## SYNTHESIS & INTEGRATION

# The freshwater biome gradient framework: predicting macroscale properties based on latitude, altitude, and precipitation

WALTER K. DODDS [ID],[1],† LINDSEY BRUCKERHOFF,[1] DAROLD BATZER,[2] ANNE SCHECHNER,[1] CASEY PENNOCK,[1] ELIZABETH RENNER,[1] FLAVIA TROMBONI [ID],[3] KARI BIGHAM,[4] AND SAMANTHA GRIEGER[5]

[1]Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA
[2]Department of Entomology, University of Georgia, Athens, Georgia 30602 USA
[3]Global Water Center and Biology Department, University of Nevada, Reno, Nevada 89557 USA
[4]Department of Biological and Agricultural Engineering, Kansas State University, Manhattan, Kansas 66506 USA
[5]School of the Environment, Washington State University, Vancouver, Washington 98686 USA

**Abstract.** Understanding global ecological patterns and processes, from biogeochemical to biogeographical, requires broad-scale macrosystems context for comparing and contrasting ecosystems. Climate gradients (precipitation and temperature) and other continental-scale patterns shape freshwater environments due to their influences on terrestrial environments and their direct and indirect effects on the abiotic and biotic characteristics of lakes, streams, and wetlands. We combined literature review, analyses of open access data, and logical argument to assess abiotic and biotic characters of freshwater systems across gradients of latitude and elevation that drive precipitation, temperature, and other variability. We explored the predictive value of analyzing patterns in freshwater ecosystems at the global macrosystems scale. We found many patterns based on climate, particularly those dependent upon hydrologic characteristics and linked to characteristics of terrestrial biomes. For example, continental waters of dry areas will generally be widely dispersed and have higher probability of drying and network disconnection, greater temperatures, greater inorganic turbidity, greater salinity, and lower riparian canopy cover relative to areas with high precipitation. These factors will influence local community composition and ecosystem rates. Enough studies are now available at the continental or global scale to start to characterize patterns under a coherent conceptual framework, though considerable gaps exist in the tropics and less developed regions. We present illustrative global-scale trends of abiotic, biotic, and anthropogenic impacts in freshwater ecosystems across gradients of precipitation and temperature to further understanding of broad-scale trends and to aid prediction in the face of global change. We view freshwater systems as occurring across arrays of multiple gradients (including latitude, altitude, and precipitation) rather than areas with specific boundaries. While terrestrial biomes capture some variability along these gradients that influence freshwaters, other features such as, slope, geology, and historical glaciation also influence freshwaters. Our conceptual framework is not so much a single hypothesis as a way to logically characterize patterns in freshwaters at scales relevant to (1) evolutionary processes that give rise to freshwater biodiversity, (2) regulatory units that influence freshwater ecosystems, and (3) the current scope of anthropogenic impacts on freshwaters and the vital ecosystem services they provide.

† **E-mail:** wkdodds@ksu.edu

## INTRODUCTION

Characteristics of terrestrial ecosystems converge across global precipitation and temperature gradients and ecologists use the concept of biomes to classify terrestrial systems across these gradients (Holdridge 1947, Whittaker 1970). Here, we ask whether such an approach would be useful to freshwater ecologists concerned with pattern and process at the broadest (macrosystem) scales. For example, an ecologist considering a mesic temperate grassland expects dominance by grasses, a role of fire in maintaining grass dominance, an evolutionary history with large grazing mammals, adaptations to seasonality, ability to withstand hot and dry conditions as well as times of ample moisture, and moderately high productivity. If we consider an Arctic freshwater habitat, we expect strong seasonal effects; it may freeze completely and will have long days with low light intensity and months of darkness. All species in these Arctic waters must be adapted to withstand cold temperatures, low-stature plants dominate wetlands, and groundwater is shallow. Limnologists already make assumptions that specific characteristics link to large-scale patterns of abiotic drivers, though they do not organize these assumptions in a coherent structure analogous to the biomes framework in terrestrial ecology.

Dodds et al. (2015) proposed a framework to describe how global patterns of temperature and precipitation might constrain stream ecology, as correlated with their corresponding terrestrial biomes. Under the stream biome gradient framework, climate was a clear determinant of stream properties including hydrology (flooding and drying), geomorphology (drainage density and channel morphology), canopy cover, seasonality, and many other core abiotic and biotic drivers of aquatic ecology. These translated to patterns of diversity and distributions of animal life history traits as well as differences in expected ecosystem rates (Dodds et al. 2015). It is unclear to what degree these patterns transfer to other surface waters (wetlands and lakes).

Here we explore the idea of biomes for streams, wetlands, and lakes. We strive to provide a predictive framework of ecological properties across the broadest spatial scales (macroscales). Macrosystem approaches are relevant to biogeography, conservation, and human scales of management (e.g., national laws relate to conservation and environmental protection) and represent a novel way to view ecology on continental scales (Heffernan et al. 2014, McCluney et al. 2014). We view this as a framework, as the prior paper Dodds et al. (2015) used the term "concept" but did not provide one simple concept, but rather a general predictive approach based on constraints imposed by climate. We understand that broad generality requires a trade-off with specific local prediction (Levins 1966), and that there will be many local exceptions to the generalizations of the framework. We hope this framework identifies macroscale patterns that freshwater scientists can use to provide expectations on how systems will vary based on large-scale drivers.

The first step is providing a definition of biome that could apply to freshwaters. Our general working definition of a biome is a unique spatial region defined by predictable abiotic and biotic characteristics (process, form, and function) of ecological interest driven by climatic factors and others that vary over broad spatial scales. As with terrestrial biomes, aquatic biomes will not have hard and fast boundaries. Transitions among biomes across space occur largely as gradients rather than as sharp edges. Biomes are not biogeographically systematic (not zoogeographic regions or ecoregions; sensu Abell et al. 2008). Ecologists define terrestrial biomes based on plant architecture and productivity even though they can contain different species that have convergent evolution leading to similar function. Aquatic primary producers may function similarly, and we explore this and other potential ways to delineate freshwater biomes. Whittaker (1970) stated biomes could be developed for aquatic systems based on physiognomy but noted that aquatic communities intergrade with each

other in different ways and are less dependent on global climatic gradients than are terrestrial habitats (presumably because water is less limiting).

We assessed patterns of both abiotic and biotic characteristics across global gradients of precipitation and temperature (driven by elevation and latitude) and additional characteristics that might be a function of elevation or latitude (e.g., glaciation and slope). We considered surface freshwater habitats, including streams, wetlands, lakes, and reservoirs. Our goal was to assess patterns of abiotic factors across global gradients and link these abiotic patterns to observed biological responses. We chose abiotic factors known to be drivers of ecological structure and function in freshwater systems. These factors include temperature, light, geological processes, hydrology, chemistry, and habitat density and distribution. Where data are lacking, we do not test predictive patterns, but hypothesize potential patterns based on logic. We intend to generate a general predictive framework of testable hypotheses but cannot test every hypothesis. Thus, this paper is a statement of approach rather than a complete application. We use a combination of literature review and data analysis (see Appendix S1 for data descriptions). For some patterns, we explore representative transects ($n = 20$) across global gradients (Fig. 1) to test predictions. The precipitation gradient transects were set to cut across landscapes keeping temperature somewhat constant, while temperature gradients were set along gradients of altitude or latitude attempting to keep precipitation roughly constant. In some cases, we find biological patterns by latitude, altitude, temperature, or precipitation and then hypothesize potential causes. We consider these potential areas for future research.

## PHYSIOGRAPHY: STREAMS, WETLANDS, AND LAKES ACROSS ABIOTIC GRADIENTS

Abiotic factors structuring freshwater biota vary across broad scales. We characterize freshwater systems across abiotic gradients known to be important drivers of ecosystem structure and function. Those abiotic characteristics can also drive ecological and evolutionary processes predictably over broad spatial scales. In this section, we evaluate and synthesize spatial gradients of

geomorphic, climatic, hydrologic, and other physiographic characteristics of lentic and lotic systems. These sections form the basis of the subsequent discussion on how climate can drive biotic processes to lead to unique freshwater biomes.

### Temperature

Temperature controls metabolism of individual organisms, ecosystem rates, the balance between actual and potential evapotranspiration (a determinant of runoff to freshwaters), and other physical factors of habitats (e.g., lake stratification, extent and duration of ice cover, dissolved oxygen levels). Daily and seasonal water temperature extremes of freshwater systems vary predictably with climate (Table 1). In smaller water bodies, canopy cover modulates diurnal swings in temperature (create a microclimate, Allen 2016), so given a constant amount of energy input, daily, and seasonal water temperatures will likely be more extreme in grasslands, tundra, and deserts and less extreme in forests (except in deciduous forests during times of no leaf cover).

Elevation and latitude control temperature; tropical systems are warmer (by up to 30°C average temperature), but less variable seasonally. With mean average temperatures of −20°C or less in high latitude systems, water is not liquid for much of the year. Ice formation exerts multiple effects on the ecology and geomorphology of aquatic environments. For instance, shallow habitats in high latitudes and altitudes may freeze completely during winter, allowing only freeze-tolerant organisms to survive. In areas with permanent ice cover, summer thawing may lead to ponds or streams on the surface of the ice that form a unique cold habitat. Ice also influences stratification of lakes and river flows. For example, intense flooding can occur following ice breakup which influences erosional processes, water quality (e.g., temperature, nutrients), in-channel and floodplain vegetation, and which can disturb aquatic organisms such as benthic macroinvertebrates and fishes (Prowse and Culp 2003).

The solubility of oxygen in water is relatively low and declines with increasing water temperatures (Dodds and Whiles 2019). This, combined with greater metabolic rates at higher temperatures (up to a point) and the prevalence of
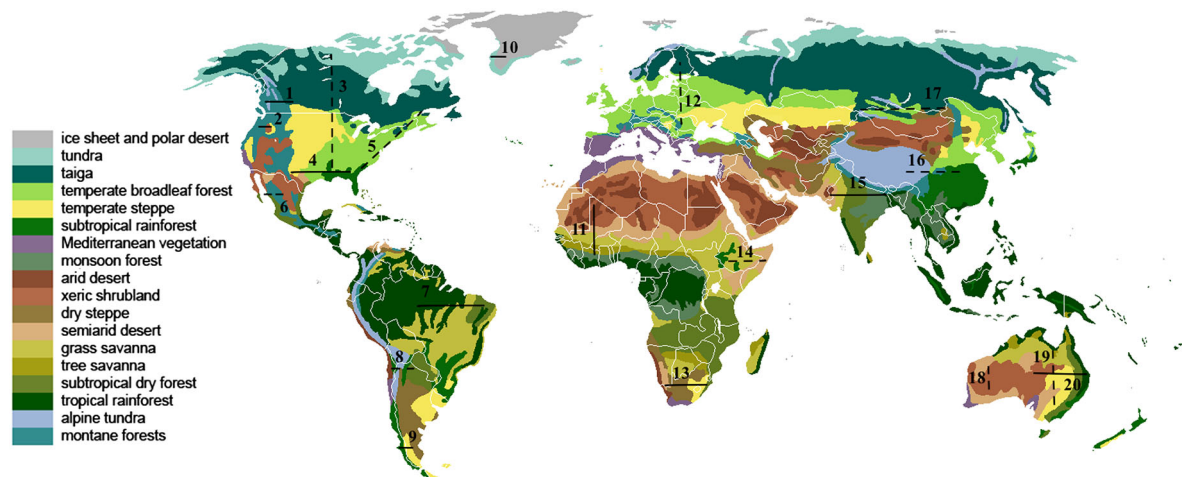
Fig. 1. Twenty transects across varying climate gradients used to investigate patterns across biome gradients. Solid black lines represent precipitation gradients drawn with temperature held relatively constant (10), while dashed black lines represent temperature gradients driven by altitude or latitude (10). Background biome image from https://commons.wikimedia.org/wiki/File:Vegetation.png.

