NRC Research Press

ARTICLE

# Surface water connectivity affects lake and stream fish species richness and composition

Katelyn B.S. King, Mary Tate Bremigan, Dana Infante, and Kendra Spence Cheruvelil

**Abstract:** Stream and lake fishes are important economic and recreational resources that respond to alterations in their surrounding watersheds and serve as indicators of ecological stressors on aquatic ecosystems. Research suggests that fish species diversity is largely influenced by surface water connectivity, or the lack thereof; however, few studies consider freshwater connections and their effect on both lake and stream fish communities across broad spatial extents. We used fish data from 559 lakes and 854 streams from the midwestern–northeastern United States to examine the role of surface water connectivity on fish species richness and community composition. We found that although lakes and streams share many species, connectivity had a positive effect on species richness across lakes and streams and helped explain species composition. Taking an integrated approach that includes both lake and stream fish communities and connectivity among freshwaters helps inform scientific understanding of what drives variation in fish species diversity at broad spatial scales and can help managers who are faced with planning for state-, regional-, or national-scale monitoring and restoration.

**Résumé :** Les poissons de cours d'eau et de lac constituent d'importantes ressources économiques et récréatives qui réagissent aux changements dans les bassins versants qui les entourent et servent d'indicateurs des facteurs de stress écologiques pour les écosystèmes aquatiques. Si des travaux de recherche indiqueraient que la diversité spécifique des poissons est largement influencée par la connectivité des eaux de surface ou l'absence de cette dernière, peu d'études se sont penchées sur les connexions de plans d'eau douce et leur effet sur les communautés de poissons de lacs et de cours d'eau à grande échelle. Nous avons utilisé des données sur les poissons de 559 lacs et 854 cours d'eau dans les États du centre-ouest et du nord-est des États-Unis pour examiner le rôle de la connectivité des eaux de surface en ce qui concerne la richesse spécifique et la composition des communautés de poissons. Nous avons constaté que, bien que les lacs et cours d'eau comptent de nombreuses espèces en commun, la connectivité a un effet positif sur la richesse spécifique des lacs et des cours d'eau en général et aide à en expliquer la composition spécifique. Une approche intégrée qui inclut les communautés tant des lacs que des cours d'eau et la connectivité des plans d'eau douce favorise une meilleure compréhension scientifique des facteurs de variation de la diversité spécifique à de grandes échelles spatiales et peut aider les gestionnaires dans la planification de la surveillance et de la restauration à l'échelle étatique, régionale ou nationale. [Traduit par la Rédaction]

## Introduction

Global biodiversity is declining rapidly, with freshwater biodiversity declining at higher rates compared with terrestrial and marine biodiversity (Butchart et al. 2010; Wiens 2016). Freshwater fish communities are good study systems for understanding changes in biodiversity because they represent multiple trophic levels that respond differently to watershed alterations, serve as an indicator of ecological stressors on aquatic ecosystems, and constitute important economic and recreational resources (Harris 1995; Drake and Pereira 2002; Esselman et al. 2011). Many natural features structure fish assemblages, and understanding the roles of these features is essential for scientists to understand how and why human disturbances are causing declines in freshwater biodiversity to conserve it (Abell 2002).

Two natural features that shape fish communities are waterbody area and surface water connectivity. Island biogeography theory (MacArthur and Wilson 1967) describes how the area and connectivity of islands influence the rates of extinction and colonization of species. In the time since this theory was proposed, studies have demonstrated that larger lakes and streams support more fish species than smaller waterbodies (e.g., Eadie et al. 1986; Osborne et al. 1992; Magnuson et al. 1998). Waterbody area not only influences extirpation rates, but can also affect fish species composition because larger lakes or streams provide a variety of habitat types (e.g., littoral versus deep water, cool versus warm pools) compared with smaller lakes or streams (e.g., Lyons 1996; Dodson et al. 2000; Wehrly et al. 2012).

Surface water connections among freshwater types provide fish access to refuge, food, habitat, and nesting sites. These facts likely underlie the positive relationships found between fish species richness and connectivity in lakes (e.g., Kratz et al. 1997; Griffiths 2015) or streams (e.g., Hitt and Angermeier 2008). Surface water connectivity also explains variation in fish community composition. For example, a study of 17 species in Swedish lowland streams found watercourse distance from a stream site to the nearest lake explained species distributions in streams (Trigal and Degerman 2015). They found this measure of connectivity was most important for species that can move between lakes and streams during low flow periods. Similarly, Olden et al. (2001) used a suite of connectivity metrics for drainage lakes in two watersheds to investigate the effects of connectivity on lake fish communities. Many connectivity measures were correlated with patterns of fish

---

Received 19 March 2020. Accepted 8 November 2020.

**K.B.S. King, M.T. Bremigan, and D. Infante.** Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, USA.
**K.S. Cheruvelil.** Department of Fisheries and Wildlife and Lyman Briggs College, Michigan State University, East Lansing, Michigan, USA.
**Corresponding author:** Katelyn B.S. King (email: kingka21@msu.edu).

Can. J. Fish. Aquat. Sci. **78:** 433–443 (2021) dx.doi.org/10.1139/cjfas-2020-0090

community composition in lakes (Olden et al. 2001). Scientists point to the importance of studying lakes, streams, and wetlands as part of an integrated freshwater landscape (Soranno et al. 2010; Fergus et al. 2017; King et al. 2019). In fact, we suggest that to study both lake and stream fish biodiversity, lakes and streams can be thought of as existing along a gradient from less connected systems (e.g., isolated lakes and headwater streams) to highly connected systems (e.g., rivers and lakes connected to other lakes).

Although studies of either lake **or** stream fish communities have demonstrated the importance of surface water connectivity for fish biodiversity, few have taken such an integrated perspective to study the similarities and differences in fish biodiversity across lakes **and** streams. Some fish species move between lakes and streams, and materials can move between connected waterbodies, providing food and nutrients. For example, lakes may be a source of predators, provide refuge during drought or freezing, and provide a variety of habitats for stream fish (Jones 2010). Some studies have applied this integrated approach to examine the biodiversity of phytoplankton, invertebrates, or the distribution of specific fish species (e.g., Pépino et al. 2017; Qu et al. 2017; Mellado-Díaz et al. 2019; Heim et al. 2019). However, to our knowledge, only two studies have investigated both lake and stream fish biodiversity. Findings from one study in Wisconsin, United States (US) indicates that streams within a relatively small extent (i.e., 12 waterbodies in one county) had higher richness than lakes they were connected to (Willis and Magnuson 2000). The other study in France demonstrates that streams and lakes may share many species, but does not explicitly consider the role of connectivity (Irz et al. 2006). Therefore, it remains unknown how patterns of fish biodiversity vary across a gradient of surface water connectivity that includes both lake and stream fish communities across a large geographic extent.

We fill this gap by asking: What are the differences and similarities in lake and stream fish species richness and composition across an integrated freshwater landscape? We quantify fish species richness (within a waterbody) and similarity (across water bodies) in over a thousand lakes and streams across the midwestern–northeastern US to determine the effects of surface water connections on fish biodiversity. After accounting for waterbody area, we expected higher richness in highly connected lakes and streams compared with isolated lakes and streams because species can move through the connected network to recolonize or find refuge from stressors. Likewise, we expected more similar species composition across highly connected lakes and streams as compared with isolated lakes and streams because surface water connections allow species that migrate to inhabit these connected systems, leading to community homogenization (e.g., Trigal and Degerman 2015). Taking an integrated freshwater landscape approach to characterize fish biodiversity is a critical first step needed to understand the influences of climate change and land use intensification on fish biodiversity for future conservation.

## Methods

### Study extent and sampling

We used data from a five-state extent (~680 664 km$^2$) in the United States that included the states of Iowa (IA), Maine (ME), Michigan (MI), New Hampshire (NH), and Wisconsin (WI) (Fig. 1). The majority of this area was glaciated during the Wisconsin glacial period (~2.6 million to 11 000 years ago) and experiences a temperate climate. Wadable streams and nonwadable rivers were included (hereinafter, streams), as well as both natural lakes and anthropogenic reservoirs (hereinafter, lakes). Lakes had an area $\geq$ 4 ha and a public access site. Individual lake sample sites were selected in MI, NH, and ME based on a stratified-random design, using surface area classes (MI: small = 4–40 ha, medium = 40–405 ha, large = >405 ha; ME–NH: small = 5–20 ha, medium = 20–500 ha, large = >500 ha), wherein sample size each year was proportional to the lake population in each class. MI also stratified based on fisheries management regions. IA and WI lakes were chosen nonrandomly, selected by experts as "important," whereby IA sampled roughly 80% of the total lake population and WI sampled all lakes > 40 ha and 20% of lakes < 40 ha. Stream sample sites were compiled from both random and nonrandom survey designs (Daniel et al. 2015). Streams in MI were selected from a stratified random sampling design, based on fisheries management regions, stream size as a function of watershed area (stream: <207 km$^2$, small river: 207–777 km$^2$, large river: >777 km$^2$), and stream temperature (cold: <17.5 °C, cold transition: 17.5–19.5 °C, warm transition: 19.5–21 °C, warm: >21 °C). Streams in ME from the Environmental Protection Agency (EPA) National Rivers and Streams Assessment were stratified by EPA ecoregion and Strahler order. Additional information about sample design was not available; however, water bodies sampled did not include fishless lakes or streams.

