Hotspots and bright spots in functional and taxonomic fish diversity

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Abstract: Planning for freshwater conservation is often secondary to that for terrestrial protected areas and rarely considers all aspects of biodiversity, such as functional biodiversity. To illustrate the application of functional diversity in conservation planning, we used data from a large-scale monitoring program to characterize patterns in functional and taxonomic fish biodiversity across coastal freshwater wetlands in northern Laurentian Great Lakes. We assessed the relationship between these 2 types of diversity to identify areas most likely to maximize conservation benefits in terms of these dimensions of biodiversity. In addition, we used an outlier analysis to find areas with unexpectedly high taxonomic or functional diversity in highly impacted watersheds, or bright spots. Taxonomic and functional fish diversity metrics were not closely related, and different areas across the basin supported highest taxonomic and functional diversities. Several bright spots had either very high taxonomic richness or functional diversity despite intensive anthropogenic land use, possibly indicating high resilience and conservation potential. These findings are relevant in the context of freshwater protected area prioritization because there are few guidelines available for nomination and selection of new freshwater protected areas.

Key words: freshwater protected areas, freshwater fish, conservation prioritization, Great Lakes, outlier analysis, functional evenness

To slow the rate of decline of the world’s freshwater biodiversity, we need to target more than just taxonomic richness. Other conservation aspects such as functional and phylogenetic diversity as well as ecological processes also play an important role in conservation management (Strecker et al. 2011). Functional diversity encompasses the universe of traits exhibited by a given assemblage. For example, fish functional diversity can include foraging habit, body size, habitat use, and reproductive and behavioral strategies (e.g., Mims et al. 2010, Stuart-Smith et al. 2013). Functional diversity is an important community attribute, which may be related to the diversity of ecosystem processes and nutrient pathways, which in turn are linked to resilience (Diaz and Cabido 2001, Folke et al. 2004, Rooney and McCann 2012). Functional diversity may also reveal more about the mechanisms by which ecological communities respond to environmental change than other diversity metrics (Poff et al. 2006) and may, therefore, be the most relevant characteristic to guide ecosystem-level restoration. However, functional diversity is not well-studied and is rarely applied to the management of protected areas.
and development of conservation frameworks (e.g., Devictor et al. 2010, Mouillot et al. 2011).

Temperate fish taxonomic diversity is only a small contributor to global diversity; however, the functional diversity of the Nearctic fish fauna is one of the most vulnerable components of diversity on the global scale (Toussaint et al. 2016). Functional extinction thresholds are often reached considerably faster than those for taxonomic extinctions (Säterberg et al. 2013). Recent studies have emphasized the need for urgent action to protect functional diversity, which is threatened disproportionately relative to taxonomic biodiversity (Toussaint et al. 2016). Furthermore, as in marine and terrestrial conservation planning, strategies developed to identify freshwater protected areas rarely address multiple dimensions of biodiversity (Strecker et al. 2011, Hermoso et al. 2015) or include habitats that support relatively high diversity despite a long history of anthropogenic stress.

Lakes, especially large ones such as the Laurentian Great Lakes, have a long history of human settlement and intense anthropogenic land use. Yet they are less frequently targeted for permanent conservation of taxonomic or functional diversity than other freshwater ecosystems (Aycrigg et al. 2013). This lack of attention may be partially attributed to the fact that, unlike headwater streams, desert springs, or isolated lakes, they have few endemic or endangered species (e.g., Matamoros et al. 2016). Freshwater protected areas, where they exist, are more likely to have been chosen based on their proximity to terrestrial protected areas or historic sites (e.g., forts or shipwrecks; Hedges et al. 2010). Nevertheless, these lacustrine fish assemblages with high total biomass and productivity contribute to important ecosystem services such as commercial and recreational fisheries (Trebitz and Hoffman 2015), and any decrease in their functional diversity is likely to have far-ranging cascading effects on ecosystem structure and functions. In addition to extensive habitat modification, nutrient deposition, and direct fishing pressure (e.g., Allan et al. 2013), the Great Lakes have experienced profound ecosystem changes due to invasive species (e.g., Smith et al. 2015). With their widespread distribution within the basin and likely more generalist habits, non-native invasive (hereafter, invasive) fish could be contributing to the erosion of overall functional diversity of lacustrine fish assemblages across the entire Great Lakes region.