Table 1. Physical and chemical patterns over climate gradients.

| Feature | High altitude | Low altitude | High latitude | Low latitude | Mesic | Xeric |
|---|---|---|---|---|---|---|
| Solar radiation | Higher | Lower | Lower | Higher | Lower | Higher |
| Ultraviolet radiation | Higher | Lower | Lower | Higher | Lower | Higher |
| Monthly irradiance minima | | | Lower | Higher (near tropics) | | |
| Water temperature | Lower | Higher | Lower | Higher | Higher | Lower |
| Water temperature extremes | No trend | No trend | Greater | Lesser | Lesser | Greater |
| Nutrients | Lower | Higher | | | Lower | Higher |
| Salinity | Lower | Higher | | | Lower | Higher |

*Note:* Blank cells are where no pattern is predicted, and no trend is indicated where a direct statistical test indicated no trend (see *Temperature, Light, and Chemistry*).

amictic lakes in tropical climates, means with all things equal, anoxic conditions will develop more frequently in aquatic habitats of warmer climates. However, ice and snow cover can also lead to anoxia, so there will be exceptions to this general pattern. Anoxia alters biogeochemical cycling and survival of many freshwater organisms. Overall, temperature provides an indirect control of ecosystem processes through its effects on metabolic rates and anoxic conditions, and we will discuss these implications more fully in the sections on ecosystem rates.

*Light*

Light fuels aquatic production, warms water, harms organisms in the form of ultraviolet radiation, and controls photolysis rates (Kirk 1994).

Latitude, altitude, cloud cover, and air pollution influence solar radiation. Incoming irradiance, photosynthetically active radiance (PAR), and ultraviolet (UV) light influence heating, photosynthesis, photolysis, and light damage, respectively.

Incoming total irradiance energy is the main force that warms water; it is greatest in tropical regions and least in high latitude regions (Fig. 2). All five of the warm-cold transects from Fig. 1 with varying latitude had a trend of increasing direct normal irradiance as latitude neared 0°. For example, along transect 3, direct normal irradiance at 44.5° latitude was 4.9 kWh·m$^{-2}$·d$^{-1}$, compared to 3.21 at 67.5° latitude.

The influence of elevation on optical atmospheric thinning causes a 50% increase in PAR over a 3 km altitude increase (Barry and Chorley
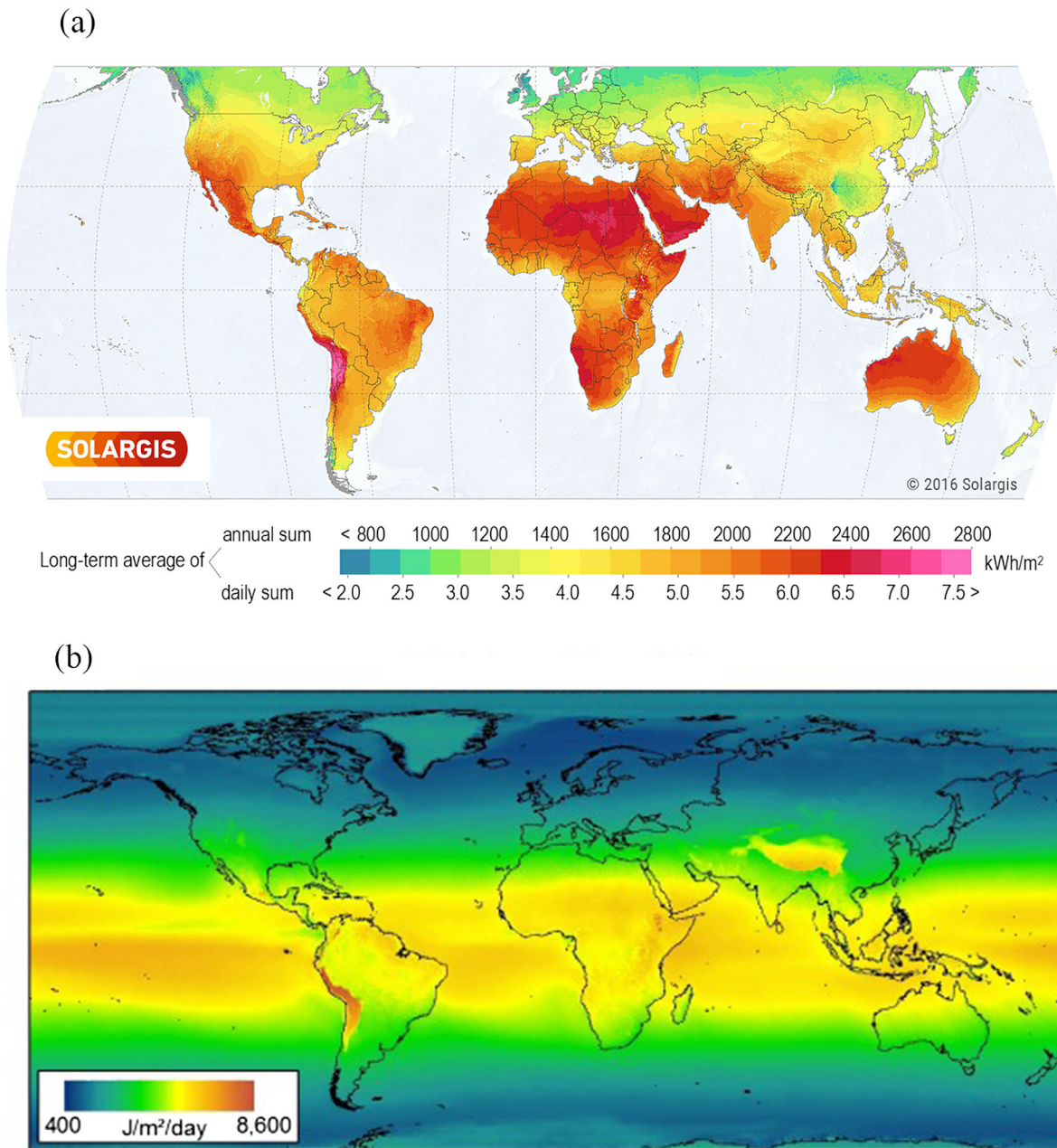
(a)



(b)



Fig. 2. (a) Global map of average daily global horizontal irradiation in kWh/m$^2$ from SolarGIS 2014 GeoModel Solar. Highlights global trends of light availability in terms of latitude and altitude. (b) Global map of annual monthly mean ultraviolet-B radiation (UV-B) from 2004 to 2013 (Beckmann et al. 2014); glUV dataset available at: https://www.ufz.de/gluv/.

2003). Incoming PAR peaks at 20° N latitude rather than at the equator, due to atmospheric moisture (Lewis 2011). Cloud cover decreases PAR and UV radiation (Häder et al. 2015) as is evident in desert areas of Australia, Northern Africa, and Southwest North America (Fig. 2). Photosynthetically active radiance declines dramatically between 20° and 70°.

High levels of UV radiation cause photolysis, which can lead to cell damage and influence chemical properties of freshwater systems. UV radiation exhibits similar latitudinal trends as other forms of irradiance, with around ten times more UV-B in the tropics than in high latitude regions (Fig. 2). Altitude also plays a role, with clear UV maxima in the Himalayan Mountains along the Tibetan Plateau and the Andes on the dry coast of South America, where UV radiation levels are around 6000 J·m$^{-2}$·d$^{-1}$, more than double the UV flux in neighboring lower altitude areas.

Additional climate-driven variables can influence the availability of incoming solar radiation once it reaches freshwater systems. Ice and snow cover influence light availability in rivers, wetlands, and lakes (Wetzel 2001), so high latitude and elevation habitats have lower light seasonally. High inorganic sediment loads can intercept a substantial amount of light. Absorption by dissolved organic carbon (DOC) reduces light availability in freshwaters. In boreal lakes, inputs of DOC increase with latitude, in turn decreasing the penetration of PAR and UV radiation in the water column during summer months (Pienitz and Vincent 2000). Paleolimnological studies of subarctic lakes indicate minimum light availability and smaller UV/PAR ratios occurred during periods of maximum vegetation coverage and higher DOC (Pienitz and Vincent 2000). Finally, in small streams, small wetlands, and forested wetlands, tree canopy can intercept light. Thus, regions of forest may have more shading than grassland, desert, or tundra regions.

*Geological processes*

Major geological processes forming river and stream networks are somewhat different from those forming wetlands and lakes, though some processes are shared (e.g., oxbow lakes and riparian wetlands). Rivers and streams form as water drains to lower topography, driven by tectonics and erosion, although glacial outburst phenomena can set river courses at temperate and higher latitudes (e.g., Waitt 1985). Fluvial geomorphologists classify streams based on morphological characteristics such as formative discharge, dominant sediment type and load, valley characteristics, and channel dimensions and profile (Leopold and Wolman 1957, Schumm 1977,

Rosgen 1996), and these characteristics all vary with changes in precipitation and seasonality.

Valley characteristics such as confinement, slope, lithology, and soils, which are functions of elevation, drive material sorting and channel pattern (Table 2). Slope and available sediment control the dominant sediment transport mechanism of streams, which can influence network structure. A global assessment indicates steeper slopes are related to narrower and less sinuous rivers and there are more rivers in areas with lower slopes (Frasson et al. 2019).

In general, bedload transport is prevalent in upland streams of steep slopes while suspended load transport dominates in lowland rivers (Church 2006). Therefore, transportable material at higher elevations tends to be cobble- to boulder-sized rock of colluvial origin, while finer materials of alluvial, eolian, lacustrine, and/or glacial origin dominate at lower elevations. Channel pattern is expected to evolve from straight to braided and/or sinuous (Leopold and Wolman 1957), while transportable bed material size decreases moving from small, higher elevation streams to large, low elevation rivers (Church 2006). Channel form generally follows a precipitation gradient; braided channels with a high sediment load and width-to-depth ratio are expected to be more prevalent in drier climates than wet ones, holding elevation constant (Dodds et al. 2015). Based on these generalizations, unstable channel forms should be more common in regions of low elevations and/or precipitation.

Wetlands occur where shallow water permanently or periodically inundates the land surface and are especially common where depth to groundwater is shallow and local geomorphology allows for positive surface water balance (Fan et al. 2013). Wetlands form from processes such as glacial scarring, tectonic interaction, succession from small lakes, and sediment input from rivers (Tooth and Viles 2014). Glacial depressions are associated with wetlands in higher latitudes and altitudes. Therefore, wetlands in more arid, lower latitude regions (uninfluenced by Pleistocene glacial cover) usually have longer formation histories (Tooth and McCarthy 2007). Arid wetlands are more dependent on surface flow as a source of water than humid wetlands and therefore should have

Table 2. Variation of geomorphological attributes of freshwater systems across gradients of precipitation and temperature driven by elevation and latitude.

| Feature | High altitude | Low altitude | High latitude | Low latitude | Mesic | Xeric |
|---|---|---|---|---|---|---|
| River slope | High gradient | Low gradient | | | | |
| Dominant transport mechanism | Bedload | Suspended | | | | |
| Transportable material | Larger | Finer | | | | |
| Turbidity (concentration) | Low | High | | | Lower | Higher |
| Channel pattern | Straight, braided | Sinuous, braided | | | More sinuous | More braided |
| Sediment load variability | Greater† | Smaller† | Smaller† | Greater† | Smaller | Greater |
| Stream width-to-depth ratio | Smaller | Greater | | | Smaller | Greater |
| Stability of channel form | Greater stability | Less stability | | | Greater stability | Less stability |
| Formation history | Shorter | Longer | Shorter | Longer | Shorter | Longer |

Note: Blank cells are where no general expected pattern is predicted.
† Over the last 1000 yr (see Dearing and Jones 2003).

longer periods of desiccation and higher levels of sedimentation. Across global gradients, we expect increased dependence on local physical topography in wetland formation with decreasing precipitation, as deeper depressions are required to meet the top of the water table.

Major processes that form wetlands and lakes include tectonic, volcanic, landslide, glacial, dissolution, fluvial, eolian, beaver dammed, coastal, and meteoric (Hutchinson 1957). Jackson et al. (2014) followed Hutchinson's synopsis of lake formation and provided a modified geomorphic classification of inland freshwater wetlands. Fluvial wetlands include stream and river floodplain wetlands, as well as beaver wetlands. Lacustrine wetlands occur at lake fringes and drying lakes. Glacial wetlands include bogs, fens, tundra, potholes, and kettles. Groundwater wetlands include dissolution and low-lying coastal plain depressions. This leaves miscellaneous inland depressions such as wind-carved playas, paleomarine depressions, buffalo wallows, and anthropogenic. The distribution of lake sizes is still not well understood as a function of climate and topography, though progress is being made on this front (Steele and Heffernan 2017).