Stream and lake fish sampling was performed once at each site by university researchers or state or federal agency personnel between 1991 and 2009 with the goal of performing general surveys of fish communities (i.e., no targeted sampling for specific species; Table 1). We compiled and integrated these data for our analyses (Alger 2009; Daniel et al. 2015). These data include both stocked and naturally occurring species; therefore, the data reflect species persistence at each site.

To account for differences in sampling methods across lakes, we selected only samples collected using fyke or trap nets and (or) electrofishing methods. Fyke nets were set overnight in the summer (June–September) in all states except IA, which also set fyke nets in October. The number of nets set increased with lake size, with a mean of three to five nets. Electroshocking was performed at night, and mean electroshocking time in MI and IA was 30 min, in WI 3.5 h, and NH and ME did not electroshock. Although the use of overnight fyke netting and nighttime electrofishing increases the chances of capturing species that live in the limnetic zone and migrate to the littoral zone at night (in addition to more littoral species), we acknowledge these sampling methods may underestimate the presence of cold-water species, especially in larger–deeper lakes. Similarly, stream sampling data included are from single-pass electrofishing methods (combined backpack and boat; Daniel et al. 2015).

All species identified as hybrids were not counted as a new species and were therefore removed from the datasets prior to analysis. "Unknown" taxa (i.e., when an individual had not been identified to the species level) were also removed. Species nonnative to the state were maintained in the dataset to investigate community composition and because the presence of non-native species may help explain biodiversity patterns.

### Fish data quality assurance

We followed methods that have been used previously to account for differences in fish sampling efforts and methods (e.g., Irz et al. 2007; Niu et al. 2012). We performed rarefaction curves to account for differences in sampling effort (Irz et al. 2007; Niu et al. 2012). In a rarefaction curve, the likelihood of catching more species increases with the number of individuals caught, until the maximum number of species is found and the curve reaches an asymptote (Gotelli and Chao 2013). We performed rarefaction curves on all lake–gear combinations and stream sites (streams only had one gear type) using the "vegan" R package (Oksanen et al. 2019) that randomly selects individuals from samples and plots the mean cumulative number of species found.

If a waterbody–gear combination did not reach an asymptote (<0.05 degrees) at 90% of the total individuals captured (Yang 2013), we concluded that sampling was not sufficient to catch all species vulnerable to that gear for biodiversity assessment and removed the entire lake or stream from analysis. Since rarefaction curves cannot be estimated from one species, if a lake–gear

**Fig. 1.** Characterizing the integrated freshwater landscape of study: (A) distribution of lake (*n* = 559) and stream sampling sites (*n* = 854); (B) distribution of lake connectivity classes ISO_lake (isolated lakes, *n* = 100), HW_lake (headwater lakes, *n* = 73), DR_lake (drainage lakes, *n* = 192), DR_lake_lake (drainage lakes connected to upstream lakes, *n* = 194); (C) distribution of stream connectivity classes HW_stream (headwater streams, *n* = 370), HW_stream_lake (headwater streams connected to a lake, *n* = 99), MID_stream (mid-order streams, *n* = 355), RIVER (rivers, *n* = 30). Connectivity classes are ordered from most isolated to most connected (top to bottom) for lakes (B) or streams (C) and detailed descriptions are in the text. Map was created using ArcGIS 10.3 Desktop (Esri 2014). Base map is from LAGOS GIS Toolbox (Soranno et al. 2015), and points were generated from our dataset. [Colour online.]

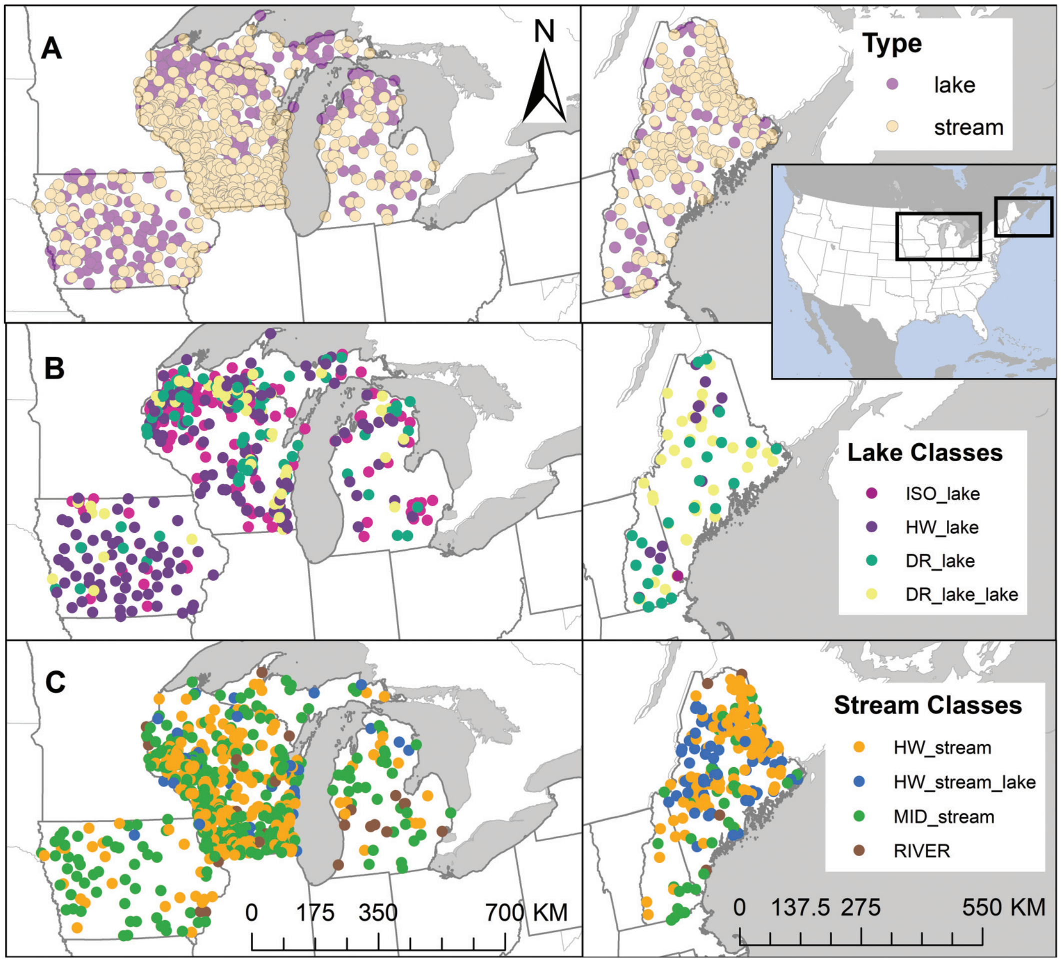


**Table 1.** Description of fish data sources, years of sampling, and gears used, organized by US state.

| State | Freshwater type | Years | Gear | Agency |
|---|---|---|---|---|
| Michigan | Lake | 2003–2006 | Shock, fyke | Michigan Department of Natural Resources |
| | Stream | 2003–2006 | Shock | Michigan Department of Natural Resources |
| Wisconsin | Lake | 2001–2005 | Shock, fyke | Wisconsin Department of Natural Resources |
| | Stream | 2001–2005 | Shock | Wisconsin Department of Natural Resources; Minnesota Pollution Control Agency |
| Iowa | Lake | 2001–2004 | Shock, fyke | Iowa State University |
| | Stream | 2001–2004 | Shock | Iowa Department of Natural Resources; Illinois Department of Natural Resources; United States Geological Survey |
| Maine | Lake | 1991–1994 | Fyke | Environmental Protection Agency's (EPA) Environmental Monitoring & Assessment Program |
| | Stream | 2006–2009 | Shock | Maine Department of Environmental Protection; EPA National Rivers and Streams Assessment |
| New Hampshire | Lake | 1991–1994 | Fyke | EPA's Environmental Monitoring & Assessment Program |
| | Stream | 1994, 1999–2001 | Shock | New Hampshire Fish and Game; United States Geological Survey |

**Fig. 2.** Connectivity gradient for lakes and streams ordered from most isolated systems (left) to highly connected systems (right): ISO_lake, HW_stream, HW_stream_lake, HW_lake, DR_lake, MID_stream, DR_lake_lake, and RIVER. Refer to Fig. 1 for description of different classes.

