different and more holistic perspectives on biodiversity and how they function (Longhi and Beisner, 2010).

The creation of the National Ecological Observatory Network (or NEON) in the United States will support efforts to understand these multiple facets of diversity in freshwater, as well as terrestrial, ecosystems. NEON consists of a network of observation facilities at the continental-scale and is designed to collect long-term ecological data to better understand how ecosystems are changing. Early synthesis efforts have described vast species diversity of multiple taxonomic groups across time and space (Li et al., 2022b). Here we show that taxonomic biodiversity across lentic freshwater NEON sites varies dramatically across space and taxa (Figure 1). Across taxonomic groups, richness varied from 2-3x between sites, with the largest differences in algal richness between the least diverse site (Suggs Lake, with an average of 75 taxa) and the most diverse site (Little Rock Lake, average 258 taxa).

<Figure 1 near here>

3.0 Patterns of Diversity

By examining patterns of diversity both across and within waterbodies, we illustrate how lakes and ponds are both similar and different compared to other types of ecosystems.

3.1 Macroecology

Across waterbodies, it is usually assumed that species diversity increases from high to low latitudes for most of the major groups of plants and animals and that the highest diversity occurs at low latitudes. In freshwaters, however, this latitudinal trend in species richness is often reversed. Tropical lakes have abbreviated zooplankton faunas compared with temperate locales (Fernando, 1980); they are depauperate in large-bodied species of copepods and cladocerans, and limnetic rotifers are likewise poorly represented. Similarly, diving beetles are more diverse in temperate regions compared to tropical regions (Morinière et al., 2016). However, fish species richness and endemicity is actually lower in north temperate lakes of glacial origin than in older lakes from tropical areas.

Community ecologists used to compare isolated freshwater systems to biogeographic islands. The relationship of species number to area containing those species is a well-known empirical observation, and a power function is widely used to describe this pattern mathematically: $S=cA^{Z}$, where S is the number of species, A the area, Z the slope of the regression line, and c a constant. It can also be expressed as log $S=c+Z\ logA$. For example, crustacean zooplankton species richness was significantly correlated with lake surface area (Dodson, 1992). The species area curve for North American lakes is statistically different from and steeper than the corresponding European curve (slopes, respectively, 0.094 and 0.054). This positive relationship was also observed for rotifers, macrophytes, and fishes (Dodson, Arnott, and Cottingham, 2000). However, others have postulated that area per se does not account for species richness, but rather, reflects the influence of other covariates, such as energy inputs, primary production, and top-down pressure by fish communities (Hessen et al., 2006; Hessen, Bakkestuen, and Walseng, 2007). Further, small and isolated lakes and ponds can have relatively high species richness, if fish are not present (Scheffer et al., 2006).

The metabolic theory of ecology has also been demonstrated to predict species richness in lakes and ponds. In this model, environmental temperature and richness are positively related, owing to physiological constraints (Allen, Brown, and Gillooly, 2002); however, support for the hypothesis has been equivocal. The metabolic theory performed poorly compared to the species richness-energy model for North American crustacean zooplankton richness (Pinel-Alloul et al., 2013), but phytoplankton richness was generally well predicted by the metabolic theory across three continents (Segura et al., 2015).

3.2 Biogeography

Many of the lakes at higher latitudes and altitudes were formed at the end of the last Ice Age. They are therefore very young compared to ancient lakes, and they acquired their fauna and flora via the rivers that supply them with water via runoff in their basin and via aerial transport by wind or animals. Dumont (1994), in a review of the species richness of the zooplankton in ancient lakes, provided evidence that these waterbodies have simple pelagic communities. The number of species regularly found in the pelagic plankton of ancient lakes (pre-Pleistocene) varies from three (Lake Tanganyika) to approximately 15 to 20 in Lakes Victoria, Biwa, and Titicaca, typically with five copepod, five cladoceran, and 10 rotifer species. In contrast, “young” lakes may have nearly double the number of species, with up to 10 copepod, 10 cladoceran, and 10 to 15 rotifer species occurring together. In the oldest lakes (Baikal, Tanganyika), which also happen to be the deepest, this simplification of richness is extreme, where the food web collapses to a linear chain.

3.3 Vertical Distribution in Within Waterbodies

Aquatic organisms are not evenly distributed along depth. Water characteristics are relatively uniform in shallow lakes and ponds, which are mixed by winds; however, deeper lakes exhibit patterns of vertical gradients for temperature and light. Briefly speaking, the lake is divided by a thermocline into an upper layer, the epiliminion, and a lower layer, the hypolimnion. Most diversity occurs in the oxygenated upper layer while the lower layer may be deoxygenated if ecosystem respiration is high (e.g., from dying phytoplankton). Photoautotrophs will largely be found in these upper, well-lit regions, but may also migrate vertically to access nutrients. In some stratified lakes therefore, biota may be depauperate, except for bacteria, at greater depths. In lakes with well-oxygenated hypolimnia, fish and other invertebrate aquatic organisms may live at deeper depths, and instead are influenced by temperature regimes. For example, cool and coldwater adapted fishes may occupy the metalimnion and hypolimnion in stratified lakes. As a consequence, zooplankton and other invertebrates may exhibit diel vertical migration (or shifts in their position in the water column) in response to predation pressure by fishes, spending daylight hours in deeper waters and migrating upwards to feed at night.

There is an exception to this rule in Lake Baikal, which is the deepest lake in the world with a maximum depth of 1620 m. The mechanism of mixing of the deep water zone is still not completely understood, but the entire water column of this lake is well oxygenated. Life for fish and invertebrates is therefore possible from the surface to maximum depth, which is exceptional for freshwater systems. Lake Baikal is therefore unique among inland systems and includes some of the deepest-occurring freshwater animals. Fish species from the family Abyssocottidae in Lake Baikal are adapted to deep water and do not occur above 400 m, with physiological adaptations including reduction in eye size and resistance to high pressures (Sideleva, 1994).

3.4 Morphometry and Species Richness

Species diversity within a lake is a function of the diversity of microhabitats: the more ecological niches in the lakes, the more species may be expected. The lake's morphometry is basic to its structure: deep, steep-sided lakes do not offer as many biotopes as shallow, flat lakes. In shallow lakes, most of the lake bottom may be colonized by plants and animals (the benthic flora and fauna), while in deep lakes, only a small part of the lake bottom is colonized, corresponding to vertical profiles in light. Generally speaking, deep lakes are dominated by planktonic organisms, usually associated with suspended particles. In shallow lakes, benthic organisms are dominant and the heterogeneity of lake bottom, as well as the development of macrophytes, may increase the diversity of benthic species.

3.5 Local Environmental Factors

Local, or within-lake, environmental factors can also affect biodiversity in freshwater lakes and ponds. Variables such as salinity, nutrients, contaminants, UV light, temperature, dissolved oxygen, pH, sediment, and biotic factors may alter species diversity. Additionally, fluctuations in these variables may also constrain biodiversity. In the Paradox of the Plankton, Hutchinson (1961) observed that the sheer diversity of phytoplankton in waterbodies could not be explained by the relatively few limiting resources that they require and given that the principle of competitive exclusion predicts that two species competing for the same resource cannot coexist. However, Hutchinson (1961) and others have observed that environmental fluctuations in time and space can prevent competitive exclusion (among other explanations). More recently, factors such as top-down predation, evolution, and turbulence have shown promise in understanding this longstanding paradox (Bracco, Provenzale, and Scheuring, 2000; Behrenfeld et al., 2021).

