RESEARCH ARTICLE

Applying the patch-matrix model to lakes: a connectivity-based conservation framework

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Abstract

Context Biodiversity conservation for terrestrial species often emphasizes land protection to help maintain connectivity among habitat patches. However, conservation of aquatic and semi-aquatic species is challenging because aquatic species (e.g., fish) move among lakes using aquatic connections (e.g., streams, wetlands), whereas semi-aquatic species (e.g., amphibians) use both aquatic connections and upland habitats.

Objectives We applied the patch-matrix model to create an aquatic and semi-aquatic connectivity framework for lakes. We applied our framework using lakes in Michigan, USA to examine (1) the relationship between aquatic and semi-aquatic connectivity for lakes and (2) the extent to which protected areas encompass aquatic and semi-aquatic connectivity among lakes.

Methods We used principal component analysis to calculate aquatic and semi-aquatic connectivity scores for lakes. We then examined relationships among aquatic and semi-aquatic connectivity scores and existing protected areas (strict and multi-use).

Results Fewer than 3% of lakes had high scores for either aquatic or semi-aquatic connectivity. Connectivity scores were generally higher in Michigan's Upper Peninsula, which is heavily forested with greater land protection. Although lake protection was overall low (16 and 32% of lake watersheds in Michigan were ≥ 10% protected under strict and multi-use protection, respectively), highly connected lakes were generally more protected than less connected lakes.

Conclusions We propose using our aquatic and semi-aquatic connectivity framework to (1) identify and prioritize lakes for conservation that are likely to have high biodiversity and conservation value and (2) generate testable hypotheses for studying the integrated terrestrial-aquatic landscape under global change.

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Introduction

Measuring, modeling, and understanding connectivity among discrete habitat patches is a traditional focus in landscape ecology and conservation planning. Inter-patch connectivity through the matrix has long been an important consideration in protected area design (Noss and Harris 1986; Minor and Urban 2008) and has attracted additional interest in the context of climate-driven species' range shifts (Hannah et al. 2007; Robillard et al. 2015). However, past applications of the patch-matrix model to conservation have been mostly terrestrial, with far fewer applications to fresh waters (Erős et al. 2012; Erős and Campbell Grant 2015). In particular, lakes have received very little attention, even though lake and stream networks are strikingly similar to networks of terrestrial nodes and linkages typically considered in landscape ecology (Olden et al. 2001; De Meester et al. 2005; Saunders et al. 2016). From a biodiversity perspective, a challenge when applying the patch-matrix model to lakes is the need to account for different types of connectivity (i.e., aquatic and semi-aquatic; Erős et al. 2012). For example, fish (Magnuson et al. 1998; Olden et al. 2001; Beisner et al. 2006) and zooplankton (Cottenie et al. 2003; Cottenie and De Meester 2003) move among lakes via streams (i.e., aquatic connectivity), whereas semi-aquatic amphibians (Fortuna et al. 2006; Ribeiro et al. 2011; Decout et al. 2012; Peterman et al. 2013; Jeliazkov et al. 2019) and reptiles (Bowne et al. 2006, Pereira et al. 2011) mainly move among lakes through upland vegetation, wet-lands, and temporary ponds (i.e., semi-aquatic con-nectivity). Although previous studies have recognized the importance of both aquatic and semi-aquatic connectivity among freshwater patches (Erős and Campbell Grant 2015, Mushet et al. 2019), no studies have integrated both forms of connectivity into a unifying conceptual framework for lakes, attempted to quantify them, nor examined them with respect to current land conservation practices.

Under rapid global change, connections among fresh waters are an essential topic of study for maintaining seasonal migrations, accessing thermal refuges, and facilitating species' range shifts (Isaak et al. 2015). Therefore, the complex aquatic-terrestrial landscape needs considering when prioritizing lands to conserve freshwater biodiversity. Ideally, protected areas would encompass diverse forms of structural connectivity (i.e., habitat contiguity; Collinge and Forman (1998)) among lakes and other fresh waters to maintain freshwater biodiversity. However, protected areas are usually designated for terrestrial features, rarely taking into account fresh waters or freshwater connectivity (Saunders et al. 2002; Abell et al. 2007). Currently, only an estimated 15–20.7% of fresh waters are protected globally (Juffe-Bignoli et al. 2014, Bastin et al. 2019). Protection of fresh waters them-selves, however, does not guarantee protection of structural connectivity, which has direct consequences for freshwater biodiversity conservation. For example, a study in the US state of Michigan found that protecting wetlands and upland vegetation that facil-itate species' movements benefits semi-aquatic but not strictly aquatic biodiversity (Herbert et al. 2010). Considering the logistical and financial challenges of monitoring freshwater biodiversity across large areas, freshwater biodiversity conservation efforts could benefit from a coarse-filter approach based on struc-tural connectivity (both aquatic and semi-aquatic). Coarse-filter conservation approaches often target community-level or geophysical diversity rather than individual species (i.e., fine-filter approach) (Hunter et al. 1988). However, it is currently unknown to what extent prioritizing conservation of aquatic connectiv-ity benefits semi-aquatic connectivity and vice versa, nor to what extent existing protected areas facilitate these two forms of connectivity. Below, we describe a framework for aquatic and semi-aquatic connectivity among lakes that can be applied as a coarse-filter conservation approach for freshwater biodiversity.

Applying the patch-matrix model to lakes: a new framework based on aquatic and semi-aquatic connectivity