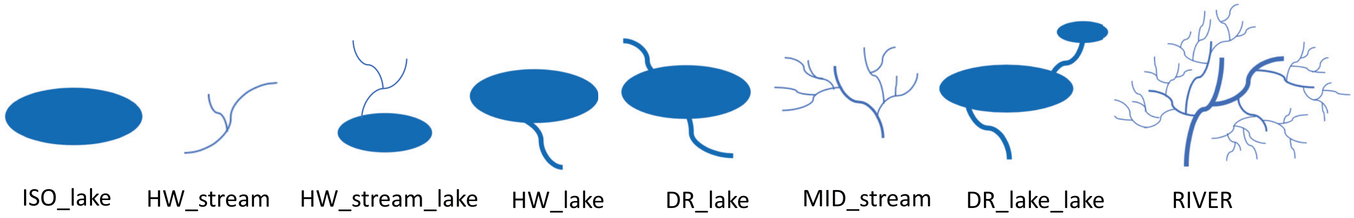


**Table 2.** The waterbody area (km$^2$) for each of the connectivity classes where area data was available.

| | | | Area (km$^2$) | | | |
|---|---|---|---|---|---|---|
| Type | Connectivity class | *n* | Minimum | Median | Mean | Maximum |
| Lake | ISO_lake | 100 | 0.056 | 0.50 | 0.67 | 3.43 |
| | HW_lake | 73 | 0.050 | 0.74 | 1.3 | 0.050 |
| | DR_lake | 192 | 0.040 | 0.55 | 1.3 | 13 |
| | DR_lake_lake | 194 | 0.054 | 2.2 | 6.1 | 60 |
| Stream | HW_stream | 204 | 0.000049 | 0.0034 | 0.0058 | 0.10 |
| | HW_stream_lake | 63 | 0.00028 | 0.0033 | 0.0049 | 0.036 |
| | MID_stream | 355 | 0.00047 | 0.024 | 0.051 | 0.92 |
| | RIVER | 30 | 0.022 | 0.31 | 0.43 | 1.6 |

**Note:** Only 652 streams of 854 streams had area data (i.e., did not have width for headwater streams).

combination or stream site only caught one species, we also considered this to be insufficient sampling, and the entire waterbody was removed from analysis. This process resulted in retention of ~94% and ~67% of lakes and streams, respectively, for analysis. Rarefaction curves were rerun for each of the remaining water bodies (across all gears) to obtain rarefaction estimates for species richness in each waterbody using the "iNEXT" R package (Hsieh et al. 2020). These rarefaction estimates for asymptotic species richness were used instead of observed species richness (count of the number of unique species) for further analysis (sensu Niu et al. 2012).

### Characterizing surface water connectivity

Lakes and streams were defined based on digital mapping provided by multiple USGS National Hydrography Dataset products. We assigned each freshwater type to classes of surface water connectivity using published metrics based on network linkages (i.e., Strahler stream order) and lake–stream connections (Soranno et al. 2017). These "connectivity" classes describe a waterbody according to its degree of surface water connectivity and provide context of watershed or network position.

More specifically, streams were classified into four classes. Three of these classes were based on Strahler stream order (Strahler 1957) using the classifications from NHDplus-V2 (USGS 2019) downloaded using the "nhdR" package (Stachelek 2019). Strahler stream order represents the position of a stream reach within the stream network, with Strahler order 1 representing the tributaries and increasing in number as one moves down a stream network. We grouped these stream orders into three classes of streams: headwater streams (first- to second-order; HW_stream; Colvin et al. 2019), mid-order streams (third- to fifth-order; MID_stream), and rivers (≥sixth-order; RIVER) (USEPA 2016). The fourth class was created by dividing the headwater streams into two classes based on whether it was directly connected to a lake. Therefore, streams in the HW_stream class are most isolated, and those in the HW_stream_lake class are directly connected to a lake.

Lakes were also classified into four connectivity classes based on surface water connections (not including dams), using the classifications from LAGOS-NE_GEO version 1.05 (Soranno et al. 2015, 2017; Soranno and Cheruvelil 2017*a*) downloaded using the "LAGOSNE" R package (Stachelek and Oliver 2019) that consider the presence–absence of inflowing and outflowing streams and the presence–absence of upstream lakes. Isolated lakes (ISO_lake) have no inflowing or outflowing streams, representing the least connected lake category; headwater lakes (HW_lake) are more connected than isolated lakes, having outflowing (but not inflowing) streams. Two categories of drainage lakes both have inflowing and outflowing streams, but differ according to the absence (DR_lake) or presence (DR_lake_lake) of an upstream lake. These eight total connectivity classes represent a gradient of surface water connectivity that can incorporate both lakes and streams as the focal system, from less connected systems such as isolated lakes and headwater streams to highly connected systems such as rivers and lakes connected to other upstream lakes (Fig. 2).

### Characterizing geographic patterns

We wanted to account for potential effects of waterbody area (MacArthur and Wilson 1967) and location (i.e., spatial autocorrelation; Dormann et al. 2007) on patterns of fish biodiversity. Lake areas were obtained from LAGOS-NE-GIS version 1.0 (Soranno et al. 2015, 2017; Soranno and Cheruvelil 2017*b*). Stream length was obtained for each reach from the NHDplus-V2 (USGS 2019), and stream width from the sampling records, when provided, were used to calculate stream area (Table 2). For cases when width was not provided, we used the Google Earth engine measuring tool on satellite imagery (Google Earth Pro 2019; MID_stream and RIVER classes); however, HW_stream and HW_stream_lake classes were not measured using Google Earth because the resolution is not fine enough to capture very small streams. Thus, 202 headwater streams were dropped, leaving 204 HW_stream and 63 HW_stream_lake samples for the subsequent ANCOVA analysis (Table 2).

Finally, to avoid possible spatial autocorrelation among connected sites with fish data, we selected the single fish sample site from all stream sites as well as from lake sites that are connected to other lakes (DR_lake_lake) in each subwatershed (USGS HUC12s) that contained the most unique species (i.e., the highest richness). HUC12s (mean = 93 km$^2$; Seaber et al. 1987) were obtained from LAGOS-NE-GIS version 1.0 (Soranno et al. 2015, 2017; Soranno and Cheruvelil 2017*b*). This approach assumes that the other sites within the subwatershed contain a subset of the species of the site with the most unique species. The final dataset used for analysis included 559 lakes and 854 streams across the five-state extent (Fig. 1; Table 1).

### Characterizing fish biodiversity

It is important to characterize biodiversity of aquatic communities using multiple metrics because two communities could have the same number of species (i.e., species richness), but contain different species (i.e., species composition; Tonn and Magnuson 1982; Downing 2005; Aggemyr et al. 2018). In addition, a system could have low species richness but contain a subset of species of a species-rich system (i.e., nestedness), or a species-poor system could have unique species compared with others in an area (Baselga 2010). Therefore, we used both species richness and composition to characterize biodiversity and understand the underlying features contributing to patterns of fish biodiversity.

Species richness was natural-log-transformed prior to analyses. We used ANOVA with post hoc least significant difference (LSD) pairwise comparison and Bonferroni adjustment to compare mean rarefaction species richness across the eight classes of freshwater connectivity. We also conducted this analysis by region, separating out the northeastern (ME and NH) from the midwestern (IA, MI, WI) waterbodies to examine the effect of geographic location on the relationship between connectivity and species richness. We also used ANCOVA to simultaneously regress connectivity class and waterbody area, as well as model the interaction between them. If the interaction was significant ($\alpha$ = 0.05), we identified significant differences in slopes among the connectivity classes using a post hoc pairwise comparison using the "emmeans" package (Lenth 2019). This approach shows the amount of variation explained by both surface water connectivity and waterbody area, as well as indicates whether the relationship between species richness and waterbody area varies with connectivity class.

To quantify differences in species composition, we calculated the mean species dissimilarity based on all possible pairwise comparisons between two connectivity classes. We chose the Sørensen dissimilarity measure, calculated using the "vegan" package (Oksanen et al. 2019), which uses the presence of a species in one system compared with another:

$$\beta = (b + c)/(2a + b + c)$$

where $a$ is the number of species shared between two connectivity classes, and $b$ and $c$ are the numbers of unique species (not shared) for each class. Sørensen dissimilarity measures range from 0 (waterbodies that have all the same species) to 1 (no species are shared across waterbodies). To identify significant differences in dissimilarity among the communities along the surface water connectivity gradient, we used permutational multivariate analysis of variance (PERMANOVA; Anderson 2017) using the "vegan" package (Oksanen et al. 2019). We repeated this analysis by region to examine the effect of geographic location (i.e., northeastern versus midwestern waterbodies) on species dissimilarity.

Correspondence analysis (CA) was performed on species presence–absence data to summarize patterns in community structure and further determine whether more connected waterbodies such as those in the RIVER and DR_lake_lake connectivity classes are more similar to each other than they are to more isolated systems. CA was performed using the "FactoMineR" package (Husson et al. 2020) and is a multivariate ordination method that organizes sites by similarities in their assemblages. CA is good for categorical variables such as species and is not as affected by datasets with many zero values compared with other ordination methods (Gauch 1982). To reduce the influence of rare species on the CA analysis, we included only species that were present in >5% of the lakes or streams in analyses. We retained the first two CA axes as summaries of between-site community assemblages for visualization purposes. The 95% ellipses were drawn based on connectivity classes or by region to visualize clustering in assemblage structure across connectivity classes or between the northeastern and midwestern US. All analyses were performed in R version 3.6.1 (R Core Team 2018). Code for analysis and data (except for WI data due to data sharing restrictions) can be found in an archived Github repository (King 2020).