4.0 Biodiversity Processes Governing Freshwater Ecosystems

One of the most pressing questions for freshwater scientists, particularly in the face of rapid global change, is to predict how biodiversity processes that govern lake and pond ecosystem function will respond to natural and anthropogenic stressors. There is substantial evidence that biodiversity is a driving process in how ecosystems function and respond to perturbations (Cardinale et al., 2012).

4.1 Ecosystem Functioning

Lakes and ponds provide numerous ecosystem functions, many of which are supported and mediated by ongoing interactions between the organisms and the physico-chemical characteristics of the system. These organism-driven ecosystem functions rely on system-wide diversity as well as individual species' traits (Vaughn, 2010) to provide services that are beneficial for humans, also called "ecosystem services" (Ehrlich and Ehrlich, 1981). Broad categories of ecosystem services include supporting (e.g., nutrient cycling, water quality), regulating (e.g,. carbon sequestration, climate regulation), provisioning (e.g., food resources, water supply, species' habitat), and recreational and cultural services.

There is substantial evidence that alterations to or loss of biodiversity can negatively affect ecosystem processes (Brönmark and Hansson, 2002), not just from the loss of species richness, but from the loss of species' traits (Cardinale et al., 2012). Further, these biodiversity-ecosystem function effects can vary substantially, depending on individual lake or pond system characteristics, their community of organisms, and/or spatial and temporal scales (Vaughn, 2010).

4.2 Bottom-Up vs. Top-Down Control of Ecosystem Function

In the classical limnological approach, competing perspectives on the forces driving community structure and associated ecosystem functions set "bottom-up" and "top-down" control as mutually exclusive processes (Hunter and Price, 1992). In systems governed by "bottom-up" control, competition for limited resources between primary producers has consequences for primary productivity and the upward flow of energy through the system to higher trophic levels (Taylor, Vanni, and Flecker, 2015). The competing and often dominant "top-down" perspective, suggests that the effects of top predators cascade down trophic levels to affect primary productivity and are responsible for controlling the state of the entire ecosystem (Gliwicz, 2002). More recent evidence suggests that these processes act simultaneously (Taylor, Vanni, and Flecker, 2015) and their relative importance varies depending on local conditions and community composition (Vaughn, 2010). The interplay between bottom-up and top-down processes can both affect and be affected by changes in biodiversity (e.g., eutrophication, fish kills, overharvest) (Taylor, Vanni, and Flecker, 2015).

Increases in limiting nutrients, predominantly phosphorus and nitrogen, alter ecosystem functions through planktonic and detrital pathways (Taylor, Vanni, and Flecker, 2015), with bottom-up consequences for biomass and composition of the phytoplankton community, as well as higher trophic levels (Hulot, Lacroix, and Loreau, 2014). However, consumers can influence the biomass and diversity of organisms at lower trophic levels directly via predation (e.g., size-selective feeding) or indirectly through interactions that alter competitive or consumer-resource interactions at lower trophic levels (e.g., trophic cascades) (Polis et al., 2000). Changes in top and intermediate predators can affect biomass, composition, and functional identities of lower trophic levels (Carpenter, Stanley, and Vander Zanden, 2011), mediate bottom-up effects by altering nitrogen and phosphorus ratios and primary production, and in turn modify ecosystem respiration, and nutrient cycling and storage. The relative strength of bottom-up and top-down processes remains a pressing ecological question in lake and pond ecosystems, particularly as these processes continue to be affected by changing natural and anthropogenic pressures, and impact management practices (Kolding et al., 2008).

4.3 Biological Diversity and Stability

Ecosystem stability is generally considered to be the ability of a system to "bounce back" to a previous state of ecosystem functioning, or to resist perturbations to ecosystem function (Downing and Leibold, 2010). Stability can be affected by cross-scale stressors where ecosystem responses are dependent on the often complex interplay between patterns of species diversity, community structure, and non-independent species' traits, which often respond directly or indirectly to the same environmental or anthropogenic stressors (Symstad et al., 2003; Ives and Carpenter, 2007). Theoretical and even empirical studies into broad patterns of diversity-stability in lake and pond ecosystems often provide opposing conclusions, largely as a result of differences in spatial or temporal scales, or different perspectives on stability as a response (e.g., productivity, resistance vs. resilience, invasibility, compensatory dynamics, and invasion/colonization and extinction dynamics). Recent empirical evidence, however, provides important avenues for further exploration. For instance, the diversity-compositional stability relationship of plankton communities varies biogeographically with latitude and altitude (Shurin et al., 2007). Additionally, dreissenid mussel invasions precipitated changes to ecosystem-wide stability in nutrient flows, which in turn, impacted food web structure (Conroy and Culver, 2005). Unpacking the complexity of the diversity-stability relationship in lake and pond ecosystems is an important research area moving forward.

4.4 Biodiversity and Food Webs

Food chains and webs are conceptual models that depict trophic, or feeding, interactions among species in a freshwater community as a network, where the diversity of organisms is represented as individual nodes. These models are often well-resolved taxonomically in freshwater systems (Thompson, Dunne, and Woodward, 2012), and provide a picture of the processes at work in ecosystems, particularly the flow of energy between organisms. These models occupy a central position in community and ecosystem ecology, as they provide useful qualitative and quantitative representations of important drivers of community composition (e.g., competition, predation) and ecosystem function (e.g., biomass distribution, energy fluxes) across trophic levels (Thompson, Dunne, and Woodward, 2012).

Changes to food web structure can result from local or broad-scale environmental or anthropogenic factors, with consequences for ecosystem-wide flows of energy and function. For instance, at the local scale, invasion by two bass species led to declines in prey-fish abundance and richness and a decrease in lake trout trophic position in Canadian lakes (Vander Zanden, Casselman, and Rasmussen, 1999). Overharvest of inland fisheries often targets the largest fish taxa, which has top-down and cascading consequences on the biomass and diversity of lower trophic levels (Allan et al., 2005). Further exploration of the role of biodiversity within food web structure and ecosystem function in response to abiotic and biotic processes has important implications for management and conservation of lake and pond ecosystems.

5.0 Threats to Biodiversity

Freshwater ecosystems support significant biodiversity. The concentration of people around freshwater systems has resulted in a much greater degree of degradation to these systems than most open marine or even terrestrial systems. As a result, freshwater biodiversity is declining at a far higher rate compared to marine and terrestrial ecosystems (Grooten and Almond, 2018). Indeed, populations of freshwater species have declined by an average of 83% since 1970, with the most severe declines in freshwater fishes. Some key threats to freshwater biodiversity are examined below.

5.1 Habitat Loss and Alteration

Competition for water may result in the total or partial desiccation of lakes and ponds through various diversions and impoundment of tributaries. Water is withdrawn most often from aquatic systems for irrigation, flood control, and urban and industrial consumption. A spectacular example is provided in the Aral Sea, a large saline lake in the terminus of an extensive inland drainage basin in south-central Asia. The need for water to irrigate crops has resulted in diversion of most of the waters flowing into the Aral Sea. These diversions, as well as poor agricultural practices, have resulted in a marked decrease in surface area (80%) and an increase in salinity (from c. 10 to >120 g/l) since the 1960s (Gaybullaev, Chen, and Gaybullaev, 2012). Fish have virtually disappeared from the lake and the diversity of associated bird and wildlife communities has decreased. Many invertebrate taxa have also disappeared (Williams and Aladin, 1991). Another more recent example is the mega-drought affecting the American Southwest. Reservoirs in the Colorado River system provide water for over 40 million people, including irrigation and municipal water. These reservoirs have declined to historic low levels as the 23-year drought has proceeded, with the two largest reservoirs, Lake Mead and Lake Powell, declining from 95% full to 25% since 2000 (Wheeler et al., 2022). These declines have resulted in massive losses of lentic aquatic habitat, with unknown, though likely significant, consequences for biodiversity.

