

# Invasive species and biotic homogenization in temperate aquatic plant communities

Ranjan Muthukrishnan  | Daniel J. Larkin

Department of Fisheries, Wildlife and Conservation Biology and Minnesota Aquatic Invasive Species Research Center, University of Minnesota-Twin Cities, St. Paul, Minnesota

## Correspondence

Ranjan Muthukrishnan, Department of Fisheries, Wildlife and Conservation Biology and Minnesota Aquatic Invasive Species Research Center, University of Minnesota-Twin Cities, St. Paul, Minnesota 55108, USA. Email: mrunj@iu.edu

## Present address

Ranjan Muthukrishnan, Environmental Resilience Institute, Indiana University, Bloomington, Indiana

## Funding information

Minnesota Aquatic Invasive Species Research Center from the Minnesota Environment and Natural Resources Trust Fund

Editor: Janne Soininen

## Abstract

**Aim:** Biotic homogenization (BH), a reduction in the distinctness of species composition between geographically separated ecological communities in a region, is an important but underappreciated potential consequence of biological invasions. While BH theory has always considered invasions, it has generally been in a relatively narrow context that the cosmopolitan nature of invasive species increases BH because of their shared presence across many locations. We sought to evaluate this component of BH as well as broader effects of invasive species on BH through changes in native communities, including overall reductions in species richness or shifts in species composition.

**Location:** Minnesota, USA.

**Time period:** 2002–2014.

**Major taxa studied:** Aquatic macrophytes, including both vascular plants and attached macroalgae.

**Methods:** We used surveys of aquatic macrophyte communities from 1,102 shallow lakes in Minnesota, USA (including 248 lakes with repeated surveys) to evaluate relationships between invasion, native species and BH.

**Results:** We found that the presence of invasive species was associated with BH and that this pattern was reflected in both the total community (i.e., with invasive species included) and in the composition of the native species community alone. We found that invaded lakes were more compositionally similar to each other than uninvaded lakes, but that both groups were becoming more similar over time—despite neither group exhibiting declines in species richness. This pattern was largely driven by shifts in the native community itself, with common species becoming more widespread and rare species becoming rarer.

**Main conclusions:** Invasive species increase measures of community similarity through their own presence in multiple locations, and also by influencing the composition of native species. These patterns have important implications for conservation and management and suggest that BH should be considered more widely in evaluating the impacts of biological invasions and developing response strategies.

## KEYWORDS

aquatic macrophytes,  $\beta$ -diversity, biotic homogenization, invasive species, lake, native species

## 1 | INTRODUCTION

Human activities have drastically reshaped ecological systems through a variety of processes, including habitat loss and degradation (Halpern et al., 2008; Hoekstra, Boucher, Ricketts, & Roberts, 2005), climate change (Hoegh-Guldberg & Bruno, 2010; Parmesan & Yohe, 2003), and the spread of invasive species (Mack et al., 2000; Vilà et al., 2011). While these processes are understood to be associated with reductions in local ( $\alpha$ ) diversity or movement of species into new regions, a less well-appreciated consequence of anthropogenic global change is biotic homogenization (BH; Olden & Rooney, 2006). As some species are extirpated, while others invade into new areas (either naturally or via human activity), geographically distinct communities can become more similar to each other, resulting in loss of  $\beta$ -diversity over time.

This loss in ecological distinctness and variability could have a variety of consequences (Olden, LeRoy Poff, Douglas, Douglas, & Fausch, 2004). Loss of species, the simplest mechanism for BH, can reduce ecosystem functioning (O'Connor & Crowe, 2005; Yachi & Loreau, 1999) and production of services (Worm et al., 2006), depending on the specific role of the species that are lost. There is also growing evidence that  $\beta$ -diversity itself plays a direct role in ecosystem functioning that is undermined by homogenization (Hautier et al., 2018; Mori, Isbell, & Seidl, 2018). BH also undermines stability and resilience of ecosystems (Downing, Nes, Mooij, & Scheffer, 2012; Tilman, Reich, & Knops, 2006), reducing ecosystems' capacity to recover after large-scale environmental disturbances or to resist biological invasions (Olden et al., 2004).

Anthropogenic impacts can drive BH through a variety of mechanisms. While loss of species is the simplest mechanism, BH – or conversely, biotic differentiation – can happen through either loss or gain of species depending on their identity and commonality (Olden & Rooney, 2006). In some cases, as with agriculture, humans purposefully spread a small subset of species across broad geographic ranges. More generally, human activity and global transport increase the likelihood of inadvertent dispersal of certain species, even within their native ranges (Nathan et al., 2008). Such increased dispersal can promote the dominance of highly competitive species by giving them access to more locations. Similarly, human development can remove natural barriers that previously prevented mixing of species or populations (Elton, 1958). Additionally, environmental changes associated with agriculture, development, or other human activities can homogenize abiotic conditions, thereby supporting a more homogeneous flora and fauna (McKinney, 2006).

From its beginning, theory around BH has explicitly considered invasive species, but often in a narrow way. Invasive species, broadly speaking, are cosmopolitan, able to spread to many locations, and tend to become locally abundant. Their ubiquity can thus drive ecological communities to become more compositionally similar (McKinney, 2004), making invasive species one of the most influential, direct drivers of BH (Olden et al., 2004). This direct influence on community similarity has been considered

the main role of invaders on BH; however, invasive species can also indirectly increase community similarity via effects on native communities. This can occur through species interactions (e.g., competitive exclusion) or invader-mediated impacts on environmental conditions that spur shifts in community composition (Byers, Wright, & Gribben, 2010; D'Antonio & Vitousek, 1992; Didham, Tylianakis, Hutchison, Ewers, & Gemmill, 2005). Thus, the influence of invasive species on BH can be differentiated between a *direct* component (invasive species' presence altering community similarity) and an *indirect* component (via concomitant effects on native species). Conversely, BH can occur simply through spread or loss of native species, independent of the influence of invasive species. These alternative mechanisms can be quantified by estimating the background rate of homogenization of communities with only native species present and contrasting this rate with that found where invaders are present. Where invaders are present, their influence can be further assessed by partitioning out the mathematical contribution (to similarity measures) of shared presence of the invasive species across locations versus changes in community similarity associated with the native community alone.

Here we investigate the role of invasive species in BH in aquatic plant communities of shallow lakes across Minnesota. Lakes are a key commercial and cultural resource in the upper Midwest (Keeler et al., 2012, 2015), and their macrophyte communities strongly influence ecosystem functioning (Carpenter & Lodge, 1986; Takamura, Kadono, Fukushima, Nakagawa, & Kim, 2003). Several emergent and submersed aquatic invasive plant species are present in Minnesota lakes and represent a significant concern for both lake users and resource managers. Several local impacts of aquatic macrophyte invasions, including reductions in  $\alpha$ -diversity, alteration of environmental conditions, and degradation of habitat for other species, have been well established (Muthukrishnan, Hansel-Welch, & Larkin, 2018; Strayer, 2010; Thomaz, Mormul, & Michelan, 2015), but we know of no research that has evaluated invasions' influence on ecological distinctiveness at regional scales, and their potential to further drive BH by impacting native communities. Because of the implications of BH for ecosystem resilience and adaptability (Olden et al., 2004), understanding these potential effects of aquatic invasions is important for informing management strategies in response to invasions.