## Results

### Species richness and connectivity

As we predicted, fish species richness was higher in more connected, downstream freshwater systems. Across the gradient of surface water connectivity from very isolated lakes and streams to highly connected lakes and streams, there was a significant difference in the mean rarefaction species richness (ANOVA; $F = 65.2$, $p < 0.001$), with richness generally increasing with connectivity (with the exception of isolated lakes; Fig. 3). A similar pattern was found when splitting the study area into the northwestern and midwestern regions (refer to online Supplemental Fig. S1[1]). LSD pairwise comparison showed that streams in the HW_stream and HW_stream_lake classes have significantly lower richness than the other connectivity classes (Fig. 3). Richness in ISO_lake, HW_lake, and DR_lake classes did not significantly differ; however, richness in these three classes was significantly lower than richness in waterbodies in the DR_lake_lake and RIVER classes (Fig. 3). On the other hand, waterbodies in the RIVERS class had significantly higher species richness than waterbodies in the MID_stream class (Fig. 3).

When including area in the model, both waterbody area and connectivity class had a significant effect on species richness (ANCOVA; $F = 56.6$, $p < 0.001$ and $F = 72.8$, $p < 0.001$, respectively) with a significant interaction ($F = 10.3$, $p < 0.001$). Although relationships significantly differed across some connectivity classes, the direction of the relationship was constant with area having a positive relationship with species richness in all connectivity classes (Fig. 4). Slopes did not significantly differ across the stream or river classes; however, slopes were significantly different ($p < 0.05$) among many of the lake connectivity classes and between lake and stream classes (e.g., DR_lake_lake was different from all three other lake connectivity classes; MID_stream was different from DR_lake_lake, DR_lake, and HW_lake). Across the lake and stream classes, slope generally decreased with increasing connectivity.

### Species composition and connectivity

When examining total fish biodiversity in lakes as compared with streams, we found that more species occur in streams ($n$ = 147) than in lakes ($n$ = 121; Supplemental Table S1[1]). Lakes had 21 unique species that were not found in streams, whereas streams had 47 species not found in lakes (Fig. 5). Despite these differences, the majority of fish species were common to both lakes and streams, with 100 species in common (Supplemental Table S1[1]; Fig. 5).

When examining the effects of surface water connectivity on species composition, we found significant differences in Sørensen dissimilarity across the lake and stream connectivity classes (PERMANOVA; $F = 73.1$, $p = 0.001$). Species assemblages were the most similar between classes of connected systems and the least similar when comparing waterbodies in connected classes with those in isolated classes (Fig. 6). These patterns held when we conducted the analysis by region (midwest and northeast PERMANOVA; $F = 69.2$, $p = 0.001$ and $F = 14.0$, $p = 0.001$, respectively; Supplemental Fig. S2[1]). For example, within a freshwater type, waterbodies in the ISO_lake class were the most dissimilar from those in the

---

[1] Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0090.

**Fig. 3.** Boxplot of log rarefaction species richness across connectivity classes. Classes with the same letter are not significantly different (least significant difference (LSD), $\alpha$ = 0.05; Bonferroni adjustment). Classes of streams (orange) and lakes (purple) are arranged in order of increasing connectivity from left to right. [Colour online.]

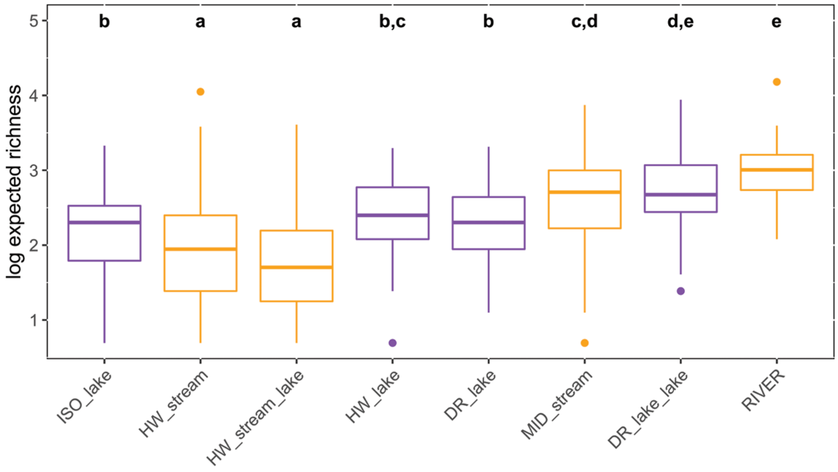
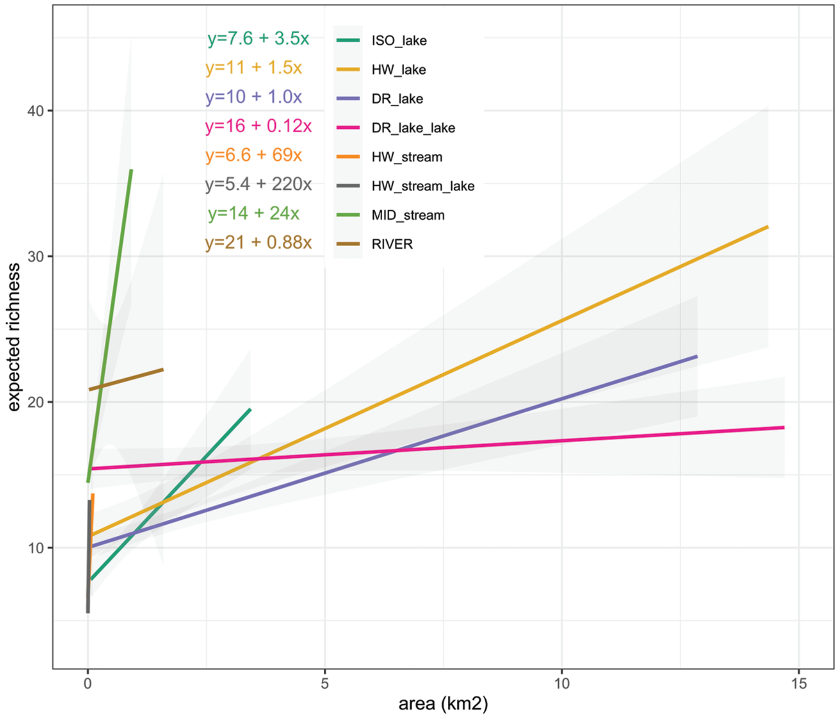


**Fig. 4.** Area and expected species richness relationships by connectivity class. Grey-shaded areas are 95% confidence intervals. Slopes were significantly different ($p < 0.05$) between DR_lake_lake and the three lake classes (DR_lake, HW_lake, and ISO_lake); between DR_lake and ISO_lake; and between MID_stream and the three lake classes (DR_lake_lake, DR_lake, and HW_lake). Slopes were not significantly different between stream and river classes. Note: some of the lakes in the DR_lake_lake class are larger than 15 km$^2$; however, the graph was truncated at 15 km$^2$ for better visualization. [Colour online.]



DR_lake_lake class, and waterbodies in the HW_stream and HW_stream_lake classes were the most dissimilar from those in the RIVER class. Across freshwater types, waterbodies in the DR_lake_lake class were more similar to those in the RIVER and MID_stream classes than the waterbodies in the ISO_lake class were to the RIVER and MID_stream classes (Fig. 6).

Correspondence analysis structured the assemblages into two dimensions that explain ~23% of the variation in species composition across sites (dimension 1: 13.5% and dimension 2: 9%; Fig. 7). The top five species contributing to the first CA axis (dimension 1, *x* axis) are black crappie (*Pomoxis nigromaculatus*), yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), pumpkinseed (*Lepomis gibbosus*), and walleye (*Sander vitreus*). The top five species contributing to the secondary CA axis (dimension 2, *y* axis) are bluntnose minnow (*Pimephales notatus*), hornyhead chub (*Nocomis biguttatus*), stonecat (*Noturus flavus*), northern hog sucker (*Hypentelium nigricans*), and the johnny darter (*Etheostoma nigrum*).

**Fig. 5** Venn diagram of lake and stream fish comparison. The top five most influential species from the correspondence analysis primary axis are listed in the shared species overlapping circle. Three of the top five species from the correspondence analysis secondary axis are listed in the streams circle; these species occurred in streams, but in <5% of lakes. Species listed in the lakes circle were found in lakes, but not streams. Images are from the Integration and Application Network, University of Maryland Center for Environmental Science (https://ian.umces.edu/symbols/) and do not necessarily reflect listed species. [Colour online.]

