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Lakeshore residential development as a driver of aquatic habitat and littoral fish communities: A cross-system study

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Abstract

Lakeshore riparian habitats have undergone intensive residential development in many parts of the world. Lakeshore residential development (LRD) is associated with aquatic habitat loss/alteration, including altered macrophyte communities and reduced coarse woody habitat. Yet habitat-mediated and other generalized effects of LRD on lake biotic communities are not well understood. We used two approaches to examine the relationships among LRD, habitat, and fish community in a set of 57 northern Wisconsin lakes. First, we examined how LRD affected aquatic habitat using mixed linear effects models. Second, we evaluated how LRD affected fish abundance and community structure at both whole-lake and site-level spatial scales using generalized linear mixed-effects models. We found that LRD did not have a significant relationship with the total abundance (all species combined) of fish at either scale. However, there were significant species-specific responses to LRD at the whole-lake scale. Species abundances varied across the LRD gradient, with bluegill (*Lepomis macrochirus*) and mimic shiners (*Notropis volucellus*) responding positively along the gradient and walleye (*Sander vitreus*) having the most negative response. We also quantified site-level habitat associations for each fish species. We found that habitat associations did not inform a species' overall response to LRD, as illustrated by species with similar responses to LRD having vastly different habitat associations. Finally, even with the inclusion of littoral habitat information in models, LRD still had significant effects on species abundances, reflecting a role of LRD in shaping littoral fish communities independent of our measure of littoral habitat alteration. Our results indicated that LRD altered littoral fish communities at the whole-lake scale through both habitat and non-habitat-mediated drivers.

KEYWORDS
anthropogenic impact, coarse woody habitat, fish–habitat relationships, habitat loss, littoral zone, macrophytes

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INTRODUCTION

There is keen interest in the ecological impacts of low-density residential development adjacent to lakes (hereafter referred to as lakeshore residential development [LRD]; Kaufmann et al., 2014; Schmieder, 2004). Shorelines of temperate lakes are disproportionately developed for residential purposes compared to surrounding forested areas (Gonzalez-Abraham et al., 2007; Radeloff et al., 2001). For example, housing density near shorelines of northern Wisconsin lakes has increased by more than 600% since the 1930s and is expected to continue increasing (Gonzalez-Abraham et al., 2007; Schnaiberg et al., 2002). The result is that many lakes are ringed with homes, and lakes lacking LRD are becoming increasingly rare. For example, roughly 8% and 30% of lakes in southern and northern Michigan, respectively, are considered to be undeveloped (Wehrly et al., 2012). Given its prevalence and ongoing expansion, LRD represents a potent but poorly understood driver of environmental change for lakes (Carpenter et al., 2007).

While in some contexts concentrating human activities can serve to spare other areas from anthropogenic impacts, in this case, LRD concentrates human impacts at the sensitive habitat interface between riparian and lake littoral zone habitats. Lake littoral zones serve as important habitat for many lake organisms and support disproportionately high biodiversity and productivity (Hampton et al., 2011; Vadeboncoeur et al., 2011; Vander Zanden & Vadeboncoeur, 2002). Many aquatic species rely on the littoral zone at some stage of their life cycle, and changes to littoral zone function can have far-reaching ecosystem impacts (Schindler & Scheuerell, 2002). A key aspect of littoral zones is that they are highly heterogeneous and structurally complex, with habitat features that include coarse woody habitat (CWH) and macrophytes (Strayer & Findlay, 2010).

Studies have linked LRD to littoral zone habitat differences or change. Some studies have found that developed lakes have decreased macrophyte abundances (Radomski, 2006; Radomski & Goeman, 2001). Developed lakes also tend to have less CWH, largely due to removal by shoreline property owners (Amato et al., 2015; Jorgensen et al., 2006). This loss of CWH as predation refugia in the littoral zone can destabilize predator–prey dynamics and lead to reductions in prey fish abundance (Gaeta et al., 2014; Helmus & Sass, 2008; Sass, Kitchell, et al., 2006). LRD may also decrease the productive capacity of fisheries, as suggested by reduced growth rates in bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) in developed lakes (Christensen et al., 1996). Similarly, macrophyte communities and overall abundance can be affected by boat traffic, dock shading, and shoreline maintenance practices (Amato et al., 2015; Asplund & Cook, 1997; Radomski et al., 2010). These changes in habitat quantity and quality may affect species interactions (predation and competition) and, thus, influence community composition at higher trophic levels (Gaeta et al., 2014; Werner et al., 1983; Werner & Hall, 1977). One might expect these habitat modifications to affect higher-order communities such as fish in complex ways.

Studies have documented adverse impacts of LRD on a wide range of taxa, including amphibians, birds, macroinvertebrates, and fish (Jennings et al., 1999; Lindsay et al., 2002; Twardochleb & Olden, 2016; Woodford & Meyer, 2003). Cross-system studies that use the lake as the unit of analysis have documented decreases in growth rates of certain fish species, along with changes in spatial distribution, and a decrease in intolerant species along lakeshore development gradients (Jennings et al., 1999; Scheuerell & Schindler, 2004; Schindler et al., 2000). While habitat changes may be a driver of biotic response, lakeshore development may also be a surrogate for other factors and stressors such as fish stocking, boating, angling, and invasive species, which may be acting at a lake scale (Muirhead & Macisaac, 2005; Post et al., 2002; Ziegler et al., 2017). Finally, there is the critically important issue of the spatial scale of drivers and responses. LRD and the associated habitat changes reflect processes that typically occur at a localized spatial scale. Studies examining lake-level responses to LRD, that is, examining biotic attributes along a LRD gradient using lakes as the unit of comparison, may miss biotic responses that occur at more localized (i.e., site-level) spatial scales.

To address current knowledge gaps relating to how fish communities respond to LRD and habitat, we analyzed a data set of 57 lakes in northern Wisconsin (Figure 1). First, we quantified habitat differences associated with LRD using linear mixed-effects models (LMMs) (Figure 1a). We then evaluated the roles of LRD (Figure 1c), littoral habitat (Figure 1b, which is itself affected by LRD, Figure 1a), and lake attributes (Figure 1d) in shaping fish communities at both lake- and site-level spatial scales using a multilevel modeling framework. Finally, we asked whether site-level fish–habitat associations inform species responses to the cross-lake LRD gradient. Our goal is to tease apart how human activities (in this case LRD) and the associated littoral habitat differences affect nearshore fish communities, taking into account responses at site- and lake-level spatial scales.