Activities in the lands surrounding waterbodies can also affect habitat. Siltation from erosion within watersheds has direct adverse effects on fish by covering spawning sites, destroying benthic food sources, and reducing water clarity for visual feeding animals. However, increased turbidity may also have indirect effects on biodiversity in lakes. Seehausen et al. (1997) provided evidence that increasing turbidity from deforestation and agricultural practices has led to a decline in cichlid diversity in Lake Victoria by interfering with coloration-based mate choice. Shoreline development and urbanization of lakes may also affect littoral zone habitat via reductions in coarse woody debris and emergent vegetation, riparian deforestation, and eutrophication. These changes have resulted in losses of terrestrial insect subsidies, alterations to macroinvertebrate functional composition, and effects on fish communities (Francis and Schindler, 2009; Twardochleb and Olden, 2016).

Connectivity between waterbodies can be important for freshwater biodiversity in several ways. Dams may affect biodiversity by restricting movement of more mobile organisms (e.g., fishes) and altering the hydrological regime (e.g., lotic to lentic, water-level fluctuations), with the strongest effects observed in tropical regions (Turgeon, Turpin, and Gregory-Eaves, 2019). By contrast, canals and pipelines may increase connectivity by connecting previously isolated waterbodies or regions. This connectivity can be a double-edged sword, facilitating spread of both native and invasive taxa. Increased connectivity resulted in homogenization of zooplankton communities across lakes and ponds, but an overall increase in regional richness, compared to earlier time periods when waterbodies were more isolated (Strecker and Brittain, 2017).

5.2 Climate Change

Climate change affects lake and pond biodiversity in myriad ways, including the direct effects of increased temperatures and other changes to thermal properties of water, but also via indirect effects, including alteration or loss of habitat, changes in the hydrological regime, salinization, brownification, and changes to food web structure (Havens and Jeppesen, 2018). Climate change impacts are more likely for cool- and cold-water adapted taxa, particularly high latitude or altitude species that cannot migrate to more thermally suitable habitats (Heino, Virkkala, and Toivonen, 2009). Paleolimnological studies have demonstrated significant restructuring of temperate and northern lake communities, with shifts from benthic or heavily silicified to pelagic diatoms concurrent with climate change (Rühland, Paterson, and Smol, 2008), as well as increasing dominance of cyanobacteria (Taranu et al., 2015). Surveys in mountain lakes have shown that climate may be more influential for lake macroinvertebrate communities at broad spatial scales compared to local scale (Boersma, Nickerson, Francis, and Siepielski, 2016). Experiments have shown variable trends of warming on species diversity, which is likely the result of complex responses in multi-species communities, particularly across several trophic levels (Stewart et al., 2013). One broad generality that has emerged is that species diversity may be less affected by climate change compared to composite measures, such as biomass, functional traits, or community composition (Stewart et al., 2013).

5.3 Overharvest

Inland fisheries are vast, contributing more than 40% of the world's finfish production, and thus have great importance for local economies and society (Lynch et al., 2016). These fisheries can include aquaculture, recreational, and commercial fishing activities; however, overfishing is a significant threat to freshwater biodiversity. Similar to marine ecosystems, inland fisheries can decrease biodiversity by fishing down the food web – targeted removal of large-bodied individuals first, then moving progressively to smaller and smaller sized fish species (Allan et al., 2005). Bycatch can also be a substantial source of mortality in freshwater fisheries (Raby, Colotelo, Blouin-Demers, and Cooke, 2011).

Overharvest is not limited to fishes. Freshwater megafauna are often targeted for their meat, skin, and eggs (He et al., 2017). Taxa such as the Siamese Crocodile (*Crocodylus siamensis*), the Chinese Giant Salamander (*Andrias davidianus*), and the Cuban Crocodile (*Crocodylus rhombifer*) are all at risk of extinction from overharvest (He et al., 2017). Historical and contemporary overharvest of molluscs for food, shell uses (e.g., buttons), and the ornamental pet trade has led to biodiversity declines and increased threats of extinction in freshwater bivalves and gastropods (Bohm et al. 2021).

5.4 Pollution and Contaminants

5.4.1 Eutrophication

The biological structure and internal biological control mechanisms of freshwater lakes are highly affected by lake water nutrient concentrations and loading. Limnologists distinguish lakes by their trophic state. Oligotrophic lakes are generally deep and are characterized by low nutrient levels and clear water. The biomass at all trophic levels is low. By contrast, eutrophic lakes are often shallow with high nutrient levels, abundant plankton, and low water clarity. One concept of lake succession considers that lakes pass through different trophic states, beginning with low productivity, gradually moving to a moderately productive or mesotrophic state to finally reach the eutrophic stage. This succession may happen in undisturbed lakes;however, eutrophication (sometimes called cultural eutrophication) is now widespread as a result of human activities.

Eutrophication is the process of enrichment of a water body due to an increase in nutrient loading. The most important nutrients causing eutrophication are phosphorus (P) and nitrogen (N), the same nutrients responsible for bottom-up control of freshwater systems. These chemicals are abundant in waters released from sewage treatment works and from surface and groundwater runoff in agricultural regions.

The most obvious consequence of eutrophication is increased phytoplankton growth, an overall increase in biomass, and a shift in species composition of the lake (Jeppesen et al., 2000). For example, at low P concentrations, shallow lakes in northern Europe are usually in a clearwater stage; submerged macrophytes are abundant and have high species richness, phytoplankton biomass is relatively low with few taxa, piscivores are abundant (though typically few species), and predation pressure on zooplankton is consequently low. Typically, at higher P concentrations there is a shift to a turbid stage: submerged macrophytes disappear, phytoplankton increase (though richness is again low, peaking at mesotrophic conditions), and the fish stock changes. The fish biomass rises and there is a shift from a system dominated by pike (*Esox lucius*) and perch (*Perca fluviatilis*) to one exclusively dominated by planktivorous-benthivorous fish, mainly bream (*Abramis brama*) and roach (*Rutilus rutilus*). Thus eutrophication can affect biodiversity through changes to species composition and loss of sensitive species.

5.4.2 Acidification

The release of sulfur, carbon, and nitrous oxides from the burning of fossil fuels may be transported great distances before being transformed chemically into sulfuric and nitric acids and deposited as rain, snow, or dust. When acid rains occur over areas where waters are poorly buffered, the chemistry and biology of freshwaters can be changed dramatically (Gunn and Sandøy, 2003). Many softwater (i.e., low concentrations of dissolved chemicals) lakes have been acidified both in North America and Europe, but evidence has accumulated for the occurrence of acidification in China, the former Soviet Union, and South America as well (e.g., Biskaborn et al., 2021). Monitoring studies indicate a general impoverishment of species numbers in lakes as they become more acidic. This trend holds across taxonomic groups, with thresholds of negative effects (and recovery) occurring around pH ~6 (Gunn and Sandøy, 2003). In many locations, recovery of biodiversity has lagged behind chemical recovery, which is thought to be related to factors such as availability of colonists from a regional species pool, biotic interactions, and water quality (Yan et al., 2003).

