Temporal dynamics of taxonomic homogenization in the fish communities of the Laurentian Great Lakes

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Abstract
Aim: As a result of the loss of native species and the spread of non-native species, fish communities are becoming increasingly homogenous globally. In the Laurentian Great Lakes, 21 native fish species have been extirpated from one or more lakes as a result of habitat alteration and destruction, overexploitation and invasive species since the 1800s. Over the same time period, 30 non-native species became established in at least one lake as a result of authorized and unauthorized introductions. This study examines temporal changes in taxonomic dissimilarity over 15 time periods spanning the last 150 years.

Location: Laurentian Great Lakes, North America.

Methods: Changes to the Great Lakes fish fauna were summarized in species lists by decade from 1870 to 2010. Taxonomic dissimilarity between and within communities was calculated using Jaccard’s dissimilarity coefficient; the relative contribution of turnover (species replacement) and nestedness (species loss) to total taxonomic dissimilarity was also calculated. To test whether the Great Lakes have homogenized, we conducted a regression on multiple-site dissimilarity values over time.

Results: Native species richness in the Great Lakes exhibits a latitudinal gradient that reflects post-glacial history and current climate. We demonstrate that the establishment of non-native species and extirpation of native species has changed fish communities in each of the Great Lakes, with communities in Lake Superior differentiating the most (~23%) and in Lake Ontario the least (~12%) since 1870. Multiple-site dissimilarity ranges between ~50% and 53% per decade, and communities have become ~5.9% more similar over time since 1870.

Main Conclusions: Species introductions and extirpations have changed community composition, resulting in the fish communities becoming significantly more similar to one another over time and, thus, homogenized. As a result, ongoing management should prevent range expansion of native and non-native species to preserve the current distinctiveness of the Great Lakes fish communities.

Keywords
biological invasions, diversity, homogenization
1 | INTRODUCTION

Multiple factors that act at different temporal and spatial scales determine which species are able to persist in a given community. The geographical barriers that have historically limited species distributions have been diminished over time by human activity, such as trade and travel, causing species to expand beyond their native ranges or disperse distances far greater than naturally possible. As a result, environmental requirements and patterns of trade and travel have become important regulating factors in the formation of new biogeographical patterns, and this has multiple consequences on species distributions (Capinha, Essl, Seebens, Moser, & Pereira, 2015). As non-native species are introduced into communities and native species expand their ranges or become extirpated, the composition of species within and between communities changes, which may result in biotic homogenization, an increased compositional similarity between communities (Olden, Poff, Douglas, Douglas, & Fausch, 2004). Although the number of studies examining biotic homogenization has exponentially increased over the past decade, to our knowledge, no study has examined homogenization through time but rather previous studies have either compared compositional similarity between two time periods or before and after a hypothesized stressor (e.g. invasions, land use change); this limits our understanding of rates of change through and at multiple points in time and, consequently, our ability to detect multiple state changes in both biotic homogenization and biotic differentiation, a decrease in compositional similarity between communities (Olden, 2006; Olden, Comte, & Giam, 2018). Here, we evaluate whether fish communities in the Laurentian Great Lakes have experienced biotic homogenization through time and how turnover and nestedness contribute to changes in biodiversity.