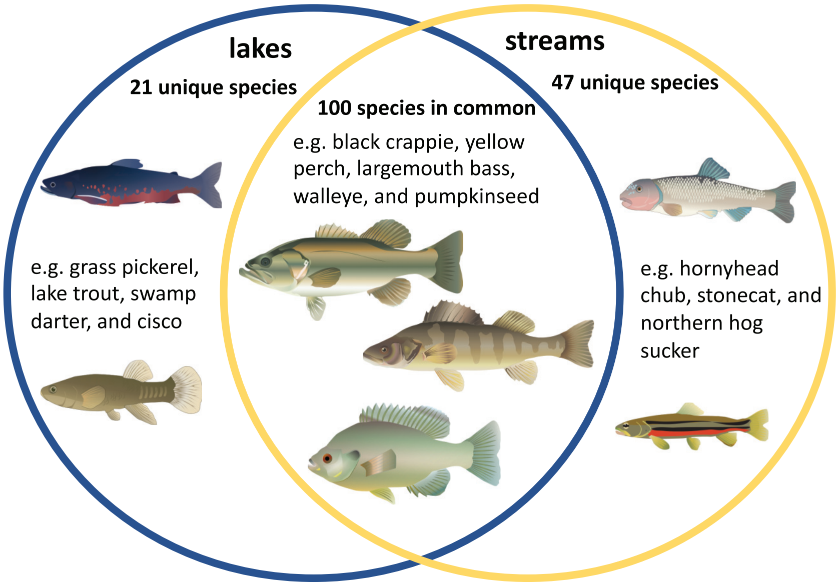
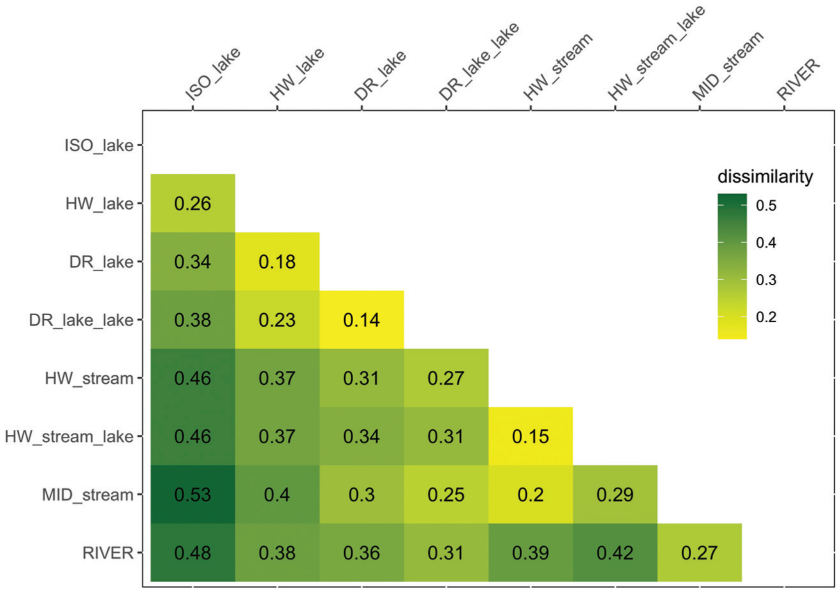


**Fig. 6.** Mean Sørensen dissimilarity index for lakes, streams, and across freshwater types based on all possible pairwise comparisons between each combination of two connectivity classes (PERMANOVA; $F = 73.1$, $p = 0.001$). Sørensen dissimilarity, which uses the presence–absence of a species, measures range from 0 (waterbodies that have all the same species) to 1 (no species are shared across waterbodies). [Colour online.]

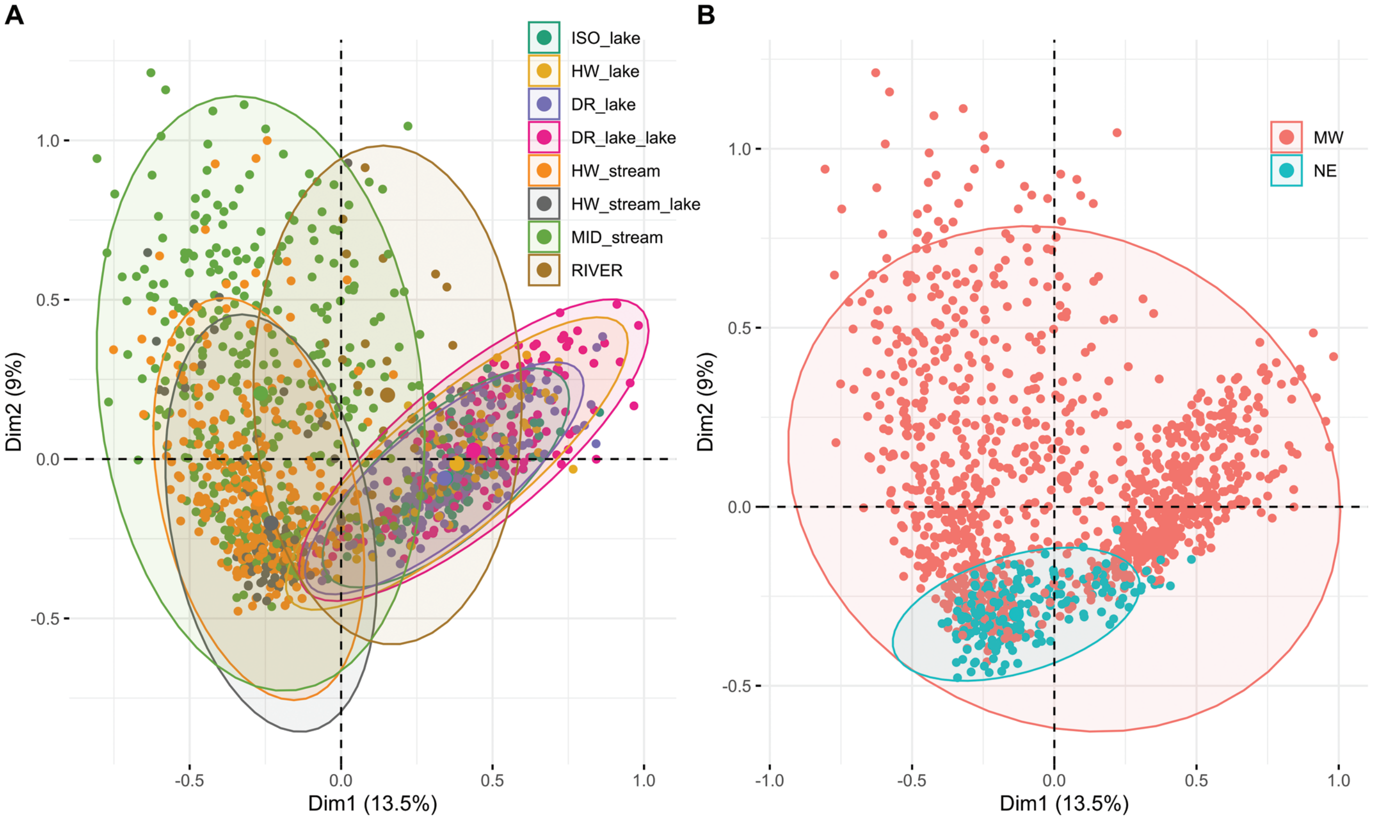


Ninety-five percent ellipses based on connectivity class and region show more divergence in assemblage structure across the eight connectivity classes than between the northeastern and midwestern regions (Fig. 7). However, both connectivity and region ellipses also show nestedness, with the northeastern sites mostly nested within the midwest and assemblages in the ISO_lake class almost completely nested within the DR_lake_lake class (Fig. 7). In contrast, HW_stream and RIVER class assemblages were divergent along the first CA axis, with the MID_stream class in between (Fig. 7*a*). Finally, the assemblage structure in lakes was more similar to waterbodies in the RIVER class than to those in the MID_stream and HW_stream classes (Fig. 7*a*).

## Discussion

Scientists will improve understanding of patterns and drivers of freshwater biodiversity by taking an integrated freshwater perspective to study both lake and stream biotic communities (Jones 2010; Chaloner and Wotton 2011; King et al. 2019). Many aquatic species make use of surface water connections to move among connected waterbodies for food, refuge, and habitat.

**Fig. 7.** Patterns in community structure from correspondence analysis of species presence–absence data. The first two axes (dimension 1 and dimension 2) that best describe community structure were selected for visualization. Connectivity classes and their 95% ellipses are drawn to visualize clustering in assemblage structure across connectivity classes (A), and region and their 95% ellipses are drawn to visualize clustering in assemblage structure based on region (B) (MW = midwest; NE = northeast). [Colour online.]



Therefore, we suggest studying both lake and stream communities along a gradient of surface water connectivity from isolated to very well-connected lakes and streams. With this approach, we found that (*i*) connectivity was positively related to species richness, (*ii*) lakes and streams shared many species, and (*iii*) connectivity helped explain variation in species composition across lakes and streams. Our results demonstrate that lakes and streams are not independent from each other and the importance of including both lakes and streams in analysis, particularly when considering communities of highly mobile organisms like fishes. Incorporating both lake and stream fish communities together in studies will improve future predictions of species distributions in response to climate and land use change and predictions of species richness and composition to unsampled water bodies.

### Species richness and connectivity

Even after accounting for regional species richness differences and waterbody area, our study supports the idea that surface water connectivity is positively correlated with species richness. The midwestern region showed a stronger relationship between connectivity and species richness than what was found in the northeastern region, likely in part because we only had fish data for one isolated lake in the northeast. Regardless, both regions showed an increase in species richness in more connected classes. It is also worth noting the results of our investigation into the ways that waterbody area and connectivity classes may be confounded. For example, slopes across stream and river connectivity classes did not differ significantly. This result may be because these classes are based on Strahler order, which can be a proxy for stream area (Hughes et al. 2011). In contrast, lake area was significantly less correlated with species richness (smaller slope) in the more connected lakes than the isolated lakes, suggesting that connectivity may dampen the effects of lake size. This result is reasonable since a larger isolated lake is likely to have more vertical habitat than a smaller isolated lake, which can result in higher species diversity, whereas both large and small connected lakes have the potential for increased habitat availability in nearby waterbodies (Jackson et al. 2001). The gear types used in this study may underestimate species richness in larger lakes since they do not target deep cold-water species; therefore, stronger relationships may be seen between area and species richness if additional gear types are used in future research.