5.4.3 Toxic Chemicals

Toxic chemicals are ubiquitous in the environment; over 350,000 thousand chemicals or chemical mixtures have been registered for manufacture and use globally (Wang, Walker, Muir, and Nagatani-Yoshida, 2020). The production, release and global transport of these chemicals leaves no aquatic system unexposed. Impacts of contaminants on aquatic biodiversity can be characterized as acutely toxic (when exposure is generally high; impacts are typically clearly connected to the compound) or chronically toxic (low exposure over an extended period of time; cause and effect can be more difficult to establish). Additionally, many of the thousands of environmental chemicals likely interact, but our understanding of whether effects are synergistic, additive, or antagonistic are limited due to the infinite number of combinations of contaminant mixtures in the environment. Broadly, impacts of toxic chemicals on aquatic systems include reductions in fitness, reproductive success, and survival, and consequently decreased biodiversity.

Environmental contaminants can largely be grouped into the following: heavy metals, pesticides, flame retardants, personal care products and pharmaceuticals, and other contaminants of emerging concern. Each group has varied but distinctive impacts on biodiversity in aquatic systems - primarily through indirect impacts on reproduction, growth, and species-specific lethal impacts (Amoatey and Baawain, 2019). For example, heavy metals (e.g., lead, arsenic, mercury) biomagnify in the food web and are typically neurotoxic; they can interfere with developmental growth and survival, increase the incidences of abnormalities, and decrease survival. Pesticides pose both acute and chronic toxicity threats to organisms; legacy pesticides like organophosphates and DDT (and its metabolite DDE) are acutely toxic, leading to, for example, neurotoxic and carcinogenic outcomes for invertebrates and fish (Bekele et al., 2021). Most modern pesticides (e.g., atrazine, glyphosate) pose chronic exposure risk to aquatic organisms, and have endocrine disrupting properties that lead to impacts such as skewed sex ratios (e.g., feminization of frogs and fish, Hayes et al., 2002) and altered timing of metamorphosis of aquatic invertebrates (Rohr and McCoy, 2010). Flame retardants are typically chlorinated (e.g., polychlorinated biphenyls, PCBs) or brominated (e.g, polybrominated diphenyl ethers, PBDEs) compounds and are lipophilic; these compounds can have negative impacts on development of fishes in particular due to their neurotoxic and endocrine-disrupting qualities. The effects of pharmaceuticals, personal care products, and contaminants of emerging concern are incredibly wide-ranging, but generally include negative impacts on endocrine function, reproduction, behavior, and fitness (Srain, Beazley, and Walker, 2021).

Recently, there has been increased attention on the potential deleterious effects of salt on freshwater taxa. Freshwater salinization has increased rapidly in recent years and has many potential sources, including sea-level rise, increased discharge from saline groundwater, irrigation, wastewater from mining and oil extraction, urbanization, and de-icing of roads with salts (Cunillera-Montcusí et al., 2022). Increasing salinity can affect organismal osmoregulation (i.e., regulation of ions to maintain equilibrium between external and internal fluids), with effects ranging from sub-lethal (e.g., reduced reproductive rates, smaller body size) to lethal, ultimately reducing taxonomic diversity (Hintz and Relyea, 2019).

5.4.4 Plastic Pollution

A topic of emerging interest is the effects of microplastics (ie. small pieces of plastic, typically <5 mm) on freshwater organisms. Plastics often are deposited in waterbodies through watershed processes, including riverine transport and the disposal of waste, garbage, and sewage (Azevedo-Santos et al., 2021). Ingestion of plastics is generally the route by which harmful effects have been observed, though entanglement in fishing nets and other plastic debris is also of concern. There is also evidence that plastics may adhere to gills, thus interfering with filtration (e.g., fishes; Azevedo-Santos et al., 2021). Additionally, the effects of plastics may be amplified by interactions with other compounds, including metals, persistent organic pollutants, and antibiotics.

The effects of plastic pollution on freshwater biodiversity are via loss of species due to lethal effects or sub-lethal effects that alter organismal fitness. Plastic ingestion has been observed in a broad range of taxa that utilize freshwater systems, including aquatic birds, mammals, amphibians, invertebrates, and fishes (Azevedo-Santos et al., 2021), suggesting that the scope of this issue is potentially enormous and warrants further research.

5.4.5 Noise and Light Pollution

Recently, there has been emerging evidence on the effects of noise and light pollution on aquatic organisms. Though little is known about how both light and noise pollution affect aquatic biodiversity, the widespread and pervasive nature of these threats suggests that there are likely consequences at the sub-lethal level, which may include changes in species distributions.

Anthropogenic noise associated with increased industrialization and traffic has increased at a rapid pace. Water is highly effective at transmitting sound, thus warranting concern for aquatic organisms, particularly fishes and invertebrates. Artificial noise may impair sensory systems, including communications, induce stress responses, alter predator-prey interactions, and affect reproduction (Slabbekoorn et al., 2010).

Ecological light pollution constitutes a broad range of different types of photopollution that interferes with natural organisms. Artificial light at night (ALAN) has increased rapidly since the 19th century, constituting a potentially large, but understudied, source of pollution in waterbodies (Holker et al., 2021). Changes in species' physiology and behavior are expected as a result of increased nocturnal light. For example, adult aquatic insects were attracted to artificial lights, interfering with overland dispersal (Perkin, Hölker, and Tockner, 2014). Urban light sources affected diel vertical migration of *Daphnia*, with fewer individuals migrating shorter distances when exposed to light (Moore et al., 2000). Artificial polarized light can also represent a source of pollution, with the potential for broad consequences across the many animal taxa that use polarization as a cue for feeding, habitat, breeding, and/or oviposition (Horváth, Kriska, Malik, and Robertson, 2009). This is particularly true for aquatic insects, such as dragonflies, mayflies, caddisflies, and water bugs, but also may affect waterbirds, fish, crustaceans, and reptiles.

5.5 Invasive Species

The introduction of invasive species into inland waters has occurred globally. These introductions can occur intentionally (e.g., fish stocking programs) as well as unintentionally (e.g., aquatic hitchhikers). Some of the main goals of deliberate introductions were initially to improve recreational fisheries and aquaculture, develop biological control of aquatic diseases, insects, and plants, or fill supposed "vacant niches" and improve wild stocks in old or newly created impoundments.

Species invasions can affect biodiversity at many levels of biological organization, including genetic, population, and community diversity. The introduction of salmonids to Patagonian lakes resulted in the loss of genetic diversity of the native *Galaxias platei* fish (Vera-Escalona, Habit, and Ruzzante, 2019). Invasion by the red swamp crayfish (*Procambarus clarkii*) precipitated rapid shifts in native tadpole development times in ponds, reducing intraspecific phenotypic variation and potentially weakening local adaptation (Melotto, Manenti, and Ficetola, 2020). The invasion of the spiny water flea, *Bythotrephes longimanus*, has reduced zooplankton community richness in the Laurentian Great Lakes in addition to smaller inland lakes (Strecker, Arnott, Yan, and Girard, 2006). Loss of native species taxonomic, functional, and phylogenetic diversity following invasion is commonly observed (e.g., Matsuzaki, Sasaki, and Akasaka, 2016); however, other responses have also been recorded (Alahuhta et al., 2018).

There are several mechanisms for these losses of biodiversity, including: predation and superior competition by invasive taxa; changes in life history, behavior, growth, and morphology of native taxa; introgression and hybridization among native and invasive taxa; transmission of parasites and pathogens; and many others (Cucherousset and Olden, 2011). Often, these factors may act in synergy, creating a challenging environment for the persistence of native species. However, in some instances, native species can adapt to novel invaders. For instance, several native fish and amphibian species shifted either their food resources or trophic position in the presence of non-native species in floodplain wetlands (Holgerson et al., 2022).