Of these lake and wetland formations, tectonic, volcanic, coastal, dissolution, and meteoric are not closely related to broad biogeographic patterns of climate, but others in Table 3 are either directly or indirectly. Coastal formations are mainly prevalent at low elevations, and glacial depressions predominate at high latitudes and/or high altitudes. Wind-scoured depressions are more common in drier areas where vegetative cover is less likely to inhibit eolian erosion. Landslide lakes are more common in areas with steeper topography (with high local elevations), and fluvial lakes and wetlands are more abundant in areas with higher densities of large rivers.

*Hydrology*

Regional climate and geology control hydrology and maintain all freshwater ecosystems. Direct precipitation, surface runoff, and groundwater are the main sources of water that feed into freshwaters. The dominant timing and form (rain or snow) of precipitation can greatly affect water availability, phenology, and intensity of effects on freshwater systems (Table 4). For all aquatic environments, depth to groundwater is a crucial aspect dictated by climate and is particularly important in dry areas. In high altitude or latitude areas, permafrost strongly limits depth to groundwater (Fan et al. 2013).

Flow patterns in streams correlate to the terrestrial biomes in which they are embedded (Dodds et al. 2015). The flow regime of streams and rivers shifts from ephemeral and flashy to more stable, groundwater-fed, perennial systems as precipitation increases, though floods still occur in mesic areas (Poff 1996, Ullrich et al. 2010). Snowmelt influences flow in high latitude or altitude areas. Mountain ranges may affect climate, inducing a rain-shadow effect on the leeward side of the range. For example, habitats found on the leeward side of a mountain range may be more ephemeral or intermittent near the range,

Table 3. Variation of hypothesized attributes related to lake and wetland formation across climate gradients.

| Feature | High altitude | Low altitude | High latitude | Low latitude | Mesic | Xeric |
|---|---|---|---|---|---|---|
| Glacial depressions | More | Less | More | Less | | |
| Wind-caused depression | | | | | Less | More |
| Landslide lakes | More | Less | | | | |
| Fluvial lakes and wetlands | Less | More | | | More | Less |
| Coastal/lakeshore | Rare | More common | | | | |

*Note:* Blank cells are where no general expected pattern is predicted.

Table 4. Gradients related to hydrology over climate gradients driven by precipitation, altitude, and latitude.

| Feature | High altitude | Low altitude | High latitude | Low latitude | Mesic | Xeric |
|---|---|---|---|---|---|---|
| Flow regime | Ephemeral on leeward side, perennial on windward side, snowmelt | Variable | Snowmelt | Stormflow | More stable, groundwater-fed, perennial | Ephemeral and flashy |
| Primary water source (wetlands) | Snowmelt | Precipitation | Snowmelt | Precipitation | Precipitation | Groundwater discharge, flow from nearby high altitude areas |
| Evapotranspiration | Lower | Higher | Lower | Higher | | |
| Actual: potential evapotranspiration | Lower | Higher | Lower | Higher | >1 | <1 |
| Seasonal variation in inundated surface area | | | Higher | Lower | | |
| Mixing and stratification | Mono- or dimictic | Variable depending on latitude | Mono- or dimictic | Amixis (tropical) | | |
| Depth to groundwater | Shallow (permafrost, shallow soil) | Variable | Shallow (permafrost, shallow soil) | Variable | Shallow | Deep |
| Spatial connectivity | | | | | Higher | Lower (closed basins, intermittent river networks) |

*Note:* Blank cells are where no general expected pattern is predicted.

shifting to more perennial systems at lower elevations further away from the range, while on the windward side, flow regime is expected to be perennial, regardless of elevation.

Wetland character is determined by the dominant sources of water (direct precipitation, surface flow, and/or groundwater; Brinson 1993). These sources control chemistry and hydroperiod or hydropattern (i.e., the general seasonal pattern of surface water inundation, Jackson et al. 2014). Thus, climate and biome gradients will dictate regional wetland character. For example, in humid climates, groundwater discharge into wetlands contributes to local hydrology, but direct precipitation and surface flow dominate (Prigent et al. 2007, Tooth and McCarthy 2007). In contrast, arid climates have fewer wetlands, which are typically sustained by groundwater discharge (e.g., spring-associated ponds, pans) or flowing surface water (e.g., fluvial wetlands). While occasional intense rains may cause floods, these events will be ephemeral, and usually insufficient to create conditions characteristic of wetlands such as hydric soils and obligate wetland biota (Keddy 2000). Arid wetlands are prone to prolonged desiccation

(Tooth and McCarthy 2007, Tooth and Viles 2014). In semi-arid climates, wetland habitat will be predominantly associated with seasonal river flooding rather than precipitation or groundwater. Along altitude gradients, precipitation drives water tables at low elevations, whereas high-elevation wetlands are more temporally stable due to snowmelt (Millar et al. 2017). We expect similar relationships with increasing water depth in wetlands with decreasing latitude (Jiménez-Alfaro et al. 2014).

Evapotranspiration is a universally important process of water loss from wetlands, varying strongly with climatic conditions (Brinson 1993, Kroes and Brinson 2004), as the balance of potential and actual evapotranspiration rates control surface flow and groundwater discharge. Emergent and adjacent macrophyte transpiration most strongly affects wetlands but can influence streams and small ponds, making the link to terrestrial biomes especially strong. Evaporation varies across temperature and humidity gradients, with potential rates being greatest in hot, dry climates, and least important in cool, humid climates. Terrestrial biome type (e.g., presence or absence of trees) will control transpiration rates, with direct influences on hydrology. For example, flooding is not completely controlled by seasonal changes in precipitation, but instead can be driven by changes in evaporation and tree transpiration rates, both of which decline in winter, allowing rivers to fill and spill into adjacent floodplains (Benke et al. 2000). These same changes also affect how much water accumulates on floodplains from direct rainfall and groundwater discharge.

Precipitation can drive inundation directly or indirectly. In warm regions, monsoonal precipitation cycles can directly cause seasonal flooding. In contrast, inundation of boreal wetlands (where snowmelt is a major water source) has little correlation with the timing of snowfall, but rather the total magnitude and pattern of warming. In humid regions like the Pantanal or Amazon Basin of South America, inundation dependence of riverine wetlands on precipitation increases with distance from the river channel. The Pantanal inundation depends upon a seasonal cycle of precipitation, but downstream areas of wetlands may lag by 6 months from periods of peak rainfall (Hamilton 2002). Across

latitudinal gradients, seasonal variation in wetland surface area increases with distance from the equator (Prigent et al. 2007).

Lakes (except saline lakes in closed basins) are less responsive to climatic fluctuations with respect to hydrology compared to streams and wetlands, but some hydrologic attributes of lakes are linked to climate, elevation, and latitude. For example, a key controlling factor of seasonal cycles and biogeochemistry in lakes is the extent and frequency of mixing and stratification (Dodds and Whiles 2019). Temperate to high altitude or latitude lakes will not mix when there is ice cover and may not stratify in the summer; therefore, mixing may only occur once (monomictic) or twice (dimictic) per year. Tropical lakes are susceptible to biogenically induced amixis (never mixing). In this case, continuous primary production in the surface waters results in organisms sinking into the profundal zone and releasing salts on decomposition, leading to higher density of the deeper waters. The biogenic activity leads to a relatively permanent state of stratification. All of the factors controlling stratification could be influenced by climatic fluctuations.

### Sediment

Incoming sediment size and load affect morphological characteristics of all freshwater systems, as well as biology and water quality. Bed material sediment size tends to decrease with decreasing elevation (Church 2006). Based on the transportable sediment available and the dominant sediment transport mechanism (Church 2006), turbidity is expected to be greater in lowland rivers where suspended load transportation dominates, vs. in steeper streams of higher elevations.

Sediment load depends on watershed sources and sinks, both of which can vary considerably over space and time. A global study conducted by Dearing and Jones (2003) using 100- to 1000-yr-old sediment records from various lakes and seas found the relative magnitude of change between the minimum sediment accumulation rate ($S_{min}$) and the maximum rate ($S_{max}$) varied along both elevation and latitudinal gradients. The dimensionless ratio $S_{max}/S_{min}$ indicated the greatest variance in accumulation in regions of high elevations, low latitudes, and/or small

drainages. However, these sediment load generalizations developed over temperature gradients may vary significantly when assessing different time scales.

Assessing sediment concentration and loads over a precipitation gradient is less complex. In general, sediment concentration should be higher in semi-arid and arid regions due to more surface exposure and, as a result, erosional events. For example, rivers in United States desert and Mediterranean biomes have roughly 3–12 times greater mean sediment concentrations than those from forested regions (Dodds and Whiles 2004). However, sediment load is generally proportional to discharge, so load should be greater in more mesic areas; Table 2 summarizes these sediment characteristics.

Characteristics of sediments can also depend upon climate. In dry regions, surface soils have lower organic carbon content than more mesic biomes (Jobbágy and Jackson 2000). Thus, sediments entering aquatic systems in drier areas are expected to have a higher inorganic content. The organic content of allochthonous sediment can strongly influence biota (Whiles and Dodds 2002).

### Chemistry

Nutrient concentration trends may vary across climatic gradients as nutrient ecoregions tend to have variable expected baseline nutrient concentrations (Smith et al. 2003). Dodds et al. (2015) hypothesized nutrient concentrations would generally be low in biomes where terrestrial vegetation is dense and moderately higher in deserts due to an increase in erosion potential. Nitrogen concentrations in undisturbed tropical watersheds are about five times greater than in similar temperate watersheds, but this is enigmatic as some also claim higher rates of denitrification to be characteristic of the tropics (Downing et al. 1999).

Climate has no clear relationship with the balance between N and P availability in freshwater. Elser et al. (2007) found little support for latitudinal variation in the autotrophic production response to nutrient enrichment. However, we have relatively few data from the tropics or arctic systems and comprehensive analyses may uncover trends with climate. Dodds and Smith (2016) noted considerable variance in total N to total P ratios at reference concentrations across ecoregions of the United States, suggesting that stoichiometric nutrient supply might link to biome.

Turner et al. (2003) documented dissolved silicate to dissolved nitrate ratio is a sensitive indicator of aquatic food web health and harmful algal blooms. Their analysis of silicate and nitrate concentrations in the world's largest rivers (37% of Earth's watershed area) indicated dissolved silicate yield increases with increasing runoff (i.e., following a precipitation gradient) but is not dependent on temperature. Thus, we expect silicate yield not to depend on latitude or altitude except as they influence precipitation.

Saline lakes are one habitat in which climate has a strong influence on chemistry, which influences biological and physical properties (Hutchinson 1957; Table 1). Saline waters are common in dry climates because terminal lake formation is possible when evaporation equals rates of input. Saline lakes can have unique chemical characteristics including high nutrient content, and chemistry depends upon the geology of the areas feeding them. Saline waters can demonstrate greater capacity for stratification, as dissolved salts have a greater influence on water density than temperature, and areas with saline waters are likely to have waters of highly contrasting salinities. Salinity has a strong influence on the types of organisms that can persist.

### Distribution, density, and size of habitats

The density and size of freshwater habitats can influence species dispersal and diversity, and other aspects of connectivity. Climate gradients obviously influence density of freshwaters (Table 5). Density is highest in wet areas, depending on geology. High-latitude areas have high densities of wetlands because evaporation rates are low and permafrost limits infiltration (Fig. 3). Continental ice sheets also flattened large areas while leaving behind many depressions that became lakes and wetlands. This is apparent in boreal and arctic latitudes of the Northern Hemisphere (45–75° N), which have the highest densities of lakes (Verpoorter et al. 2014).