We found that the more isolated water bodies, such as headwater streams and isolated lakes, had lower richness than the highly connected water bodies, likely due to the fact that these isolated systems are harder to recolonize after extinction events (Griffiths 2015). Interestingly, isolated lakes had higher species richness than the two isolated stream classes. This result is likely in part because, although isolated lakes do not have connections that provide fish species with other lakes or streams for refuge, food, and breeding habitat, lakes provide a wide range of these habitats both vertically and horizontally. For example, fish species may use the shallow nearshore areas for breeding and feeding and may seek refuge in the deep, cold hypolimnion during warm periods or in the daytime when visual predation is high (Jackson et al. 2001). At the other end of the surface water connectivity gradient, rivers and highly connected lakes had higher species richness than more isolated waterbodies. This result supports previous research that showed that connectivity supports the movement of species within and among freshwater types (e.g., Magnuson et al. 1998; Olden et al. 2001; Beisner et al. 2006; Hitt and Angermeier 2008). We found a pattern of higher species richness in more connected waterbodies over a broad geographic extent and for both stream and lake fish communities.

### Species composition and connectivity

Our study of hundreds of lakes and streams across a broad geographic extent provides evidence that existing variation in fish species composition can be partially explained by surface water connectivity. Within a freshwater type, we found that fish assemblages in mid-order streams overlap with both headwater streams and rivers, which is likely because these systems are central in the river network (Hitt and Angermeier 2011). Additionally, the majority of the compositional differences between isolated lakes and highly connected lakes was due to isolated lakes having a low species richness. Most species found in the isolated lakes reflected that of the more connected lakes. Nested patterns have been shown to be influenced by a combination of lake size and isolation, which reduce a fish's access to refugia and (or) colonization routes, as well as predators (e.g., largemouth bass, walleye, yellow perch), that can influence the presence of smaller prey species (Braoudakis and Jackson 2016).

Across freshwater types, species composition in lakes overlapped more with rivers than with streams, likely because rivers are highly connected systems that provide similar habitat and water temperatures as lakes (Irz et al. 2006). Much of this compositional overlap between lakes and rivers, and divergence between lakes and streams, can be attributed to the species that had the most influence on the primary CA axis (black crappie, yellow perch, largemouth bass, pumpkinseed, and walleye), which were very prevalent in lakes, somewhat prevalent in rivers, and less common in streams (Supplemental Table S1[1]). The distribution of these common species, and thus prevalence in lakes as compared with streams, may have been partly due to stocking (especially of walleye) because they are recreationally and economically important. Human transfer of species can lead to homogenized communities among lakes, and some of these species can influence the presence of native species because they are littoral predators (Jackson et al. 2001).

Although there was some overlap in species composition across connectivity classes, we also found some differences across connectivity classes. The species that had the most influence on the secondary CA axis were the hornyhead chub (in streams and rivers but in <5% of lakes and therefore absent from the CA analysis), stonecat (in streams but not in rivers or lakes), and northern hog sucker (in mid-order streams and rivers, but in <5% lakes and headwater streams and therefore absent from the CA analysis). In addition, the tessellated darter (*Etheostoma olmstedi*) and the pugnose minnow (*Opsopoeodus emiliae*), both of which have specific habitat requirements and are nonmigratory, were observed in headwater streams only. Although high variability in flow may make it difficult for headwater streams to support many species, these systems commonly have heterogeneous habitats and good water quality, thus creating unique habitats for species (Jackson et al. 2001).

### Limitations and future directions

To understand broad-scale patterns and drivers of fish biodiversity, we advocate taking an integrated approach that includes both lake and stream fish communities and considers surface water connectivity. However, there are many ways scientists can characterize surface water connectivity. For example, more continuous metrics that incorporate the distance from the stream reach to the nearest lake or that describe the network structure or position of a lake or stream in the network may give further insight into our research findings (Tonkin et al. 2018). Additionally, including data about dams that block dispersal and reduce surface water connectivity will help us to understand regional patterns of biodiversity (Cooper et al. 2016). In fact, much remains to be understood about the conditions that result in positive or negative effects of connectivity or fragmentation (e.g., by dams) on biodiversity (Fausch et al. 2009; Jackson and Pringle 2010).

Further analysis of community structure across broad spatial extents and multiple freshwater types may also be necessary for understanding the role of connectivity in determining fish communities. For example, connectivity may have different effects on biodiversity depending on ecological context, such as land cover or use or terrain (e.g., Magnuson et al. 1998; Henriques-Silva et al. 2019). Our study included wide ranges in many ecological context features, which likely underlies some of the differences we found in fish composition across the northeastern and midwestern US (Abell et al. 2008; Troia and McManamay 2020). However, the fact that the top two CA axes were able to explain 23% of the assemblage structure across such a broad spatial extent and for a large number of lake and stream species speaks to the importance of connectivity for species composition at broad spatial scales. Therefore, taking an integrated freshwater landscape perspective that considers lake and stream fish communities across a broad spatial extent can elucidate how connectivity affects biodiversity differently depending on how connectivity is characterized and the surrounding ecological context.

### Taking an integrated freshwater perspective to understand and conserve biodiversity

Knowledge about the biotic similarities and differences among lakes and streams may provide insight for future freshwater conservation decisions. As climate and land use are altered by human activities around the globe, surface water connections will become even more important for maintaining fish biodiversity, as they will be able to move (or not move) to different parts of their local network during dry periods, to escape warming waters, or to find more oxygen-rich waters (Tonn and Magnuson 1982; McCluney et al. 2014). Increases in water temperature can shift habitat in favor of warm-water tolerant species (e.g., Hansen et al. 2017), and increases in human-induced habitat fragmentation can reduce the ability of fish to move to previously connected waterbodies (Allan et al. 2005). For example, a recent project by the United States Geological Survey modeled water temperatures in lakes and streams to predict fish habitat change with warming temperatures and states that "an integrated assessment of stream and lake temperatures under climate change is necessary for decision-making" (Read 2017). This project shows a movement toward a more integrated freshwater landscape perspective to understand the effects of climate change on freshwater ecosystems. Quantifying surface water connectivity and temperatures will be important for predicting future fish species diversity and community composition (Isaak et al. 2015).

Although we found that surface water connectivity can be positively correlated with species richness, it is important to consider the ways that connectivity can also facilitate the presence of non-native species. For example, isolated waterbodies are more protected from species that migrate, such as the invasive sea lamprey (*Petromyzon marinus*) or the introduced brown trout (*Salmo trutta*) that outcompete native brook trout (*Salvelinus fontinalis*). These two non-native species were not observed in any isolated lakes in our study, demonstrating the potential refugia that these isolated systems may provide for vulnerable fish. Unfortunately for conservationists, surface water connectivity can have complex effects on biodiversity that require managers to incorporate both goals of maximizing species richness and minimizing spread of invasive species into broad-scale conservation plans (Fausch et al. 2009; Jackson and Pringle 2010).

Successful management and conservation of freshwater biodiversity depends on more research and study designs that work across lakes and streams and that explicitly incorporate surface water connectivity. For example, state and federal agencies could incorporate both lake and stream co-located sites into their monitoring programs. Based on our research, we suggest that protecting fresh waters across a range of connectivity will protect the most biodiversity within a region (McCullough et al. 2019) and that including both lakes and streams in conservation and restoration plans will protect species distributions (Erős et al. 2018; Acreman et al. 2019). Because fresh waters are connected to each other, watershed- and regional-level management strategies that include lakes and streams will be more effective than site-level management.

## Acknowledgements

We thank Patrick Hanley, Ian McCullough, Lauren Rodriguez, Nicole Smith, and Joe Stachelek for providing feedback on early drafts and two anonymous reviewers for their constructive feedback. We also thank Maggie Haite, Sophie Morin, and Margaret Brown for help with data mining. We also thank all of the data providers, including the Michigan Department of Natural Resources Status and Trends Program. This research was partially supported by US National Science Foundation Macrosystems Biology program (EF No. 1638679), Michigan State University Environmental Science and Policy Summer Research Fellowship, and the Robert C. Ball and Betty A. Ball Fisheries and Wildlife Fellowship.

## References

Abell, R. 2002. Conservation biology for the biodiversity crisis: a freshwater follow-up. Conserv. Biol. **16**(5): 1435–1437. doi:10.1046/j.1523-1739.2002.01532.x.

Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., et al. 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. BioScience, **58**(5): 403–414. doi:10.1641/B580507.

Acreman, M., Hughes, K.A., Arthington, A.H., Tickner, D., and Dueñas, M.A. 2019. Protected areas and freshwater biodiversity: a novel systematic review distils eight lessons for effective conservation. Conserv. Lett. **13**: 1–14. doi:10.1111/conl.12684.