We applied the patch-matrix model to create an aquatic and semi-aquatic connectivity framework for lakes that builds on the graph-based theoretical framework traditionally used in terrestrial ecology. Our conceptual framework treats lakes as focal patches within the integrated aquatic-terrestrial land-scape (Fig. 1). At one extreme are "isolated" lakes that have no aquatic connections and are surrounded by a landscape that is impenetrable for overland movements (Fig. 1c). At the other extreme are highly "connected" lakes with abundant, permanent aquatic connections and a permeable surrounding landscape
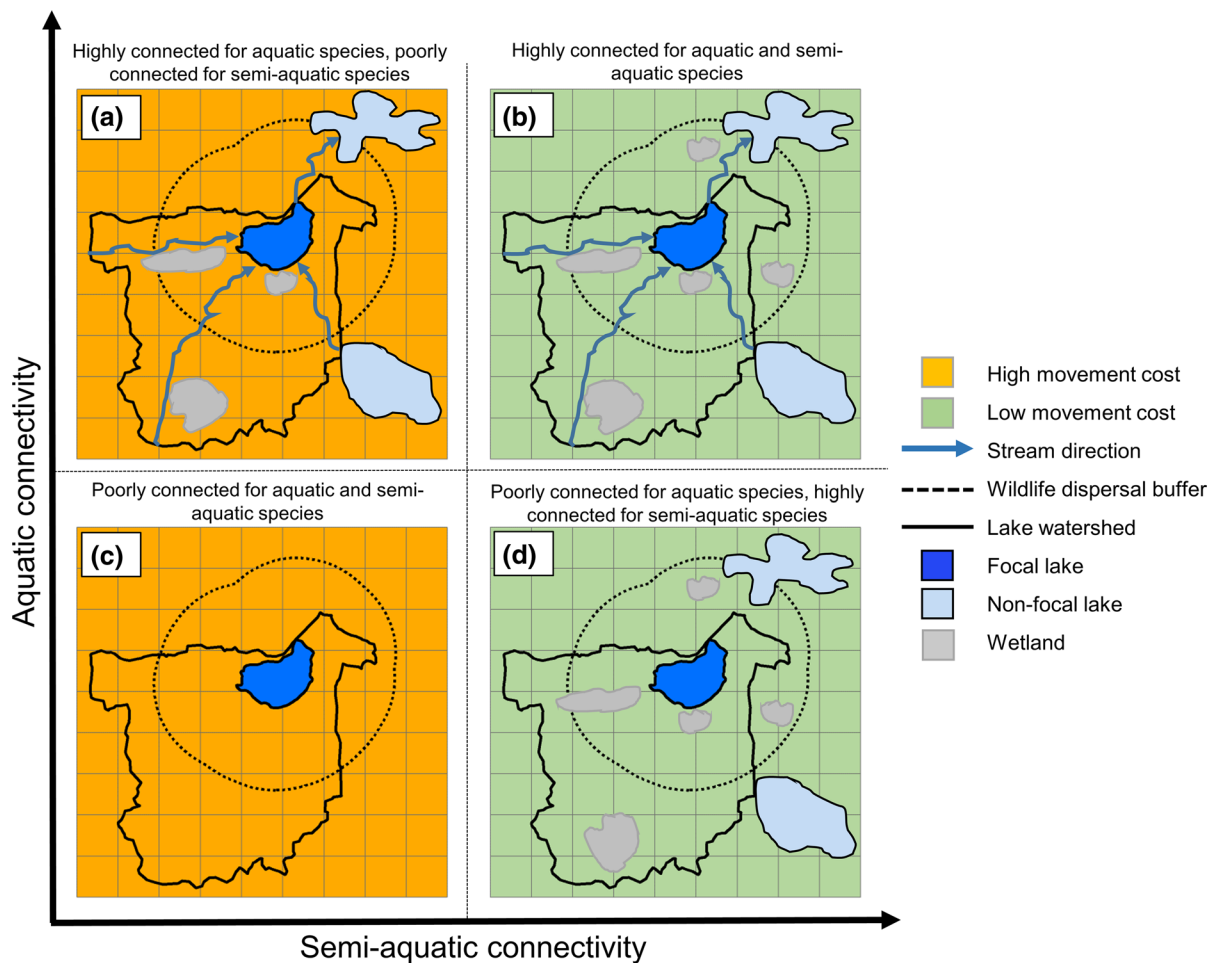
Fig. 1 Conceptual framework for aquatic and semi-aquatic connectivity of lakes, which are treated as discrete habitat patches. The four quadrants represent extreme examples along aquatic and semi-aquatic connectivity gradients. Lakes with high levels of aquatic connectivity (**a**) have inflow and outflow streams, enabling organisms to travel to other lakes, wetlands, or streams both against and with flow direction. Their watersheds have high densities of streams that connect to other lakes as well as wetlands connected to streams and lake shorelines. Lakes with high levels of semi-aquatic connectivity (**d**) are surrounded by aquatic (e.g., lakes and wetlands) and terrestrial (e.g., vegetation types) features that facilitate movements among lakes. Buffer zones represent dispersal distances of semi-aquatic species (often species- and/or life-stage specific) around focal lakes; non-focal lakes within buffers are accessible from the focal lake. Wetlands or small lakes can make non-focal lakes beyond buffers accessible by serving as stepping-stones. Movement costs across the landscape are low due to minimal anthropogenic development and abundant natural vegetation and non-focal aquatic features. Lakes with high levels of aquatic and semi-aquatic connectivity (**b**) share characteristics of a and d. Lakes with no aquatic connections or stepping-stones and that exist in non-permeable (i.e., highly developed) landscapes are the most isolated (**c**)

that facilitates overland movements (Fig. 1b). These examples represent endpoints of two axes; most lakes will likely have some intermediate degree of connectivity, which can vary depending on species, life stage (e.g., different movement ecologies), or time (e.g., seasonal or episodic precipitation or snowmelt).

Aquatic connectivity among lakes is determined by the presence, configuration, and permanence of lakes, streams, and wetlands in both local and network watersheds (for lakes in networks of upstream and downstream lakes), as well as dispersal abilities of species. In general, connected lakes have watersheds with high densities of undammed streams and wetlands, particularly wetlands adjacent to lake shorelines and streams (Fig. 1a, c). Additionally, these lakes have both inflows and outflows, which can connect

focal lakes to other lakes outside its local watershed. Aquatic species capable of swimming (e.g., fish) can access lakes both upstream and downstream of focal lakes (depending on flow velocity), whereas immotile species (e.g., phytoplankton) can only access downstream lakes. In hydrologically isolated lakes, many aquatic species, notably fish, may be absent (Scheffer et al. 2006).

Semi-aquatic connectivity among lakes depends on semi-aquatic species' dispersal abilities and landscape permeability, which is influenced by the presence, distribution, and configuration of both terrestrial and aquatic features such as vegetation, anthropogenic development (particularly roads and land use), topography, and other waterbodies. Therefore, connected lakes are typically surrounded by features with minimal resistance to wildlife movements (e.g., natural vegetation, waterbodies) (Fig. 1 b, d). However, species- or life stage-specific dispersal capacities may be particularly important for semi-aquatic species (Patrick et al. 2012), with longer dispersal capabilities facilitating greater connectivity among lakes. Therefore, lakes in close proximity to other lakes and with permeable landscape features among them generally have greater levels of semi-aquatic connectivity. One way that semi-aquatic connectivity is distinct from aquatic connectivity is that dispersal distances may extend into watersheds of non-focal lakes, and small lakes or wetlands may function as stepping-stones among larger lakes, potentially facilitating connectivity beyond the standard dispersal distance from the focal lake (Pereira et al. 2011). Overall aquatic and semi-aquatic connectivity of lakes thus depends on the integrated aquatic-terrestrial landscape, encompassing watersheds of focal and connected lakes, as well as areas surrounding lakes within dispersal distances for semi-aquatic species.