Another infrequently considered but possibly critical issue for freshwater conservation is the identification of areas that have sustained high taxonomic and functional diversity despite considerable anthropogenic pressure. By paying more attention to these areas, both managers and researchers could garner additional information about local factors contributing to resilience and could further diversify conservation investment. Bright spot analysis is a method that derives from economic theory (Pretty et al. 2006) and focuses on identifying positive outliers in the relationship between stress and relevant biotic metrics (Cinner et al. 2016). Bright spot analysis has shown promise for identifying such conservation targets as coral reefs that sustain high fish biomass despite high human pressure (Cinner et al. 2016) and agricultural areas that exceed expectations for bird diversity and landscape multifunctionality (Frei et al. 2018); however, it has not been widely applied to freshwater conservation.

In this study, we focused on functional trends in fish assemblages by analyzing data from the ongoing Great Lakes Coastal Wetland Monitoring (GLCWM) Program of the US Environmental Protection Agency (EPA). The program’s goal is to “implement a standardized basin-wide coastal wetland monitoring program that will be a powerful tool to inform decision-makers on coastal wetland conservation and restoration priorities throughout the Great Lakes basin” (Uzarski et al. 2017). We used fish abundance data from the GLCWM initiative to examine patterns in functional and taxonomic diversity and how these 2 types of diversity respond to stress. We explored whether coastal wetland fish taxonomic diversity is closely related to functional diversity, tested whether these taxonomic-functional trends are similar for native and invasive species, and identified areas that have the greatest potential for conservation as measured by prominent functional or taxonomic diversity hotspots or both. We assessed whether taxonomic and functional diversity are associated with anthropogenic stress, approximated by watershed land use. Finally, we applied a novel concept of bright spots (positive outlier) analysis to identify areas supporting high diversity despite having high levels of anthropogenic stress.

MATERIALS AND METHODS

Study area

This study focused on the coastal freshwater wetlands of the northern Laurentian Great Lakes (GL) including lakes Superior, Michigan, and Huron. The lakes are glacial in origin, deep, cold, and meso-oligotrophic (e.g., Dove and Chapra 2015). Major types of land use and land cover in the region include large coastal cities, intense agriculture, forestry, and sparse shoreline development. Large expanses of the Great Lakes coastline are high-energy wave-swept habitats. Coastal wetlands are less prevalent, but they harbor high diversity of fishes (e.g., Vadeboncoeur et al. 2011, Trebitz and Hoffman 2015). These temperate freshwater wetlands are hydrologically connected to the lakes and are characterized by ice cover and scour in winter and natural long- and short-term water fluctuations caused by variation in precipitation and fetch. Most of these wetlands have submerged or emergent macrophytes or both. Greater connectivity among wetlands at local to regional spatial scales (vs e.g., series of isolated lakes) ensures that few of the observed trends are due to biogeographic limitations. We did not include the lower Great Lakes (Ontario and Erie) because they are considerably different from the
northern Great Lakes in their fish fauna, anthropogenic stress levels, and drivers of assemblage composition.