METHODS

Study area

The data we analyzed were collected by researchers at the University of Wisconsin–Madison Center for

Limnology from 2001 to 2004. The 57 study lakes are in Vilas County, Wisconsin, USA, in the Northern Highlands Lake District (Figure 2). This area is primarily second-growth forest, low relief, and formerly glaciated landscape (Magnuson et al., 2006). Roughly a third of the landscape is made up of rivers, wetlands, and lakes

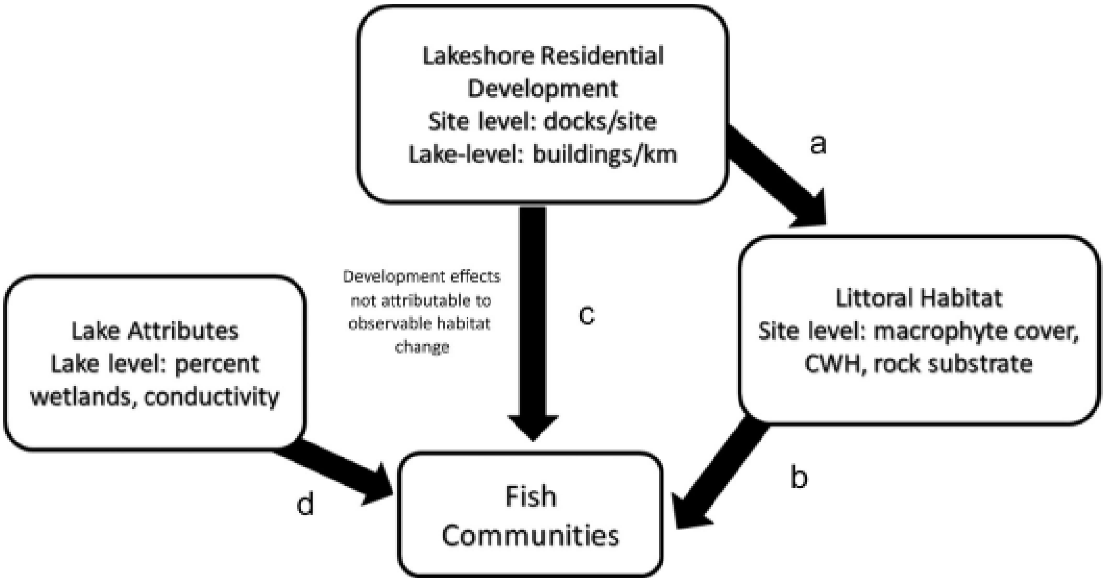

FIGURE 1 Conceptual framework for considering how lakeshore residential development (LRD) affects littoral habitat and, ultimately, fish communities. First, we hypothesized that LRD affects littoral habitat, such as macrophyte cover, coarse woody habitat (CWH), and substrate characteristics (a). In turn, littoral habitat may affect fish communities (b). LRD may have generalized effects on fish communities that are independent of LRD effects on littoral habitat (c). Finally, lake attributes that are largely unrelated to LRD may also affect fish communities (d).

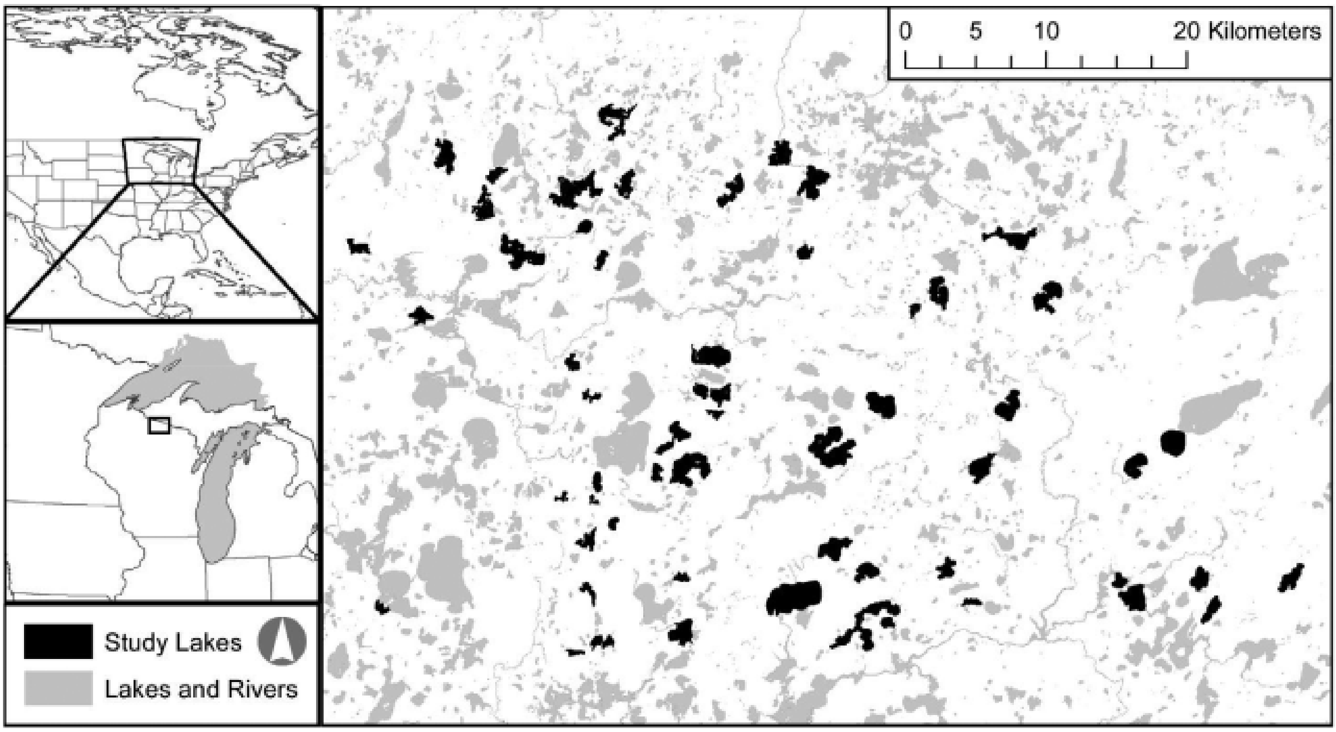

FIGURE 2 Map of northern Wisconsin, United States, showing location of the 57 study lakes. Study lakes are shaded black, other lakes are gray.