Study objective and questions

We tested our aquatic and semi-aquatic connectivity framework using approximately 6000 lakes ≥ 4 ha in Michigan, USA and examined the extent to which protected areas encompass aquatic and semi-aquatic connectivity among lakes. We asked the following:

1. To what extent do lakes with high levels of aquatic connectivity also have high levels of semi-aquatic connectivity?

2. To what extent do existing protected areas facilitate aquatic and semi-aquatic connectivity among lakes?

Finally, we discuss application of our framework for integrating fresh waters into conservation planning and studying responses of lake biodiversity to global change.

Methods

Study area

This study was conducted in both peninsulas (Upper and Lower) of the US state of Michigan. Michigan has a humid continental climate with four distinct seasons. Mean annual temperatures generally decrease with latitude, ranging 3–10 °C based on 1981–2010 normals (PRISM Climate Group 2004). Mean annual precipitation is generally greatest in the southwestern part of the state (> 1000 mm) and lowest in the northeastern Lower Peninsula and western Upper Peninsula (< 700 mm) based on 1981–2010 normals (PRISM Climate Group 2004). The Great Lakes are responsible for the longitudinal gradient in precipitation, which occurs throughout the year (Andresen 2017). Precipitation falls primarily as snow in winter, but can vary from 900 to over 5500 mm annually from the southeastern Lower Peninsula to the northwestern Lower and northern Upper Peninsulas, respectively, particularly due to lake effect processes (Andresen 2017).

Land use and land cover in Michigan follow distinct regional patterns. The Lower Peninsula is dominated by agriculture and urban development in the south and a mixture of forest and agriculture in the north (Pugh 2018). Nearly half of the state's 10 million human population lives in metropolitan Detroit in southeastern Michigan. In contrast, the Upper Peninsula is mostly forested and contains just 3% of the state population, despite comprising 29% of the state's total land area (Pugh 2018). Surface waters are abundant throughout the state, including extensive networks of streams, wetlands, and lakes (Fergus et al. 2017). Although the Upper Peninsula contains some hills reaching approximately 600 m, Michigan overall has little topographic relief, particularly in the agriculture-dominated Lower Peninsula.

Geospatial datasets

We used permanent lakes $\geq$ 4 ha as focal lake "patches", obtained from LAGOS-NE-GIS v. 1.0 (Soranno and Cheruvelil 2017b). We chose this size cutoff for focal lakes because lakes > 4 ha are more likely to be managed and monitored than smaller lakes (Michigan Status and Trends; Hayes et al. 2003); however, we included small lake polygon features (0.1–4 ha) obtained from NHD Plus v. 2 (USGS 2018) as potential stepping-stones in dispersal buffers (for semi-aquatic wildlife) around larger focal lakes. Wetlands within dispersal buffers were quantified using the National Wetlands Inventory (USFWS 2018). Watershed polygons (LAGOS-NE-GIS v. 1.0) and measures of watershed aquatic connectivity (LAGOS-NE-GEO v. 1.05; Soranno and Cheruvelil 2017a) were obtained from the database LAGOS-NE (Soranno et al. 2017). We used the US Protected Areas Database (PADUS) v. 1.4 (USGS 2016) to map Michigan protected areas and to account for different protection statuses (Fig. 2). Consistent with similar studies (Herbert et al. 2010, Jenkins et al. 2015,
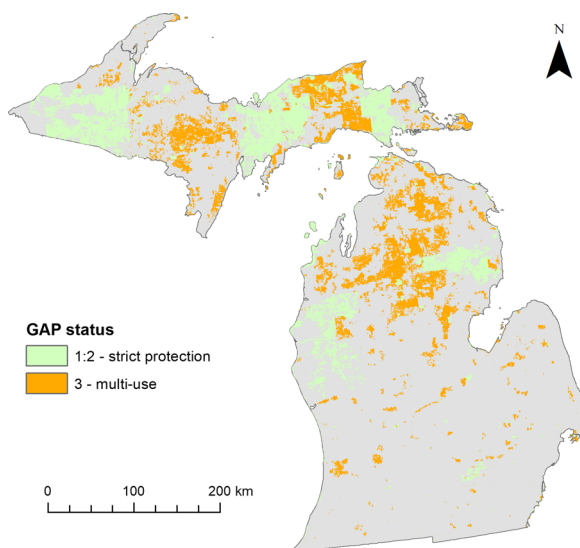
Panlasigui et al. 2018), we considered lands under Gap Analysis Program (GAP) status 1–3 as protected. We considered GAP status 1–2 as strictly protected (e.g., national parks, wilderness areas), recognizing that status 3 lands allow some resource extraction (e.g., national forests that allow timber harvests). We excluded status 4 lands because these have no legally-mandated, permanent protection and comprise a small proportion of protected areas compared to lands under status 1–3.

Quantifying aquatic and semi-aquatic connectivity for lakes

We used principal component analysis (PCA) to condense aquatic and semi-aquatic connectivity variables into two dimensions, respectively (performing separate PCAs for aquatic and semi-aquatic). We chose PCA because we were focused on quantifying composite indices of aquatic and semi-aquatic connectivity rather than the relative importance of individual contributing connectivity variables. We maximized use of available information in the different contributing variables by using all principal components in calculating aquatic and semi-aquatic connectivity scores. In n-dimensional space, the length of the longest diagonal (distance to origin) is the square root of the sum of the squares of the legs (i.e., side lengths) (Yeng et al. 1990). Therefore, regardless of the number of principal components, the distance from the origin represents a composite aquatic or semi-aquatic connectivity score by extension of the Pythagorean theorem. PCA results are fully summarized in Supplementary material 1 (Figs. S1–S2, Tables S1–S2). Aquatic and semi-aquatic connectivity scores ranged from 0.07 to 14.63, with larger scores indicating greater connectivity. We used the traditional 2-dimensional Pythagorean theorem to calculate a combined aquatic/semi-aquatic connectivity score for each lake. We used R v. 3.5.1 for all R analyses (R Core Team 2018). Data and R scripts are available on Zenodo (McCullough 2019).