Fish sampling

In the GLCWM sampling protocol, site selection follows a rotating panel design that covers the majority of Great Lakes coastal wetlands and major geomorphic wetland types (riverine, barrier-beach protected, and lacustrine coastal wetlands), with 20% of all wetland sites to be sampled annually from 2011 to 2020. Fish are sampled with fyke nets according to standard protocols (Uzarski et al. 2017) from late June through early September. Fyke nets are placed in morphotypically-similar vegetation stands and in water depths between 0.2 and 1.0 m. These morphotype stands were vegetated areas composed of >75% of plants with similar physical structure (e.g., >75% cattail, sedge, bulrush, floating or submersgent). Three fyke nets with 0.475-cm mesh, and either 0.5- or 1.0-m frame height (based on water depth), are set overnight (>12 h) in each morphotype. From 1 to 3 morphotypes are sampled at each site to ensure the most complete representation of the different habitats present within a wetland. When more than 1 morphotype was sampled at a site, we randomly subsampled net data to standardize sampling effort to 3 nets/site. Then, species-specific fish abundance (i.e., catch counts) within a site was averaged across the 3 nets to provide a more accurate representation of site-level diversity. The analyses in this study included data collected between 2011 and 2016 (last year for which data were available). Each site corresponded to a wetland associated with a separate watershed. When multiple years of fish data were available for a given site, only the first year of sampling was included in our analyses to avoid pseudo-replication of the watershed landuse stressor data (whereas averages were not calculated to avoid artificially inflating richness-based metrics). This analysis included a total of 256 unique coastal wetland sites.

Functional diversity

Our functional diversity assessment was based on species-specific trait information. Trait information was available for all identified species. Instances when species were identified only to genus or family level represented <5% of all records. One site had no native species and was removed from the analyses. Functional richness and evenness (see below) could not be calculated for sites with fewer than 3 species (6 sites), so the total n for these comparisons was 249. We chose to include juvenile fish in our analysis even though it could introduce some inaccuracies—i.e., they may differ from adults in some important trait states. However, these individuals are important contributors to overall functional diversity and ecosystem function and also indicate presence of adults. For most species, juveniles gradually converge with adults in their functional traits, so we applied adult trait states to juvenile fishes. Several species of infrequently caught predatory fishes (Grass Pickerel, Walleye, Longnose Gar, Northern Pike, Bowfin) were detected primarily as juveniles. These species are piscivorous from an early age and are important for functional diversity analyses. Juvenile fish were an important contributor to absolute and relative abundance for the following species: Yellow Perch, White Sucker, bullheads, Black Crappie, Smallmouth and Largemouth Bass, and Golden Shiner. All of these species were relatively common, so the bias introduced by considering juveniles was more likely to affect evenness-based measures.

We selected the following 15 traits based on their availability across species encountered in our study as well as their ecological importance: spawn timing, temperature and microlocation preference, fecundity, parental care, egg size and incubation, longevity, total length, mouth position, body shape, trophic guild, adult microhabitat, adult food, and overall tolerance (Table S1). Trait information was derived from FishBase (Froese and Pauly 2017) and trait databases based on published literature (Scott and Crossman 1973, Barbour et al. 1999, Hubbs and Lagler 2004). Detailed descriptions of trait states, trait data sources, and explanations of trait selection are available in the Supplemental Materials (Table S1).

Functional diversity indices we considered included functional richness ($F_{ric}$) and functional evenness ($F_{eve}$) (Villéger et al. 2008), Rao’s Quadratic entropy ($RaoQ$), and functional dispersion ($F_{disp}$) (Laliberté and Legendre 2010). $F_{ric}$ is calculated as a convex hull volume of possible trait combinations and can be conceptualized as the number of unique trait value combinations in a community when only nominal and ordinal traits are present (Villéger et al. 2008, Laliberté et al. 2014). $F_{eve}$ reflects the distribution of abundances in trait space (similar to taxonomic evenness), and is orthogonal to $F_{ric}$ (Mason et al. 2005). $RaoQ$ accounts for the relative abundances of species and for the trait differences between species by measuring differences between 2 randomly selected individuals with replacement (Botta-Dukát 2005). $F_{disp}$, which is very closely related to $RaoQ$, is the weighted mean distance in multidimensional trait space of individual species to the weighted centroid of all species, where weights correspond to relative species abundances (Laliberté and Legendre 2010). In addition to these functional metrics, we calculated taxonomic richness ($T_{ric}$) as the number of species and taxonomic evenness as Pielou evenness. All of the above indices were calculated with and without the invasive species.