Aggemyr, E., Auffret, A.G., Jädergård, L., and Cousins, S.A.O. 2018. Species richness and composition differ in response to landscape and biogeography. Landsc. Ecol. **33**: 2273–2284. doi:10.1007/s10980-018-0742-9.

Alger, B.M. 2009. Measuring anthropogenic disturbances in a hydrogeomorphic-based lake classification built using fish assemblages in 360 north-temperate lakes. M.Sc. thesis, Department of Fisheries and Wildlife, Michigan State University, East Lansing, Mich.

Allan, D.J., Palmer, M., and Poff, N.L. 2005. Climate change and freshwater ecosystems. *In* Climate change and biodiversity. *Edited by* T.E. Lovejoy and L. Hannah. Yale University Press, New Haven, Conn. pp. 272–290.

Anderson, M.J. 2017. Permutational multivariate analysis of variance (PERMANOVA). *Edited by* N. Balakrishnan et al. Wiley StatsRef: Statistics Reference Online. Wiley Online Library. Available from https://onlinelibrary.wiley.com/doi/10.1002/9781118445112.stat07841.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecol. Biogeogr. **19**(1): 134–143. doi:10.1111/j.1466-8238.2009.00490.x.

Beisner, B.E., Peres-Neto, P.R., Lindström, E.S., Barnett, A., and Longhi, M.L. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology, **87**(8712): 2985–2991. doi:10.1890/0012-9658(2006)87[2985:TROEAS]2.0.CO;2. PMID:17249222.

Braoudakis, G.V., and Jackson, D.A. 2016. Effect of lake size, isolation and top predator presence on nested fish community structure. J. Biogeogr. **43**: 1425–1435. doi:10.1111/jbi.12731.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., et al. 2010. Global biodiversity: indicators of recent declines. Science, **328**: 1164–1168. doi:10.1126/science.1187512. PMID:20430971.

Chaloner, D.T., and Wotton, R.S. 2011. Overview: the links that bind aquatic ecosystems. J. N. Am. Benthol. Soc. **30**: 751–761. doi:10.1899/10-125.1.

Colvin, S.A.R., Sullivan, S.M.P., Shirey, P.D., Colvin, R.W., Winemiller, K.O., Hughes, R.M., et al. 2019. Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. Fisheries, **44**(2): 73–91. doi:10.1002/fsh.10229.

Cooper, A.R., Infante, D.M., Wehrly, K.E., Wang, L., and Brenden, T.O. 2016. Identifying indicators and quantifying large-scale effects of dams on fishes. Ecol. Indic. **61**: 646–657. doi:10.1016/j.ecolind.2015.10.016.

Daniel, W.M., Infante, D.M., Hughes, R.M., Tsang, Y., Esselman, P., Wieferich, P.C., et al. 2015. Characterizing coal and mineral mines as a regional source of stress to stream fish assemblages. Ecol. Indic. **50**: 50–61. doi:10.1016/j.ecolind.2014.10.018.

Dodson, S.I., Arnott, S.E., and Cottingham, K.L. 2000. The relationship in lake communities between primary productivity and species richness. Ecology, **81**: 2662–2679. doi:10.1890/0012-9658(2000)081[2662:TRILCB]2.0.CO;2.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography, **30**(5): 609–628. doi:10.1111/j.2007.0906-7590.05171.x.

Downing, A. 2005. Relative effects of species composition and richness on ecosystem properties in ponds. Ecology, **86**(3): 701–715. doi:10.1890/03-0239.

Drake, M.T., and Pereira, D.L. 2002. Development of a fish-based index of biotic integrity for small inland lakes in Central Minnesota. N. Am. J. Fish. Manage. **224**(22): 1105–1123. doi:10.1577/1548-8675(2002)022<1105:DOAFBI>2.0.CO;2.

Eadie, J.M., Hurly, T.A., Montgomerie, R.D., and Teather, K.L. 1986. Lakes and rivers as islands: species–area relationships in the fish faunas of Ontario. Environ. Biol. Fishes, **15**: 81–89. Available from https://link.springer.com/content/pdf/10.1007/BF00005423.pdf

Erős, T., O'Hanley, J.R., and Czeglédi, I. 2018. A unified model for optimizing riverscape conservation. J. Appl. Ecol. **55**(4): 1871–1883. doi:10.1111/1365-2664.13142.

Esri. 2014. ArcGIS desktop: release 10.3. Environmental Systems Research Institute, Redlands, Calif.

Esselman, P.C., Infante, D.M., Wang, L., Wu, D., Cooper, A.R., and Taylor, W.W. 2011. An index of cumulative disturbance to river fish habitats of the conterminous United States from landscape anthropogenic activities. Ecol. Restor. **29**(1–2): 133–151. doi:10.3368/er.29.1-2.133.

Fausch, K.D., Rieman, B.E., Dunham, J.B., Young, M.K., and Peterson, D.P. 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conserv. Biol. **23**(4): 859–870. doi:10.1111/j.1523-1739.2008.01159.x.

Fergus, C.E., Lapierre, J.F., Oliver, S.K., Skaff, N.K., Cheruvelil, K.S., Webster, K., et al. 2017. The freshwater landscape: lake, wetland, and stream abundance and connectivity at macroscales. Ecosphere, **8**(8): e01911. doi:10.1002/ecs2.1911.

Gauch, H.G., Jr. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge.

Google Earth Pro. 2019. NOAA. Available from https://www.google.com/earth [accessed 1 November 2019].

Gotelli, N.J., and Chao, A. 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. Encycl. Biodivers. Second Ed. **5**: 195–211. doi:10.1016/B978-0-12-384719-5.00424-X.

Griffiths, D. 2015. Connectivity and vagility determine spatial richness gradients and diversification of freshwater fish in North America and Europe. Biol. J. Linn. Soc. **116**(4): 773–786. doi:10.1111/bij.12638.

Hansen, G.J.A., Read, J.S., Hansen, J.F., and Winslow, L.A. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biol. **23**(4): 1463–1476. doi:10.1111/gcb.13462. PMID:27608297.

Harris, J.H. 1995. The use of fish in ecological assessments. Aust. J. Ecol. **20**: 65–80. doi:10.1111/j.1442-9993.1995.tb00523.x.

Heim, K.C., Arp, C.D., Whitman, M.S., and Wipfli, M.S. 2019. The complementary role of lentic and lotic habitats for Arctic grayling in a complex stream–lake network in Arctic Alaska. Ecol. Freshw. Fish, **28**(2): 209–221. doi:10.1111/eff.12444.

Henriques-Silva, R., Logez, M., Reynaud, N., Tedesco, P.A., Brosse, S., Januchowski-Hartley, S.R., et al. 2019. A comprehensive examination of the network position hypothesis across multiple river metacommunities. Ecography, **42**(2): 284–294. doi:10.1111/ecog.03908.

Hitt, N.P., and Angermeier, P.L. 2008. Evidence for fish dispersal from spatial analysis of stream network topology. J. N. Am. Benthol. Soc. **27**(2): 304–320. doi:10.1899/07-096.1.

Hitt, N.P., and Angermeier, P.L. 2011. Fish community and bioassessment responses to stream network position. J. N. Am. Benthol. Soc. **30**(1): 296–309. doi:10.1899/09-155.1.

Hsieh, T.C., Ma, K.H., and Chao, A. 2020. iNEXT: interpolation and extrapolation for species diversity. R package version 2.0.2. Available from https://CRAN.R-project.org/package=iNEXT.

Hughes, R.M., Kaufmann, P.R., and Weber, M.H. 2011. National and regional comparisons between Strahler order and stream size. J. N. Am. Benthol. Soc. **30**(1): 103–121. doi:10.1899/09-174.1.

Husson, F., Josse, J., Le, S., and Mazet, J., 2020. FactoMineR: multivariate exploratory data analysis and data mining. R package version 2.2. Available from https://CRAN.R-project.org/package=FactoMineR.

Irz, P., Odion, M., Argillier, C., and Pont, D. 2006. Comparison between the fish communities of lakes, reservoirs and rivers: can natural systems help define the ecological potential of reservoirs? Aquat. Sci. **68**: 109–116. doi:10.1007/s00027-005-0812-3.

Irz, P., Michonneau, F., Oberdorff, T., Whittier, T.R., Lamouroux, N., Mouillot, D., and Argillier, C. 2007. Fish community comparisons along environmental gradients in lakes of France and north-east USA. Global Ecol. Biogeogr. **16**: 350–366. doi:10.1111/j.1466-8238.2006.00290.x.

Isaak, D.J., Young, M.K., Nagel, D.E., Horan, D.L., and Groce, M.C. 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Global Change Biol. **21**(7): 2540–2553. doi:10.1111/gcb.12879.

Jackson, C.R., and Pringle, C.M. 2010. Ecological benefits of reduced hydrologic connectivity in intensively developed landscapes. BioScience, **60**(1): 37–46. doi:10.1525/bio.2010.60.1.8.

Jackson, D.A., Peres-Neto, P.R., and Olden, J.D. 2001. What controls who is where in freshwater fish communities — the roles. Can. J. Fish. Aquat. Sci. **58**(1): 157–170. doi:10.1139/f00-239.