Aquatic connectivity

The aquatic connectivity variables we used were watershed stream density, proportion of watersheds covered by stream-connected wetlands, and proportion of lake shorelines adjacent to wetlands (occurring

Fig. 2 Protected areas of Michigan based on Gap Analysis Program (GAP) status in US Protected Areas Database (PADUS) v. 1.4. GAP status 1: managed for biodiversity with natural disturbances allowed to proceed or mimicked. GAP status 2: managed for biodiversity with natural disturbances suppressed. Status 1 and 2 lands are considered strictly protected. GAP status 3: managed for multiple uses and subject to extractive activities (e.g., mining or logging) or off-highway vehicle use. Gray background represents unprotected land

within 30 m lake buffers) (Table 1). We considered but ultimately excluded dam density and watershed proportions covered by non-focal lakes ($\geq$ 4–10 ha) due to low variability across study watersheds. We also excluded total watershed wetland cover due to high correlation with stream-connected wetlands (r = 0.76). We extracted all variables for Michigan lakes $\geq$ 4 ha using the LAGOSNE R package (Stachelek and Oliver 2017).

Semi-aquatic connectivity

We used buffers around focal lakes to quantify semi-aquatic connectivity (Table 1). We evaluated buffer widths by reviewing previous studies of semi-aquatic amphibian and reptile dispersal. We chose a 1500 m buffer to encompass maximum dispersal distances by most semi-aquatic amphibians (reviewed by Smith and Green 2005) and reptiles (reviewed by Roe and Georges 2007). We counted the number of small lake (0.1–4 ha) and wetland patches within buffers to quantify the availability of aquatic habitats accessible via overland movements (we excluded streams because they may be reached via aquatic movements). We counted number of lake patches rather than area of lakes because lakes were often only partially within buffers. In addition, we quantified the proportion of buffers covered by lake edge and wetland habitat, calculated as the perimeter of overlapping lakes and wetlands translated to 900 m² cells [matching

resolution of the National Land Cover Database; NLCD (USGS 2011)] divided by buffer area. We focused on lake edge rather than core habitat to represent potential lake entry points and to reflect semi-aquatic species' preference for shallow habitat along lake margins. All aforementioned connectivity variables were calculated in R using GIS functions in the raster (Hijmans 2017), rgeos (Bivand and Rundel 2018), and spatialEco (Evans 2018) packages. Finally, we calculated the cost distance from focal lakes to the nearest non-focal lake ($\geq$ 4 ha) using a cost surface derived from a combined land cover, waterbody, and road raster dataset (Fig. S3). Cost values were assigned based on mean movement costs estimated in Patrick et al. (2012) for 6 semi-aquatic amphibian and reptile species native to Michigan. These species were the green frog (*Lithobates clamitans*), American toad (*Anaxyrus americanus*), red-spotted newt (*Notophthalmus viridescens*), common snapping turtle (*Chelydra serpentina*), painted turtle (*Chrysemys picta*), and wood turtle (*Glyptemys insculpta*), all of which use lakes as habitat for at least part of the year. We opted to create a generalized cost surface so that landscape permeability within buffers would pertain to a diverse suite of semi-aquatic species. Development of the cost surface and calculation of cost distances are described in detail in Supplementary Material 1.

Table 1 Aquatic and semi-aquatic connectivity variables for lakes

Aquatic	Data sources(s)	Semi-aquatic	Data source(s)
Watershed stream density (m/ha)	LAGOS-NE-GEO v. 1.05	Number of lake patches (0.1–4 ha) within dispersal buffer	NHD Plus[a] v. 2 medium resolution
Watershed stream-connected wetland cover (prop.)	LAGOS-NE-GEO v. 1.05	Number of wetland patches within dispersal buffer	National Wetlands Inventory
Shoreline wetland cover (prop.)	LAGOS-NE-GEO v. 1.05	Lake edge area within dispersal buffer (prop.)	NHD Plus v. 2 medium resolution
		Wetland area within dispersal buffer (prop.)	National Wetlands Inventory
		Cost distance to nearest lake	NLCD[b] 2011, NHD Plus v. 2, TIGER[c]

[a]National Hydrography Dataset

[b]National Land Cover Database

[c]Topologically Integrated Geographic Encoding and Referencing

Lake connectivity and protected areas

We calculated the proportion of lake watersheds and dispersal buffers for each focal lake ≥ 4 ha) protected under strict protection (GAP status 1–2) and multi-use (GAP status 1–3) using the Tabulate Area tool in ArcGIS v. 10.6.0. We next associated these proportions with connectivity scores (aquatic and semi-aquatic individually) using Pearson correlation coefficients. We opted for separate analyses for focal watersheds and dispersal buffers because semi-aquatic species may travel outside the watersheds of focal lakes.

Results

Aquatic and semi-aquatic connectivity of lakes

Aquatic and semi-aquatic connectivity scores were generally low across Michigan lakes. The correlation between aquatic and semi-aquatic connectivity scores was weak (r = 0.14), indicating that few lakes had high scores along both axes (Fig. 3). Frequency
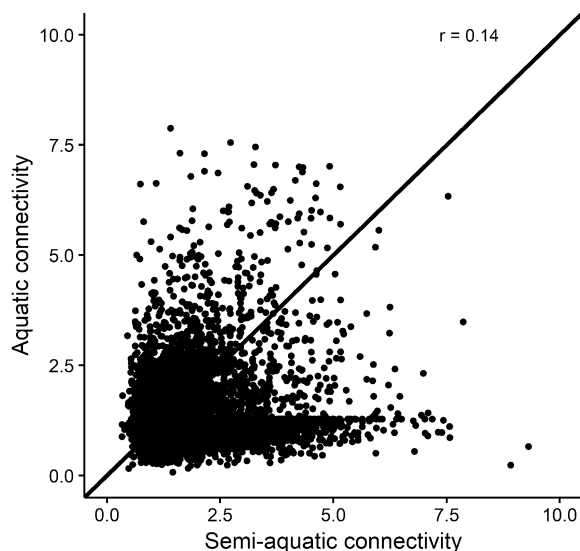

Fig. 3 Association between aquatic and semi-aquatic lake connectivity PCA scores for Michigan lakes ≥ 4 ha (n = 6213) (per Fig. 1). The combined aquatic/semi-aquatic connectivity score is the distance from the plot origin. R value is the Pearson correlation coefficient. Thick black line is 1:1 fit. Due to axis limits, 7 lakes are not shown (maximum values for aquatic, semi-aquatic, and combined scores were 10.5, 14.6 and 14.7, respectively)

distributions demonstrated that aquatic, semi-aquatic, and combined connectivity scores were 2 or lower for the majority of lakes, indicating that highly connected lakes were relatively rare (Fig. 4). Lake connectivity scores were overall higher for semi-aquatic connectivity than for aquatic connectivity (Fig. 4). Overall, many Michigan lakes fell into the least-connected quadrant C of our aquatic and semi-aquatic connectivity framework (Fig. 1).