Even though wetlands are abundant at high latitudes, wetlands are also widely dispersed throughout the tropics in lower latitudes (Fig. 3; Mitsch et al. 2009, Fan et al. 2013, Gumbricht

Table 5. Patterns of distribution, density, and habitat size of streams, wetlands, and lakes across climate gradients.

| Feature | High altitude | Low altitude | High latitude | Low latitude | Mesic | Xeric |
|---|---|---|---|---|---|---|
| Drainage density | | | Lower | Higher | Higher | Lower |
| Perennial stream density | Lower | Higher | No trend | No trend | Higher | Lower |
| Wetland and lake density | Lower | Higher | Higher | Lower | Higher | Lower |

*Note:* Blank cells are where no pattern is predicted, and no trend is indicated where a direct statistical test in this paper or one cited in the text indicated no trend (see *Distribution, density, and size of habitats*).

et al. 2017). Wetland density is high in mesic areas and increases with decreasing elevation because riparian wetlands follow many large rivers (e.g., the Amazon) and flood plains are wider where there is little topographic relief (Tooth and Viles 2014). In arid climates, river inflows and local physical topography (i.e., tectonic depression and windblown sediments) promote surface water retention and therefore support wetland formation.

We used global data for delineated stream networks (Appendix S2) to assess the distribution of rivers across all continents except Antarctica. The number of rivers within an area generally decreased as temperature increased (Fig. 4). Area-corrected densities of flowing water increased with distance from the equator.

Perhaps this is related to increased temperatures and evaporation as well as drier conditions at 30° north and south of the equator driven by Hadley cells, coupled with potential underestimation of river density in wetter tropical areas. There appear to be slightly more streams per unit area in higher latitude areas of the Northern Hemisphere (Fig. 4). Rivers are relatively evenly distributed across the Southern Hemisphere, while in the Northern Hemisphere, the highest and most variable densities of streams are found around 50–60° N (Fig. 4). Interestingly, we found no clear trends between the density of rivers and elevation or precipitation at a global scale (Appendix S2). This could be an artifact of our method to extract densities, which does not take into account stream size or water volume.
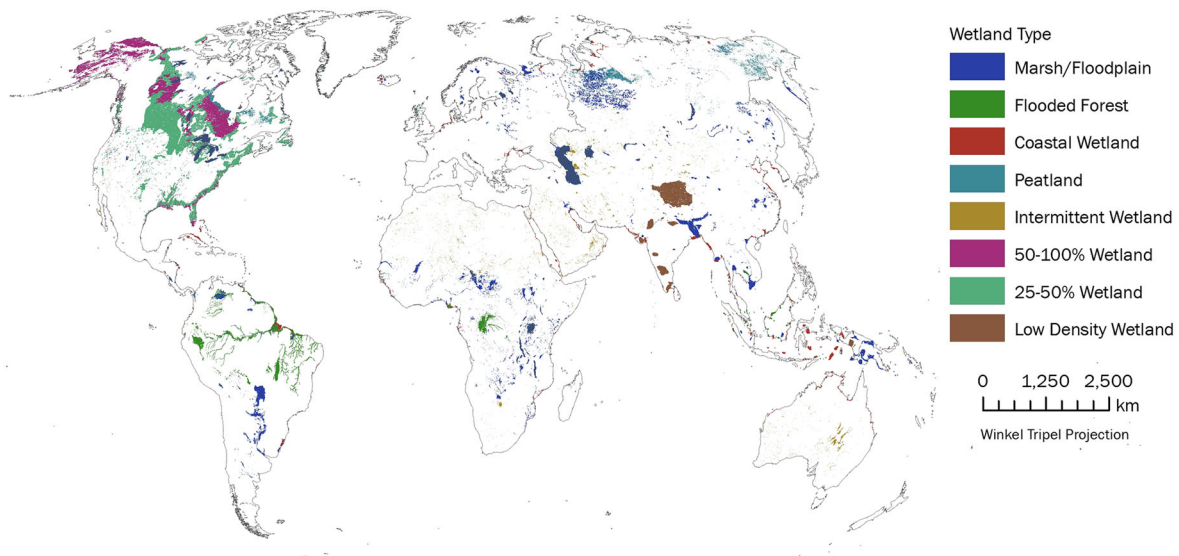


Fig. 3. Global distribution of different types of wetlands. Spatial data were compiled from multiple sources by Lehner and Döll (2004). Because wetlands can exhibit seasonal variations in extent, boundaries are difficult to delineate. Wetland classifications containing percentages therefore represent the proportion of wetland within the area based on extents defined by multiple data sources.
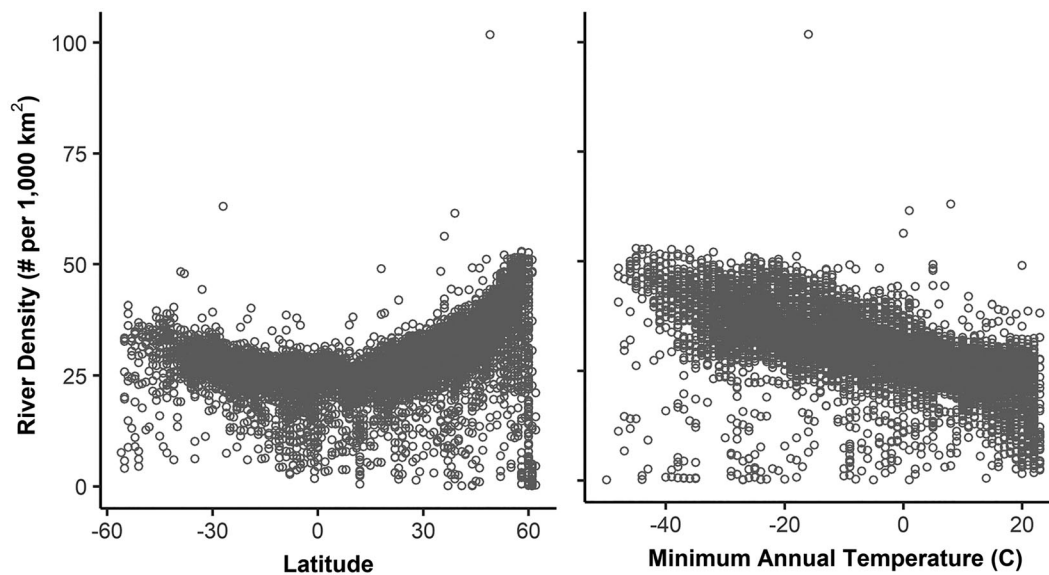
Fig. 4. Distribution of number of river segments within 1000-km$^2$ grids distributed globally in relation to latitude and temperature. Spatial data were obtained from Lehner et al. (2008; rivers) and Fick and Higmans (2017; temperature).

Small streams (1st order) contribute most to the length of rivers globally, while moderate-sized rivers (5th–9th order) contribute most to stream area (Downing et al. 2012). Bifurcation ratios (Leopold 1962, Welcomme 1976) predict the size distribution of rivers to be similar globally, even across regions with different climates. Downing et al. (2012) compared the size distribution of rivers in the United States and Africa and found similar ratios of stream area to land area between the two continents (0.56% and 0.30%, respectively). They concluded that the proportion of area covered by rivers is small (less than 1%) regardless of geographic region. These comparisons were made at very broad scales (continents), and they were not specifically designed to capture precipitation and temperature gradients.

Verpoorter et al. (2014) found a general decreasing trend of lake density, area, and perimeter, from north to south across the globe. Similar to patterns of wetlands, lake densities are highest in boreal and arctic latitudes of the Northern Hemisphere (45–75° N, Appendix S2). The low total number of lakes in the Southern Hemisphere in part relates to lower proportion of land mass relative to the Northern

Hemisphere. We found even when correcting for land area, a greater proportion of terrestrial area was covered by lake habitats in the Northern Hemisphere relative to the Southern Hemisphere, although a peak in lake coverage exists just below the equator (Fig. 5). This high density of lakes at high latitudes is likely due to the large number of glaciated lakes in those regions. The area covered by lake habitats also decreases with increasing elevation. Over half of the global density, perimeter, and area of lakes is located at elevations lower than 500 m above sea level (Verpoorter et al. 2014). While lake density and size decrease with increasing temperature across elevation and latitudinal gradients (Appendix S2), our analysis of global lakes indicated the highest proportion of lake surface area/total land area was found at intermediate levels of precipitation (Fig. 5).

Although we classify freshwater habitats into lakes, rivers, wetlands, these different habitats interact with one another to form mosaics of freshwater habitat. The summed connectivity of these different habitats may be important for both ecological and evolutionary phenomena. We combined global datasets of freshwater distributions (Appendix S1) to assess patterns of
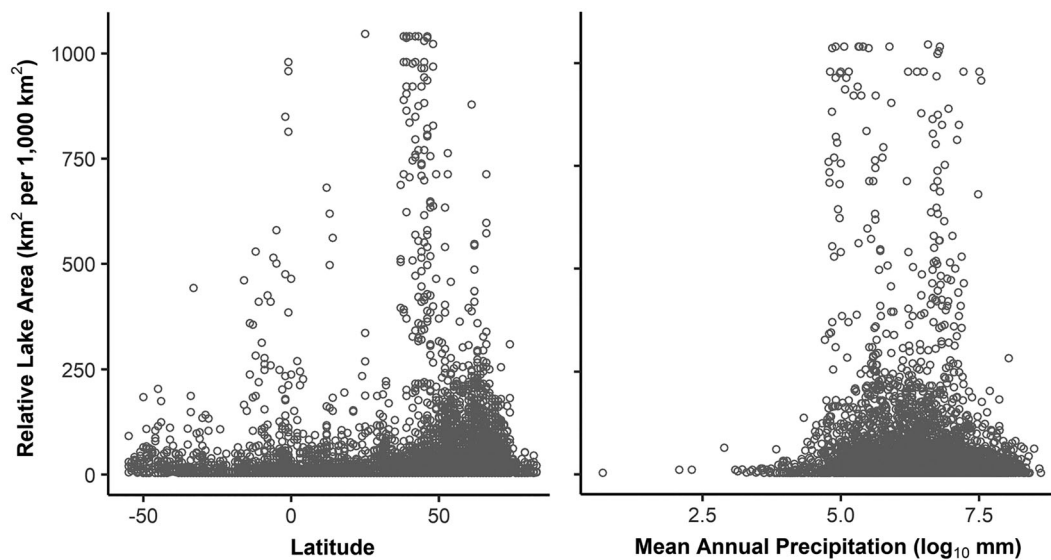
Fig. 5. Total surface lake area within 1000-km$^2$ grids distributed across the globe in relation to latitude and precipitation. Lake area data were obtained from the Global Lakes and Wetlands Database (Lehner and Döll 2004) and temperature data from Fick and Higmans (2017).

hydrologic connectivity across temperature and precipitation gradients globally (analysis described in Appendix S2). We used patch cohesion values of small landscapes (10,000 km$^2$) across the globe to compare connectivity of all freshwater habitats. Patch cohesion measures the physical connectedness of freshwater habitat patches by relating the perimeter of freshwater patches to the total area of freshwater habitat within each sub-landscape unit (Gustafson 1998). Higher values indicate more connectivity or aggregation of freshwater habitats within a landscape, while lower numbers indicate freshwater habitats are dispersed and fragmented across the landscape. Our analysis indicated higher connectivity within landscapes at latitudes around 50° and around the equator (Fig. 6). Connectivity was greatest at intermediate elevation and precipitation levels. Overall, the large area of lakes and wetlands in the Northern Hemisphere and around the equator drive connectivity across large (latitudinal) temperature gradients, although we see the highest connectivity at high temperatures (Fig. 6). In wetter climates, where streams have a high drainage density (i.e., channels per unit area), there is a greater probability that wetlands and lakes will be linked by flowing water, and wetlands and lakes will also tend to have greater

numbers per unit area (with less distance between them).

Glaciation can lead to relatively sharp patterns of connectivity. Similar to our analysis, Fergus et al. (2017) analyzed lake, wetland, and stream connectivity at the southern extent of glaciation of Eastern North America. They found areas that had been covered by the continental ice sheet had more connected lakes and wetlands. Areas immediately south of the glaciation had less connected wetlands and lakes but more connected streams and rivers.