(Carpenter et al., 2007). The lakes vary in terms of productivity, plant communities, fish communities, morphometry, and hydrology (Kratz et al., 1997). Some of this variability is related to a lake's position in the landscape (Riera et al., 2000; Soranno et al., 1999). Lakes lower in the landscape tend to be larger and connected to other water bodies via surface waters and tend to have higher fish species richness (Kratz et al., 1997). Generally, lakes higher in the landscape have less groundwater input and rely more on precipitation inputs compared to lakes lower in the landscape (Perales et al., 2020; Pint et al., 2003; Webster et al., 1996). Because these inputs vary in ion concentration, conductivity is used as a proxy for landscape position (Webster et al., 2000). The region is a popular tourism and outdoor recreation destination because of the high density of lakes and rivers (Jorgensen et al., 2006). As a result, lakeshores have been extensively developed, and LRD continues to expand (Brown et al., 2005; Carpenter et al., 2007; Gonzalez-Abraham et al., 2007).

Selection of lakes and sampling sites

The study lakes were selected to span gradients in LRD intensity and landscape position (Carpenter & Kratz, 2022). Quintiles of the following indices were used to select lakes that spanned both gradients: conductivity as a proxy for landscape position and buildings per kilometer of lake shoreline to approximate LRD intensity. For buildings per kilometer, the number of buildings were counted within a 100-m buffer of each lake and divided by the lake perimeter. This was done using imagery collected in 1996. While the imagery was collected several years before the fish sampling was conducted, residential development in this region is incremental, and we felt confident that changes in development would be minor. Lake conductivity ranged from 15 to 120 μS/cm, while buildings per kilometer ranged from 0 to 46. Study lakes had a maximum depth range of 4–26 m and ranged from 29 to 666 ha.

Nearshore fish surveys

Eight sites were surveyed for fish in each lake, with the location of sites corresponding to the major and minor cardinal directions (Carpenter et al., 2023). To sample nearshore fish communities, a boom style electrofishing boat (DC) was used to shock a 100-m section of shoreline at each site. Each lake was sampled after sunset, and electrofishing was conducted along a 1- to 2-m depth contour. Dip netters attempted to net all fish regardless of species or size. We report all fish catches as the number of fish per site and restricted our analysis to the following 10 most frequently sampled species: bluegill (*L. macrochirus*), bluntnose minnow (*Pimephales notatus*), largemouth bass (*M. salmoides*), mimic shiner (*Notropis volucellus*), pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieu*), walleye (*Sander vitreus*), white sucker (*Catostomus commersonii*), and yellow perch (*Perca flavescens*). See Appendix S1: Table S1 for total fish catches, which include littoral fish species that might have been undersampled.

Shoreline and littoral zone habitat surveys

Macrophytes, substrate characteristics, riparian forest density, docks, and CWH were characterized at each of the eight sites (Alexander et al., 2013; Carpenter, Kratz, Marburg, Provencher, & Turner, 2013; Carpenter, Kratz, Marburg, Provencher, Turner, et al., 2013). The macrophyte surveys consisted of divers swimming a transect from shore to the 2-m depth contour or a length of 50 m. Divers characterized macrophytes using 0.25-m^2 survey hoops every meter along the transect. Species composition, mean macrophyte coverage, and a macrophyte growth form score (0–5) were documented for each hoop. We focused our analysis on mean macrophyte cover (in percentage). See Alexander et al. (2008) for a more in-depth analysis of this macrophyte data set. Additionally, each site received a qualitative characterization of substrate composition along the 0.5-m depth contour, with the following substrate size categories receiving scores from 0 to 2: silt, organic debris, rocks, pebbles, and sand. We restricted our analysis to the sand and rock scores based on the number of nonzeroes present. To quantify riparian (terrestrial) habitat, the number of living trees with ≥5 cm dbh were counted in three 10 × 10 m plots per site and reported as number of trees per 100 m^2.

Analysis of LRD relationship with nearshore habitat

We used LMMs to examine the relationship between LRD at two spatial scales (lake and site level) and lakeshore habitat variables at the site level (Table 1; Gelman & Hill, 2006). We modeled littoral habitat variables as a function of buildings per kilometer (lake level), docks per site (site level), and a lake-level random effect to account for the hierarchical nature of the

TABLE 1 The response of site-level lakeshore habitat metrics ("dependent variable") to lakeshore residential development (LRD) measured at both the site level (in docks per site) and lake level (in buildings per kilometer).

Lakeshore habitat variables (dependent)	LRD variables (independent)	Fixed effect	SE	p
CWH/site	Intercept	4.024	0.669	0.000
	Docks/site	−0.212	0.202	0.296
	Buildings/km	**−0.133**	0.043	0.003
Macrophyte cover (%)	Intercept	12.350	6.221	0.052
	Docks/site	1.147	1.050	0.275
	Buildings/km	0.373	0.255	0.150
	Conductance	0.257	0.085	0.004
No. trees/100 m^2	Intercept	15.165	0.995	< 0.001
	Docks/site	**−1.225**	0.367	0.001
	Buildings/km	**−0.141**	0.064	0.032
Sand score	Intercept	1.213	0.069	< 0.001
	Docks/site	0.053	0.033	0.110
	Buildings/km	**0.014**	0.005	0.003
Rock score	Intercept	0.706	0.062	0.000
	Docks/site	−0.011	0.031	0.709
	Buildings/km	**−0.013**	0.004	0.002

Note: Values reported are fixed-effect coefficients and SEs from linear mixed-effects models (LMMs) of LRD on lakeshore habitat. Buildings per kilometer is the lakewide measure of LRD, docks per site is the site-level measure of LRD. Significant ($p < 0.05$) correlations between LRD and habitat variables are in bold. Coefficients are estimated from an individual LMM for each lakeshore habitat variable, which had lake as a random effect.