Anthropogenic stress

To test whether taxonomic richness and functional diversity were associated with large-scale stressors, we calculated AgDev (Johnson et al. 2015, Host et al. 2019), a composite stress index based on separate scores for agriculture and development in a given watershed. Catchments
were delineated in ArcHydro based on 10-m Digital Elevation Models (Hollenhorst et al. 2007). The agriculture stress score for the USA side was derived from % agricultural land from Wolter et al. (2006). Canadian landuse scores were derived from the 2000 Provincial Land Cover and National Land and Water Information Service from Land Information Ontario. Development was based on % urban land use, population density (USA and Canadian census 2006), and road density (ESRI ArcGIS 9.3; Streetcarto data from the 2003 Tele Atlas Dynamap Transportation version 5.2). We chose the maximum of these normalized values to represent development stress (Dev) for each watershed. The combined stressor gradient (AgDev) equals the Euclidean distance of normalized Ag and Dev scores from the origin (0, 0). We also tested diversity metrics against a more comprehensive stressor gradient, RankSum (D. G. Uzarski, Central Michigan University, unpublished report). RankSum is based on measurable stress characteristics ranked across all study sites. Some describe local water quality (transparency, chlorophyll a, total phosphorus, soluble reactive phosphorus, total nitrogen, ammonia, nitrate, temperature, dissolved oxygen, pH, and conductivity, see Elias et al. 2008 for method details), and others describe land use (proportion of developed land, agriculture, native vegetation, and wetlands within 1-km and 20-km buffers of each wetland site).

Statistical approaches

We performed linear regression analyses to relate measures of diversity to each other and to the stressor gradients. Residual distributions were checked with the qqnorm function. No transformations were necessary with the exception of abundance of invasive species, which was log-transformed. In addition, higher-level polynomial models were fitted to test for a saturating relationship between functional and taxonomic richness. We used the Akaike Information Criteria (AICc) to identify the most parsimonious models. Relationships were visualized by applying weighted regression with bootstrapped smoothers (Schönbrodt 2012). This function calculates smoothers from 1000 bootstraps of the original sample followed by calculation of density estimates for each vertical cut through the bootstrapped smoothers, which are then visualized by shade intensity (Schönbrodt 2012). We used a Poisson regression model to test for the relationship between native richness and probability of invasive presence. To determine trait overlap between native and invasive species, we computed Gower’s dissimilarity and mapped the locations of all species in principal coordinate (PCoA, Villéger et al. 2008) space.

Bright spots were operationally defined as areas with high diversity despite high levels of watershed stress, in contrast to hotspots, which are areas of highest absolute diversity. The upper 20th percentile of sites along stressor as well as diversity gradients was considered in the bright spots analyses of positive outliers. In its more conventional form, this analysis identifies outliers as data points beyond a certain cut-off of standard deviations—e.g., more than 2× the standard deviation (SD) of the relationship between diversity metrics and stress (Cinner et al. 2016) or one or more SDs in landscape multifunctionality or diversity from the expected relationship (Frei et al. 2018).

Family-wise error rate corrections were applied to related groups of tests. All analyses were conducted in R (version 3.3.2; R Core Development Team 2016) with stats (R Core Development Team 2016), FD (Laliberté and Legendre 2010, Laliberté et al. 2014), cluster (Maechler et al. 2017), ape (Paradis et al. 2004), and rfishbase (Boettiger et al. 2012) packages. Diversity trends were mapped with QGIS (version 2.18; QGIS Development Team; available from: https://qgis.org/en/site/forusers/download.html).