Using plant community composition data from 1,102 lakes, including 248 lakes with repeated surveys, we quantified community similarity across lakes with and without invasive plant species, changes in similarity over time, changes in overall species richness, and the relative contributions of native and invasive species to community similarity. To investigate the potential influence of species invasions on BH, we tested the hypotheses that: (a) lakes with invasive species are on average more similar than lakes without invasive species, (b) lakes with invasive species are increasing in similarity at a faster rate than uninvaded lakes, (c) species richness decreases more in invaded lakes than uninvaded lakes, and (d) greater similarity among invaded lakes is driven by

both the presence of invasive species and changes in native species composition.

## 2 | METHODS

### 2.1 | Survey data

Between 2002 and 2014, the Minnesota Department of Natural Resources conducted 1,662 vegetation surveys in 1,102 shallow lakes across Minnesota (Figure 1). The lakes represent a broad range of conditions found across the state, including varying levels and types of surrounding land use, human activity, and management. For a subset of 289 lakes, surveys were repeated in multiple years; however, 41 of these lakes were managed using water-level drawdowns, which greatly alters vegetation, and so were excluded from the repeated-survey analyses. This left a set of 248 lakes where changes in community similarity could be assessed over time. Of the full set of lakes, 616 had at least one invasive macrophyte species, while 181 of the lakes with multiple surveys were invaded. Many lakes contained multiple invasive species (up to four), but it was most common for lakes to only have a single invasive species.

For each survey, the thrown-rake method was used to quantify macrophyte communities at littoral locations on a point-intercept grid placed on each lake (Madsen & Wersal, 2017; Spears et al., 2009). At each location, all macrophytes (aquatic vascular plants and macroalgae) found were identified to species or the lowest feasible taxon. Throughout, we refer to taxa as 'species' for clarity, although this includes some identified only to genus (see Supporting Information Table S1 for a full list of taxa). The number of points surveyed within a lake varied as a function of lake size ( $61.7 \pm 37.9$ ; mean  $\pm$  SD).

We determined invasive status of species in Minnesota based on established lists (Milburn, Bourdaghs, & Husveth, 2007; USDA National Resources Conservation Service, 2016); six were present in our surveys: *Lythrum salicaria* (purple loosestrife), *Myriophyllum spicatum* (Eurasian watermilfoil), *Phalaris arundinacea* (reed canarygrass), *Potamogeton crispus* (curly-leaf pondweed), *Typha angustifolia* (narrow-leaf cattail) and *Typha*  $\times$  *glauca* (hybrid cattail). Recent surveys have suggested that *Typha* stands in the region generally include hybrid genotypes, even those that may have previously been recorded as the native *Typha latifolia* (Travis, Marburger, Windels, & Kubátová, 2010). Thus, we treated all *Typha* records in the dataset as invasive and as a single taxonomic unit when counting species richness. We also reran analyses, while differentiating *Typha* to the lowest reported taxon and found no qualitative differences in results, indicating low sensitivity to this conservative approach to *Typha* taxonomy. Similarly, both invasive European and native genotypes of *Phragmites australis* occur in Minnesota, but lineages were not discriminated in our dataset. Based on recent statewide surveys of *P. australis* populations (J. Bohnen, unpubl. data) and the rarity of hybridization between native and invasive *P. australis* (Fant, Price, &

Larkin, 2016; Saltonstall, Castillo, & Blossey, 2014), it is likely that the large majority of *P. australis* occurrences in the dataset were native and we have treated them accordingly.

### 2.2 | Data analysis

To determine lake-level species richness and community composition across the full set of 1,102 lakes, we aggregated data from individual sampling points to the lake level using the most recent survey available for each lake. No macrophytes were observed in the most recent survey for 33 lakes; these were dropped from subsequent analyses. We classified lakes where at least one invasive species was present as 'invaded'. To evaluate community similarity for invaded and uninvaded lakes we calculated Jaccard dissimilarity ( $J_d$ ) between lakes (Jaccard, 1912) where

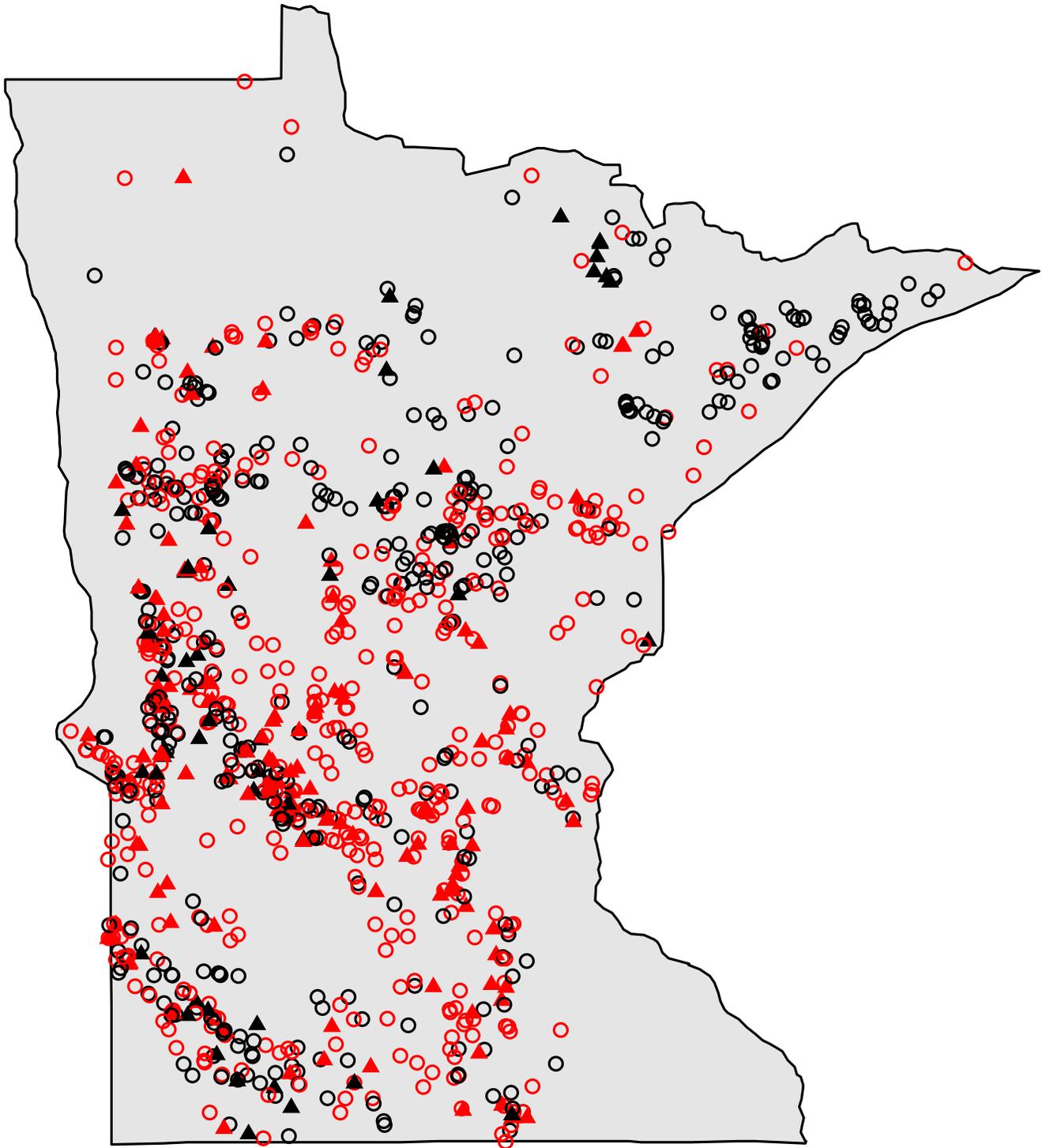
$$J_d = \frac{2B_d}{1+B_d} \quad (1)$$

and  $B_d$  is the Bray–Curtis dissimilarity (Bray & Curtis, 1957) between lakes, calculated based on species presence/absence,

$$B_d = 1 - \frac{\text{\#of species in common}}{\text{\#of species in site a} + \text{\#of species in site b}}. \quad (2)$$