## Biotic Characteristics Across Biome Gradients: What Is a Freshwater Biome?

Plant architecture and productivity are the key features of terrestrial biomes. Dominant plant types (e.g., type of macrophytes or phytoplankton) might connect less strongly to aquatic than to terrestrial habitats across climate gradients as water limitation is a key determinant of plant productivity and form in terrestrial environments. Emergent plants in wetlands follow climate patterns (e.g., short stature or mosses at high altitudes or latitudes), but trends in other producers (e.g., periphyton, submerged macrophytes) may tie less closely to climate as we
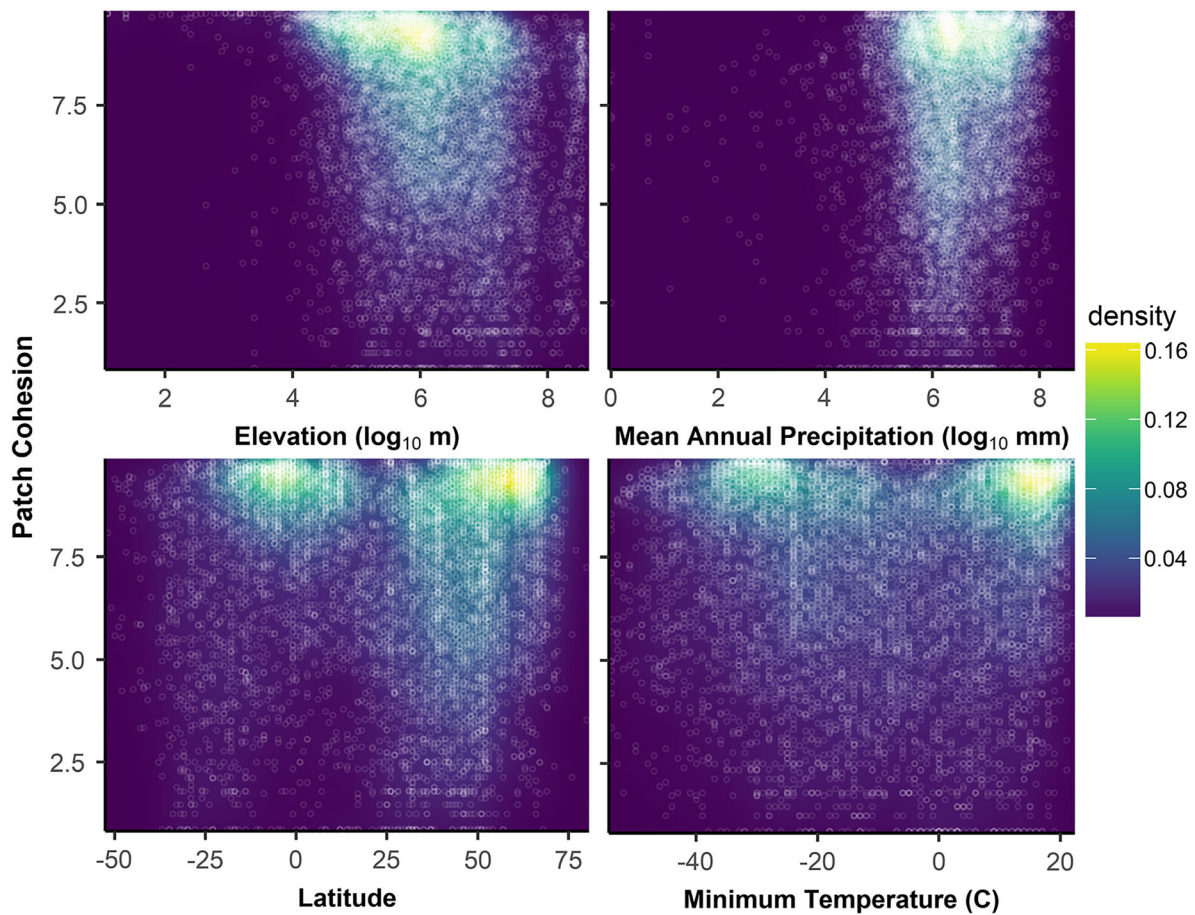
Fig. 6. Patch cohesion, a measure of connectivity, of all freshwater habitats across the globe varied across global gradients of elevation, precipitation, latitude, and temperature. White dots represent individual landscapes (1000 km$^2$), and heat map colors represent the density of landscape exhibiting given values of patch cohesion and latitudes. Higher values of patch cohesion represent greater degree of connectivity between freshwater habitat patches. Freshwater spatial data were combined from Lehner and Döll (2004) and Lehner et al. (2008), and climate data were obtained from Fick and Higmans (2017). See Appendix S2 for geoprocession explanation.

discuss below. Thus, any categorization of freshwater biomes may require consideration of variables in addition to the plant physiognomy that forms the primary basis of terrestrial biome classification. Such variables could include ecosystem rates in addition to productivity, community architecture, or functional types or diversities of primary producers and other organisms. Here, we consider how climatic gradients influence predictability of these potential variables. We consider primary producers, invertebrates, and vertebrates in this context as well as other

biological characteristics such as ecosystem rates, food chain length, and trophic state.

### Ecosystem rates

Gross primary production (GPP), ecosystem respiration (ER), and their balance, net ecosystem production (NEP), are fundamental ecosystem rates that control biogeochemistry as well as system productivity. The balance between GPP and ER indicates the primacy of autochthonous or allochthonous carbon sources and potential energy pathways in the system. These can be

influenced by climate, as well as additional ecosystem processes, such as nutrient uptake and retention (Table 6).

*Gross primary production.*—Stream GPP increases with temperature and latitude (Bernot et al. 2010). This is likely due to indirect and confounding variables, including light availability (discussed in *Light*). The rates of GPP in streams across biomes are discussed in more detail elsewhere (Dodds et al. 2015, Bernhardt et al. 2018). Bernhardt et al. (2018) suggest that position in the river continuum is potentially a more important control on metabolism than the biome the river is embedded in.

In wetlands dominated by emergent vegetation, light or nutrients likely limit GPP, so latitude, altitude, and cloud cover could limit production of emergent vegetation. Temperature and length of growing season are also important drivers of wetland plant production. Middleton and McKee (2004) considered factors limiting bald cypress production across about 10 degrees latitude. Cold temperatures and shorter growing seasons limited production at higher latitudes while respiration and water loss limit production at lower latitudes, making the relationship between latitude and production curvilinear. Brinson et al. (1981) found a similar curvilinear relationship with wetland net biomass production. Lowest biomass production occurred in wetlands in southern Florida (lowered fertility) and northern Canada (lower temperatures). Northern ombrotrophic (deriving nutrients from atmospheric moisture) bogs had minimal nutrient availability or water flow and were lowest in biomass production.

At constant temperature, important influences in biomass production include water availability, water flow, and nutrient availability. Brinson et al.'s (1981) expansive freshwater wetland study indicated the importance of moisture gradients to wetland GPP. In forested wetlands, GPP was higher in floodplain forests (which had high nutrients and water levels) than in shallow cypress ponds (reliant mostly on precipitation). In non-forested wetlands, GPP was greatest in riverine marshes and lowest in stagnant, nutrient-poor wetlands. Overall, GPP was greater in non-forested wetlands than in forested wetlands. Unlike most terrestrial systems, bryophytes can contribute significantly to overall ecosystem productivity of wetlands (Brinson et al. 1981, Peregon et al. 2008). *Sphagnum* mosses exhibit strong correlations with climate gradients; growth and productivity are positively correlated with increased temperature and precipitation. Climate variables affect herb or shrub production less directly, with productivity being influenced more by water levels. Shrubs can grow better in shallower water, while herbs and grasses are more productive under deeper water conditions (Thornman and Bayley 1997).

Many factors could influence broad biogeographic patterns of GPP in lakes, but light is a key variable (Lewis 2011). Light interacts with nutrient concentrations to drive the magnitude and temporal variability of GPP. Across 7500 lakes globally, daily GPP rates in Northern

Table 6. Ecosystem rates as they vary over climate gradients driven by precipitation, altitude, and latitude.

| Feature | High altitude | Low altitude | High latitude | Low latitude | Mesic | Xeric |
|---|---|---|---|---|---|---|
| Ecosystem respiration | Lower | Higher | Lower | Higher | Higher | Lower |
| Gross primary production | | | | | Higher | Lower |
| Net ecosystem production | | | Lower | Higher (near tropics) | Lower (in small systems, more riparian canopy light interception) | Higher (in small systems, less riparian light interception) |
| Wetland primary production | Lower | Higher | Lower | Higher | | |
| Sphagnum production | | | | | Higher | Lower |
| Wetland net ecosystem production | Higher | Lower | Lower | Higher | | |
| Wetland pH | | | Lower | Higher | Lower | Higher |

*Note:* Blank cells are where no general expected pattern is predicted.

Hemisphere temperate lakes increased with increased surface irradiance, whereas daily GPP in tropical lakes decreased with increased light availability due to photoinhibition (Staehr et al. 2016). Greater irradiance warmed lakes and weakened thermal stratification in tropical lakes relative to temperate lakes (Lewis 1996). Warmer temperatures combined with more efficient nutrient cycling and less variable solar irradiance make primary production twice as high in tropical lakes relative to temperate lakes (Lewis 2011).

*Ecosystem respiration and decomposition.*—Ecosystem respiration can indicate heterotrophic activity in addition to respiration by primary producers. Many freshwaters are net heterotrophic and have more allochthonous than autochthonous carbon input (Dodds and Cole 2007). In general, respiration rates respond to temperature similarly across terrestrial, marine, and freshwater lakes and rivers (Yvon-Durocher et al. 2012). Young et al. (2004) proposed leaf decomposition and metabolism as priority functional ecosystem indicators, as they collectively represent the autochthonous and allochthonous basis of freshwater food webs and energy systems. Decomposition has been studied more in streams, but trends are likely to apply to wetlands and lakes. In general, decomposition rates of litter in streams increase as latitude and lignin content drop and temperature, precipitation, and nutrient availability rise (Zhang et al. 2008, Boyero et al. 2016). Leaf decomposition rate is also driven by litter quality (LeRoy and Marks 2006) and is therefore likely to vary among terrestrial biomes with different vegetation inputs. Leaf decomposition rates increase by 5–21% with a 1–4°C increase in temperature based on broad-scale meta-analysis (Follstad Shah et al. 2017). This increase is less than expected from metabolic theory but leads to substantial expected differences in rates from high latitude to the tropics. Supporting this, Tiegs et al. (2019) report an impressive experiment using constant substrata type to measure decomposition that demonstrated higher rates of decomposition at lower latitudes.

Ecosystem respiration in streams largely increases with increasing temperature and decreasing altitude (Mulholland et al. 2001, Dodds et al. 2015). In streams, ER appears to be largely unconnected from precipitation gradients because of metabolic compensation, with aquatic primary producers dominating when canopy cover is low (discussed in Dodds et al. 2015).

Woody inputs to freshwater systems may also be important both with respect to respiration rates and as habitat for freshwater animals. Across terrestrial biomes, woody vegetation is associated with humid climates, so woody debris input is greatest in regions of high precipitation. Tree canopy cover, and thus large woody debris input, can also vary across gradients of temperature and light availability, but is strongly associated with certain terrestrial biomes. Obviously, large woody debris input to rivers, wetlands, and lakes will be greatest in forested biomes and less in grasslands, tundra, and semi-arid to arid deserts.

*Net ecosystem production.*—Freshwater mesocosm experiments suggest warmer habitats will have lower net ecosystem production because respiration rates are more strongly influenced by temperature than GPP (Yvon-Durocher et al. 2010). This result was verified for streams using instream measures of metabolism across a wide array of biomes (Song et al. 2018). The later measurements included organisms adapted to the streams that were investigated, circumventing a potential criticism of the mesocosm experiments.

A few studies indicate wetland NEP increases with elevation. Millar et al. (2017) found NEP was positively correlated with water table depth and negatively correlated with air temperature. At higher altitudes, wetlands are less dependent on rain, due to increased ice and snowmelt. Additionally, Lovell and Menges (2013) also found soil moisture across a modest elevation gradient to be the primary factor controlling growth patterns of wetland plants.

Any factor that limits light to aquatic habitats could decrease NEP. For example, greater inorganic turbidity in desert areas could limit production. Cloudy areas, areas with highly tannic waters (dystrophic), dense canopy cover, and prolonged ice cover can all decrease NEP.

*Other metabolic rates.*—Nitrogen cycling rates in streams do not vary predictably across climate gradients as indicated by broadly geographically distributed stream isotopic tracer measurements. Tank et al. (2018) found no relationship between ammonium uptake rates and temperature for streams, indicating limitation by other factors. Mulholland et al. (2009) found little evidence for

temperature effects on stream denitrification rates across temperate biomes.