1.1 | Biogeography, connectivity and community saturation

The primary determinant that shaped the current biogeography of freshwater fishes in the Laurentian Great Lakes (lakes Erie, Huron, Michigan, Ontario and Superior), hereafter referred to as the Great Lakes, was the retreat of the most recent glaciation during the Wisconsin glacial period 80,000–10,000 years before present (YBP) (Dyke & Evans, 2003). During the maximum extent of the Wisconsin glaciation, there were no known freshwater habitats in the Great Lakes basin other than a small ice-free highland in Wisconsin (Bailey & Smith, 1981; Mandrak & Crossman, 1992; Underhill, 1986). Fishes that occurred in the Great Lakes prior to the last glacial period were either extirpated or displaced into southern refugia. Current distributions suggest that the Mississippi and Atlantic coastal refugia were the main origins of species colonizing the Great Lakes basin following post-glacial retreat, with the Beringian and Missourian refugia also hypothesized sources (Bailey & Smith, 1981; Mandrak & Crossman, 1992). Subsequent colonization occurred via active dispersal through corridors of suitable aquatic habitat from 15,000 YBP, when the ice sheet began to recede, until about 6,000 YBP, when isostatic rebound isolated the basin from refugial areas, forming the current drainage basin (Bailey & Smith, 1981; Mandrak & Crossman, 1992). The Great Lakes remained isolated until canal construction commenced in the 19th century. Dispersal of species between Lake Ontario and Lake Erie was facilitated by the Welland Canal, in 1824, which by-passed Niagara Falls (Bailey & Smith, 1981). In 1825, the completion of the Erie Barge Canal allowed the dispersal of species from the Atlantic coast (Daniels, 2001). Isolation of the Great Lakes from the Mississippi drainage remained until 1848, when the Illinois and Michigan Canal, later replaced by the Chicago Sanitary and Ship Canal (Chicago SSC), reconnected the Great Lakes via Lake Michigan to the Mississippi River (Bailey & Smith, 1981). The Chicago SSC has been the second largest pathway for fish introductions into the Great Lakes after shipping (Mandrak & Cudmore, 2010).

Due to the limited time since the last glaciation, recolonization may have not resulted in saturated fish communities. A saturated community is characterized by a maximal level of local richness, dependent on area or ecological limits such that additional species cannot be added without local extinctions (Mateo, Mokany, & Guisan, 2017). To date, studies have provided equivocal evidence for the occurrence of saturation (see Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). One of the central goals in invasion biology is to predict which species will be successful and a number of hypotheses have been developed to explain invasion success (see Lockwood, Hoopes, & Marchetti, 2013), including the idea that, as saturation in a community increases, the probability of invasion decreases (Lonsdale, 1999). At the community level, the accumulation of non-native species should theoretically slow down over time as the number of possible colonizers from the regional species pool becomes depleted and the number of available niches declines. However, a number of studies have shown the opposite, that is that communities show no sign of saturation in the number of non-native species able to establish (Cornell & Lawton, 1992; Moyle & Light, 1996; Pinto-Sánchez, Crawford, & Wiens, 2014; Seebens et al., 2017). The Great Lakes fish fauna show no signs of saturation in the accumulation of non-native species; 30 species have become successfully established since 1870, and an additional 39 have been found in the basin but have not established reproducing populations (Mandrak & Cudmore, 2010), substantially changing the fish fauna of the region.

1.2 | Taxonomic homogenization

The fish community composition of the Great Lakes has changed dramatically since European settlement, which brought new species and new technology to the region (e.g. shipping, more efficient fishing equipment). Their settlement had large impacts on the native fish communities leading to species declines and extirpations, and deliberate stocking of species, which remains a threat to native species even though the last stocking of a new non-native species occurred in the 1980s (Mandrak & Cudmore, 2010). The number of successfully established non-native species has increased over time, with surges in the late 1800s, 1950s and 1980s, and impacts on the native community have ranged from relatively benign to high
negative ecological impacts through predation, competition, disruption of trophic structure and disease transmission (Crossman, 1991; Mandrak & Cudmore, 2010). Within the Great Lakes basin, the introduction of non-native species has occurred through a variety of pathways including, but not limited to, commercial shipping, dispersal, live trade, recreational boating and angling, and stocking (Mandrak & Cudmore, 2010). In total, 69 fish species are known to have been introduced into the Great Lakes basin, 30 of which have established reproducing populations (Mandrak & Cudmore, 2010). As new non-native species become introduced and established, and existing species expand their current range, the fish fauna of the Great Lakes will continue to change with a variety of potential consequences.