Abbreviation: CWH, coarse woody habitat.

data. We included the following habitat variables: CWH density (in CWH per site), macrophyte cover (in percentage), sandiness (sand score), rockiness (rock score), and the number of living trees in the riparian buffer (number of trees per 100 m^2). We developed a single model for each habitat variable, with buildings per kilometer as our lake-level LRD variable and docks per site as the site-level measure of LRD. Sites within a lake differed regarding the degree of development, but in general, buildings per kilometer was positively related to docks per sites ($p < 0.0001$, marginal $r^2 = 0.16$; Nakagawa & Schielzeth, 2013). All models were fit using restricted maximum likelihood, and *p*-values for random effects are derived from likelihood ratio tests of a full model against a model with the random effect removed. All models have the same structure, except for macrophyte cover, which includes conductance because of its importance in structuring macrophyte communities (Table 1; Alexander et al., 2008; Mikulyuk et al., 2011).

Multilevel modeling of fish, habitat, and LRD

We used generalized linear mixed-effects models (GLMMs) to examine the relationship between fish communities, LRD, and littoral habitat variables (Gelman & Hill, 2006). To examine species-specific responses to different predictor variables, we included random intercepts and slopes for each species (Jackson et al., 2012). To do this, we included catch per site as the response (dependent) variable, a random intercept per species (1 j species), slope terms of predictor variables across species (predictor variable j species), and the main effects of the included predictor (independent) variables. This approach reduces the probability of making type 1 errors associated with parameterizing a model for each species because species with weak relationships will have slopes closer to zero compared to species with stronger relationships (Gelman & Hill, 2006). *p*-values for each species' random effect were derived from likelihood ratio tests of the full model against a model with the species random effect excluded (Zuur, 2009). By including species-specific random slopes for each predictor variable, we could estimate the relationship for all species and predictor variables included in the model (Jackson et al., 2012). Significant species-specific random effects imply changes in fish community composition. An advantage of this modeling framework is to allow us to draw inferences about differences in individual species abundance relationships and community structure within a single analysis. This multilevel modeling approach has better power to detect the significance of environmental drivers on communities compared to more traditional methods, especially among collinear predictors (i.e., redundancy analysis, canonical correspondence analysis, nonmetric multidimensional scaling; Jackson et al., 2012).

We categorized our covariates as one of three types of variables: lake-level environmental variables, indices of LRD intensity, and site-level habitat features (Figure 1). The model included the abundance of species as the response variable with a Poisson error distribution, which is commonly implemented for count data (Zuur, 2009; Zuur et al., 2007). We also included a random effect for lake to model dependency among observations within a lake, a random effect for site to capture the site dependency among fish from the same site, and an observation-level random effect (Harrison, 2014). Due to the emphasis on understanding LRD as a driver of fish communities and the challenges of drawing inferences from a cross-system study, the a priori model included lake attributes that are hypothesized to be important in structuring fish communities but are believed to be unaffected by LRD in this region (Kratz et al., 1997; Magnuson et al., 2006; Riera et al., 2000). This included conductance (in microsiemens per centimeter) and percent wetland in a 500-m buffer around a lake (% wetland). We also include site-level habitat data (number of CWH per site, macrophyte cover, rockiness) and buildings per kilometer and docks per site as lake- and site-level indices of LRD, respectively. Our LMMs and GLMMs were fit using lme4 in R (Bates et al., 2015, version 4.2.1; R Project for Statistical Computing, Vienna, Austria).

RESULTS

Effects of lakeshore development on habitat: Whole-lake and within-lake scales

Our LMMs indicated that four of five nearshore habitat characteristics were significantly related to LRD ($p < 0.05$, Table 1, Figure 3). CWH per site, number of trees