RESULTS

Native species richness and functional diversity

We found a total of 71 native species across 256 sites, with site-specific richness ranging from 1 to 21 unique species. When considering only native species, there was a modest but statistically significant relationship between functional (Fric) and taxonomic richness (r² = 0.48, p < 0.0001; Fig. 1). In testing for saturation of Fric with species richness, the 2nd-order polynomial had a similar fit (r² = 0.47, p < 0.0001), but was not selected based on AICc (49.2 vs 50.9 for linear and 2nd -order models, respectively). The 2 measures of functional dispersion, Fdis and RaoQ, were closely related (r² = 0.93, p < 0.0001), so we focused only on RaoQ in all subsequent comparisons. Species richness was not signif-

Figure 1. Relationship between taxonomic richness (number of species) and functional fish richness (Fric) across northern Great Lakes coastal wetlands (n = 249, 6 sites omitted because Fric could not be calculated on <3 species) visualized with weighted watercolor regression with bootstrapped smoothers. Shading intensity indicates smoother density/bootstrapping-based confidence intervals, with decreasing intensity indicating increasing confidence intervals. Linear regression r² = 0.48, p < 0.0001.
significantly related to RaoQ ($p = 0.58$, Fig. 2A), whereas Pielou evenness was ($p < 0.0001$) (B) across northern Great Lakes coastal wetlands. Shading intensity indicates smoother density/bootstrapping-based confidence intervals, with decreasing intensity indicating increasing confidence intervals. Note that superimposition of layers is a result of single-point bootstrapping.

Richness hotspots did not overlap geographically with functional diversity hotspots (Fig. S2A–C). Highest species richness of fishes (upper quintile of distribution, 19–21 species) occurred in several wetlands in the North Channel of Lake Huron, St Louis Bay in Lake Superior, and Green Bay in Lake Michigan (Fig. S2A). Functional diversity hotspots occurred in Saginaw Bay and eastern Georgian Bay of Lake Huron as well as eastern Green Bay and south-eastern Lake Michigan (Fig. S2C).

Diversity metrics in the context of invasive species

At least 1 invasive fish species was found in ½ of all coastal wetlands in this study, and multiple invasive fish species were captured at approximately 11% of sites. We found a total of 12 invasive species, of which Common Carp and Round Goby were the most abundant. Sites with higher native richness had a marginally higher probability of having at least 1 invasive species ($p = 0.034$) and a greater number of invasive species (Poisson $p = 0.0039$).

Native vs total (including invasive) $F_{ric}$ and RaoQ were closely related ($r^2 > 0.88$ and $p < 0.0001$ for all comparisons; Fig. S3A, B); therefore, functional diversity relationships did not change with inclusion of invasive species. When examining only the sites with invasive species, overall functional diversity (native and invasive species combined, RaoQ$\text{all}$) was not related to the number of invasive species present at a site ($p = 0.37$). The abundance of invasive species, however, was weakly but significantly negatively correlated with RaoQ$\text{all}$ ($r^2 = 0.10$, $p = 0.0009$, Fig. S4). Functional richness ($F_{ric\text{all}}$) was not related to the number of invasive species or their abundance ($p > 0.05$). Invasive species mostly overlapped with natives in their functional traits based on their position in principle coordinate space of the Gower’s distance matrix (Fig. S5).

Stressor-diversity relationships and bright spots

We also examined the most prominent outliers for the relationship between native species diversity indices and watershed stress. Overall, we found no significant relationship between AgDev watershed stress and diversity indices (native richness: $p = 0.12$, $F_{ric}$ $p = 0.56$; RaoQ: $p = 0.81$; Fig. 3A, B). For the more comprehensive stressor measure, RankSum, there was also no relationship with taxonomic richness ($p = 0.75$) or RaoQ ($p = 0.10$). Because of these weak associations, we identified high diversity–high stress outliers (bright spots) by intersecting the upper 20% of sites based on both diversity metrics and watershed stress. Our analysis revealed several prominent bright spot candidates, or areas with unusually high taxonomic richness (Fig. 4A, Fig. S6A) or functional diversity (Fig. 4, Fig. S6B) in proximity to the most degraded watersheds. In both cases, different areas were identified as bright spots depending on whether taxonomic richness or functional diversity was considered (Table S2).