This increase in biotic exchange may contribute to biotic homogenization, which is the increase in similarity at the genetic, taxonomic and/or functional level as non-native species are introduced into a community and native species become extirpated, which can fundamentally change the global or regional distribution of species (Olden et al., 2004; Rahel, 2000; Taylor, 2004). As species establish in a novel community, local diversity (\(\alpha\)) may increase, but this generally results in a reduction of diversity between communities (\(\beta\)), which may have profound ecological and/or evolutionary implications (Olden & Rooney, 2006). Quite often, the regional loss of native species is outnumbered by the addition of non-native species (Rahel, 2010; Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011). Changes between historical and present-day communities have been well documented (see, e.g. Baiser, Olden, Record, Lockwood, & McKinney, 2012; Rahel, 2010; Villéger et al., 2011; Winter et al., 2009), and in aquatic systems, similarity has been shown to increase over time (see Rahel, 2002). However, less is known about how the accumulation of non-native species may continuously affect biotic homogenization through time.

Biotic homogenization occurs continuously through time, but studies to date have been limited to a comparison of two periods of time, generally between historical/pre-European/pre-human settlement and present-day communities. The degree of homogenization is captured by the reduction in \(\beta\) diversity between these two time periods. By comparing only two time periods, how \(\beta\) diversity varies through time is often overlooked, but may provide more information on the impact of changes in community composition. For example, biotic differentiation may occur closer to the historical period as non-native species become introduced, while a transition towards gradual homogenization may occur later in time as native species become extirpated, suggesting that rates of biotic homogenization may vary through time (Olden, 2006).

Classic dissimilarity indices (e.g. Jaccard, Sørensen) used to quantify taxonomic homogenization may reflect two phenomena: turnover and dissimilarity due to nestedness (Baselga, 2010; Baselga, Jiménez-Valverde, & Niccolini, 2007). Turnover, or species replacement, reflects the replacement of some species by others between communities, despite any potential differences in species richness (Baselga, 2010). Nestedness, or species loss, accounts for differences in composition due to species richness between nested communities where the composition of the poorest community is a subset of the composition of the richest community, reflecting the ordered loss of species, usually due to dispersal limitations (Baselga, 2010). Determining how nestedness and turnover change over time can have profound management implications when examining biotic homogenization. Taxonomic homogenization can occur when both turnover and nestedness decrease if unique species become extirpated in the richest community and the same non-native species become widespread. It can also occur when unique species are introduced into the poorest community and the increase in turnover is lower than the decrease in nestedness or, alternatively, when unique species become extirpated in the poorest community and the decrease in turnover is higher than the increase in nestedness (Villéger & Brosse, 2012). Examining nestedness and turnover through time provides information on how the introduction of non-native species and subsequent extirpation of native species impacts the level of dissimilarity through changes in species richness and the number of species shared between communities.

The Great Lakes provide an ideal system to examine how the addition of non-native species and loss of native species has affected similarity in community composition over time. Both extirpations and successful introductions have been well documented from the historical communities (1870) to present (2010), allowing for long-term, large-scale and high-resolution temporal data necessary to examine how biotic homogenization occurs continuously over a long time period. We test three hypotheses: (a) fish communities in each basin have changed over time, specifically, Lake Erie changed the most due to impacts of excess nutrient loading, changes in watershed connections and the number of non-native species introduced, while Lake Superior will have changed the least given its geographical isolation and harsher environmental conditions; (b) lakes Huron and Michigan will have the most similar fish communities as they are joined at the same lake level, while Lake Superior will have a fish community most dissimilar to the other Great Lakes given its geographical isolation; and (c) as a result of introductions and extirpations, on average, fish communities have become more similar over time (i.e. homogenized) across the five basins, with changes in nestedness and turnover indicative of homogenization.

2 METHODS

Using species lists (Roth, Mandrak, Hrabik, Sass, & Peters, 2013) and data on species extirpations and successful introductions (Mandrak & Cudmore, 2010), we compiled a dataset of freshwater fish occurrences for the Laurentian Great Lakes basin (lakes Erie, Huron, Michigan, Ontario, Superior; Table 1) by decade from 1870 (historical fish community) to 2010 (present-day community). This dataset included 182 freshwater fish species; 152 native and 30 established non-native species (Roth et al., 2013). At least 39 additional non-native species have been introduced into the Great Lakes basin, but have not yet established reproducing populations (Mandrak & Cudmore, 2010). In total, three taxa have become
globally extinct, 15 species have become extirpated, and many species have declined close to extirpation (Mandrak & Cudmore, 2010; Roth et al., 2013).