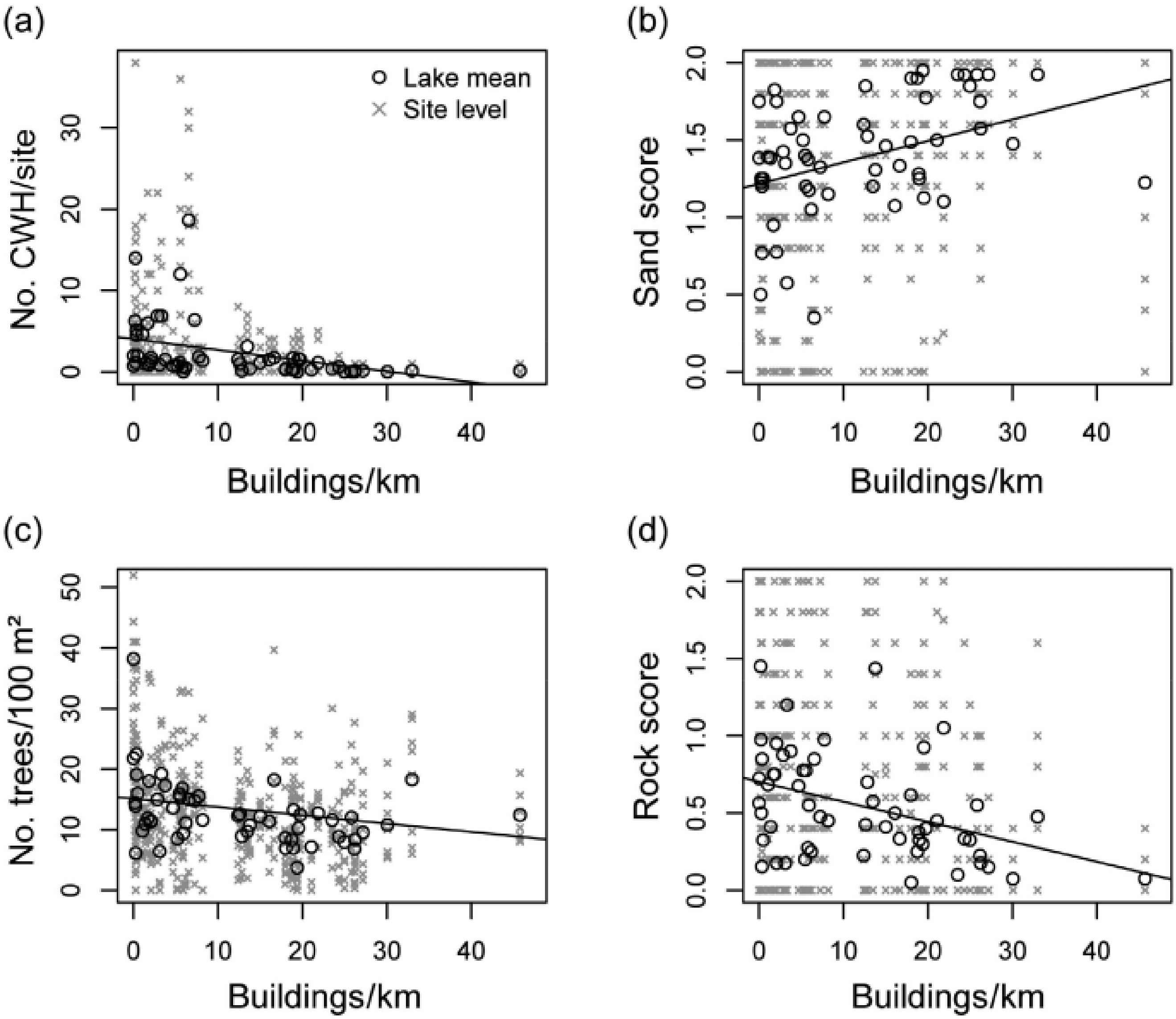

FIGURE 3 Scatter plots showing relationship between (a) coarse woody habitat density (in CWH per site), (b) sand score, (c) trees per site, (d) rock score, and lake-level lakeshore residential development (LRD) (in buildings per kilometer). Circles represent a lake mean for a variable, and the gray *x* values represent the eight site-level measurements for each lake. Trendlines show the buildings-per-kilometer fixed effect derived from the linear mixed-effects models for each lakeshore habitat variable (Table 2), with probabilities <0.05. Macrophyte cover (in percentage) was not significantly related to LRD at either the lake level (in buildings per kilometer) or site level (in docks per site) and is not shown.

per 100 m^2, and the sand and rock scores of a site were related to LRD at the whole-lake scale. Additionally, number of trees per 100 m^2 was significantly related to LRD at the site level. Both CWH per site and rock scores were negatively related to LRD at the whole-lake scale. Mean macrophyte cover was not significantly related to LRD at either scale but was positively associated with conductance. Sand score was positively related at the whole-lake scale, while number of trees per 100 m^2 was negatively related at both scales of lakeshore development. In summary, LRD and littoral/riparian habitat were closely related. Specifically, more developed lakes tend to have less CWH, fewer trees in the riparian buffer, and finer substrate compared to less developed lakes. More developed sites tend to have lower densities of riparian forests.

Multilevel modeling of fish, habitat, and LRD

Overall fish abundance was positively related to conductivity (fixed effect = 0.535, $p < 0.05$, Table 2). All the species-specific random effects were significant ($p < 0.001$) except for docks per site, which suggests that the lake-level environmental variables, lake-level LRD (in buildings per kilometer), and site-level habitat characteristics explained significant among-species variation in abundance (Table 2). The fish-habitat associations among species were confirmatory for species with well-known habitat preferences (Figure 4b; Becker, 1983). For example, bluegill, largemouth bass, and pumpkinseed are often associated with macrophytes (Figure 4b). Similarly, smallmouth bass and walleye showed positive associations with rocky areas. Species also differed in their lake-level relationship with LRD (Figure 4a). Because habitat is included in the models, we interpret the species-specific relationships with buildings per kilometer as the population-level effect of development on fish abundance that is not explained by habitat, while also noting that lakeshore habitat is also related to LRD, as shown in Table 1.

TABLE 2 Coefficients and random effects from Poisson generalized linear mixed-effects model.

Variable	Fixed effects	Random effects
Intercept	−0.739*	0.866***
Lake attribute		
Lake level: conductance	0.535**	0.124***
Lake level: % wetland	−0.022	0.058***
Lakeshore residential development		
Lake level: buildings/km	0.221	0.087***
Site level: docks/site	−0.009	0.000
Littoral habitat		
Site level: no. CWH/site	0.051	0.074***
Site level: macrophyte cover (%)	0.080	0.295***
Site level: rock score	0.059	0.079***
Lake random effect	...	0.674***
Site random effect	...	0.075
Observation level random effect	...	2.958***

Note: The random effects intercepts are the species-specific intercepts for each specific predictor variable (1 j species). All other random effects are variances of species-specific slopes (predictor variable j species). The fixed effects are main effects and represent the mean response of all species combined. Lake random effect and site random effect are lake-level and site-level random effects to account for the hierarchical nature of our sampling design (i.e., [1 j lake name], [1 j site]). All predictor variables were scaled and centered. Docks per site, buildings per kilometer, and no. coarse woody habitat (CWH) per site were log-transformed while conductance, % wetland, macrophyte cover (in percentage), and rock score were not.
*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Species with similar ecosystem responses to LRD differed in their habitat associations (Figure 4b). Although weak, white suckers and walleye both had negative relationships with buildings per kilometer, while these two species had almost opposite habitat associations. This was also true of species found to have positive relationships with LRD. Bluegill, mimic shiners, and pumpkinseed had the strongest positive relationships with buildings per kilometer but differed in the types of sites within a lake that they were most abundant. Bluegill and pumpkinseed preferred sites with more macrophyte cover but exhibited slightly different preferences for CWH and rockiness of a site, while mimic shiners showed a strong preference for open areas, having negative associations with coarse substrate, macrophyte cover, and CWH (Figure 3b).