**DISCUSSION**

Our temperate large lakes study revealed that taxonomic richness does not predict functional diversity (whereas Pielou evenness and functional diversity were significantly but not strongly related) and that these 2 dimensions of biodiversity had mostly non-overlapping hotspots. Globally, functional and taxonomic diversity are not closely related, suggesting that regional species traits are not a random subgroup of the worldwide pool of traits (Toussaint et al. 2016). Similarly, low correspondence has been observed in other systems including global (Stuart-Smith et al. 2013) and regional (Lefcheck et al. 2014, Granger et al. 2015) patterns.
in marine fish diversity as well as in other taxa (e.g., birds; Devictor et al. 2010).

Species richness of these coastal freshwater wetlands may be important on local scales, but as a young, high-latitude, oligotrophic system, the northern Great Lakes support low overall diversity and levels of endemism (e.g., Matamoros et al. 2016). On the global scale, lake size, age, and latitude have been demonstrated to be the best predictors (all positive except latitude) of the probability of occurrence and abundance of endemic fish species (Hanly et al. 2017). In contrast, functional diversity of the Nearctic fish fauna is one of the most vulnerable worldwide (Toussaint et al. 2016, but see Vitule et al. 2017 for discussion of incomplete functional diversity information for tropical fauna). Another study focusing on temperate regions found that functional homogenization in European riverine fish assemblages was 6× greater than taxonomic homogenization (Villéger et al. 2014). This underscores the importance of a more explicit consideration of functional biodiversity in freshwater conservation, and the need to protect functional diversity hotspots even in systems that may not merit increased conservation efforts in terms of their contribution to global taxonomic diversity. Our results have implications for monitoring as well because multiple dimensions of biodiversity may need to be represented by different indicator species (Sattler et al. 2014, Stuart-Smith et al. 2015). There was little functional redundancy in our system, as we did not detect saturation or leveling of functional richness with the number of species observed at a site (based on AICc model details).

Functional traits summarized in our functional diversity metrics are relevant in a whole-system context. For example, loss of functional diversity may result in reduced prey availability for terrestrial predators, piscivorous birds (which could be affected by prey size or reduced range of spawn timing and spawn microhabitats), and reduced within-food-web linkages. There is a need for further studies to fully understand the connection between functional diversity and ecosystem function, but reduced functional diversity appears to lead to changes in ecosystem functions such as simplification of food webs, diminished capacity for particulate organic matter processing, and top-down effects on zooplankton grazing and changes in overall productivity (Danovaro et al. 2008, Vaughn 2010).

Large secondary consumers are more susceptible to functional than taxonomic extinction, and a loss of even a small proportion of their population may trigger declines in other connected species, as demonstrated in a modeling study of ecologically effective population sizes (Säterberg et al. 2013). These findings contradict simulations of species extinctions in grasslands, which could lose large numbers of species without changes in the functional properties of those assemblages (Sundstrom et al. 2012). However, even in that case, species loss reduced redundancy, which would likely compromise overall resilience.

Although invasive species are widespread in Great Lakes wetlands, understanding their effects on functional diversity is difficult in this large-scale observational study, because these effects depend on whether invaders are simply added to an existing assemblage or replace native (particularly functionally distinct) species. We saw no effect of the number of invasive species per site on overall functional diversity and only a weak effect of invasives abundance, indicating a possible weak erosion of functional diversity as invasive species become more dominant. Invasive species are more likely to be trophic generalists (Romanuk et al. 2009), which may lead to the functional homogenization of native assemblages (Olden et al. 2004). This trophic skew can have important implications for ecosystem productivity and overall trophic structure (Reynolds and Bruno 2012). Most of the invasive fish species observed in our study were omnivores, partly confirming this theoretical prediction (Romanuk et al. 2009). Their functional space generally overlapped with that of the native species. In this system, however, homogenization effects may be more difficult to demonstrate because of the positive relationship between native species richness and presence of invasive species.
Many, but not all, previous studies have demonstrated declines in functional diversity with increasing anthropogenic pressure (Villéger et al. 2010, Schmera et al. 2017). For example, Infante et al. (2009) observed lower functional trait diversity in fish and macroinvertebrates in stream catchments with more agriculture. Likewise, functional trait space was lower in streams with low habitat-quality scores (Pease et al. 2015). The weak relationship between fish functional diversity and watershed land use observed in this study most likely has complex causes, confounded by the fact that large expanses of shallow coastal areas that support the most diverse fish assemblages spatially coincide with areas of dense human settlement (e.g., Saginaw Bay, Green Bay).