Dissimilarity measurements were calculated using the vegdist function (with method = 'jaccard') from the vegan package (Oksanen et al., 2015) in R version 3.5.1 (which was used for all analyses; R Core Team, 2018). We then calculated the Jaccard similarity ( $J_s$ ) as  $J_s = 1 - J_d$ . We measured  $J_s$  for each uninvaded lake with respect to all other uninvaded lakes and calculated the mean similarity value ( $\bar{J}_s$ ) for each lake. We repeated this process for all invaded lakes, measuring similarity against other invaded lakes. Additionally, we calculated similarity between invaded lakes based on only the native species present to quantify BH not driven directly by invader presence. We tested for an effect of invasion on BH by comparing the mean similarities (for all species and for native species only) of invaded and uninvaded lakes using a t-test. We also compared multivariate community similarity between uninvaded and invaded lakes, again considering all species and only native species (in this case excluding lakes that had no native species), using analysis of similarity (Clarke, 1993; using the anosim function from the vegan package, with method = 'jaccard' and 10,000 permutations).

As different geographic regions could potentially correlate with abiotic environmental differences that would limit the potential set of species that can co-occur we conducted additional analyses to evaluate if there was an effect of the spatial scale of regions used to calculate  $\beta$ -diversity. To do this we separated lakes into smaller regions and calculated  $B_d$  and  $\bar{J}_s$  (as above) for each lake based only on comparison with other lakes in the region (when there were at least five invaded or uninvaded lakes in the geographic region), rather than across the



**FIGURE 1** Locations of all sampled lakes. Invaded locations are coloured red and uninvaded locations are black. Open circles indicate locations with only a single sampling time point and filled triangles represent lakes sampled in multiple years

entire dataset. We conducted these additional analyses at two spatial scales, counties and the four Minnesota Department of Natural Resources administrative regions, and compared average similarities of invaded and uninvaded lakes using *t*-tests at each spatial scale.

To examine temporal patterns of BH, we conducted further analyses using data from the 248 lakes with repeated survey data. For

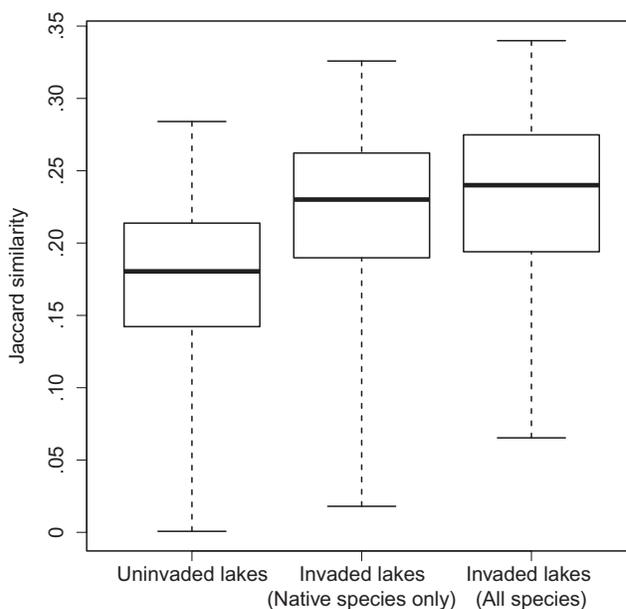
these lakes, we calculated mean similarity between invaded lakes and between uninvaded lakes for both the earliest and most recent surveys of each lake. On average, the time between surveys was  $6.0 \pm 2.9$  years, with a maximum of 12 years. We evaluated whether the change in similarity over time was different between invaded and uninvaded lakes by analysing mean similarity using a linear

mixed effects model (using the lmer function from the lme4 package; Bates, Mächler, Bolker, & Walker, 2015), which included time period, invasion status and their interaction as fixed effects and lake identity as a random effect to account for repeated measures (surveys). We evaluated statistical significance using a parametric bootstrap approach with the PBmodcomp function (from the pbrtest package; Halekoh & Højsgaard, 2014), which compares models both with and without the parameter of interest. To evaluate if these patterns were driven by changes in species richness, we then conducted analogous comparisons using richness as the response variable. We also separated the plant community by general growth form into emergent and aquatic (submersed and floating) categories and evaluated changes in BH and species richness for each group using the same methods as above.

We further analysed data from the repeated-survey lakes by quantifying changes in the presence of individual species between time points to evaluate if changes in lake similarity were based on the presence of invaders or shifts in native species assemblages. For each species in the dataset, we identified the total number of lakes where it was present, the number of lakes where it was absent during the initial survey but present at the later time point (new colonizations), and the number of lakes where the species was present during the initial survey but not seen in the later time point (losses); we did this separately for invaded and uninvaded lakes. We then calculated the proportion of lakes where each species was a new colonist and the proportion where it was lost, and related those values to the overall commonness of the species as indicated by the number of times it occurred across the entire dataset of 1,102 lakes. This allowed us to evaluate the relative rarity or commonness of species being lost from or added to lakes.

### 3 | RESULTS

Overall, there was high variability in lake-level species richness ( $10.64 \pm 7.30$ ; mean  $\pm$  SD; range 0–44). Measures of lake similarity (Figure 2) showed relatively high distinctiveness for both uninvaded ( $\bar{J}_s = .176 \pm .049$ ;  $\bar{J}_s$  can range from 0 to 1 with a value of 1 indicating identical assemblages in all locations) and invaded lakes ( $\bar{J}_s = .220 \pm .055$ , excluding invasive species from calculations). However, invaded lakes had significantly higher similarity values ( $t = 13.782$ ,  $df = 1,022.1$ ,  $p < .001$ ). When distinctiveness of invaded lakes was calculated with invasive species included, similarity of invaded lakes was similar ( $\bar{J}_s = .232 \pm .055$ ), which was also significantly higher than uninvaded lakes ( $t = 17.731$ ,  $df = 1,027.3$ ,  $p < .001$ ). Community composition of uninvaded lakes was also significantly different from invaded lakes when considering all species [analysis of similarity (ANOSIM) statistic ( $R = .016$ ;  $p < .001$ ) or just native species ( $R = .008$ ;  $p = .007$ ). Similar relative patterns were observed at all spatial scales (county level analysis only native species  $t = 4.044$ ,  $df = 803.5$ ,  $p < .001$ ; county level analysis all species  $t = 6.777$ ,  $df = 820.83$ ,  $p < .001$ ; region level analysis only native species  $t = 6.957$ ,  $df = 889.78$ ,  $p < .001$ ; region level analysis all species