DISCUSSION

Fish community structure was influenced by environmental variables, site-level habitat features, and the number of buildings per kilometer. Our study suggests there are overall differences in the littoral fish community along a LRD gradient. Our modeling approach allowed us to identify the species with the most considerable differences in abundance along lake-level LRD gradients while also quantifying fish–habitat associations and relationships between LRD and habitat. Initially, we hypothesized that by combining our understanding of fish–habitat associations with changes in habitat associated with LRD, we would be able to predict species-specific responses to LRD. However, we found that fish species had unique habitat associations that did not

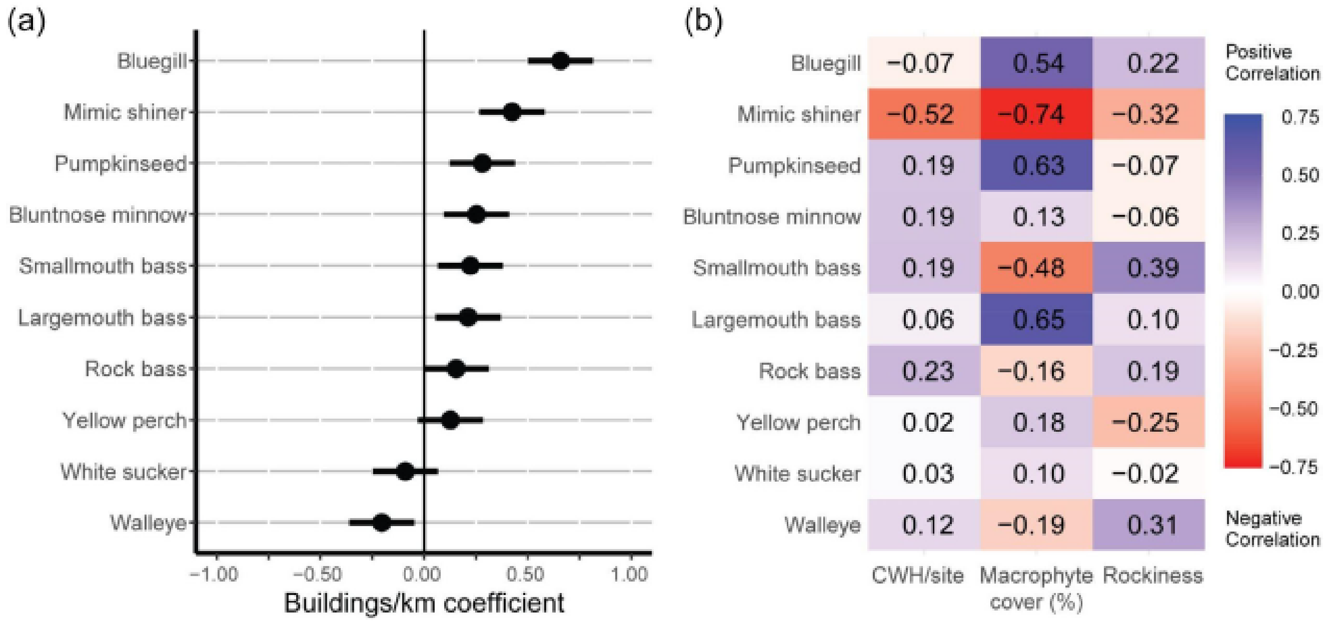

FIGURE 4 (a) Species-specific responses to lakeshore residential development (LRD) (in buildings per kilometer). Points are the sums of fixed and species-specific random effects from the Poisson generalized linear mixed-effects models (GLMMs) in Table 2. Error bars are ±SEs. (b) Heatmap of site-level habitat associations for each species. Values shown are the sums of fixed and species-specific random effects from the Poisson GLMM. Positive values indicate that a species is more abundant at sites and in lakes with the associated characteristic. Note that both panels use values derived from the same model and are plotted differently to facilitate interpretation of a species' response to LRD and their corresponding habitat associations.

inform their lake-level responses to LRD. Fish species with similar responses to LRD could have dramatically different habitat associations, indicating that the resultant effects of LRD on fish communities are more complicated than translating changes in habitat to less or more fish with specific habitat associations.

LRD and habitat

There was a predictable and straightforward relationship between LRD and shoreline habitat features. In general, the habitat modifications we document agree with the literature (Jacobson et al., 2016). Developed lakes are generally characterized by a loss of CWH and altered aquatic macrophyte communities (Christensen et al., 1996; Radomski, 2006; Radomski et al., 2010). Macrophyte species richness and coverage are negatively impacted by lakeshore development (Beck et al., 2013; Radomski & Goeman, 2001; Sass et al., 2010). In some cases, macrophyte species richness and coverage were reduced by roughly 50% along developed shorelines (Bryan & Scarnecchia, 1992). While we did not document a significant relationship between macrophyte cover and LRD, Alexander et al. (2008) present a more in-depth analysis of this macrophyte data set and documented that increased LRD most noticeably impacted floating and emergent macrophytes. Other cross-system studies and studies tracking changes through time using historical aerial imagery have documented significant reductions of emergent and floating macrophyte coverage in more developed lakes (Radomski, 2006; Radomski & Goeman, 2001). As a result of development, macrophyte cover has been reduced by around 15% to 28% in northern temperate lakes (Radomski, 2006; Radomski & Goeman, 2001).

Developed lakes have less CWH due to direct removal and loss of riparian forests, with potential impacts lasting decades due to slow natural replacement (Amato et al., 2015; Elias & Meyer, 2003; Francis & Schindler, 2006; Marburg et al., 2006, 2009). We documented a significant negative lake-level effect of LRD on CWH (see Marburg et al., 2006 for a more detailed treatment of this CWH data set). In general, the abundance of CWH in the littoral zone is highly variable in relatively undeveloped lakes (≤10 buildings/km) and is affected by biotic and abiotic factors (Czarnecka, 2016). However, in highly developed lakes (≥10 buildings/km), the variability of the abundance of CWH in the littoral zone is significantly reduced. Specifically, relatively undeveloped lakes surveyed in northern Wisconsin varied from zero to over 700 pieces of CWH per kilometer in the littoral zone. In comparison, in more developed lakes, this figure ranged from zero to under 200 pieces of CWH per kilometer (≥5 cm in diameter; Marburg et al., 2006). This loss of CWH has been linked to reduced growth rates in bluegill and largemouth bass (Schindler et al., 2000), dramatic changes in fish foraging behavior, and the disruption of predator–prey dynamics (Ahrenstorff et al., 2009; Sass, Kitchell, et al., 2006). Additionally, we document a site- and lake-level positive relationship between sandiness and LRD. This may be due to shoreline maintenance practices by property owners, as some report maintaining or having a beach (Amato et al., 2015; Jorgensen et al., 2006). Although the specific implications of this suite of habitat differences associated with LRD are unclear, we know that fish communities broadly respond to changes in habitat, with specific examples of habitat losses resulting in significant changes (Gaeta et al., 2014; Olson et al., 1998; Sass, Kitchell, et al., 2006).