We quantified taxonomic homogenization as the per cent change in community dissimilarity between decades from 1870 to 2010 using Jaccard’s dissimilarity index for multiple sites as outlined in Baselga (2010), which avoids potential issues of covariance in averaging pairwise similarities when comparing the composition of more than two communities (Diserud & Ødegaard, 2007). This multiple-site index extends the pairwise measure to three or more communities by accounting for shared species across all sites and unique species found in only one site (Baselga, 2010, 2012). To test whether there were significant changes in dissimilarity between all five lakes, we completed a regression on dissimilarity values over time. A significant positive slope would indicate that differentiation has occurred, while a significant negative slope would indicate that homogenization has occurred.

We calculated pairwise dissimilarity using Jaccard’s dissimilarity index between all possible pairs of lakes by decade to determine which communities are most similar and different. Additionally, we calculated pairwise dissimilarity between each decade and the historical fish community (1870) in each lake, and quantified the per cent change to determine which community has changed the greatest from the historical community. We calculated the relative contribution of turnover (i.e. species replacement; Equation 1, adapted from Baselga, 2012) and nestedness (i.e. species loss; Equation 2, adapted from Baselga, 2012) to total dissimilarity, where dissimilarity is equivalent to 1–Jaccard’s similarity index (Baselga, 2010) between each decade and the historical fish community in each lake and across all lakes by decade using the multiple-site index. For components of nestedness and turnover, \( a \) is the number of species present in both sites, \( b \) is the number of species present in the first but not the second, and \( c \) is the number of species present in the second but not the first. To determine how patterns are changing over time, we calculated the per cent change in turnover and nestedness between 1870 and 2010. All analyses were performed in R 3.4.2 (R Core Team, 2017), and the ‘betapart’ package was used to calculate components of turnover, nestedness and Jaccard’s dissimilarity coefficient (Baselga, Orme, Villéger, Bortoli, & Leprieur, 2017).

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\beta_{\text{Tes}} = \frac{\max(b,c) - \min(b,c)}{a + b + c} \times \frac{a}{a + 2 \min(b,c)}
\]

\[
\beta_{T} = \frac{2 \min(b,c)}{a + 2 \min(b,c)}
\]

3 | RESULTS

We found that the fish community of each of the lakes has changed over time, becoming more dissimilar to the historical community as native species become extirpated and non-native species become introduced (Figure 1). Comparing the present-day community to that of the historical (1870) in each lake, we found that Lake Ontario has changed the least, increasing in dissimilarity from the historical community by 12.4%, while Lake Superior has changed the most, increasing in dissimilarity from the historical community by 23.2%. Lakes Erie, Huron and Michigan increased in dissimilarity from the historical community, by 20.8%, 21.4% and 18.8%, respectively (Figure 1). When comparing dissimilarity between lakes, we found that, for each decade, Lake Huron and Lake Michigan have the most similar composition, whereas Lake Erie

| Table 1 | Number and status of extant native, extirpated/extinct and non-native fish species for each community in the Laurentian Great Lakes basin |
|---|---|---|---|---|---|---|
| Status | Erie | Huron | Michigan | Ontario | Superior | Total |
| Total Extant Native | 112 | 102 | 117 | 107 | 72 | 140 |
| Extirpated/Extinct | 9 | 8 | 9 | 7 | 3 | 18 |
| Introduced, Established | 23 | 21 | 23 | 15 | 20 | 30 |
| Introduced, Failed | 13 | 13 | 13 | 14 | 5 | 39 |
and Lake Superior have the most dissimilar composition, and, in general, Lake Superior was most dissimilar to all other Great Lakes (Figure 2). Lakes Erie and Michigan, Erie and Ontario, Erie and Superior, Huron and Michigan, Huron and Superior, Michigan and Superior, and Ontario and Superior have become significantly less dissimilar to one another over time ($p < .01$ for all comparisons; Figure 3). Although dissimilarity decreased between lakes Erie and Huron, Huron and Michigan, and Michigan and Ontario, these patterns were not significant (Figure 3). The multiple-site dissimilarity across lakes declined significantly, 1870–2010, by 5.9% (Adjusted $R^2 = .7816$, slope = $-0.021866$, $p = 7.4942 \times 10^{-6}$ (Figure 4), indicating that the lakes have become homogenized (i.e. more similar in community composition) over time. Through time, dissimilarity both increased and decreased between decades (Figure 4), reflecting the ongoing addition of non-native species and loss of native species. When considering pairwise comparisons, the changes between decades are largely driven by Lake Erie becoming more similar to all other lakes.