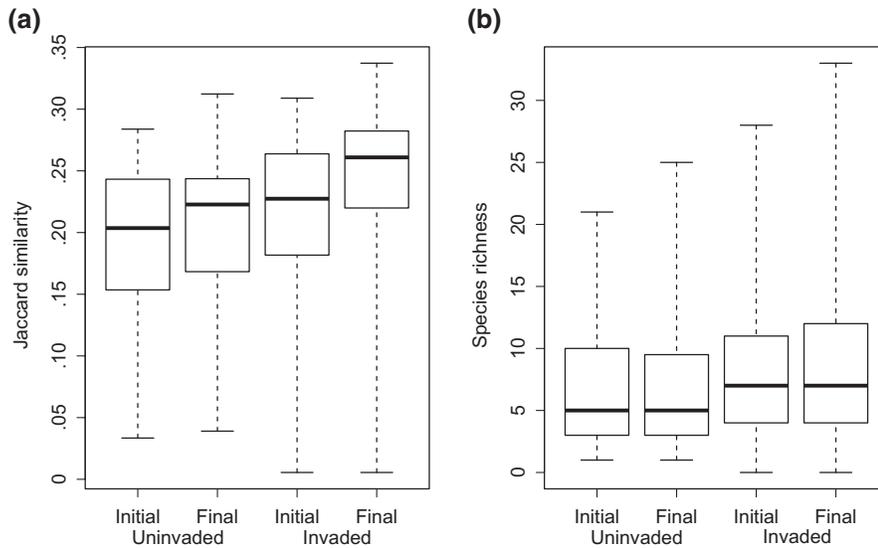


**FIGURE 2** Community similarity of aquatic macrophytes (measured as mean Jaccard similarity) in uninvaded and invaded lakes in Minnesota. Additionally, community similarity was calculated for invaded lakes excluding invasive species (to evaluate similarity of the native community itself) and using all species. The difference between the second and third boxplots represents the direct mathematical contribution of invasive species themselves to community similarity

$t = 10.253$ ,  $df = 881.37$ ,  $p < .001$ ), although as would be expected, average similarity between lakes was greater at smaller spatial scales (Supporting Information Figure S1).

Evaluation of lakes with repeated surveys showed an overall trend toward increasing similarity (Figure 3a; significant positive main effect of time in Table 1). Additionally, invaded lakes were more similar to each other than uninvaded lakes, even at their initial sampling time point (significant main effect of invasion status in Table 1). Invaded lakes also increased in similarity between initial and final surveys but not significantly more than uninvaded lakes (positive but non-significant interaction term in Table 2). Species richness was marginally higher in invaded lakes ( $8.51 \pm 5.90$ ; Figure 3b, main effect of invasion status in Table 2) than uninvaded lakes ( $6.79 \pm 5.47$ ), but this difference was relatively consistent over time (no significant time or interaction effects). Broadly similar patterns were seen when plant communities were split by growth form (Supporting Information Figures S2 and S3). The aquatic (submersed and floating) plant community showed significant main effects of time and invasion as well as a significant interaction between time and invasion status indicating greater rates of BH in invaded lakes (Supporting Information Table S2) but no significant patterns with species richness (Supporting Information Table S3). The emergent plant community showed similar trends in BH and species richness, again with statistically significant patterns only in BH (Supporting Information Tables S4 and S5).

Examining changes in individual species, uninvaded lakes showed a slight tendency for more species losses than colonizations (centroid



**FIGURE 3** Changes in (a) community similarity and (b) species richness of aquatic macrophytes in invaded and uninvaded lakes over time in Minnesota lakes with repeated surveys

Parameter	Estimate	Standard error	Test statistic	p value	Significant
Intercept	0.192	0.008	25.271		
Time (final)	0.015	0.008	1.897	.061	
Invasion (invaded)	0.025	0.009	2.784	.005	*
Time × invasion (final and invaded)	0.010	0.009	1.001	.319	

Note. Asterisks indicate parameters that were statistically significant ( $\alpha=.05$ ) in the analysis.

Parameter	Estimate	Standard error	Test statistic	p value	Significant
Intercept	6.701	0.707	9.478		
Time (final)	0.179	0.482	0.371	.710	
Invasion (invaded)	1.370	0.828	1.656	.097	
Time × invasion (final and invaded)	0.705	0.565	1.248	.210	

**TABLE 1** Statistical results for linear model evaluating changes in community similarity ( $\beta$ -diversity) between invaded and uninvaded lakes. Estimate values are for the condition in parentheses.

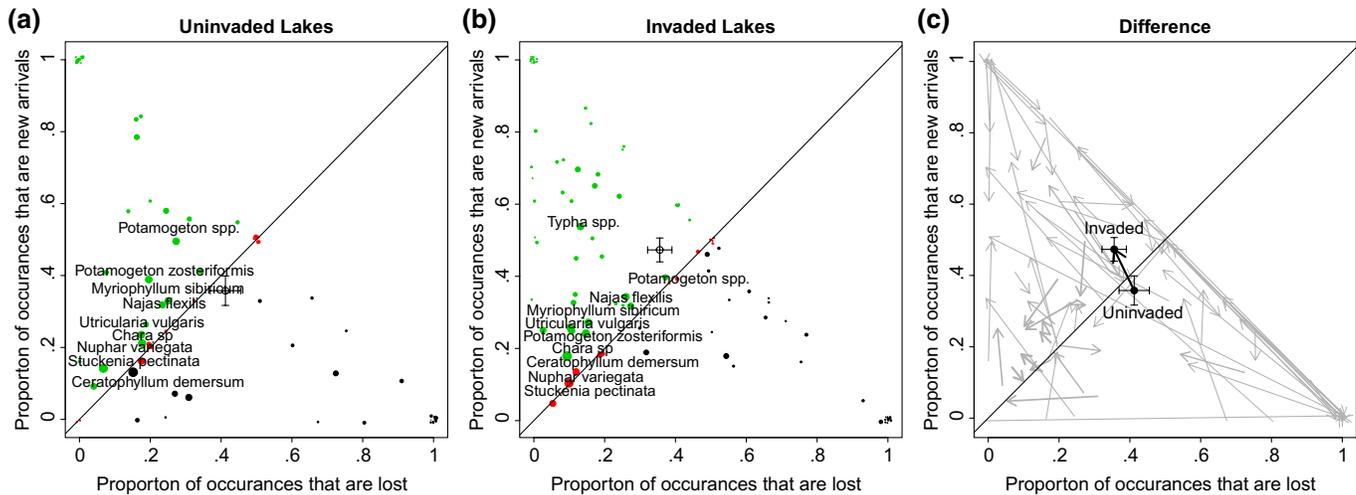
**TABLE 2** Statistical results for linear model evaluating changes in species richness between invaded and uninvaded lakes. Estimate values are for the condition in parentheses

lies below the 1:1 line in Figure 4a). Additionally, while less-common species were slightly more likely to be lost than gained in uninvaded lakes (more small circles below the 1:1 line than above in Figure 4a), common species were about equally likely to be lost or to be new colonists. In contrast, far more species were new colonists rather than lost in invaded lakes (centroid above the 1:1 line in Figure 4b) and many of the new colonizers were common species. This suggests that the increase in BH in invaded lakes was driven primarily by common species becoming more common and rarer species being lost. Species in invaded lakes also tended to lie further away from the origin, and closer to the line from (0,1) to (1,0), indicating their presence in those lakes was less constant.