Jones, N.E. 2010. Incorporating lakes within the river discontinuum: longitudinal changes in ecological characteristics in stream–lake networks. Can. J. Fish. Aquat. Sci. **67**(8): 1350–1362. doi:10.1139/F10-069.

King, K. 2020. Code and data for lake and stream fish species richness and composition. Github repository code and data. Zenodo. Available from http://doi.org/10.5281/zenodo.4266961.

King, K., Cheruvelil, K.S., and Pollard, A. 2019. Drivers and spatial structure of abiotic and biotic properties of lakes, wetlands, and streams at the national scale. Ecol. Appl. **29**: e01957. doi:10.1002/eap.1957. PMID:31240779.

Kratz, T., Webster, K., Bowser, C., Magnuson, J., and Benson, B. 1997. The influence of landscape position on lakes in northern Wisconsin. Freshw. Biol. **37**(1): 209–217. doi:10.1046/j.1365-2427.1997.00149.x.

Lenth, R. 2019. Emmeans: estimated marginal means, a.k.a. least-squares means. R package version 1.4.1. Available from https://CRAN.R-project.org/package=emmeans.

Lyons, J. 1996. Patterns in the species composition of fish assemblages among Wisconsin streams. Environ. Biol. Fishes, **45**: 329–341. doi:10.1007/BF00002524.

MacArthur, R.H. and Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Magnuson, J.J., Tonn, W.M., Banerjee, A., Toivonen, J., Sanchez, O., and Rask, M. 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. Ecology, **79**: 2941–2956. doi:10.1890/0012-9658(1998)079[2941:IVEITA]2.0.CO;2.

McCluney, K.E., Poff, L., Palmer, M.A., Thorp, J.H., Poole, G.C., Williams, B.S., et al. 2014. Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. Front. Ecol. Environ. **12**(1): 48–58. doi:10.1890/120367.

McCullough, I.M., King, K.B.S., Stachelek, J., Diaz, J., Soranno, P.A., and Cheruvelil, K.S. 2019. Applying the patch-matrix model to lakes: a connectivity-based conservation framework. Landsc. Ecol. **34**: 2703–2718. doi:10.1007/s10980-019-00915-7.

Mellado-Díaz, A., Sánchez-González, J.R., Guareschi, S., Magdaleno, F., and Velasco, M.T. 2019. Exploring longitudinal trends and recovery gradients in macroinvertebrate communities and biomonitoring tools along regulated rivers. Sci. Total Environ. **695**: 133774. doi:10.1016/j.scitotenv.2019.133774. PMID:31422332.

Niu, S.Q., Franczyk, M.P., and Knouft, J.H. 2012. Regional species richness, hydrological characteristics and the local species richness of assemblages of North American stream fishes. Freshw. Biol. **57**(11): 2367–2377. doi:10.1111/fwb.12016.

Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. 2019. vegan: community ecology package. R package version 2.5-6. Available from https://CRAN.R-project.org/package=vegan.

Olden, J.D., Jackson, D.A., and Peres-Neto, P.R. 2001. Spatial isolation and fish communities in drainage lakes. Oecologia, **127**(4): 572–585. doi:10.1007/s004420000620. PMID:28547495.

Osborne, L.L., Kohler, S.L., Bayley, P.B., Day, D.M., Bertrand, W.M., Wiley, M.J., and Sauer, R. 1992. Influence of stream location in a drainage network on the index of biotic integrity. Trans. Am. Fish. Soc. **121**: 635–643. doi:10.1577/1548-8659(1992)121<0635:IOSLIA>2.3.CO;2.

Pépino, M., Rodríguez, M.A., and Magnan, P. 2017. Incorporating lakes in stream fish habitat models: are we missing a key landscape attribute? Can. J. Fish. Aquat. Sci. **74**(5): 629–635. doi:10.1139/cjfas-2016-0221.

Qu, Y., Wu, N., Guse, B., and Fohrer, N. 2017. Riverine phytoplankton shifting along a lentic–lotic continuum under hydrological, physiochemical conditions and species dispersal. Sci. Total Environ. **619–620**: 1628–1636. doi:10.1016/j.scitotenv.2017.10.139. PMID:29066197.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Read, J.S. 2017. An integrated assessment of lake and stream thermal habitat under climate change. Report for Northeast Climate Science Center. USGS. ScienceBase-Catalog Version: 2.165.1. Available from https://www.sciencebase.gov/catalog/item/5a53d604e4b01e7be2308760.

Seaber, P.R., Kapinos, F.P., and Knapp, G.L. 1987. Hydrologic units maps, US Geological Survey Water Supply Paper 2294. Section 508. Available from http://www.usgs.gov/accessibility.html.

Soranno, P., and Cheruvelil, K. 2017*a*. LAGOS-NE-GEO v1.05: A module for LAGOS-NE, a multi-scaled geospatial and temporal database of lake ecological context and water quality for thousands of U.S. Lakes: 1925–2013. Environmental Data Initiative. Available from http://dx.doi.org/10.6073/pasta/b88943d10c6c5c480d5230c8890b74a8 [accessed 23 September 2019].

Soranno, P., and Cheruvelil, K. 2017*b*. LAGOS-NE-GIS v1.0: A module for LAGOS-NE, a multi-scaled geospatial and temporal database of lake ecological context and water quality for thousands of U.S. Lakes: 2013–1925. Environmental Data Initiative. Available from http://dx.doi.org/10.6073/pasta/fb4f5687339bec467ce0ed1ea0b5f0ca [accessed 23 September 2019].

Soranno, P.A., Cheruvelil, K.S., Webster, K.E., Bremigan, M.T., Wagner, T., and Stow, C.A. 2010. Using landscape limnology to classify freshwater ecosystems for multi-ecosystem management and conservation. BioScience, **60**(6): 440–454. doi:10.1525/bio.2010.60.6.8.

Soranno, P.A., Bissell, E.G., Cheruvelil, K.S., Christel, S.T., Collins, S.M., Fergus, C.E., et al. 2015. Building a multi-scaled geospatial temporal ecology database from disparate data sources: fostering open science and data reuse. GigaScience, **4**(1). doi:10.1186/s13742-015-0067-4. PMID:26140212.

Soranno, P.A., Bacon, L.C., Beauchene, M., Bednar, K.E., Bissell, E.G., Boudreau, C.K., et al. 2017. LAGOS-NE: a multi-scaled geospatial and temporal database of lake ecological context and water quality for thousands of U.S. lakes. Gigascience, **6**(12): 1–22. doi:10.1093/gigascience/gix101. PMID:29053868.

Stachelek, J. 2019. Tools for working with the National Hydrography Dataset. R package. Available from https://cran.r-project.org/package=nhdR.

Stachelek, J., and Oliver, S. 2019. LAGOSNE: interface to the lake multi-scaled geospatial and temporal database. R package version 2.0.1. Available from https://cran.r-project.org/package=LAGOSNE

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union. **38**: 913–920. doi:10.1029/TR038i006p00913.

Tonkin, J.D., Altermatt, F., Finn, D.S., Heino, J., Olden, J.D., Pauls, S.U., and Lytle, D.A. 2018. The role of dispersal in river network metacommunities: patterns, processes, and pathways. Freshw. Biol. **63**: 141–163. doi:10.1111/fwb.13037.

Tonn, W.M., and Magnuson, J.J. 1982. Patterns in the species composition and richness of fish assemblages in Northern Wisconsin lakes. Ecology, **63**(4): 1149–1166. doi:10.2307/1937251.

Trigal, C., and Degerman, E. 2015. Multiple factors and thresholds explaining fish species distributions in lowland streams. Global Ecol. Conserv. **4**: 589–601. doi:10.1016/j.gecco.2015.10.009.

Troia, M.J., and McManamay, R.A. 2020. Biogeographic classification of streams using fish community– and trait–environment relationships. Divers. Distrib. **26**(1): 108–125. doi:10.1111/ddi.13001.

USEPA. 2016. National rivers and streams assessment 2008–2009. US Environmental Protection Agency, Washington, D.C. EPA/841/R-16/007.

USGS. 2019. National hydrography dataset. Technical Report. United States Geological Survey. Available from https://nhd.usgs.gov/.

Wehrly, K.E., Breck, J.E., Wang, L., and Szabo-Kraft, L. 2012. A landscape-based classification of fish assemblages in sampled and unsampled lakes. Trans. Am. Fish. Soc. **141**: 414–425. doi:10.1080/00028487.2012.667046.

Wiens, J.J. 2016. Climate-related local extinctions are already widespread among plant and animal species. PLoS Biol. **14**: e2001104. doi:10.1371/journal.pbio.2001104. PMID:27930674.

Willis, T.V., and Magnuson, J.J. 2000. Patterns in fish species composition across the interface between streams and lakes. Can. J. Fish. Aquat. Sci. **57**(5): 1042–1052. doi:10.1139/f00-028.

Yang, W., Ma, K., and Kreft, H. 2013. Geographical sampling bias in a large distributional database and its effects on species richness–environment models. J. Biogeogr. **40**(8): 1415–1426. doi:10.1111/jbi.12108.