Turetsky et al. (2014) found many factors influenced methane release from wetlands as based on analysis of data from 71 northern, temperate, and subtropical wetlands. Permanently, wet areas had emission rates influenced by the capacities of plants to transport methane from sediments to the atmosphere. In wetlands that dried, which predominate in drier climates, hydroperiod and temperature were key controlling factors.

Lewis (2002) suggests rates of denitrification are substantially greater in tropical than temperate lakes. In lakes that stratify, the greater hypolimnetic temperatures and prolonged periods of stratification make depletion of dissolved oxygen more rapid and more likely, leading to conditions that favor denitrification. Presumably, similar arguments would apply to methanogenesis in lakes, so rates are likely greater in tropical than temperate lakes.

### Trophic structure

Some aspects of food web structure that might be influenced by climatic gradients include trophic cascades, food web complexity and stability, and food chain length (Table 7). However, many of these are insufficiently cataloged to generalize across biomes. In very harsh habitats (including high salinity habitats and the freshwaters of Antarctica), multicellular animals are rare or absent. In these cases, food chain lengths are short. Attempts to generalize the importance of omnivory across broad geographic areas have been inconclusive. For example, Füreder (2007) found decreased omnivory with increasing temperature because greater diversity allowed for more specialization, while Gonzalez-Bergonzoni et al. (2012) found increasing omnivory with increasing temperature because of food limitation.

Fernández et al. (2017) analyzed ecosystem complexity across a latitudinal gradient and quantified complexity using several metrics such as emergence, self-organization, homeostasis, and autopoiesis (the potential of an ecosystem to develop organization). They found no significant global pattern of any metric of complexity across the latitudinal gradient, but they did observe complexity driven largely by photoperiod and seasonality, which should relate to latitude.

Norman et al. (2017) reviewed isotopic experiments from streams across several continents to describe the efficiency of nitrogen transfer from primary uptake compartments, such as epilithon and detritus, to animals. They found nitrogen transfer rates were greater with open canopy. This indicates that biomes with low riparian vegetation around streams (and potentially wetlands and small lakes) should have greater rates of nitrogen transfer into animal components of the ecosystem.

Relationships among food chain length and gradients of temperature, latitude, elevation, or precipitation are weak in rivers, wetlands, and lakes (Post et al. 2000, Vander Zanden and Fetzer 2007). Jardine et al. (2015) found species shifts from tropical to temperate areas of Australia but found no latitudinal differences in community structure in the streams. However, Irons et al. (1994) found a positive correlation between stream invertebrate leaf litter processing rates and latitude, which suggests invertebrates matter more with respect to nutrient recycling and food chain length at higher latitudes. Dodds et al. (2015) noted some evidence that food chain length in streams will increase across a latitudinal gradient toward the tropics.

Food chain length in lakes is probably driven more by trophic state than by latitude, altitude, or precipitation. A global synthesis of lake food chain lengths found weak or no relationships with ecosystem size, mean annual air temperature, or latitude (Vander Zanden and Fetzer 2007). However, there is ample evidence that climate-dependent factors influence lakes. These factors include changes in phosphorus loading (Vollenweider 1968, Schindler 1977, Jeppesen et al. 2005), mixing regime and stratification, oxygen saturation, and frequency of extreme wind events (Mooji et al. 2005, Blenckner et al. 2007, Kernan et al. 2009). Additionally, lakes experience changes in trophic structure driven by temperature (Gyllström et al. 2005, Beklioglu et al. 2007, Jeppesen et al. 2007, Meerhoff et al. 2007*a*, *b*) and by complex interactions between temperature, nutrients, and physical forces (Jeppesen et al. 2009). Thus, climate gradients may be linked to food chain length, but

Table 7. Variation of biological properties over climate gradients from literature, data patterns analyzed, or logical argument.

| Feature | High altitude | Low altitude | High latitude | Low latitude | Mesic | Xeric |
|---------|---------------|--------------|---------------|--------------|-------|-------|
| Canopy cover | Lower | Higher | Lower | Higher | Higher | Lower |
| Macrophyte diversity | | | Lower | Higher (Neo and Afro tropics) | | |
| Wetland species | Less trees | Greater woody vegetation | Greater C:N, less trees | Lesser C:N, more trees | Greater woody vegetation | Greater herbaceous vegetation |
| Non-fish vertebrate diversity: freshwater turtle diversity | Lower | Higher | | | | |
| Fish species richness | Lower | Higher | Lower | Higher | Higher | Lower |
| Percentage endemic species | | | No trend | No trend | No trend | No trend |

*Note:* Blank cells are where no pattern is predicted, and no trend is indicated where a direct statistical test indicated no trend (see *Patterns of animal diversity across freshwater biomes*).

anthropogenic eutrophication can override this potential interaction.

### Aquatic microbial diversity

Microbes obviously respond to temperature, light, and nutrients, so aquatic microbial communities should relate to climate gradients. However, global surveys of microbial diversity are limited given the relatively recent ability to identify the dominant taxonomic units of bacteria and archaea from the natural environment. Even global surveys of eukaryotic microbes are rare. In subarctic ponds in Norway and Finland, diatom and cyanobacteria richness followed a unimodal trend with increased elevation, non-cyanobacteria richness decreased, while heterotrophic bacterial diversity was more directly related to elevation and terrestrial productivity (Teittinen et al. 2017). A meta-analysis on freshwater bacteria of lakes found pH to be a very influential environmental variable and latitude a weak, but significant, variable in influencing bacterial community composition (Newton et al. 2011). These findings, and others (Koopman and Carstens 2011, Newton et al. 2011, Antoniades et al. 2014), suggest aquatic microbial diversity, at least to some extent, can be related to terrestrial biodiversity patterns, and thus should link to the biomes freshwaters are embedded in. This is a promising area for future research.

### Primary producers: distribution and diversity

Freshwater macrophytes exhibit complex patterns of diversity across global climate gradients.

We found little comparative information on latitudinal patterns of phytoplankton diversity or community structure in lakes and wetlands, or periphyton in streams. Therefore, our following discussion focuses on macrophytes. Many freshwater macrophytes have broad geographic ranges, but diversity is highest in the Neotropics, intermediate in the Oriental, Nearctic, and Afrotropics, lower in the Palearctic and Australasia, even lower in the islands of the Pacific, and lowest in Antarctica (Chambers et al. 2008). Of the 412 macrophyte genera, 39% are endemic to a single biogeographic region, with the highest rates of endemism found in the Neotropics and Afrotropics. Grimaldo et al.'s (2017) analysis of macrophyte diversity in warm, calcareous rivers in Africa and the Americas found latitude was the strongest driver of diversity and could predict macrophyte richness. Although broad temperature gradients drive patterns of macrophyte diversity, local factors can have strong impacts on diversity, especially the presence of invasive species (O'Hare et al. 2012, Grimaldo et al. 2017).

Wetland vegetation composition and structure varies in response to surrounding terrestrial environment, water source, salinity, nutrient availability, and climate conditions. Obviously, forested wetlands (e.g., swamps, boreal bogs) are dominated by perennial woody plants, whereas non-forested wetlands (e.g., marshes) are dominated by annual or perennial emergent or submersed plants (Brinson et al. 1981). Generally, dominant wetland species tend to follow

precipitation gradients. Dominant species showed high turnover across rainfall gradients in coastal wetlands, with more woody vegetation in wetter areas and graminoid marshes in drier climates (Osland et al. 2014). Wetland plant species are characterized by their tolerance for inundation. Woody plants are associated with a higher moisture index and seasonally flooded wetlands, while emergent plants are tolerant of prolonged flooding (Garris et al. 2015).

Wetland vegetation also varies with latitude. Collantes et al. (2009) found floristic composition of Argentinian freshwater wetlands changes along a latitudinal gradient, due to variations in factors such as soil pH, base cations, and soil C:N ratio. The C:N increased with increasing latitude (most likely due to slow decomposition rates), and pH increased with rainfall (caused by base cation leaching). Studies of rich fens across Europe similarly suggested compositional shifts in species with latitude (Jiménez-Alfaro et al. 2014), with vascular plants responding more strongly to latitude shifts than bryophytes. Based on prior published studies, we predict a transition from woody to herbaceous wetland plants from wet to dry regions. Wetland net biomass production and primary production should generally be higher in lower latitude, warmer regions.

### Patterns of animal diversity across freshwater biomes

There are around 126,000 described freshwater animal species, making up approximately 9.5% of known global diversity (Balian et al. 2008). This estimate is likely low, as large geographical gaps in knowledge of species diversity exist, especially across invertebrate groups of Central Africa, South America, and South-East Asia. Due to knowledge gaps in tropical systems, current estimates of diversity that indicate highest levels of freshwater diversity in the Palearctic zoogeographic region may be inaccurate. We will focus our discussion of animal diversity patterns on vertebrates and arthropods because these groups have been most thoroughly described.

A broad consensus exists that aquatic invertebrate communities in streams, rivers, wetlands, and lakes vary strongly across climatic gradients. This variation occurs among terrestrial biomes, and hypotheses about factors controlling this variation are emerging. For stream invertebrate fauna, assessing latitudinal gradients in diversity has been a major focus of study, particularly between the temperate and tropical zones (e.g., Boulton et al. 2008). Generally, major invertebrate groups vary in their diversity responses to latitude (Table 8). Vinson and Hawkins (2003) observed Ephemeroptera and Trichoptera richness declined with increasing altitude, while Plecoptera richness increased with altitude, up to 2500 m, and then declined. More direct links to biome gradients for stream invertebrates are also found in Vinson and Hawkins (2003). They grouped their 493 collections of stream insects into biogeographic regions (8) and biomes (9). While both biogeographic region and biome explained significant variation in the generic richness of individual and combined Ephemeroptera, Plecoptera, and Trichoptera richness, biome tended to account for about twice the variation relative to biogeographic region. In general, forested biomes tend to support a greater richness of Ephemeroptera, Plecoptera, and Trichoptera taxa than do arid or tundra biomes, with grassland biomes having intermediate richness.

Meta-analyses addressing freshwater wetland aquatic invertebrates also point toward the importance of biomes. Batzer and Ruhí (2013) compiled global family-level taxa lists from 447 individual wetlands, largely from North America and Europe. Multivariate community analyses of this fauna identified 11 distinct groups of wetlands, many of which corresponded to biome variation (e.g., desert depressions, semi-arid (i.e., grassland) depressions, alpine ponds, northern boreal forest wetlands, Mediterranean ponds). This geographic variation dwarfed macroinvertebrate community variation between temporarily and permanently flooded habitats, typically considered a major ecological transition for wetland invertebrates (Batzer and Wissinger 1996, Wellborn et al. 1996, Wissinger 1999). However, temporary and permanent wetland subgroupings were often evident within geographic locations. Ruhí et al. (2013) examined wetland invertebrate generic composition among 225 temporary wetlands located in the Nearctic and western Palearctic. Genera in the harsh arid and cold climates tended to concentrate in a few higher taxonomic groupings, and in the more benign climates, genera were spread across many higher

Table 8. Summary of literature on diversity of some stream invertebrate groups as a function of latitude.

| Group | High latitude | Low latitude |
| --- | --- | --- |
| Amphipoda | More diverse | Less diverse (Väinölä et al. 2007) |
| Coleoptera | Less diverse | More diverse (Brown 1981, Jäch and Balke 2008) |
| Ephemeroptera | Peaks at 30° S and 40° N | Peak at 10° N (Vinson and Hawkins 2003) less diverse in general (Pearson and Boyero 2009) |
| Hemiptera | Less diverse | More diverse (Polhemus and Polhemus 2008) |
| Odonata | Less diverse | More diverse (Pearson and Boyero 2009) |
| Plecoptera | Peaks at 30° S and 40° N | Less diverse (Vinson and Hawkins 2003, Pearson and Boyero 2009) |
| Trichoptera | Peaks at 30° S and 40° N | Lower (Vinson and Hawkins 2003) or no pattern (Pearson and Boyero 2009) |

taxa. This suggests harsh climate conditions filter some groups, but those adapted for the conditions can proliferate. For example, the diversity of large branchiopods (fairy shrimps, clam shrimps, tadpole shrimps) tends to be greatest in wetlands with harsh environmental conditions (see Boix and Batzer 2016).