When examining the relative contribution of turnover and nestedness to multiple-site dissimilarity between communities, we found that both nestedness and turnover generally contribute equally to overall patterns; however, this is driven by extremes in one or more communities. Nestedness and turnover have both decreased over time, by 3% and 11.2%, respectively. Nestedness, or species loss, contributes very little to observed pairwise patterns between communities except in the case of comparisons with Lake Superior (Figure 2). Nestedness is highest between Lake Michigan and Lake Superior while turnover, or species replacement, is generally lowest between these two communities (Figure 2). Although nestedness is higher between Lake Superior and all other communities, turnover, or species replacement, increases in importance over time and accounts for approximately half of the dissimilarity between Lake Superior and Lake Erie, and approximately one-third of the dissimilarity between Lake Superior and Lake Ontario. There is an intermediate level of nestedness between Lake Michigan and Lake Huron, and turnover contributes very little to dissimilarity between these two communities (Figure 2). When examining the contribution of turnover to dissimilarity between communities, we found that it contributes most to the dissimilarity between Lake Erie and all other communities, and Lake Ontario and all other communities. Turnover was highest between lakes Erie and Ontario until 1980 when it became highest between Lakes Superior and Erie, and then in 2010, it became highest between lakes Huron and Ontario. Turnover was lowest between Lake Michigan and Lakes Huron and Superior.
DISCUSSION

Although many studies have documented changes between historical and present-day communities (see Baiser et al., 2012; Rahel, 2010; Villéger et al., 2011; Winter et al., 2009 for examples), to our knowledge, no study has examined patterns of biotic homogenization by decade over multiple time periods. Over time, we found that each community differentiated as non-native species were introduced and became established. We also determined that the similarity between communities has significantly increased over time, indicating homogenization, particularly when examined in conjunction with temporal patterns of nestedness and turnover. Additionally, we found evidence of an increase in homogenization punctuated by periods of differentiation, indicating the need for more studies that examine rates of change over time.

We hypothesized that fish communities in each basin have changed over time, specifically, Lake Erie changed the most while Lake Superior changed the least, and this hypothesis was partially supported. We did find that each community changed over time, with the present-day communities, on average, 19.3% different from the historical community, mostly driven by the establishment of a total 30 non-native species regionally (Mandrak & Cudmore, 2010; Roth et al., 2013). This is consistent with the findings of Taylor (2010), which showed differentiation occurring at the smallest spatial scale.

However, while we hypothesized Lake Erie changed the most, we found that Lake Superior, which we expected to change the least due to its geographical location and harsh environmental conditions, had, in fact, changed the most over the 150-year time period. This observed change likely reflects that Lake Superior has proportionally gained the most non-native species and lost the fewest native species. Lake Ontario had the least change, approximately 12.4%, reflecting that it had proportionally gained the least number of non-native species, followed by Lake Michigan, which changed approximately 18.8% over time. This pattern is expected given that both lakes are closest to the two refugia contributing the greatest number of species following deglaciation (i.e. Mississippi and Atlantic coastal refugia); the larger change in Lake Michigan likely reflects the greater number of non-native species dispersing northward via the Mississippi basin.