One of the major problems in freshwater species introductions is their irreversibility, at least on the scale of a human's lifetime. Once introduced and established, it is impossible or nearly so, given current technology, to eradicate a fish, invertebrate, or plant species from a large natural water body. As a consequence, we are likely to see a continued reduction in native aquatic biodiversity and an increased homogenization of the world's freshwater biota.

6.0 Conclusion

Biodiversity of lakes and ponds can be understood through various lenses, including a system’s geological origin, degree of connectivity, and local- to broad-scale abiotic and biotic processes. Our understanding of freshwater biodiversity has grown with new tools and technologies. Diversity provides numerous benefits through freshwater ecosystem services, though these benefits are threatened by a suite of human-mediated environmental stressors.

Acknowledgements

AS and AM were funded by the National Science Foundation (award 1926610).

References

Alahuhta, J., Erös, T., Kärnä, O.-M., Soininen, J., Wang, J., and Heino, J. 2018. Understanding environmental change through the lens of trait-based, functional, and phylogenetic biodiversity in freshwater ecosystems. **27**, 263–273.

Allan, J.D., Abell, R., Hogan, Z., Revenga, C., Taylor, B.W., Welcomme, R.L., and Winemiller, K. 2005. Overfishing of inland waters. *Bioscience* **55**, 1041–1051.

Allen, A.P., Brown, J.H., and Gillooly, J.F. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**, 1545–1548.

Amoatey, P., and Baawain, M.S. 2019. Effects of pollution on freshwater aquatic organisms. *Water Environment Research* **91**, 1272–1287.

Anton-Pardo, M., Ortega, J.C.G., Melo, A.S., and Bini, L.M. 2019. Global meta-analysis reveals that invertebrate diversity is higher in permanent than in temporary lentic water bodies. *Freshwater Biology* **64**, 2234–2246.

Azam, F., Fenchel, T., Field, J., Gray, J., Meyer-Reil, L., and Thingstad, F. 1983. The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* **10**, 257–263.

Azevedo-Santos, V.M., Brito, M.F.G., Manoel, P.S., Perroca, J.F., Rodrigues-Filho, J.L., Paschoal, L.R.P., Gonçalves, G.R.L., Wolf, M.R., Blettler, M.C.M., Andrade, M.C., et al. 2021. Plastic pollution: A focus on freshwater biodiversity. *Ambio* **50**, 1313–1324.

Balian, E.V., Segers, H., Lévèque, C., and Martens, K. 2008. The Freshwater Animal Diversity Assessment: an overview of the results. *Hydrobiologia* **595**, 627–637.

Behrenfeld, M.J., O’Malley, R., Boss, E., Karp-Boss, L., and Mundt, C. 2021. Phytoplankton biodiversity and the inverted paradox. *ISME Communications* **1**, 1–9.

Bekele, T.G., Zhao, H., Yang, J., Chegen, R.G., Chen, J., Mekonen, S., and Qadeer, A. 2021. A review of environmental occurrence, analysis, bioaccumulation, and toxicity of organophosphate esters. *Environmental Science and Pollution Research International* **28**, 49507–49528.

Biskaborn, B.K., Narancic, B., Stoof-Leichsenring, K.R., Pestryakova, L.A., Appleby, P.G., Piliposian, G.T., and Diekmann, B. 2021. Effects of climate change and industrialization on Lake Bolshoe Toko, eastern Siberia. *Journal of Paleolimnology* **65**, 335–352.

Boersma, K.S., Nickerson, A., Francis, C.D., and Siepielski, A.M. 2016. Climate extremes are associated with invertebrate taxonomic and functional composition in mountain lakes. *Ecology and Evolution* **6**, 8094–8106.

Bracco, A., Provenzale, A., and Scheuring, I. 2000. Mesoscale vortices and the paradox of the plankton. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**, 1795–1800.

Brönmark, C., and Hansson, L.-A. 2002. Environmental issues in lakes and ponds: current state and perspectives. *Environmental Conservation* **29**, 290–307.

Buckel, J., Otto, J.C., Prasicek, G., and Keuschnig, M. 2018. Glacial lakes in Austria - Distribution and formation since the Little Ice Age. *Global and Planetary Change* **164**, 39–51.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., et al. 2012. Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.

Carpenter, S.R., Stanley, E.H., and Vander Zanden, M.J. 2011. State of the world's freshwater ecosystems: Physical, chemical, and biological changes. *Annual Review of Environment and Resources* **36**, 75–99.

Céréghino, R., Boix, D., Cauchie, H.-M., Martens, K., and Oertli, B. 2014. The ecological role of ponds in a changing world. *Hydrobiologia* **723**, 1–6.

Chambers, P.A., Lacoul, P., Murphy, K.J., and Thomaz, S.M. 2008. Global diversity of aquatic macrophytes in freshwater. *Hydrobiologia* **595**, 9–26.

Conroy, J.D., and Culver, D.A. 2005. Do dreissenid mussels affect Lake Erie ecosystem stability processes? *The American Midland Naturalist* **153**, 20–32.

Cristescu, M.E., Adamowicz, S.J., Vaillant, J.J., and Haffner, D.G. 2010. Ancient lakes revisited: from the ecology to the genetics of speciation. *Molecular Ecology* **19**, 4837–4851.

Cucherousset, J., and Olden, J.D. 2011. Ecological impacts of nonnative freshwater fishes. *Fisheries* **36**, 215–230.

Cunillera-Montcusí, D., Beklioğlu, M., Cañedo-Argüelles, M., Jeppesen, E., Ptacnik, R., Amorim, C.A., Arnott, S.E., Berger, S.A., Brucet, S., Dugan, H.A., et al. 2022. Freshwater salinisation: a research agenda for a saltier world. *Trends in Ecology & Evolution* **37**, 440–453.

Dodson, S.I. 1992. Predicting zooplankton species richness. *Limnology and Oceanography* **37**, 848–856.

Dodson, S.I., Arnott, S.E., and Cottingham, K.L. 2000. The relationship in lake communities between primary productivity and species richness. *Ecology* **81**, 2662–2679.

Downing, A.L., and Leibold, M.A. 2010. Species richness facilitates ecosystem resilience in aquatic food webs: Species richness facilitates resilience. *Freshwater Biology* **55**, 2123–2137.

Downing, J. 2010. Emerging global role of small lakes and ponds: Little things mean a lot. *Limnetica* **29**, 9–24.

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M., et al. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography* **51**, 2388–2397.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Leveque, C., Naiman, R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L.J., et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* **81**, 163–182.

Dumont, H.J. 1994. On the diversity of the Cladocera in the tropics. *Hydrobiologia* **272**, 27–38.

Ehrlich, P.R., and Ehrlich, A.H. 1981. Extinction: the causes and consequences of the disappearance of species (New York: Random House).

Fernando, C.H. 1980. The species and size composition of tropical freshwater zooplankton with special reference to the oriental region (South East Asia). *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie* **65**, 411–426.

Francis, T.B., and Schindler, D.E. 2009. Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. *Oikos* **118**, 1872–1882.

Gaybullaev, B., Chen, S.-C., and Gaybullaev, D. 2012. Changes in water volume of the Aral Sea after 1960. *Applied Water Science* **2**, 285–291.