For lake invertebrates, studies of broad geographic variation have focused on crustacean zooplankton (Cladocera and Copepoda), and data collected thus far are more ambiguous in terms of biome gradients. Dodson (1992) assessed species richness across 66 North American lakes of varying latitude, size, depth, and trophic status. Latitude was not a significant predictor of richness, although lake size and productivity were. However, Gillooly and Dodson (2000) found Cladocera size across Western Hemisphere lakes was greater in the north temperate zone than in equatorial or polar regions, suggesting a temperature effect. Havens et al. (2014) confirmed body sizes of assorted crustacean zooplankton in lakes declines with increasing water temperatures associated with latitudinal change. Beaver et al. (2014) also found more small bodied species in warmer waters when they assessed 102 western U.S. reservoirs across three ecoregions.

Vertebrates (other than fishes) dependent on freshwater habitats to complete at least some part of their life cycle follow variable relationships across temperature and precipitation gradients. Amphibian and freshwater turtle richness have positive relationships with precipitation and temperature; richness is greatest near the equator and decreases toward the poles (Buckley and Jetz 2007, Buhlmann et al. 2009). Individual amphibian groups, however, display complex patterns of richness. Plethodontid salamander

richness increases with decreasing latitude, probably more related to colonization times following glacial periods than temperature (Kozak and Wiens 2012). Anuran richness exhibits both positive and negative relationships with temperature across elevation gradients depending on latitude and precipitation (Navas 2002). Freshwater turtle diversity typically increases with decreasing elevation (Buhlmann et al. 2009). Richness of birds that specialize on riverine habitats is greatest at moderate-to-low elevations, though there is potentially a hotspot in high elevations of south-central–South-East Asia where numerous ranges overlap (Buckton and Ormerod 2002).

Some relationships with fish diversity and climate gradients are clear. Antarctic freshwater habitats are mostly too harsh to support fish. However, their presence may also be limited by dispersal. Intermittent habitats and saline habitats characteristic of drier areas are often devoid of fishes.

Abell et al. (2008) delineated 426 freshwater ecoregions combining river-, wetland-, and lake-dwelling species across the globe and observed both the total number and density of fish species (total number/ecoregion area) were generally highest at low latitudes. We further assessed fish species richness and endemism along transects of climate gradients (Fig. 1) using the same dataset (see Appendix S1 for data description, and Appendix S3 for analysis details) to assess broad-scale patterns of freshwater fish diversity.

Our analyses generally agreed with Abell et al. (2008), but we found mixed responses for some metrics across climate gradients. Specifically, fish species richness significantly increased with increases in minimum annual temperature (simple linear regression: $F_{1,46} = 12.6$, $R^2 = 0.21$, $P < 0.001$), and log richness significantly increased

as mean annual precipitation increased ($F_{1,29} = 65.3$, $R^2 = 0.69$, $P < 0.0001$; Fig. 7). Percentage of endemic species showed no obvious trends with gradients of either temperature or precipitation (Fig. 7). We did not generate regression models for this relationship due to the lack of linear pattern and the relatively large number of zeroes (Appendix S3).

The absence of any obvious relationship between endemism and temperature and precipitation suggests factors other than climate may be more important in determining distributions of endemic species. The historical availability of extinction refugia or rates of allopatric speciation could be more important than current climate gradients for endemic species distributions globally (Collen et al. 2014). Future analyses of diversity in rivers, lakes, and wetlands separately, or

data compiled at finer spatial scales may provide more insight into these relationships.

### Variation in life history

Many factors influence life history of aquatic organisms, but some (e.g., intermittence, mean temperature, and seasonality) are more likely than others to vary across biome gradients. Ephemeral habitats have clear impact on life history, as organisms that inhabit them must have desiccation resistant stages or the ability to retreat to refugia during dry periods. Such adaptations are rarer with more complex animal body architecture and with greater size. Hydrology plays a large role in the life history patterns for freshwater shrimp (Hancock and Bunn 1997) and many other freshwater taxa (Lytle and Poff 2004). However, there is much variation within and among
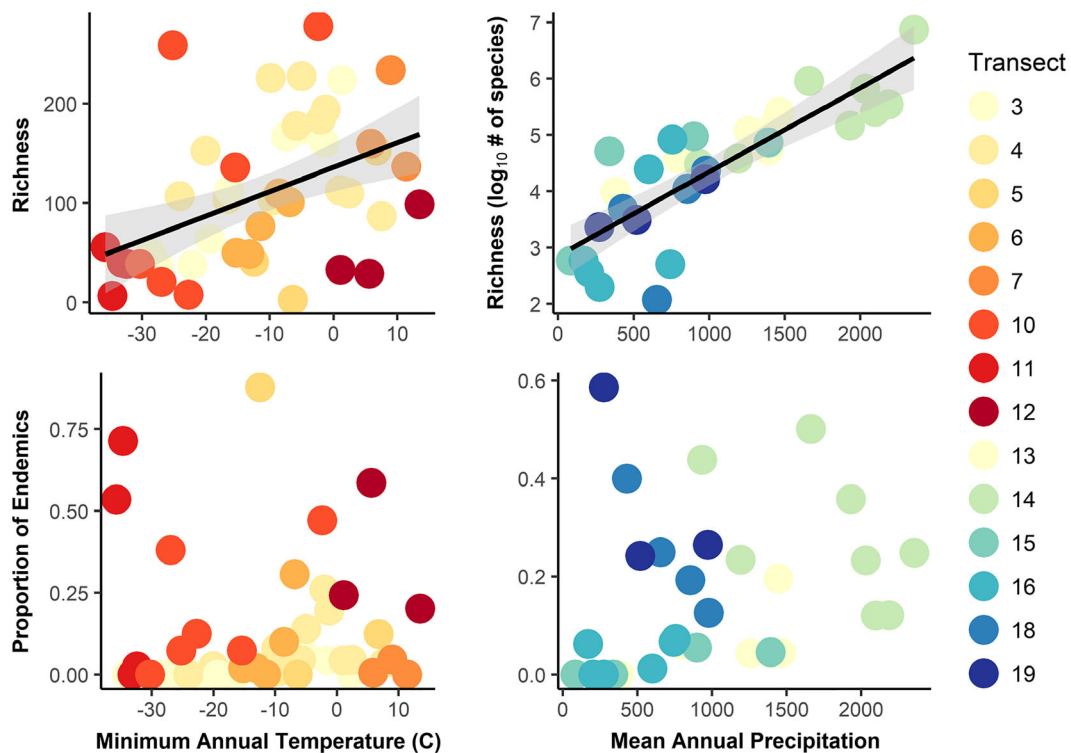


Fig. 7. Bi-plots of fish richness and percentage endemism per ecoregion across global precipitation and temperature transects (Fig. 1) obtained from freshwater ecoregions developed by Abell et al. (2008). We used linear regression to test for trends in species richness (number of species). Richness, which was log transformed across precipitation transects to improve normality, exhibited a significant positive relationship with both temperature ($F_{1,46} = 12.6$, $R^2 = 0.21$, $P < 0.001$) and precipitation ($F_{1,29} = 65.3$, $R^2 = 0.69$, $P < 0.0001$), while the proportion of endemic species per ecoregion did not exhibit any clear linear trends.

groups, and both abiotic and biotic factors will drive variation in life history patterns across taxa.

Temperature is important to invertebrate life history, with warmer temperatures increasing primary productivity and leading to more food sources for growth by invertebrates (Huryn and Wallace 2000). Temperature, latitude, and photoperiod affected the abundance of various species of immature zooplankton. Higher temperatures advanced phenology of all groups and copepod hatch rates were highest at midlatitudes, during periods of high temperature and long days. Rotifers had greater numbers of hatches at lower latitudes, although hatch success was greater for shorter days (Jones and Gilbert 2016).

Wissinger (1999) diagrammed how hydroperiod variation may control biota in North American wetlands, though his results probably apply to other parts of the world. Wetland hydroperiod variation in permanence, duration, predictability, phenology, and harshness (of both wet and dry phases) all were predicted to affect biota related in large part to invertebrate life history strategies. Wetland characteristics of certain hydroperiods were often defined by biome type (e.g., desert pools, northern peatlands, California marshes).

Patterns of fish life history strategies (Winemiller 2005, Mims et al. 2010) vary in response to local environmental variables, and these patterns likely translate into patterns across global climate gradients. Mims et al. (2010) observed opportunistic life history strategies (small bodied, early maturation, low juvenile survivorship) were most prominent in the southeast portion of the United States, periodic strategists (large body, high fecundity, late maturation, low juvenile survivorship) in the northwest portion, and equilibrium strategists (moderate maturation age, low fecundity, high juvenile survivorship) in the northern part of the country. This study suggested a latitudinal gradient, with equilibrium strategists being more dominant at higher latitudes than periodic strategists. Using a similar dataset, Mims and Olden (2012) found opportunistic strategists were associated with variable flows, while equilibrium strategists were associated with predictable flows, and additionally periodic strategists occurred in areas with high flow seasonality. This same pattern was detected in Australian fish assemblages (Olden and Kennard 2010). Bunn and Arthington (2002) found many fishes from highly variable flow regimes have evolved strategies that allow for strong recruitment despite disturbances, including fishes which spawn in months with low and stable flows and avoid months with high and unpredictable flows. As flow regimes are driven by climatic variability, this suggests that biomes can constrain fish life history strategy.

## PREDICTIVE ECOLOGY, THE FRESHWATER BIOME GRADIENT FRAMEWORK, AND ANTHROPOGENIC IMPACTS

### The framework

Even before Alexander von Humboldt published the concept of life zones in the geography of plants (von Humboldt and Bonpland 1807), humanity had words for grasslands, tundra, deserts, and forests. Perhaps humans grasp the concept of terrestrial biomes more readily as our colloquial vocabulary had classified them before the idea of biomes was formalized scientifically. However, we view terrestrial biomes as scientific constructs meant to facilitate generalizations and comparisons, and we assert that they actually occur across gradients of abiotic factors rather than representing discreet ecosystem states.

Our review and analyses throughout this paper suggest many—but not all—characteristics of lakes, streams, and wetlands are linked to the terrestrial biome in which the freshwater system is embedded. Still, there are certain pitfalls in using terrestrial biomes to delineate freshwater biomes. Classifying freshwater systems based off terrestrial biomes alone is problematic because it ignores heterogeneity both within and among terrestrial biomes, and because some aquatic ecosystems traverse traditional terrestrial biome delineations.

One of the most important shortcomings is geology, a factor not considered with respect to traditional terrestrial biomes. The geology a watershed is embedded in has strong effects on hydrology and chemistry of freshwaters in addition to geomorphology. An additional problem arises when considering classifications assuming altitude and latitude as proxies for temperature to delineate biomes. In the terrestrial biome framework, tundra would occur at high altitude

and latitude. However, high-elevation tundra at lower latitudes, compared to Arctic tundra, would have substantial slope (which Arctic tundra may or may not), less pronounced annual variation in day length, substantially greater PAR and UV influx, and lower levels of dissolved oxygen saturation.

We think that freshwater systems, being distributed across abiotic gradients used to delineate terrestrial biomes, can be characterized further given specific combinations of abiotic factors. This is the core of a biome gradient approach, rather than attempting to draw prescribed lines on a map delineating specific regions. Thus, there is merit in classifying freshwater biomes based on combinations of factors that determine the surrounding terrestrial biome (altitude, latitude, and precipitation). Furthermore, there is value in refining predictions based on that information to create a conceptual framework specific to freshwater biomes.

This framework could then be used to predict how a system might behave, what system vulnerabilities to anthropogenic pressures exist, and how we might restore or protect ecological functions. Essentially, we can create a broad baseline expectation based on the climate a habitat is found in. One could consider different freshwater types (rivers, lakes, and wetlands) as biomes in their own regard, but we view these types as more similar to habitat variance within terrestrial biomes. For example, a mountainous, coniferous forested area may have meadows, wetlands, rocky areas, and shrub-dominated regions, but ecologists would still consider the area as a single terrestrial biome. The relative distribution of the different types may vary with freshwater biome (e.g., deep, low-conductivity lakes may be relatively rare in very dry habitats, and ephemeral streams and wetlands may be relatively common).