Fish–habitat associations

Although linking LRD-related habitat alteration to littoral fish communities has been difficult, habitat plays an integral role in structuring fish communities (Gaeta et al., 2014; Kraft et al., 2015; Sass, Gille, et al., 2006; Sass, Kitchell, et al., 2006). In general, the fish–habitat associations we quantify are confirmatory of many other fish–habitat studies (Figure 4b; Becker, 1983; Moyle, 2002). For example, well-studied species such as walleye, smallmouth bass, and rock bass were positively associated with rockier sites, which is well documented by several studies (Edwards et al., 1983; McMahon et al., 1984). The same was true of less well-studied species, such as mimic shiners, which were negatively associated with CWH, macrophyte cover, and the rockiness of a site. Other studies found that mimic shiners preferred shallow habitats and were negatively associated with most plant species (Moyle, 1973). Additionally, our models identified bluegill, pumpkinseed, and largemouth bass as being more abundant than other fish species at more vegetated sites, which others have found (Hoyer & Canfield, 1996; Werner & Hall, 1977, 1979). All this is to say that, despite having well-resolved fish–habitat associations, it is challenging to predict how or which species will respond to localized habitat alteration due to development (Rose, 2000).

Among species, variation in abundance was significantly related to the number of buildings per kilometer. Our models indicate that walleye was most negatively affected by LRD, although the relationship is weak, while bluegill and mimic shiners were the most positively affected (Figures 4a and 5). While identifying which species were most responsive is of value, we were interested in the role of habitat alterations in affecting fish communities. Our lakes exhibit the typical changes in habitat associated with increased LRD, and the fish–habitat associations we quantify are unsurprising (Figures 3 and 4b). However, we found it surprising that the lake-level LRD fish responses were not easily explained by habitat associations. Thus, making predictions about which species will be impacted by habitat changes is not as simple as documenting impacts on habitat and understanding habitat associations for individual species, as we have done. Initially, we hypothesized that within-lake distributions of fish would reflect their lake-level responses, but that was not apparent in our analysis. The reality is that the lake-level differences in the fish community we document are likely a result of many drivers, including LRD associated habitat modifications.

LRD and fish communities

While we had no expectations regarding which fish would respond positively or negatively to lakeshore development, it is interesting to note that walleye and bluegill had the strongest responses to LRD according to our analysis (Figures 4a and 5), as both species are valued game species and are known to be affected by recreational anglers. Recently, walleye have been the focus of many studies because many stocks in the Midwestern United States have declined over the past 20 years (Embke et al., 2019; Pedersen et al., 2018; Rypel et al., 2018). Recent studies have concluded that many Walleye populations in our study region are close to or are overharvested by recreational anglers (Embke et al., 2019). Similarly, recreational harvest can be a strong driver of bluegill size structure (Rypel, 2015; Rypel et al., 2016). However, understanding the effect of increased harvest in the context of increasing LRD is complex because LRD-related drivers may mask each other. Specifically, theoretical work has suggested that it is possible to mask the positive effects of increased predatory fish harvest for prey species with the negative effect of reductions in CWH as predation refuge (Roth et al., 2007). Another consideration is fish stocking, which can be accompanied by its own complex suite of changes as more developed lakes tend to rely more on stocking as part of managing local fisheries (Eby et al., 2006; Ziegler et al., 2017). Thus, increased harvest and stocking, against a backdrop of habitat alteration, may be contributing to the lake-level effects of LRD on fish communities we quantify. LRD is associated with many drivers that interact and alter fish communities. While it is unclear how habitat alteration affects fish communities, we argue that habitat conservation and restoration efforts should continue given our qualitative understanding of its importance.