Connectivity scores were generally greater in Michigan's Upper Peninsula (Fig. 4), despite the Upper Peninsula containing only 29.4% of Michigan lakes ≥ 4 ha. This result is likely because the Upper Peninsula is heavily forested and largely undeveloped (Fig. 2). The highest aquatic connectivity scores were found mostly in the Upper Peninsula and the northern Lower Peninsula; however, high semi-aquatic connectivity scores were dispersed throughout both peninsulas (Fig. 4). When connectivity scores were combined for both aquatic and semi-aquatic connectivity, lakes with high connectivity scores increased in number and were scattered across Michigan, with the majority in the Upper Peninsula.

Lake connectivity and protected areas

Most lake watersheds and buffers were not well protected in Michigan. In general, the proportions of lake watersheds and buffers in protected areas in Michigan were low (medians < 0.01) in both strict and multi-use protected areas (Fig. 5). Only 16 and 32% of all lake watersheds in Michigan were ≥ 10% protected under strict and multi-use protection, respectively (Fig. 5). In fact, just 6 and 10% of lake watersheds were ≥ 90% protected for strict and multi-use protection, respectively. Similarly, 16 and 31% of buffers were ≥ 10% protected under strict and multi-use protection, respectively, and only 4% were ≥ 90% protected under strict or multi-use protection. Lakes with the greatest watershed and buffer proportions protected (≥ 0.60) under strict protection were predominantly found in the Upper Peninsula and in both the Upper Peninsula and northern Lower Peninsula when protection was expanded to multi-use (Fig. 6, S4).

Although we found positive correlations (r = 0.28–0.56) between lake connectivity scores (aquatic and semi-aquatic) and land protection (strict and multi-use), these associations were affected by a

Fig. 4 Maps and frequency distributions for aquatic, semi-aquatic, and combined aquatic/semi-aquatic connectivity scores for Michigan lakes ≥ 4 ha (n = 6213). Aquatic and semi-aquatic correspond to Y and X axes, respectively, in Fig. 3. Combined scores are the distance from the origin in Fig. 3. Points were overlaid with higher scores on top for visual emphasis. Due to axis limits, 7 lakes are not shown (maximum values for aquatic, semi-aquatic, and combined scores were 10.5, 14.6 and 14.7, respectively)
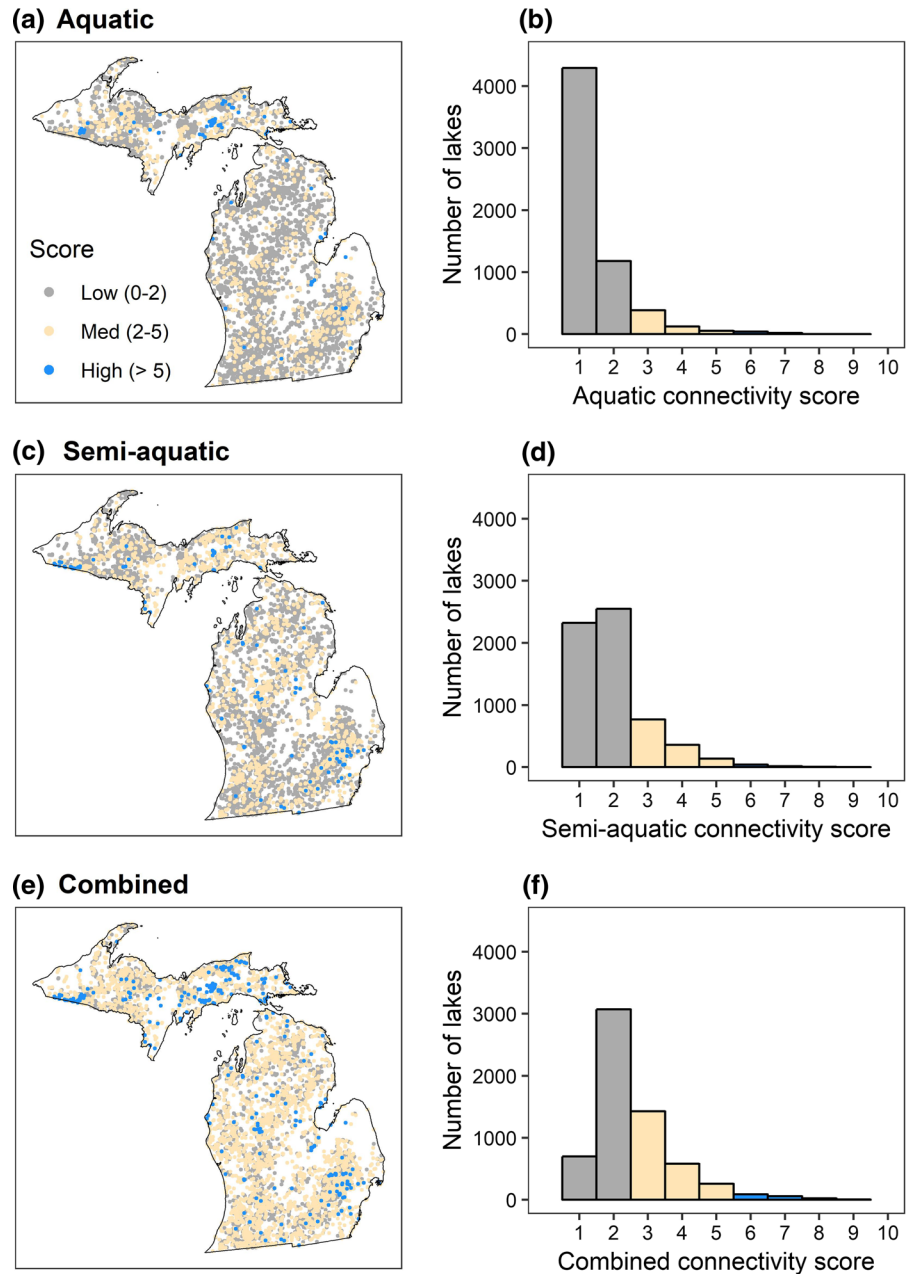

large number of lakes with low levels of protection (Fig. 7). The relatively low number of highly protected lake watersheds and buffers may be attributed to Michigan having a relatively low amount of protected land (approximately 12 and 22% under strict and multi-use protection, respectively), and to those protected areas being fragmented (Fig. 2), particularly in the Lower Peninsula. Generally, we would expect large, contiguous protected areas to contain more

highly connected lakes because such areas are more likely to contain entire lake watersheds (or dispersal buffers) and minimize connectivity barriers (e.g., land use/cover change, dam building) for aquatic and semi-aquatic species.