Identification of specific habitat factors associated with greater taxonomic richness and functional diversity was outside of the scope of this study. However, our previous

Figure 4. Spatial correspondence between watershed landuse stress (AgDev normalized composite stressor index, unitless) (A) and fish richness and functional diversity shaded from light (low) to dark (high) (B).

study, based on a different regional dataset, demonstrated that only a small proportion of variation in diversity can be consistently attributed to physical habitat drivers (Kovalenko et al. 2018). Smaller-scale habitat factors (water quality, habitat alteration), high connectivity and resulting recolonization, and species turnover caused by harsh winter conditions (Langer et al. 2016) likely override the importance of at least some of the watershed stressors. Previous studies of biodiversity identified the importance of habitat complexity (including habitat variables not measured in our study) for both tropical freshwater riverine fish (Ribeiro et al. 2016) and coral reef fish (Richardson et al. 2017). In practice, the lack of relationship between landuse and fish diversity metrics (and the presence of bright spots) may imply that protecting the most pristine areas in terms of direct anthropogenic impact may not always accomplish biodiversity objectives and, therefore, may not always be the optimal allocation of conservation efforts.

In this study, we identified several bright spots, or focal areas that sustain high fish functional diversity and taxonomic richness in coastal wetlands within the most anthropogenically altered watersheds in northern Great Lakes (Table S2). These positive outliers could be further examined to understand local factors that may be contributing to what likely is an example of increased resilience. Alternatively, if temporal consistency of these trends is supported, then these areas could be of interest for conservation despite our incomplete knowledge of what explains such resilience. The fact that this monitoring program samples a large proportion of existing wetlands with standardized, consistent protocols lends promise to direct identification of high-value areas.

Finally, the Great Lakes have more than 100 protected areas in a multitude of different categories, but they lack a unified framework of management and effectiveness assessment (Parker et al. 2017). Based on a preliminary visual assessment, few of our functional biodiversity hotspots or bright spots, overlapped with existing Great Lakes protected areas (e.g., Marine Protected Areas of the Great Lakes; NOAA 2016). One exception was the Southwest Michigan Underwater Preserve, which, however, does not grant any protection for fish fauna. Similarly, in the Colorado River basin, there was only 15% overlap between conservation scenarios emphasizing different dimensions of biodiversity and current protected areas with permanent conservation status (Strecker et al. 2011). Likewise, a study on the Iberian Peninsula found that Europe’s largest reserve network (Natura 2000; available from: http://ec.europa.eu/environment/nature/natura2000/index_en.htm), primarily designed to protect terrestrial biodiversity, covered less than 20% of freshwater species ranges (Hermoso et al. 2015).

Conservation of functional and taxonomic biodiversity in littoral habitats is essential for protecting Great Lakes fish fauna. Despite the low total area of coastal habitats compared with open water, only 8% of all Great Lakes fish species are exclusively pelagic (Vadeboncoeur et al. 2011), and ecosystem services of coastal wetland habitats far exceed their geographic extent (Trebitz and Hoffman 2015). There is mounting public support for creating additional freshwater protected areas and reserves; therefore, it is essential to consider functional diversity and resilient bright spot outliers from this perspective. Finally, it is important to recognize that focusing on uninvaded, mostly remote, and highly pristine areas for biodiversity conservation efforts may be misaligned with both hotspots and bright spots of native taxonomic and functional diversity.

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