## 4 | DISCUSSION

Invasive species can have numerous impacts on ecosystems (Pyšek et al., 2012; Vilà et al., 2011), but evaluation of their potential effects on BH have been limited—despite invasive species

being central to the original conceptualization of BH (McKinney, 2004). Most studies that consider invasion effects on BH focus on the broad geographic distribution of invasive species and how their presence itself leads to greater similarity in community composition (McKinney, 2004). Often overlooked are the pathways by which invasions can drive BH through impacts to native communities. We found that the presence of invasive plant species in Minnesota lakes was associated with greater similarity in plant community composition, eroding ecological distinctiveness across the landscape. Furthermore, this pattern arose not only from the mathematical contribution of invaders' widespread presence across lakes, but also through attendant shifts in native species composition. The patterns we observed were consistent with these changes not being driven by changes in lake-level species richness, but rather by re-sorting of species composition. Invaded lakes overall had more volatility in species composition, while uninvaded lakes were more stable. Rare species were more likely to be lost and common species were more likely to be new colonizers in invaded lakes than in uninvaded lakes. Such shifts, and associated



**FIGURE 4** Relative consistency of the presence of individual aquatic macrophyte species in (a) uninvaded and (b) invaded Minnesota lakes. Each circle represents an individual species and position along the y axis indicates the proportion of lakes in which the species was found and for which it was a new colonist (i.e., the species was not present in the initial survey, but then observed in a subsequent survey). The position along the x axis indicates the proportion of lakes in which the species was found but later lost (i.e., the species was present in the initial survey, but then not observed in a subsequent survey). Circles that lie closer to the origin indicate species that were more often present at both time points in a given lake. Green circles represent species that were new colonists more often than they were lost, black circles indicate species that were lost more often than they were new colonists, and red circles indicate species that were new colonists or lost in roughly the same number of lakes. The size of individual circles indicates the commonality of the species across all lakes and all circles are slightly jittered to make overlapping data points more visible. The names of the 10 most common species have been overlaid near their individual data points. Panel (c) shows vectors that indicate the shift in location of individual species from uninvaded to invaded lakes, and the centroids of the mean position of all species ( $\pm 1$  SE) are plotted in black

loss of  $\beta$ -diversity, could have important implications for functioning, stability and resilience of these ecosystems (Mori et al., 2018; Olden et al., 2004) and should be considered in conservation and management decision-making (McKnight et al., 2007; Pressey, Humphries, Margules, Vane-Wright, & Williams, 1993).

Invasive species have been recognized as a key mechanism of global ecological change, but understanding the potential impacts of invasions remains a somewhat contentious topic (Davis, 2003; Gurevitch & Padilla, 2004). Loss of  $\alpha$ -diversity through competitive exclusion is the most commonly considered mechanism by which invasive species can influence ecological systems (Clavero, Brotons, Pons, & Sol, 2009; Grice, 2006; Molnar, Gamboa, Revenga, & Spalding, 2008). However, loss of  $\alpha$ -diversity is not the only way invasive species can influence ecosystems (Levine et al., 2003; Vilà et al., 2011). In Minnesota lake-plant communities, invasions did not reduce species richness at the whole-lake scale, although competitive exclusion was previously reported at finer spatial scales (Muthukrishnan et al., 2018). Nonetheless, there appeared to be reorganization of community structure, potentially indicating invaders are driving BH via a broader environmental impact, akin to the effects of urbanization on BH (Blair, 2001). However, while invaded lakes had overall greater biotic similarity, both invaded and uninvaded lakes increased in similarity over the study time period. Thus, a causal effect of invasive species on BH remains uncertain. A significant positive interaction between invasion status and time, such that the rate of BH was higher for invaded lakes, would be stronger evidence that invaders specifically drive BH. Our data

were consistent with such a pattern, but the results were not definitive (positive but non-significant interaction term). We also observed broadly similar patterns for both emergent and aquatic plant communities (see Supporting Information Figures S2 and S3) with aquatic plants (both submersed and floating) showing the clearest indication of higher rates of BH in invaded lakes. This difference may arise from stronger species interactions and higher species turnover for aquatic plants, which allows BH to be observed more rapidly, than emergent ones. Alternatively, the emergent plant community includes more rare species, which sometimes were essentially terrestrial species that infrequently are observed in the edge habitat of lakes. The high incidence of rare species drives down overall community similarity and may make it difficult to identify BH with the approaches employed here. Nonetheless, the general consistency in patterns between taxonomic groups offers an additional indication of the robustness of our results. It is possible that other factors, such as human disturbances, increase both invasion and BH, and thus their relationship is driven by a broader factor controlling both processes. Yet, previous work that directly evaluated the relationship between environmental change and  $\beta$ -diversity in lakes found no significant pattern (Angeler & Drakare, 2013), suggesting invasions may be a particularly influential component of global change. While causal relationships are difficult to discern from the observational data we analysed here, analysis of large-scale observational data can offer a valuable complement to experimental efforts when dealing with complex systems (Elliott, Cheruvilil, Montgomery, & Soranno, 2016; Kelling et al., 2009). Observational studies can provide a spatial and

temporal extent unlikely to be feasible experimentally, and including a large number of independent lakes with a range of variation offers the potential for more robust patterns. These factors are likely to be critical for studying topics such as BH that are emergent outcomes of multiple processes acting across large spatial and temporal scales. These results should encourage further work that directly tests the alternative possibilities raised here.

The relationship between invasions and BH could be driven by a variety of mechanisms with different implications for community trajectories and effective management. Invasive species have been shown to competitively exclude native species in these systems (Muthukrishnan et al., 2018), which may disproportionately impact rare and less-competitive species, leading to greater relative abundance of common species. Invasive plant species tend to grow in high-density aggregations, which can potentially change water flow patterns (Cornacchia et al., 2018), nutrient cycling (Geddes, Grancharova, Kelly, Treering, & Tuchman, 2014), or light availability (Urban, Titus, & Zhu, 2009). All of these can, in turn, influence community dynamics. But it is not clear, a priori, if invasions would likely increase or decrease any of these conditions, or what the implications would be for BH. Single, widespread invasive species that have strong habitat-modifying influences, such as zebra mussels, may offer the most likely scenario for increasing BH by pulling many systems toward a particular environmental condition and reducing heterogeneity (Rahel, 2002). But this may not be the case for invasive species in general.

This uncertainty about the relationship between invasions and BH has a number of implications. It is notable that these lakes still retain significant heterogeneity ( $\bar{J}_s$  values generally below .25, although this does increase slightly when comparisons are made at smaller spatial scales) and hence diversity, such that current community-level impacts may be limited. This may be due in part to the geographic range of our comparisons and the fact that anthropogenic drivers of biotic mixing (and the associated expansion of invasive species) are relatively recent, both of which will reduce measures of community similarity. Yet, the patterns of change suggest that heterogeneity will continue to erode, which may eventually have more consequential impacts. It is also possible that prevailing environmental changes are promoting both invasion and homogenization in tandem. For example, lakes that become invaded are likely to have higher connectivity – via landscape features or human movement – to other lakes (Benjamin, Dunham, & Dare, 2007). This allows for not only higher invader propagule pressure, but also higher propagule pressure for native species, particularly those that are widespread and abundant, that is, common species. Additionally, invasions are frequently associated with habitat degradation or changes in water quality (Didham, Tylianakis, Gemmill, Rand, & Ewers, 2007; Linde, Izquierdo, Moreira, & Garcia-Vazquez, 2008). A number of environmental correlates aligned with anthropogenic impacts (e.g., Secchi depth, chlorophyll *a* concentrations) are associated with invasion in Minnesota lakes specifically (Muthukrishnan et al., 2018). Such conditions may promote invasive species as ‘passengers’ of change (*sensu* MacDougall & Turkington, 2005) and are likely to favour common

native species that employ a more generalist or environmentally tolerant strategy versus rarer species with narrower environmental niches (Devictor, Julliard, & Jiguet, 2008). There is also extensive evidence of environmental changes driving shifts in macrophyte communities (Jeppesen, Peder Jensen, Søndergaard, Lauridsen, & Landkildehus, 2000; Sand-Jensen et al., 2008) even leading to BH (Salgado et al., 2018). These mechanisms are not mutually exclusive and multiple processes could be driving the overall patterns we observed. But our findings suggest that a plausible mechanism needs to explain not only statistical patterns of homogenization (which could be driven by invader presence alone) but also shifts toward wider distributions of common species.