In the remainder of this section, we use the freshwater biome perspective to hypothesize how abiotic and biotic factors of aquatic ecosystems might change with increasing anthropogenic impact. We explore how the intensity of these impacts varies predictably across latitudinal, altitudinal, and precipitation gradients in conjunction with human population densities. This exercise is intended to illustrate some of the

potential strengths of a biome gradient framework as applied to continental waters.

### Climate change

The potential synergistic effects between climate change and other anthropogenic pressures on freshwater systems (e.g., fragmentation and habitat loss; Markovic et al. 2017) are quickly being realized. Global warming and associated climate change will have pervasive effects at macrosystem scales on structure and function of all freshwater communities; lakes and streams are important sentinels of global change (Williamson et al. 2008). Conservation and management could be facilitated by understanding how these changes could alter the expected freshwater biome type in a region. Arctic and high-elevation lakes will experience more warming (Mountain Research Initiative 2015, Kraemer et al. 2017). Warming could lead to increased species diversity in eutrophic systems and decreased diversity in oligotrophic systems (Binzer et al. 2015). Jeppesen et al. (2009) reported that warmer lakes are more sensitive to external changes such as increased nutrient loading or water-level fluctuations, suggesting that temperate lakes undergoing warming may have heightened sensitivity to eutrophication. Marino et al. (2018) analyzed empirical studies of how experimental warming strengthened or weakened trophic cascades. They found that warming strengthened top-down control in colder environments but weakened it in warm environments. We previously discussed how warming will shift system metabolism by decreasing NEP.

A changing climate will also affect precipitation amount, type, duration, intensity, and timing. This will influence hydrology and alter requirements for land and water management (Goudie 2006). A shift in hydrology can impact stream morphology, leading to excessive erosion and/or deposition until a new dynamic equilibrium is reached (Lane 1955). These kinds of morphological adjustments can have serious implications for the biota of many streams, wetlands and lakes (Cluer and Thorne 2014). Goudie (2006) hypothesized that river stability will be impacted the most in cold, tropical, and arid regions of the globe. Furthermore, these effects on river stability could be compounded by

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human impacts that disrupt flood rhythms (Jardine et al. 2015).

Wetlands are particularly vulnerable to climate changes in terms of the quality and quantity of their water sources. This vulnerability will be predominantly driven by hydropattern alterations from changing precipitation and temperature regimes. Temperature increase could decrease water levels and increase vegetation cover in semi-permanent wetlands (Erwin 2009). Macrophyte growth is predicted to increase with climate warming due to higher temperatures and reductions in water tables (Jeppesen et al. 2009).

Global warming has led to longer ice-free seasons in lakes and rivers around the world (Magnuson et al. 2000). Earlier ice-off associated with warming will lead to large shifts in lake ecology because many physical and chemical parameters in these lakes will change (Preston et al. 2016). Climate change will likely trigger shifts in the phenology of lakes (see Heino et al. 2009) by changing the timing of stratification patterns and duration of ice cover; it will also likely influence the biotic characteristics of zooplankton communities (Jones and Gilbert 2016). These changes could alter diversity, abundances, and phenology of zooplankters within lakes, and responses may diverge across latitudes due to differences in optimal hatching cues and life history strategies. We can potentially use information from areas of lower latitudes to predict future conditions at any current latitude.

### Land use changes and reservoirs

Land use changes have widespread influences on streams, wetlands, and lakes. Streams receive more pollutants and have altered hydrology, wetlands are drained and converted to agricultural or urban uses, and lakes receiving waters from impaired streams will be degraded as well (Dodds and Whiles 2019). Read et al. (2015) found lake water quality is heavily driven by local factors, especially land use within the watershed.

Changes in land use, particularly riparian modification, alter inputs of terrestrial vegetation into freshwaters. Large woody debris can be a significant allochthonous source of organic carbon in freshwater ecosystems, and anthropogenic alterations to large woody debris inputs have had lasting negative impacts on these

ecosystems (Brooker 1985, Gurnell and Sweet 1998). The relative amount of large woody debris naturally occurring in systems is a function of the biome in which they occur, and restoration of these inputs should take into account the biome context.

Dams impact flowing waters across the globe, greatly influencing the hydrology, channel stability, and ecosystem functioning of rivers and streams (Cluer and Thorne 2014, Fox et al. 2016). We assessed the number of reservoirs across gradients of temperature, latitude, elevation, and precipitation, focusing on the difference between lake and reservoir surface coverage within a given area. Similar to natural lakes, most reservoirs are located below 500 m above sea level (Appendix S2). More reservoirs occur in the Northern Hemisphere, with the highest density of reservoirs occurring around 50° N (Appendix S2). This differs from densities of natural lakes, which have higher densities between 60° and 70° N (Lehner and Döll 2004, Verpoorter et al. 2014). The distribution of lakes across northern midlatitudes corresponds to higher densities of reservoirs in areas with moderate-to-high mean annual temperatures. Across gradients of precipitation, reservoirs have high densities in relatively dry landscapes, with the highest density of reservoirs occurring in areas receiving an average of only 500–1000 mm of precipitation per year (Appendix S2). We also compared the relative amount of area covered by natural lakes and reservoirs across the same global gradients (Fig. 8). Reservoir surface area is only higher than natural lake area at low elevations, though lake area is typically still higher. Reservoir area exceeds lake area at relatively high levels of precipitation, but lake area is typically still higher, and there are no clear spikes in reservoir/lake area across temperature and latitudinal gradients. Lake area exceeds reservoir area following similar patterns of global lake surface area, with lakes exceeding reservoir area in northern midlatitudes, and just below the equator.

### Water abstraction

Highest levels of groundwater abstraction occur at midlatitudes (Wada et al. 2010). Although these latitudes generally have more surface water, large drier areas such as the Great Plains of the United States have been converted
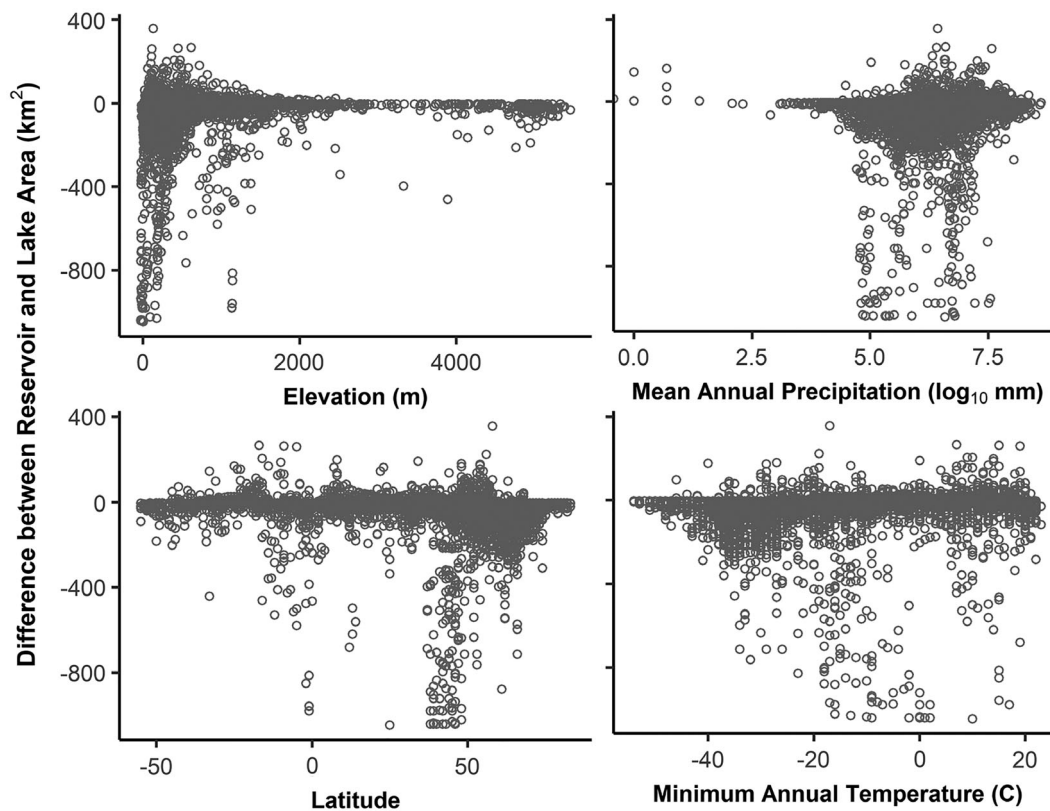
Fig. 8. The difference between reservoir areas relative to lake area within 1000-km² areas as an index of relative human impact on water surface area. Negative values indicate larger area of lakes, while positive values indicate larger area of reservoirs. Reservoir and lake area data were obtained from the Global Lakes and Wetlands Database (Lehner and Döll 2004) and climate data from Fick and Higmans (2017).

to crop production based on groundwater abstraction. These drier areas, such as northeast Pakistan, northwest India, northeast China, the central and western USA, Yemen, and southeast Spain, have high groundwater depletion rates (Wada et al. 2010), and surface waters are disappearing from these areas. Where data are available, threats to human water security follow similar trends across latitudinal and precipitation gradients, though high human population densities in areas with relatively high precipitation can still face significant water scarcity threats (Vörösmarty et al. 2010). Global water abstraction, paired with global climate change and habitat loss, will likely have a profound impact on freshwater systems, especially regarding nutrient dynamics and concentrations, water quality, salinity, and trophic structure (Jeppesen et al. 2015).

*Aquatic pollution*

Heavy metals, pharmaceuticals, microplastics, acid precipitation, nutrients, and other pollutants are common impacts on freshwater habitats; one can detect aquatic pollutants such as trace organic compounds in the most remote areas of the Arctic and Antarctic. The impact of volatile persistent organochlorine compounds increases with increasing latitude and altitude due to condensation (Wania and Mackay 1993). The concentrations of many pollutants may vary predictably or unpredictably across gradients in freshwater biomes. A study of mercury and methylmercury concentrations in fish tissue from across the western USA and Canada found no consistent latitudinal geospatial patterns at the continental scale (Eagles-Smith et al. 2016). However, their results suggested a modest correlation between methylmercury concentration and

precipitation levels. For African fishes, latitude, trophic level, and mass were all positive predictors of mercury (Hg) concentration (Hanna et al. 2014). In a global review of Hg biomagnification in aquatic food webs, Lavoie et al. (2013) reported a positive relationship between Hg trophic magnification and latitude; they hypothesized that the trend reflected decreasing temperatures from south to north, which would in turn drive lower biomagnification rates due to differences in Hg assimilation and excretion associated with temperature. Overall, continental-scale analyses of freshwater pollution patterns are lacking and warranted in a time of unprecedented anthropogenic change.

## Conclusion

Our conceptual framework is not so much a single hypothesis as a logical way to characterize patterns in freshwaters at scales relevant to evolutionary processes that gave rise to freshwater biodiversity, to the scales at which regulatory units interact with the environment, and the current scope of anthropogenic impacts on ecosystems that provide vital ecosystem services (Dodds et al. 2013). Many of our observations in this paper are obvious (e.g., freshwaters in drier areas will be sparser and prone to drying), but a broad framework including the ramifications of broad-scale gradients from basic geomorphology and hydrology to ecosystem and community responses has not been approached, as far as we know. While much has been published on some characteristics of freshwaters across continental scales, there is much more to learn. For example, far less is known about tropical waters than temperate ones with respect to diversity and ecosystem rates. Another key issue is mapping biodiversity at the appropriate scale (McManamay et al. 2018). Many biotic characteristics (e.g., food chain length, food web connectivity, rates of production and decomposition, endemism, and omnivory) have been poorly studied across broad spatial scales. Characterization of broad patterns requires substantially more data to find patterns in inherently noisy ecological data. As researchers in developing countries expand their scope of study, and government agencies become more comprehensive in their monitoring programs while making their data freely available,

we will be able to further test predictions made under the freshwater biome gradient framework. As we refine this framework, it will allow better predictive ability at macrosystem scales based on the resulting expected ecological baselines and how they will be altered in a changing world.

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