It is also important to note that across all lakes in our study, proportions of watersheds and buffers protected were moderately correlated for strict (r = 0.68) and multi-use (r = 0.66) lands. Watersheds,

Fig. 5 Frequency distributions of protection for lake watersheds (top row) and dispersal buffers (bottom row) for strictly protected (left column) and multi-use protected (right column) lands
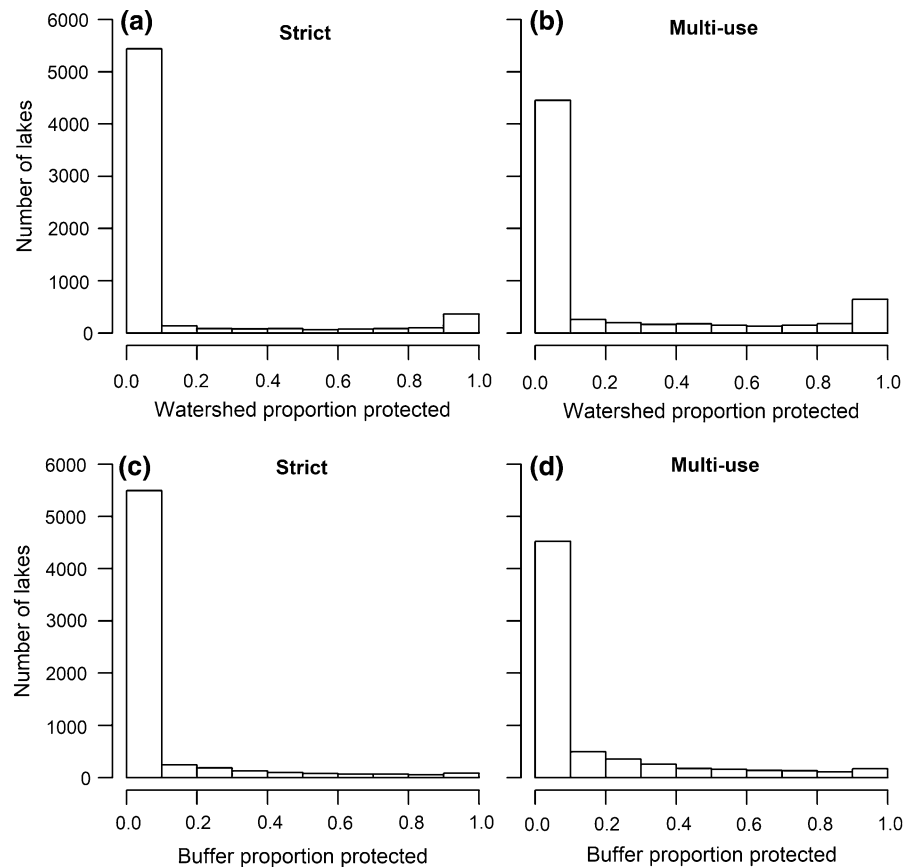
however, were considerably smaller than buffers (medians: 166 and 954 ha, respectively). Therefore, watershed protection does not necessarily translate into protection for semi-aquatic species that move large distances across watershed boundaries.

Discussion

Past landscape ecology and conservation efforts, including designating protected areas, have been focused on terrestrial rather than aquatic habitats (Saunders et al. 2002). Here, we applied the patch-matrix model to lakes to represent aquatic and semi-aquatic connectivity within the integrated aquatic-terrestrial landscape, using the state of Michigan as a case study. We then quantified the relationship between aquatic and semi-aquatic connectivity and the proportions of lake watersheds and semi-aquatic species' dispersal buffers for Michigan lakes that had been incidentally protected by land conservation

practices. Below, we describe applications of this connectivity framework, with a focus on conserving freshwater biodiversity and predicting responses to global change.

Applying the aquatic and semi-aquatic connectivity framework to conservation planning

Our aquatic and semi-aquatic connectivity framework can be used as a coarse-filter approach for conservation of lakes and their biodiversity based on structural connectivity. The framework is potentially widely applicable because it depends on commonly available geospatial datasets. Few studies have combined aquatic and semi-aquatic connectivity into a single conservation planning framework for fresh waters (Hermoso et al. 2012; Mushet et al. 2019), and we are aware of no such studies for lakes. Identifying highly connected lakes could help prioritize lakes for conservation that are important for facilitating functional connectivity (i.e., movement outside habitat and
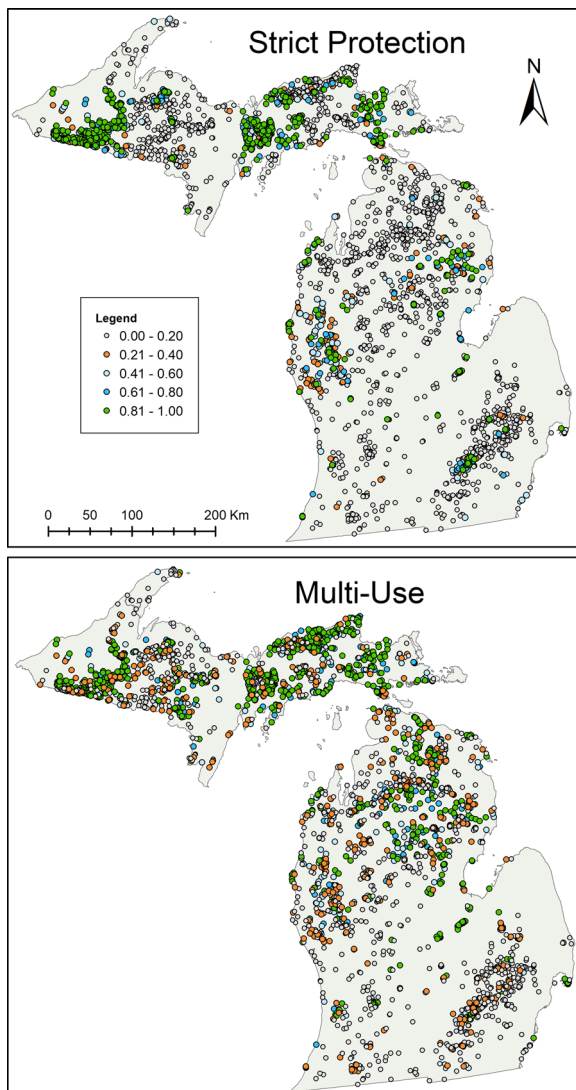
Fig. 6 Maps of proportion of lake watersheds protected under strict (top) and multi-use protection (bottom). Corresponding maps for proportion of dispersal buffers protected are in Supplementary material 1 (Fig. S4)

through the matrix; Collinge and Forman (1998)) and species' range shifts in response to climate change. On the other hand, highly connected lakes may be disproportionately vulnerable to invasive species (Panlasigui et al. 2018), and hydrologically isolated lakes may harbor regionally unique populations, species or communities (Griffiths 2015). Therefore, it is important to clarify the role of connectivity in conservation objectives and incorporate the full range of connectivity (i.e., isolated to highly connected) in conservation planning for fresh waters.