Invasion-driven BH has important implications for understanding the impacts of invasion and guiding conservation and management decision-making. Changes in  $\alpha$ -diversity of native species are a common way to quantify invader impacts (Pyšek et al., 2012)—or the apparent lack thereof (Sax, Gaines, & Brown, 2002). But analyses based on  $\alpha$ -diversity alone can miss important community-level changes when richness remains relatively constant (or even increases) despite broader regional shifts of rare species becoming rarer and common species more common. Where invaders change community composition through habitat modification, in lieu of or in addition to changes imparted through direct competition, their impacts may be disproportionately large relative to invader abundance, and removal of the invader alone may be an insufficient management response (Cuddington & Hastings, 2004; Lishawa, Lawrence, Albert, & Tuchman, 2015). Additionally, analogous to genetic diversity within species (Sgrò, Lowe, & Hoffmann, 2011), reduction in regional diversity of communities can decrease resilience to disturbances, such as diseases or changing climatic or environmental conditions (Adger, Hughes, Folke, Carpenter, & Rockström, 2005; Lavorel, 1999). This can occur when rare members of the regional species pool possess traits adapted for the novel conditions and contribute to ecosystem functioning (Chapin III et al., 2000).

BH has been considered in a variety of aquatic and terrestrial systems, with both plant and animal studies supporting the significance of BH (Olden & Rooney, 2006). But a synthesis that addresses the influence of system type on BH has not yet been established. Aquatic systems have provided some of the strongest examples of BH (e.g., Olden & Poff, 2004; Radomski & Goeman, 1995), yet it is difficult to predict if BH would be a more or less likely consequence of invasions in aquatic versus terrestrial systems. There is some evidence that aquatic plant communities, particularly at higher latitudes, are more strongly controlled by abiotic constraints than terrestrial communities (Muthukrishnan et al., 2018; Santamaría, 2002), which would suggest lower ability for aquatic invaders to influence community structure or composition through species interactions. At the same time, because lakes are often distinct spatial units and dispersal between them is limited and highly influenced by human movement (Johnson & Carlton, 1996), rare species are at greater risk of local extinction, with low potential for rescue, increasing the risk of BH. This reinforces the need for more explicit evaluation of habitat modification and direct competition between

invasive and native species to improve understanding of lake community dynamics.

While there is no shortage of reasons why invasive species are a major global concern (McGeoch et al., 2010; Pejchar & Mooney, 2009; Vilà et al., 2011; Vitousek, D'antonio, Loope, Rejmanek, & Westbrooks, 1997), their potential to promote BH has perhaps been underappreciated. Our results also identify BH over surprisingly short time-scales, often a decade or less, in contrast to major BH studies that have documented impacts over intervals of many decades (Minnesota fishes c. 40 years, Radomski & Goeman, 1995; California fishes c. 150 years, Marchetti et al., 2001; Wisconsin plants c. 50 years, Rooney, Wiegmann, Rogers, & Waller, 2004; island birds 100 + years, Cassey, Lockwood, Blackburn, & Olden, 2007). It remains uncertain if this more rapid BH is because of the impact of invasive species or simply a ratcheting up of anthropogenic impacts on natural systems, but nonetheless the speed is important to recognize. These patterns are also broadly aligned, in terms of extent and time-scale, with changes in BH associated with invasion in wetland ecosystems of Illinois (Price, Spyreas, & Matthews, 2018). We also cannot explicitly discriminate if invasions were a direct or indirect cause of BH in our study system, or if both invasion and BH simply covaried with broader drivers of change. Nonetheless, invasions in these temperate lake communities were correlated with a reduction in ecological novelty across spatial and temporal scales, despite there not having been significant declines in species richness. This has important implications for conservation and management (Olden et al., 2004) and suggests that regional diversity across the landscape, and not just local diversity, should be more widely incorporated into conservation and management applications, such as monitoring community change, evaluating invasive species impacts, and developing restoration and recovery plans.

#### ACKNOWLEDGMENTS

Funding for this project was provided through the Minnesota Aquatic Invasive Species Research Center from the Minnesota Environment and Natural Resources Trust Fund. We thank N. Hansel-Welch, A. Geisen, and the Shallow Lakes Program in general for their extensive efforts collecting and organizing field data. This work was also benefitted by the suggestions of two anonymous referees. The authors declare no conflicts of interest.

#### AUTHOR CONTRIBUTIONS

RM and DJL designed the study and analyses. RM analysed the data and wrote the initial draft of the manuscript. Both authors participated in data interpretation and revising the manuscript.

#### DATA AVAILABILITY STATEMENT

All macrophyte community data and analysis scripts for analyses in this study are archived and available from the Dryad Digital Repository, <https://doi.org/10.5061/dryad.15dv41nt2>

#### ORCID

Ranjan Muthukrishnan  <https://orcid.org/0000-0002-7001-6249>

#### REFERENCES

- Adger, W. N., Hughes, T. P., Folke, C., Carpenter, S. R., & Rockström, J. (2005). Social-ecological resilience to coastal disasters. *Science*, *309* (5737), 1036–1039.
- Angeler, D. G., & Drakare, S. (2013). Tracing alpha, beta, and gamma diversity responses to environmental change in boreal lakes. *Oecologia*, *172*, 1191–1202. <https://doi.org/10.1007/s00442-012-2554-y>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.
- Benjamin, J. R., Dunham, J. B., & Dare, M. R. (2007). Invasion by non-native brook trout in panther creek, Idaho: Roles of local habitat quality, biotic resistance, and connectivity to source habitats. *Transactions of the American Fisheries Society*, *136*, 875–888. <https://doi.org/10.1577/T06-115.1>
- Blair, R. B. (2001). Birds and butterflies along urban gradients in two ecoregions of the United States: Is urbanization creating a homogeneous fauna? In J. L. Lockwood & M. L. McKinney (Eds.), *Biotic homogenization* (pp. 33–56). Boston, MA: Springer US.
- Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, *27*, 326–349. <https://doi.org/10.2307/1942268>
- Byers, J. E., Wright, J. T., & Gribben, P. E. (2010). Variable direct and indirect effects of a habitat-modifying invasive species on mortality of native fauna. *Ecology*, *91*, 1787–1798. <https://doi.org/10.1890/09-0712.1>
- Carpenter, S. R., & Lodge, D. M. (1986). Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany*, *26*, 341–370. [https://doi.org/10.1016/0304-3770\(86\)90031-8](https://doi.org/10.1016/0304-3770(86)90031-8)
- Cassey, P., Lockwood, J. L., Blackburn, T. M., & Olden, J. D. (2007). Spatial scale and evolutionary history determine the degree of taxonomic homogenization across island bird assemblages. *Diversity and Distributions*, *13*, 458–466. <https://doi.org/10.1111/j.1472-4642.2007.00366.x>
- Chapin, F. S. III, Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., ... Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, *405*, 234–242. <https://doi.org/10.1038/35012241>
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Clavero, M., Brotons, L., Pons, P., & Sol, D. (2009). Prominent role of invasive species in avian biodiversity loss. *Biological Conservation*, *142*, 2043–2049. <https://doi.org/10.1016/j.biocon.2009.03.034>
- Cornacchia, L., van de Koppel, J., van der Wal, D., Wharton, G., Puijalon, S., & Bouma, T. J. (2018). Landscapes of facilitation: How self-organized patchiness of aquatic macrophytes promotes diversity in streams. *Ecology*, *99*, 832–847. <https://doi.org/10.1002/ecy.2177>
- Cuddington, K., & Hastings, A. (2004). Invasive engineers. *Ecological Modelling*, *178*, 335–347. <https://doi.org/10.1016/j.ecolmodel.2004.03.010>
- D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, *23*, 63–87. <https://doi.org/10.1146/annurev.es.23.110192.000431>
- Davis, M. A. (2003). Biotic globalization: Does competition from introduced species threaten biodiversity? *BioScience*, *53*, 481–489. [https://doi.org/10.1641/0006-3568\(2003\)053\[0481:BGDCFJ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0481:BGDCFJ]2.0.CO;2)
- Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, *117*, 507–514. <https://doi.org/10.1111/j.0030-1299.2008.16215.x>
- Didham, R. K., Tylianakis, J. M., Gemmill, N. J., Rand, T. A., & Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution*, *22*, 489–496. <https://doi.org/10.1016/j.tree.2007.07.001>
- Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., & Gemmill, N. J. (2005). Are invasive species the drivers of ecological