Gliwicz, M.Z. 2002. On the different nature of top-down and bottom-up effects in pelagic food webs: Top-down versus bottom-up effects. *Freshwater Biology* **47**, 2296–2312.

Grooten, M., and Almond, R.E.A. 2018. Living Planet Report - 2018: Aiming Higher (Gland, Switzerland: WWF).

Gunn, J.M., and Sandøy, S. 2003. Introduction to the Ambio Special Issue on biological recovery from acidification: Northern Lake Recovery Study. *Ambio* **32**, 162–164.

Havens, K., and Jeppesen, E. 2018. Ecological Responses of Lakes to Climate Change. *Water* **10**, 917.

Hayes, T.B., Collins, A., Lee, M., Mendoza, M., Noriega, N., Stuart, A.A., and Vonk, A. 2002. Hermaphroditic, demasculinized frogs after exposure to the herbicide atrazine at low ecologically relevant doses. *Proceedings of the National Academy of Sciences* **99**, 5476–5480.

He, F., Zarfl, C., Bremerich, V., Henshaw, A., Darwall, W., Tockner, K., and Jähnig, S.C. 2017. Disappearing giants: a review of threats to freshwater megafauna. *WIREs Water* **4**, e1208.

Heino, J., Virkkala, R., and Toivonen, H. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* **84**, 39–54.

Hessen, D.O., Bakkestuen, V., and Walseng, B. 2007. Energy input and zooplankton species richness. *Ecography* **30**, 749–758.

Hessen, D.O., Faafeng, B.A., Smith, V.H., Bakkestuen, V., and Walseng, B. 2006. Extrinsic and intrinsic controls of zooplankton diversity in lakes. *Ecology* **87**, 433–443.

Hintz, W.D., and Relyea, R.A. 2019. A review of the species, community, and ecosystem impacts of road salt salinisation in fresh waters. *Freshwater Biology* **64**, 1081–1097.

Holgerson, M.A., Barnard, M., Ahn, B., Hayes, M.P., and Strecker, A.L. 2022. Freshwater floodplain habitats buffer native food webs from negative effects of nonnative centrarchids and bullfrogs. *Freshwater Science* **41**, 327–341.

Holker, F., Bolliger, J., Davies, T.W., Giavi, S., Jechow, A., Kalinkat, G., Longcore, T., Spoelstra, K., Tidau, S., Visser, M.E., et al. 2021. 11 Pressing Research Questions on How Light Pollution Affects Biodiversity. *Frontiers in Ecology and Evolution* **9**,.

Horváth, G., Kriska, G., Malik, P., and Robertson, B. 2009. Polarized light pollution: a new kind of ecological photopollution. *Frontiers in Ecology and the Environment* **7**, 317–325.

Hugot, J.-P., Baujard, P., and Morand, S. 2001. Biodiversity in helminths and nematodes as a field of study: an overview. *Nematology* **3**, 199–208.

Hulot, F.D., Lacroix, G., and Loreau, M. 2014. Differential responses of size-based functional groups to bottom-up and top-down perturbations in pelagic food webs: a meta-analysis. *Oikos* **123**, 1291–1300.

Hunter, M.D., and Price, P.W. 1992. Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**, 724–732.

Hutchinson, G.E. 1961. The paradox of the plankton. *American Naturalist* **95**, 137–145.

Ives, A.R., and Carpenter, S.R. 2007. Stability and diversity of ecosystems. *Science* **317**, 58–62.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., and Landkildehus, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology* **45**, 201–218.

Jones, N.E. 2010. Incorporating lakes within the river discontinuum: longitudinal changes in ecological characteristics in stream-lake networks. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1350–1362.

King, K.B.S., Bremigan, M.T., Infante, D., and Cheruvelil, K.S. 2021. Surface water connectivity affects lake and stream fish species richness and composition. *Canadian Journal of Fisheries and Aquatic Sciences* **78**, 433–443.

Kolding, J., van Zwieten, P., Mkumbo, O., Silsbe, G., and Hecky, R. 2008. Are the Lake Victoria fisheries threatened by exploitation or eutrophication? Towards an ecosystem-based approach to management. In The Ecosystem Approach to Fisheries, G. Bianchi, H.R. Skjoldal, and Food and Agriculture Organization of the United Nations, eds. (Wallingford, UK ; Cambridge, MA : Rome: CABI ; Food and Agriculture Organization of the United Nations), pp. 309–354.

Li, D., Record, S., Sokol, E., Bitters, M., Chen, M., Chung, A., Helmus, M., Jaimes, R., Jansen, L., Jarzyna, M., et al. 2022a. Standardized NEON organismal data (neonDivData) (Environmental Data Initiative).

Li, D., Record, S., Sokol, E.R., Bitters, M.E., Chen, M.Y., Chung, Y.A., Helmus, M.R., Jaimes, R., Jansen, L., Jarzyna, M.A., et al. 2022b. Standardized NEON organismal data for biodiversity research. *Ecosphere* **13**, e4141.

Longhi, M.L., and Beisner, B.E. 2010. Patterns in taxonomic and functional diversity of lake phytoplankton: Taxonomic and functional diversity of lake phytoplankton. *Freshwater Biology* **55**, 1349–1366.

Lynch, A.J., Cooke, S.J., Deines, A.M., Bower, S.D., Bunnell, D.B., Cowx, I.G., Nguyen, V.M., Nohner, J., Phouthavong, K., Riley, B., et al. 2016. The social, economic, and environmental importance of inland fish and fisheries. *Environmental Reviews*.

MacKeigan, P.W., Garner, R.E., Monchamp, M.-È., Walsh, D.A., Onana, V.E., Kraemer, S.A., Pick, F.R., Beisner, B.E., Agbeti, M.D., da Costa, N.B., et al. 2022. Comparing microscopy and DNA metabarcoding techniques for identifying cyanobacteria assemblages across hundreds of lakes. *Harmful Algae* **113**, 102187.

Matsuzaki, S.S., Sasaki, T., and Akasaka, M. 2016. Invasion of exotic piscivores causes losses of functional diversity and functionally unique species in Japanese lakes. *Freshwater Biology* **61**, 1128–1142.

May, R.M. 1994. Biological Diversity: Differences between Land and Sea. *Philosophical Transactions: Biological Sciences* **343**, 105–111.

Melotto, A., Manenti, R., and Ficetola, G.F. 2020. Rapid adaptation to invasive predators overwhelms natural gradients of intraspecific variation. *Nature Communications* **11**, 3608.

Messager, M.L., Lehner, B., Grill, G., Nedeva, I., and Schmitt, O. 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. *Nature Communications* **7**, 13603.

Moore, M.V., Pierce, S.M., Walsh, H.M., Kvalvik, S.K., and Lim, J.D. 2000. Urban light pollution alters the diel vertical migration of *Daphnia*. *Internationale Vereinigung Für Theoretische Und Angewandte Limnologie: Verhandlungen* **27**, 779–782.

Morinière, J., Van Dam, M.H., Hawlitschek, O., Bergsten, J., Michat, M.C., Hendrich, L., Ribera, I., Toussaint, E.F.A., and Balke, M. 2016. Phylogenetic niche conservatism explains an inverse latitudinal diversity gradient in freshwater arthropods. *Scientific Reports* **6**, 26340.

Oertli, B., Joye, D.A., Castella, E., Juge, R., Cambin, D., and Lachavanne, J.-B. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation* **104**, 59–70.