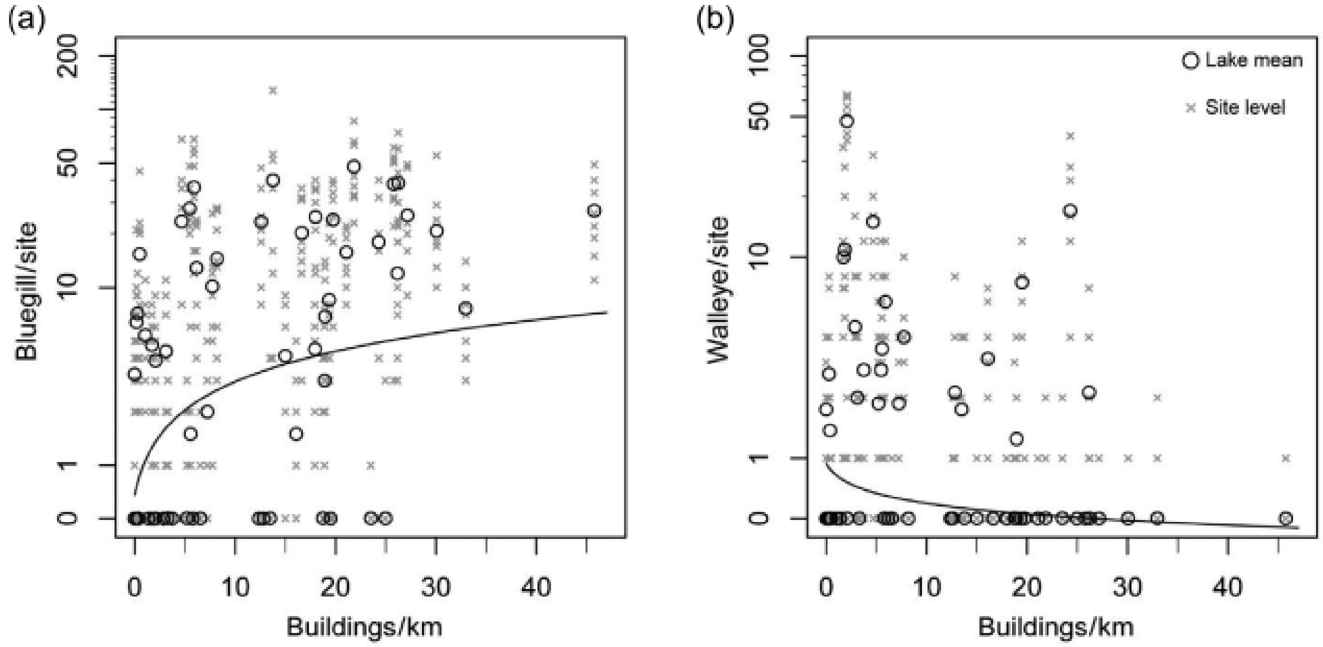

FIGURE 5 Relationship between (a) bluegill and (b) walleye abundance and buildings per kilometer. Circles represent the mean number of fish sampled for each lake, and the gray *x* values represent the number of fish sampled at a given site. Trendlines show species-specific responses to lakewide lakeshore residential development (from model in Table 2) while holding all other variables constant at the mean value. Values are back-transformed and plotted on a log scale. Catches ≤1 are plotted as 0 s.

Surprisingly, only a handful of studies have investigated changes or differences in fish communities across LRD gradients, with some of these studies documenting differences in fish communities. For instance, Jennings et al. (2009) investigated species richness patterns across lakes in northern Wisconsin and concluded more game species were present in more developed lakes, perhaps reflecting an increased likelihood of stocking associated with more developed lakes (Radomski & Goeman, 1995; Ziegler et al., 2017). In addition, more developed lakes in northern Minnesota had a lower fish index of biotic integrity scores and exhibited altered macrophyte-associated fish communities (Drake & Pereira, 2002; Dustin & Vondracek, 2017). Others have shown that individual species abundances can have complex, nonlinear relationships with LRD, and the shape of the relationship may be related to lake morphometry (Lewin et al., 2014). While it is challenging to draw general conclusions on the relationship between fish communities and LRD, understanding this relationship will continue to be an important topic for future research. Nonetheless, our analysis showed that increased LRD was associated with lake-level differences in the fish communities.

Other studies have investigated how LRD-induced habitat alterations affect the fine-scale distributions of fish and typically conclude that local habitat modifications can lead to different communities among sites within a lake (Jennings et al., 1999). The abundance of species tends to be lower on more developed shorelines (Bryan & Scarnecchia, 1992; Lewin et al., 2014; Poe et al., 1986). For example, 18 of 20 species were more abundant along natural shorelines compared to more developed shorelines in a large eutrophic lake in Iowa (Bryan & Scarnecchia, 1992). However, it is important to note that other studies documented more moderate effects of LRD on the local distribution of fishes (Taillon & Fox, 2004). While many studies have concluded that LRD affects fish in some way, it can be unclear whether the documented relationships translate to lake-level changes in fish communities. For instance, LRD can affect the spawning behavior of centrarchids (Lawson et al., 2011; Reed & Pereira, 2009), but it is unclear whether this translates to altered fish communities. In theory, if spawning habitat is not limiting, then fish can spawn elsewhere with little or no effect on the structure or function of the fish community. While these studies have contributed to our understanding of how LRD may affect fish communities, our understanding will benefit from considering multiple approaches (Carpenter, 1998).

There is a notable lack of studies quantifying the effects of LRD on fish communities through time, although Taillon and Fox (2004) noted a loss of six cyprinids and a cyprinodontid fish when they compared their surveys done in the 2000s to those conducted in the 1970s. The authors suggest that the most sensitive species may have already responded to decades of increasing

LRD. It is reasonable to believe that in some lakes, the fish community has already responded. Thus, the cumulative and slow unfolding impacts on habitat by LRD make it incredibly difficult to study but make it an appropriate candidate for long-term study (Carpenter, 1998). Another promising approach may be the use of process-driven, mechanistic models to understand how changes in habitat affect fish population vital rates and, thus, help resolve ecosystem-level fish–habitat relationships (Hayes et al., 2009; Rose, 2000). While we opted to use GLMMs because we were interested in understanding individual species responses, path analysis has been effectively used to explore more integrated measures of fish community responses to habitat alterations (McManamay et al., 2015). These points do not negate the value of comparative studies; rather, we argue for more diverse research approaches when possible.

CONCLUSION

In conclusion, LRD represents an incremental change to lakeshores, often occurring over many decades. Consequently, we grapple with trying to understand cumulative impacts on habitat occurring over generations of the organisms that are being impacted. In our study, we documented lake-level differences in fish communities across development gradients, differences in habitat associated with LRD, and fish–habitat associations. However, we found that lake-level differences in fish communities did not follow a simple conceptual model of LRD impacts on habitat and fish species associated with habitat decrease at the lake level. Thus, we argue that LRD represents a syndrome with many symptoms that result in changes in fish communities. In addition to habitat alteration, LRD is associated with a higher reliance on stocking and increased recreational angler harvest. A critical step in managing this ubiquitous and ever-increasing driver is to better understand the broad pattern, which we have attempted at informing here. Although it is challenging to understand the processes that lead to the observed differences in fish community, we must continue researching the individual and interacting drivers associated with increasing LRD. Finally, operationally, we understand that littoral habitat is critical for healthy fish populations, so we must continue conserving and restoring littoral habitats.

AUTHOR CONTRIBUTIONS

K. Martin Perales conceptualized the research, conducted analyses, and wrote the manuscript. M. Jake Vander Zanden contributed to research conceptualization and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data utilized for this research are from the Environmental Data Initiative as follows: fish data (Carpenter et al., 2023; https://doi.org/10.6073/pasta/7ffcc1989a69f22c855fbeaec5b2f4b8); riparian habitat data (Carpenter, Kratz, Marburg, Provencher, & Turner, 2013; https://doi.org/10.6073/pasta/9ed5adfa40aad99e73a5d972fab83b27); littoral habitat data (Carpenter, Kratz, Marburg, Provencher, Turner, et al., 2013; https://doi.org/10.6073/pasta/27ec6e0d5a6cb1c663633e7b3c45912f); littoral macrophyte data (Alexander et al., 2013; https://doi.org/10.6073/pasta/271d3260d3a6368d7516419ec63826e4); lake characteristic data (Carpenter & Kratz, 2022; https://doi.org/10.6073/pasta/9e7189731df1dc7f9b4d724693d62f84).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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