- change? *Trends in Ecology and Evolution*, 20, 470–474. <https://doi.org/10.1016/j.tree.2005.07.006>
- Downing, A. S., van Nes, E. H., Mooij, W. M., & Scheffer, M. (2012). The resilience and resistance of an ecosystem to a collapse of diversity. *PLoS ONE*, 7, e46135. <https://doi.org/10.1371/journal.pone.0046135>
- Elliott, K. C., Cheruvilil, K. S., Montgomery, G. M., & Soranno, P. A. (2016). Conceptions of good science in our data-rich world. *BioScience*, 66, 880–889. <https://doi.org/10.1093/biosci/biw115>
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. Chicago, IL: University of Chicago Press.
- Fant, J. B., Price, A. L., & Larkin, D. J. (2016). The influence of habitat disturbance on genetic structure and reproductive strategies within stands of native and non-native *Phragmites australis* (common reed). *Diversity and Distributions*, 22, 1301–1313.
- Geddes, P., Grancharova, T., Kelly, J. J., Treering, D., & Tuchman, N. C. (2014). Effects of invasive *Typha × glauca* on wetland nutrient pools, denitrification, and bacterial communities are influenced by time since invasion. *Aquatic Ecology*, 48, 247–258. <https://doi.org/10.1007/s10452-014-9480-5>
- Grice, A. C. (2006). The impacts of invasive plant species on the biodiversity of Australian rangelands. *The Rangeland Journal*, 28, 27–35. <https://doi.org/10.1071/RJ06014>
- Gurevitch, J., & Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution*, 19, 470–474. <https://doi.org/10.1016/j.tree.2004.07.005>
- Halekoh, U., & Højsgaard, S. (2014). A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models—The R package pbrktest. *Journal of Statistical Software*, 59, 1–32.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., ... Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, 319, 948–952. <https://doi.org/10.1126/science.1149345>
- Hautier, Y., Isbell, F., Borer, E. T., Seabloom, E. W., Harpole, W. S., Lind, E. M., ... Hector, A. (2018). Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nature Ecology and Evolution*, 2, 50–56. <https://doi.org/10.1038/s41559-017-0395-0>
- Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, 328(5985), 1523–1528.
- Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, 8, 23–29. <https://doi.org/10.1111/j.1461-0248.2004.00686.x>
- Jaccard, P. (1912). The distribution of the flora in the alpine zone. *New Phytologist*, 11, 37–50.
- Jeppesen, E., Peder Jensen, J., Søndergaard, M., Lauridsen, T., & Landkildehus, F. (2000). Trophic structure, species richness and biodiversity in Danish lakes: Changes along a phosphorus gradient. *Freshwater Biology*, 45, 201–218. <https://doi.org/10.1046/j.1365-2427.2000.00675.x>
- Johnson, L. E., & Carlton, J. T. (1996). Post-establishment spread in large-scale invasions: Dispersal mechanisms of the zebra mussel *Dreissena polymorpha*. *Ecology*, 77, 1686–1690. <https://doi.org/10.2307/2265774>
- Keeler, B. L., Polasky, S., Brauman, K. A., Johnson, K. A., Finlay, J. C., O'Neill, A., ... Dalzell, B. (2012). Linking water quality and well-being for improved assessment and valuation of ecosystem services. *Proceedings of the National Academy of Sciences USA*, 109, 18619–18624. <https://doi.org/10.1073/pnas.1215991109>
- Keeler, B. L., Wood, S. A., Polasky, S., Kling, C., Filstrup, C. T., & Downing, J. A. (2015). Recreational demand for clean water: Evidence from geotagged photographs by visitors to lakes. *Frontiers in Ecology and the Environment*, 13, 76–81. <https://doi.org/10.1890/140124>
- Kelling, S., Hochachka, W. M., Fink, D., Riedewald, M., Caruana, R., Ballard, G., & Hooker, G. (2009). Data-intensive science: A new paradigm for biodiversity studies. *BioScience*, 59, 613–620. <https://doi.org/10.1525/bio.2009.59.7.12>
- Lavelle, S. (1999). Ecological diversity and resilience of Mediterranean vegetation to disturbance. *Diversity and Distributions*, 5, 3–13. <https://doi.org/10.1046/j.1472-4642.1999.00033.x>
- Levine, J. M., Vilà, M., Antonio, C. M. D., Dukes, J. S., Grigulis, K., & Lavelle, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences*, 270(1517), 775–781.
- Linde, A. R., Izquierdo, J. I., Moreira, J. C., & Garcia-Vazquez, E. (2008). Invasive tilapia juveniles are associated with degraded river habitats. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18, 891–895. <https://doi.org/10.1002/aqc.928>
- Lishawa, S. C., Lawrence, B. A., Albert, D. A., & Tuchman, N. C. (2015). Biomass harvest of invasive *Typha* promotes plant diversity in a Great Lakes coastal wetland. *Restoration Ecology*, 23, 228–237.
- MacDougall, A. S., & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, 86, 42–55. <https://doi.org/10.1890/04-0669>
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, 10, 689–710. [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Madsen, J. D., & Wersal, R. M. (2017). A review of aquatic plant monitoring and assessment methods. *Journal of Aquatic Plant Management*, 55, 1–12.
- Marchetti, M. P., Light, T., Feliciano, J., Armstrong, T., Hogan, Z., Viers, J., & Moyle, P. B. (2001). Homogenization of California's fish fauna through abiotic change. In J. L. Lockwood & M. L. McKinney (Eds.), *Biotic Homogenization* (pp. 259–278). Boston, MA: Springer US.
- McGeoch, M. A., Butchart, S. H. M., Spear, D., Marais, E., Kleynhans, E. J., Symes, A., ... Hoffmann, M. (2010). Global indicators of biological invasion: Species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, 16, 95–108. <https://doi.org/10.1111/j.1472-4642.2009.00633.x>
- McKinney, M. L. (2004). Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography*, 13, 47–53. <https://doi.org/10.1111/j.1466-882X.2004.00059.x>
- McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127, 247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- McKnight, M. W., White, P. S., McDonald, R. I., Lamoreux, J. F., Sechrest, W., Ridgely, R. S., & Stuart, S. N. (2007). Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. *PLoS Biology*, 5, e272. <https://doi.org/10.1371/journal.pbio.0050272>
- Milburn, S. A., Bourdaghs, M., & Husveth, J. J. (2007). *Floristic quality assessment for Minnesota wetlands*. St. Paul, MN: Minnesota Pollution Control Agency.
- Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6, 485–492. <https://doi.org/10.1890/070064>
- Mori, A. S., Isbell, F., & Seidl, R. (2018). B-diversity, community assembly, and ecosystem functioning. *Trends in Ecology and Evolution*, 33, 549–564.
- Muthukrishnan, R., Hansel-Welch, N., & Larkin, D. J. (2018). Environmental filtering and competitive exclusion drive biodiversity-invasibility relationships in shallow lake plant communities. *Journal of Ecology*, 106, 2058–2070. <https://doi.org/10.1111/1365-2745.12963>
- Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., & Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution*, 23, 638–647. <https://doi.org/10.1016/j.tree.2008.08.003>
- O'Connor, N. E., & Crowe, T. P. (2005). Biodiversity loss and ecosystem functioning: Distinguishing between number and identity of species. *Ecology*, 86, 1783–1796. <https://doi.org/10.1890/04-1172>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., ... Wagner, H. (2015). *vegan: Community ecology*