Given that lakes Huron and Michigan are at the same elevation with no natural barriers to dispersal between the communities, we hypothesized that these two communities would have the most similar fish communities while Lake Superior would have a fish community most dissimilar to the other Great Lakes and this hypothesis was supported. Lake Superior likely has a fish community most different from the other communities because it is the farthest from glacial refugia (Mandrak, 1995) and has the harshest climate (Munawar, 1978) and the least habitat diversity (Grigorovich et al., 2003).
Biotic homogenization is a continuous process, which requires moving beyond the conventional comparison of two points in time. While numerous studies have compiled evidence for biotic homogenization globally and across taxa (see Baiser et al., 2012; Olden, 2006), followed by biotic homogenization once those non-native species become widespread across the landscape and cause extirpations of native species, we found that observed patterns were more complex. The similarity between communities increased when comparing the dissimilarity in each decade to that of the historical community in 1870. However, when comparing the dissimilarity of the communities between each decade, we found an overall trend of biotic homogenization with periods of differentiation occurring: 1870–1910 similarity increased between decades, 1910–1950 similarity generally decreased between decades (with the exception of 1940), 1950–1990 similarity again increased, and 1990–2010 similarity again began to decrease between decades. This could indicate that differentiation occurs as non-native species are introduced into a community but, once they reach the stage of spreading, communities begin to become more similar in their composition. These results show that rates of change vary through time and that only comparing two points of time limits our understanding of biotic homogenization as a continuous process.

When partitioning total pairwise dissimilarity into turnover and nestedness components, we found that the underlying patterns between communities were different. There is a clear difference between the processes regulating the $\beta$ diversity of the Great Lakes communities; nestedness almost solely accounts for patterns between lakes Huron, Michigan and Superior, while turnover almost completely accounts for patterns between lakes Erie and Ontario and the patterns that these two communities have with lakes Huron and Michigan. On average, turnover and nestedness contribute relatively equally through time between Lake Superior and lakes Erie and Ontario. These results reflect that the Mississippi refugia acted as a main source of species following deglaciation, and the nestedness that occurs between lakes Huron, Michigan and Superior reflects the ordered loss of species from Lake Michigan to Lake Huron and from Lake Huron to Lake Superior due to post-glacial dispersal limitations. The turnover, or species replacement, that occurs in lakes Erie and Ontario may reflect the isolation of these two communities from the each other and the rest of the Great Lakes prior to the construction of the Welland Canal and indicates that the species composition between these two communities are, in fact, distinct: between the two communities, including non-native species, there are a total of 53 unique species and 110 shared species for all species present between 1870 and 2010. These patterns of turnover and nestedness provide further evidence for post-glacial processes structuring the composition of communities in the Great Lakes and also indicate that management would be most cost-effective in maintaining the current distinctiveness of three geographical areas: (a) Lake Erie; (b) lakes Huron, Michigan and Superior; and (c) Lake Ontario.
Within communities, the accumulation of species should decrease over time as the regional pool becomes depleted of potential colonizers. Since 1870, a total of 30 non-native species have become successfully established and a further 39 species have been identified in the Great Lakes basin but have not yet established reproducing populations (Mandrak & Cudmore, 2010). This accumulation of species, including both range expansion of native species and the introduction, establishment and spread of non-native species, has increased steadily over the past 150 years and shows no signs of saturation in the Great Lakes. While each lake has experienced extinctions over time, species richness has continued to increase (Mandrak & Cudmore, 2010). The number of introductions exceeds the number of extirpations in this system, contributing more to homogenization and is consistent with the findings of other studies examining community changes in freshwater fish communities in North America (e.g. Rahel, 2000; Taylor, 2004; Taylor, 2010). Although the lakes have changed and become more similar in taxonomic composition over time, they still remain taxonomically distinct, suggesting that there are still potential colonizers from the regional pool that could establish in a new lake given dispersal and niche space opportunities. As a result, the fish fauna of the Great Lakes show no signs of saturation, and management should focus on maintaining current the taxonomic composition within each community.

The addition of non-native species and loss of native species can have dramatic consequences on $\beta$ diversity, and in the Great Lakes system, the accumulation of non-native species and extirpation of native species has changed species composition, causing communities to become significantly more similar over time and, thus, have homogenized; this could have impacts on ecosystem stability, resilience and/or functioning and could provide a framework for research going forward. Therefore, there should be ongoing efforts to prevent range expansion of both native, particularly with respect to ballast water release, and non-native species to preserve the distinctiveness of the fish community in each lake.

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DATA AVAILABILITY STATEMENT

Data may be available from the authors upon request.

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