Conservation planning efforts often seek to identify priority areas for protection, which in the freshwater realm, are often river watersheds or sub-watersheds (Nel et al. 2009; Erős et al. 2018). The protected area is a mainstay of the conservation toolbox, but many studies have previously pointed out that protected areas are not necessarily effective for conserving freshwater biodiversity and ecosystems due to challenges associated with connectivity and the exogenous nature of many threats (e.g., nutrient loading, damming, non-native fish stocking) (Saunders et al. 2002; Herbert et al. 2010). In addition to the terrestrial focus of conservation biology, these challenges likely help explain why freshwater protected areas are rare relative to terrestrial reserves (Abell et al. 2007). Several studies, however, have designed conservation planning frameworks for joint consideration of terrestrial and freshwater ecosystems, recognizing shared threats and conservation benefits (Adams et al. 2014). For example, maintaining riparian vegetation regulates stream temperatures (Larson and Larson 1996) and provides terrestrial movement corridors or thermal refuges (Krosby et al. 2018). A potential challenge to achieving both terrestrial and freshwater targets in conservation planning, however, is the need for a planning unit (e.g., watersheds, land parcels) that is relevant for terrestrial, semi-aquatic, and aquatic species. Although our finding of a moderate correlation between protection of lake watersheds and protection of semi-aquatic species' dispersal buffers ($r = 0.66–0.68$) suggests that watershed protection can simultaneously encompass some habitat for aquatic and semi-aquatic species at regional scales, focusing on watersheds may be impractical if they have not been mapped, or incompatible with conservation goals if there are particular semi-aquatic species of interest that disperse outside of the watershed.

Applying the aquatic and semi-aquatic connectivity framework to global change ecology lake research

Our aquatic and semi-aquatic connectivity framework can be used to make several general hypotheses rooted in island biogeographic theory and community ecology for future research on biodiversity-connectivity relationships in lakes (and other fresh waters), particularly under global change. Similar to large, connected islands, large, connected lakes could experience more

Fig. 7 Associations
between lake connectivity
scores (aquatic and semi-
aquatic) and protection
(strict and multi-use) of lake
watersheds (top row) and
dispersal buffers (bottom
row). R values are Pearson
correlation coefficients
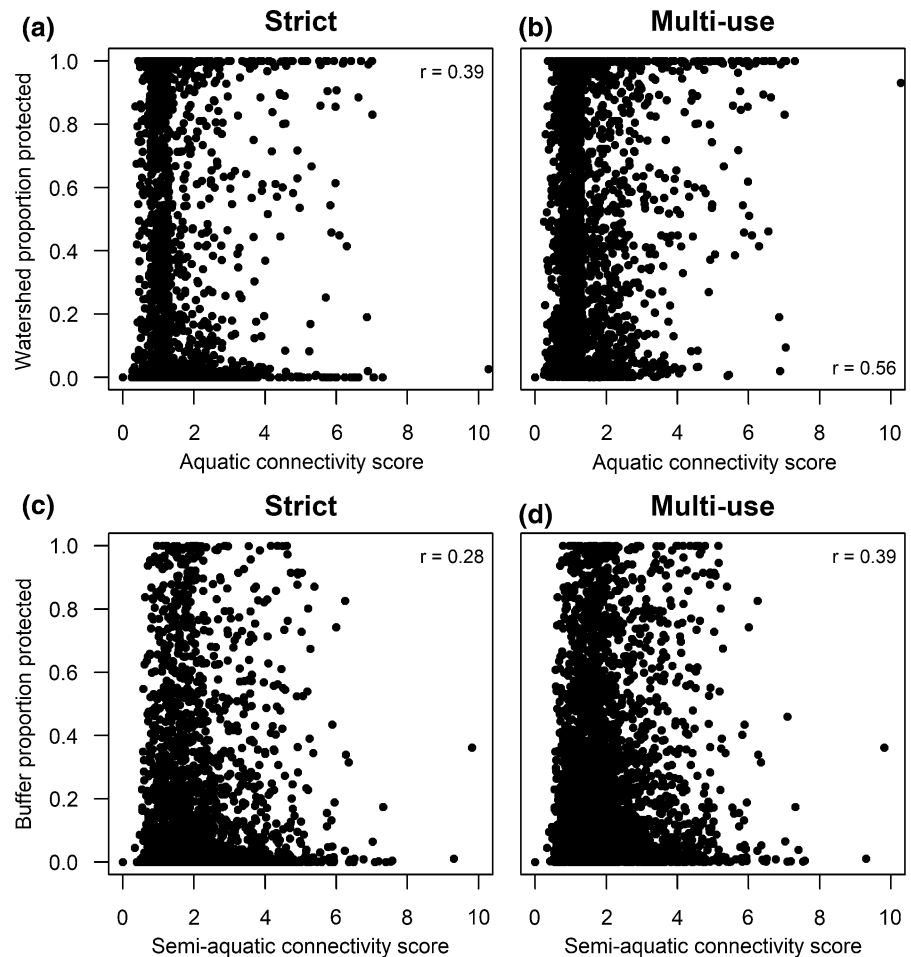
species' colonizations and thus greater biodiversity, but species interactions and ecological context likely also matter (Hortal et al. 2014). Past research has found mixed support across taxa for the transferability of island biogeographic theory (i.e., species-area relationships, effects of isolation) to lake species diversity and abundance (Lassen 1975; Browne 1981; Oertli et al. 2002). Small, hydrologically isolated lakes are commonly fishless, but also contain high diversities of plants, amphibians, invertebrates, and birds, due both to the absence of fish and the unique, often shallow biophysical environment (Scheffer et al. 2006). The paucity of biogeographic studies of aquatic and semi-aquatic species, however, likely reflects the data limitations associated with this area of research; accurate measures of lake species presence, absence, and abundance are difficult and expensive to collect across large areas. Although there has been extensive

research on connectivity within small networks of (often temporary) ponds for amphibians (e.g., Marsh and Trenham 2001) and reptiles (e.g., Bowne et al. 2006), there has been considerably less broad-scale, biogeographic research on larger, permanent lakes. Relatively cost-effective species' detection methods such as environmental DNA analysis, however, could improve and expand assessments of species' past and current presence and abundance in lakes across large areas (Thomsen et al. 2012). Therefore, the time is right for exploring these ideas in a global change context at broad spatial and temporal scales. Below we provide three hypotheses based on our aquatic and semi-aquatic connectivity framework intended to spur such research.