- package. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, *19*, 18–24. <https://doi.org/10.1016/j.tree.2003.09.010>
- Olden, J. D., & Poff, N. L. (2004). Ecological processes driving biotic homogenization: Testing a mechanistic model using fish faunas. *Ecology*, *85*, 1867–1875. <https://doi.org/10.1890/03-3131>
- Olden, J. D., & Rooney, T. P. (2006). On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, *15*, 113–120. <https://doi.org/10.1111/j.1466-822X.2006.00214.x>
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37–42. [10.1038/nature01286](https://doi.org/10.1038/nature01286)
- Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution*, *24*, 497–504. <https://doi.org/10.1016/j.tree.2009.03.016>
- Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright, R. I., & Williams, P. H. (1993). Beyond opportunism: Key principles for systematic reserve selection. *Trends in Ecology and Evolution*, *8*, 124–128. [https://doi.org/10.1016/0169-5347\(93\)90023-I](https://doi.org/10.1016/0169-5347(93)90023-I)
- Price, E. P. F., Spyreas, G., & Matthews, J. W. (2018). Biotic homogenization of regional wetland plant communities within short time-scales in the presence of an aggressive invader. *Journal of Ecology*, *106*, 1180–1190. <https://doi.org/10.1111/1365-2745.12883>
- Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*, 1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>
- Radomski, P. J., & Goeman, T. J. (1995). The homogenizing of Minnesota lake fish assemblages. *Fisheries*, *20*, 20–23. [https://doi.org/10.1577/1548-8446\(1995\)020<0020:THOMLF>2.0.CO;2](https://doi.org/10.1577/1548-8446(1995)020<0020:THOMLF>2.0.CO;2)
- Rahel, F. J. (2002). Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics*, *33*, 291–315. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150429>
- Rooney, T. P., Wiegmann, S. M., Rogers, D. A., & Waller, D. M. (2004). Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology*, *18*, 787–798. <https://doi.org/10.1111/j.1523-1739.2004.00515.x>
- Salgado, J., Sayer, C. D., Brooks, S. J., Davidson, T. A., Goldsmith, B., Patmore, I. R., ... Okamura, B. (2018). Eutrophication homogenizes shallow lake macrophyte assemblages over space and time. *Ecosphere*, *9*, e02406. <https://doi.org/10.1002/ecs2.2406>
- Saltonstall, K., Castillo, H. E., & Blossey, B. (2014). Confirmed field hybridization of native and introduced *Phragmites australis* (Poaceae) in North America. *American Journal of Botany*, *101*, 211–215. <https://doi.org/10.3732/ajb.1300298>
- Sand-Jensen, K., Pedersen, N. L., Thorsgaard, I., Moeslund, B., Borum, J., & Brodersen, K. P. (2008). 100 years of vegetation decline and recovery in Lake Fure, Denmark. *Journal of Ecology*, *96*, 260–271. <https://doi.org/10.1111/j.1365-2745.2007.01339.x>
- Santamaría, L. (2002). Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecologica*, *23*, 137–154. [https://doi.org/10.1016/S1146-609X\(02\)01146-3](https://doi.org/10.1016/S1146-609X(02)01146-3)
- Sax, D. F., Gaines, S. D., & Brown, J. H. (2002). Species invasions exceed extinctions on Islands worldwide: A comparative study of plants and birds. *The American Naturalist*, *160*, 766–783. <https://doi.org/10.1086/343877>
- Sgrò, C. M., Lowe, A. J., & Hoffmann, A. A. (2011). Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, *4*, 326–337. <https://doi.org/10.1111/j.1752-4571.2010.00157.x>
- Spears, B. M., Gunn, I. D. M., Carvalho, L., Winfield, I. J., Dudley, B., Murphy, K., & May, L. (2009). An evaluation of methods for sampling macrophyte maximum colonisation depth in Loch Leven, Scotland. *Aquatic Botany*, *91*, 75–81. <https://doi.org/10.1016/j.aquabot.2009.02.007>
- Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*, 152–174. <https://doi.org/10.1111/j.1365-2427.2009.02380.x>
- Takamura, N., Kadono, Y., Fukushima, M., Nakagawa, M., & Kim, B.-H.-O. (2003). Effects of aquatic macrophytes on water quality and phytoplankton communities in shallow lakes. *Ecological Research*, *18*, 381–395. <https://doi.org/10.1046/j.1440-1703.2003.00563.x>
- Thomaz, S. M., Mormul, R. P., & Michelan, T. S. (2015). Propagule pressure, invasibility of freshwater ecosystems by macrophytes and their ecological impacts: A review of tropical freshwater ecosystems. *Hydrobiologia*, *746*, 39–59. <https://doi.org/10.1007/s10750-014-2044-9>
- Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*, 629–632. <https://doi.org/10.1038/nature04742>
- Travis, S. E., Marburger, J. E., Windels, S., & Kubátová, B. (2010). Hybridization dynamics of invasive cattail (Typhaceae) stands in the Western Great Lakes Region of North America: A molecular analysis. *Journal of Ecology*, *98*, 7–16. <https://doi.org/10.1111/j.1365-2745.2009.01596.x>
- Urban, R. A., Titus, J. E., & Zhu, W.-X. (2009). Shading by an invasive macrophyte has cascading effects on sediment chemistry. *Biological Invasions*, *11*, 265–273. <https://doi.org/10.1007/s10530-008-9231-4>
- USDA National Resources Conservation Service. (2016). The PLANTS Database. Retrieved from <https://plants.sc.egov.usda.gov/>
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., ... Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*, 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Vitousek, P. M., D'antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, *21*, 1–16.
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., ... Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, *314*(5800), 787–790
- Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences USA*, *96*, 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>

## BIOSKETCHES

**Ranjan Muthukrishnan** is a research scientist at the Environmental Resilience Institute at Indiana University and is interested in processes that drive major changes in community structure and factors that make communities resilient to those changes. Much of his work focuses on biological invasions as a major mechanism of global ecological change and he integrates both empirical and theoretical approaches, often synthesized through the use of computational models.

**Daniel J. Larkin** is an assistant professor in the Department of Fisheries, Wildlife, and Conservation Biology at the University of Minnesota–Twin Cities. He conducts applied research in plant ecology, focusing on biodiversity conservation, ecological restoration, and management of biological invasions in aquatic, wetland and terrestrial ecosystems.

**How to cite this article:** Muthukrishnan R, Larkin DJ. Invasive species and biotic homogenization in temperate aquatic plant communities. *Global Ecol Biogeogr.* 2020;00:1–12.  
<https://doi.org/10.1111/geb.13053>

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.