Olden, J.D., Jackson, D.A., and Peres-Neto, P.R. 2001. Spatial isolation and fish communities in drainage lakes. *Oecologia* **127**, 572–585.

Palmer, M.A., Covich, A.P., Finlay, B.J., Gibert, J., Hyde, K.D., Johnson, R.K., Kairesalo, T., Lake, S., Lovell, C.R., Naiman, R.J., et al. 1997. Biodiversity and Ecosystem Processes in Freshwater Sediments. *Ambio* **26**, 571–577.

Perkin, E.K., Hölker, F., and Tockner, K. 2014. The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshwater Biology* **59**, 368–377.

Pinel-Alloul, B., André, A., Legendre, P., Cardille, J.A., Patalas, K., and Salki, A. 2013. Large-scale geographic patterns of diversity and community structure of pelagic crustacean zooplankton in Canadian lakes. *Global Ecology and Biogeography* **22**, 784–795.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., and Maron, J. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* **15**, 473–475.

Raby, G.D., Colotelo, A.H., Blouin-Demers, G., and Cooke, S.J. 2011. Freshwater Commercial Bycatch: An Understated Conservation Problem. *BioScience* **61**, 271–280.

Richardson, D.C., Holgerson, M.A., Farragher, M.J., Hoffman, K.K., King, K.B.S., Alfonso, M.B., Andersen, M.R., Cheruveil, K.S., Coleman, K.A., Farruggia, M.J., et al. 2022. A functional definition to distinguish ponds from lakes and wetlands. *Scientific Reports* **12**, 1–13.

Rohr, J.R., and McCoy, K.A. 2010. A Qualitative Meta-Analysis Reveals Consistent Effects of Atrazine on Freshwater Fish and Amphibians. *Environmental Health Perspectives* **118**, 20–32.

Rühland, K., Paterson, A.M., and Smol, J.P. 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. *Global Change Biology* **14**, 2740–2754.

Scheffer, M., van Geest, G.J., Zimmer, K., Jeppesen, E., Sondergaard, M., Butler, M.G., Hanson, M.A., Declerck, S., and De Meester, L. 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos* **112**, 227–231.

Seehausen, O., Alphen, J.J.M. van, and Witte, F. 1997. Cichlid Fish Diversity Threatened by Eutrophication That Curbs Sexual Selection. *Science* **277**, 1808–1811.

Segura, A.M., Calliari, D., Kruk, C., Fort, H., Izaguirre, I., Saad, J.F., and Arim, M. 2015.

Metabolic dependence of phytoplankton species richness. *Global Ecology and Biogeography* **24**, 472–482.

Sheath, R.G., and Wehr, J.D. 2015. Introduction to the freshwater algae. In Freshwater Algae of North America: Ecology and Classification, Wehr, J.D., R.G. Sheath, and J.P. Kociolek, eds. (London: Academic Press), pp. 1–11.

Shurin, J.B., Arnott, S.E., Hillebrand, H., Longmuir, A., Pinel-Alloul, B., Winder, M., and Yan, N.D. 2007. Diversity-stability relationship varies with latitude in zooplankton. *Ecology Letters* **10**, 127–134.

Sideleva, V.G. 1994. Speciation of endemic Cottoidei in Lake Baikal. *Advances in Limnology* **44**, 441–450.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., and Popper, A.N. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution* **25**, 419–427.

Smith, S.V., Renwick, W.H., Bartley, J.D., and Buddemeier, R.W. 2002. Distribution and significance of small, artificial water bodies across the United States landscape. *Science of The Total Environment* **299**, 21–36.

Srain, H.S., Beazley, K.F., and Walker, K.R. 2021. Pharmaceuticals and personal care products and their sublethal and lethal effects in aquatic organisms. *Environmental Reviews* **29**, 142–181.

Stewart, R.I.A., Dossena, M., Bohan, D.A., Jeppesen, E., Kordas, R.L., Ledger, M.E., Meerhoff, M., Moss, B., Mulder, C., Shurin, J.B., et al. 2013. Mesocosm Experiments as a Tool for Ecological Climate-Change Research. In Advances in Ecological Research, G. Woodward, and E.J. O'Gorman, eds. (Academic Press), pp. 71–181.

Strayer, D.L., and Dudgeon, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* **29**, 344–358.

Strecker, A.L., Arnott, S.E., Yan, N.D., and Girard, R. 2006. Variation in the response of crustacean zooplankton species richness and composition to the invasive predator Bythotrephes longimanus. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2126–2136.

Strecker, A.L., and Brittain, J.T. 2017. Increased habitat connectivity homogenizes freshwater communities: historical and landscape perspectives. *Journal of Applied Ecology* **54**, 1343–1352.

Symstad, A.J., Chapin, F.S., Wall, D.H., Gross, K.L., Huenneke, L.F., Mittelbach, G.G., Peters, D.P.C., and Tilman, D. 2003. Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *BioScience* **53**, 89.

Taranu, Z.E., Gregory-Eaves, I., Leavitt, P.R., Bunting, L., Buchaca, T., Catalan, J., Domaizon, I., Guilizzoni, P., Lami, A., McGowan, S., et al. 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. *Ecology Letters* **18**, 375–384.

Taylor, J.M., Vanni, M.J., and Flecker, A.S. 2015. Top-down and bottom-up interactions in freshwater ecosystems: Emerging complexities. In Trophic Ecology: Bottom-Up and Top-Down Interactions Across Aquatic and Terrestrial Ecosystems, (Cambridge: Cambridge University Press), pp. 55–85.

Thompson, R.M., Dunne, J.A., and Woodward, G. 2012. Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics: Freshwater food webs - a review. *Freshwater Biology* **57**, 1329–1341.

Turgeon, K., Turpin, C., and Gregory-Eaves, I. 2019. Dams have varying impacts on fish communities across latitudes: a quantitative synthesis. *Ecology Letters* **22**, 1501–1516.

Twardochleb, L.A., and Olden, J.D. 2016. Human development modifies the functional composition of lake littoral invertebrate communities. *Hydrobiologia* **775**, 167–184.

Vander Zanden, M.J., Casselman, J.M., and Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401**, 464–467.

Vander Zanden, M.J., and Vadeboncoeur, Y. 2020. Putting the lake back together 20 years later: what in the benthos have we learned about habitat linkages in lakes? *Inland Waters* **10**, 305–321.

Vaughn, C.C. 2010. Biodiversity losses and ecosystem function in freshwaters: Emerging conclusions and research directions. *BioScience* **60**, 25–35.

Vera-Escalona, I., Habit, E., and Ruzzante, D.E. 2019. Invasive species and postglacial colonization: their effects on the genetic diversity of a Patagonian fish. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20182567.

Wang, Z., Walker, G.W., Muir, D.C.G., and Nagatani-Yoshida, K. 2020. Toward a Global Understanding of Chemical Pollution: A First Comprehensive Analysis of National and Regional Chemical Inventories. *Environmental Science & Technology* **54**, 2575–2584.

Wheeler, K.G., Udall, B., Wang, J., Kuhn, E., Salehabadi, H., and Schmidt, J.C. 2022. What will it take to stabilize the Colorado River? *Science* **377**, 373–375.

Williams, D.D. 1997. Temporary ponds and their invertebrate communities. *Aquatic Conservation: Marine and Freshwater Ecosystems* **7**, 105–117.

Williams, W.D., and Aladin, N.V. 1991. The Aral Sea: Recent limnological changes and their conservation significance. *Aquatic Conservation: Marine and Freshwater Ecosystems* **1**, 3–23.