H1 Highly connected lakes have greater biodiversity than poorly connected lakes.

Whereas some studies have examined the role of hydrologic connectivity in zooplankton metapopulations (Cottenie et al. 2003; Cottenie and De Meester 2003) and many studies have shown relationships between fish populations and connectivity within river networks for both native anadromous (Fullerton et al. 2010) and invasive species (Coulter et al. 2018), no studies have examined broad-scale patterns of aquatic and semi-aquatic biodiversity in lakes as a function of both aquatic and semi-aquatic connectivity (sensu Fig. 1). Hypothetically, the availability of both types of connections should enable colonizations and continued gene flow for both aquatic and semi-aquatic species. In addition, connectivity enhances seasonal migrations among lakes (e.g., fish seeking thermal refuge from warm, shallow lakes to cool, deep lakes). Effects of climate warming on the availability of thermal habitat for fish has been a topic of concern in streams and rivers (Eaton and Scheller 1996; Brewitt and Danner 2014), but has not been studied in the context of connected lakes. Lakes with declines in thermal habitat, particularly for cool- and cold-water fish species, may be subject to local extinctions without the hydrologic connections necessary for warming-induced range shifts (Isaak et al. 2015; Hansen et al. 2017).

H2 Biodiversity in lakes depends on type of connectivity, species interactions, and local and regional ecological context.

An extension of H1 is that lakes with high levels of aquatic connectivity (Fig. 1, quadrant a) should have more aquatic biodiversity, whereas lakes with high levels of semi-aquatic connectivity (Fig. 1, quadrant d) should have more semi-aquatic biodiversity due to the dominance of respective connectivity pathways. Hydrologically isolated lakes are difficult for fish to colonize naturally and past studies have shown increased diversity of zooplankton (Donald et al. 2011), macroinvertebrates (Schilling et al. 2009), waterbirds (Haas et al. 2007), and amphibians (Hecnar and M'Closkey 1997) in the absence of fish. In lakes with high levels of both aquatic and semi-aquatic connectivity (Fig. 1, quadrant b), which our analysis of Michigan lakes suggests are rare, diversity should be determined more so by species interactions and habitat heterogeneity than dispersal limitations. Large, multi-basin lakes with varying morphometry often support deep, cold-water habitats (e.g., suitable for

salmonids) and shallow, warm-water habitats (e.g., suitable for amphibians and reptiles). Past research, however, suggests that lakes without abundant aquatic connections may actually have greater biodiversity than lakes with such connections (Scheffer et al. 2006; Davies et al. 2010). These lakes may contribute to higher regional diversity or harbor unique species as opposed to a subset of species found in other lakes within the region (Scheffer et al. 2006; Pool et al. 2014). In addition, differences in regional landscape context such as land use or topography may change the influence of connectivity in structuring lake communities (e.g., Magnuson et al. 1998). Therefore, varying levels of aquatic and semi-aquatic connectivity likely interact with both local and regional ecological context to determine species composition in and among lakes (Scheffer et al. 2006).

H3 Biodiversity in lakes depends on dynamic connectivity, particularly under global change.

The role of dynamic connectivity (spatial and temporal) for both aquatic and semi-aquatic species is a largely unstudied topic. Episodic "windows of opportunity" have been shown to be important for the establishment of plant populations, including long-distance events (Eriksson and Fröborg 1996), but this concept has not been widely demonstrated for aquatic or semi-aquatic wildlife (Campbell Grant et al. 2010; Zylstra et al. 2019). Permanent aquatic landscape features afford greater connectivity among lakes than seasonal or intermittent features (e.g., vernal pools). Particularly in dry landscapes, above-average precipitation can increase the abundance and size of temporary lakes and wetlands (i.e., stepping-stones) across landscapes, potentially facilitating greater dispersal success to lakes for semi-aquatic organisms (Bishop-Taylor et al. 2017). Above-average precipitation can also increase the volume and duration of non-permanent streams, potentially increasing aquatic migrations to permanent streams and lakes. Conversely, extensive warm periods with low amounts of precipitation may reduce the abundance and size of lakes, tributaries, and wetland stepping-stones, increasing lake isolation (McMenamin et al. 2008). Therefore, static connectivity metrics likely have limited usefulness in dry landscapes where connectivity is highly dynamic (Bishop-Taylor et al. 2018). Amphibians are expected to be particularly sensitive to climate change owing to their unique physiology

and dispersal limitations (Lawler et al. 2010), so dynamic connectivity among lakes may play a major role in local extinctions and colonizations. Land use/cover change alters landscape structure and therefore may also influence connectivity among lakes (e.g., wetland draining, logging, residential development). As such, some lakes may grow increasingly isolated under global change due to changes in the distribution and abundance of aquatic habitats and land use/cover.

Conclusion

Numerous, recent species extinctions have been documented in lakes across taxonomic groups at mid to high latitudes (Ricciardi and Rasmussen 1999; Ricciardi et al. 2002; Burkhead 2012; Ding et al. 2017). Most of the world's lakes are distributed across high latitudes (e.g., Canada, northern Europe and Eurasia) (Verpoorter et al. 2014), and the current status of their biodiversity is not well known. We developed an aquatic and semi-aquatic connectivity framework for lakes that can be used as a coarse-filter for conserving freshwater biodiversity based on structural connectivity. Our framework is flexible and relies on available geospatial data layers, and therefore could be applied to many US regions outside of Michigan and around the globe. Not only can our framework be used to prioritize lakes for conservation that facilitate functional connectivity and species' range shifts among lakes, it can also identify lakes vulnerable to invasive species and motivate future research on patterns of biodiversity along freshwater connectivity gradients. All of these applications will ultimately be useful for further incorporating fresh waters into regional conservation planning.

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