Yan, N.D., Leung, B., Keller, W., Arnott, S.E., Gunn, J.M., and Raddum, G.G. 2003. Developing conceptual frameworks for the recovery of aquatic biota from acidification. *Ambio* **32**, 165–169.

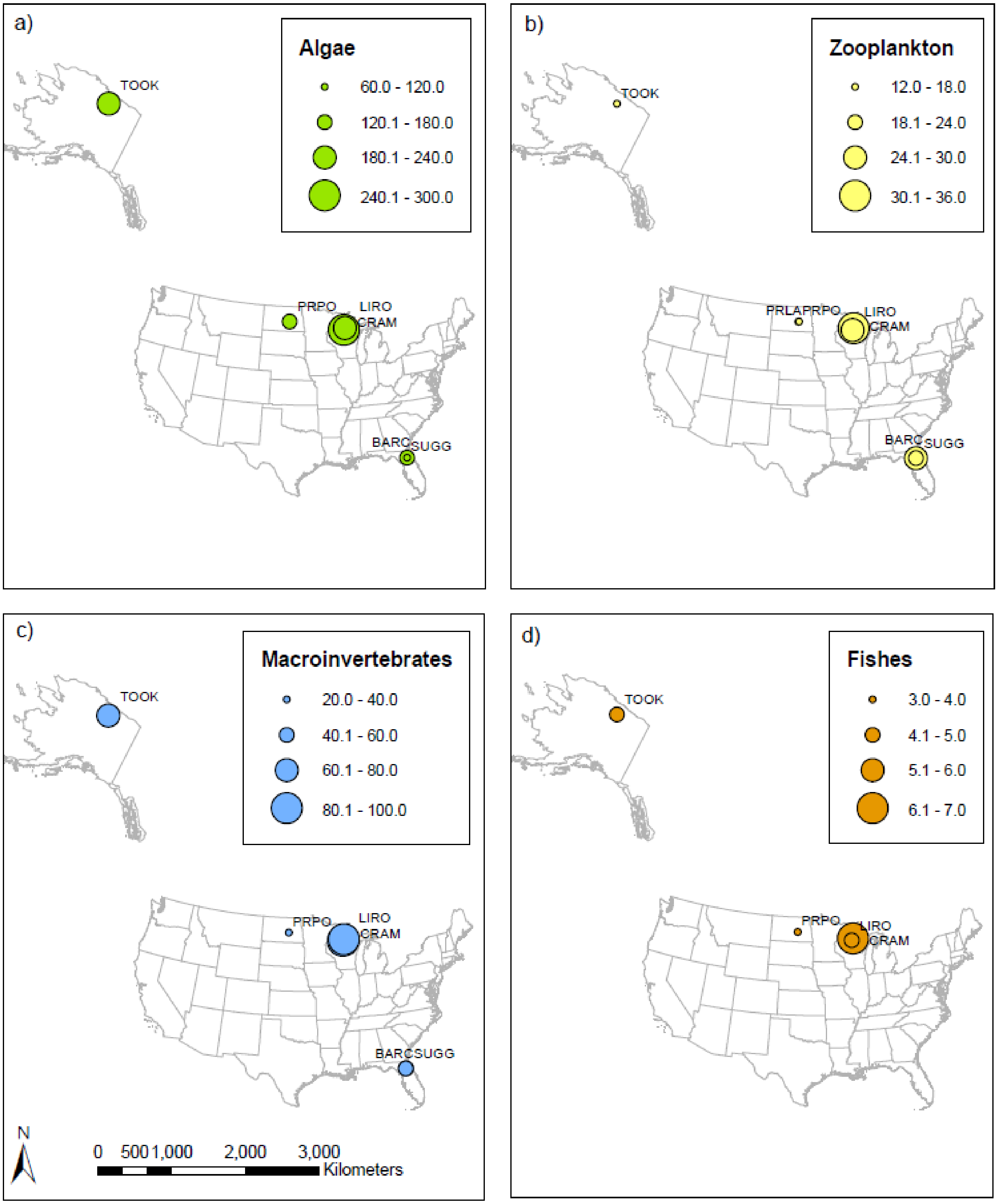
Yannarell, A.C., and Kent, A.D. 2009. Bacteria,distribution and community structure. In Encyclopedia of Inland Waters, G.E. Likens, ed. (Oxford: Academic Press), pp. 201–210.

Zarnetske, P.L., Baiser, B., Strecker, A., Record, S., Belmaker, J., and Tuanmu, M.-N. 2017. The interplay between landscape structure and biotic interactions. *Current Landscape Ecology Reports* **2**, 1–18.

Table 1. Total species diversity of major freshwater animals, by zoogeographic region. Reprinted from Hydrobiologia, 595, Balian et al., The Freshwater Animal Diversity Assessment: An overview of the results, 627-637, Copyright (2008), with permission from Springer. PA = Palearctic, NA = Nearctic, AT = Afrotropical, NT = Neotropical, OL = Oriental, AU = Australasian, ANT = Antarctic, PAC = Pacific and Oceanic Islands

	PA	NA	AT	NT	OL	AU	PAC	ANT	World
Other phyla	3,675	1,672	1,188	1,337	1,205	950	181	113	6,109
Annelida	870	350	186	338	242	210	10	10	1,761
Mollusca	1,848	936	483	759	756	557	171	0	4,998
Crustacea	4,499	1,755	1,536	1,925	1,968	1,225	125	33	11,990
Arachnida	1,703	1,069	801	1,330	569	708	5	2	6,149
Collembola	338	49	6	28	34	6	3	1	414
Insecta	15,190	9,410	8,594	14,428	13,912	7,510	577	14	75,874
Vertebrates	2,193	1,831	3,995	6,041	3,674	694	8	1	18,235
Total	30,316	17,072	16,789	26,186	22,360	11,860	1,080	174	125,530

Figure 1. Average annual taxonomic richness at National Ecological Observatory Network (NEON) lentic freshwater sites across the US for a) algae (phytoplankton and periphyton), b) zooplankton, c) macroinvertebrates, and d) fishes. Data were obtained from Li et al. (2022a). Only taxa identified to genus or species level were included. Timeframes for each data product and details are in Li et al. (2022b). Note that not all taxa are sampled at all sites. Site abbreviations: BARC = Lake Barco, CRAM = Crampton Lake, LIRO = Little Rock Lake, PRLA = Prairie Lake, PRPO = Prairie Pothole, SUGG = Lake Suggs, TOOK = Toolik Lake.


a)
Algae
60.0 - 120.0
120.1 - 180.0
180.1 - 240.0
240.1 - 300.0
TOOK
PRPO
LIRO
CRAM
BARC
SUGG
b)
Zooplankton
12.0 - 18.0
18.1 - 24.0
24.1 - 30.0
30.1 - 36.0
TOOK
PRLA
PRPO
LIRO
CRAM
BARC
SUGG
c)
Macroinvertebrates
20.0 - 40.0
40.1 - 60.0
60.1 - 80.0
80.1 - 100.0
TOOK
PRPO
LIRO
CRAM
BARC
SUGG
N
0 500 1,000 2,000 3,000
Kilometers
d)
Fishes
3.0 - 4.0
4.1 - 5.0
5.1 - 6.0
6.1 - 7.0
TOOK
PRPO
LIRO
CRAM

1016

1017

Permissions

Table 1 was reprinted from Hydrobiologia, 595, Balian et al., The Freshwater Animal Diversity Assessment: An overview of the results, 627-637, Copyright (2008), with permission from Springer.