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ARTICLE

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# Habitat complexity, connectivity, and introduced fish drive pond community structure along an urban to rural gradient

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## Abstract

Urbanization can influence local richness (alpha diversity) and community composition (beta diversity) in numerous ways. For instance, reduced connectivity and land cover change may lead to the loss of native specialist taxa, decreasing alpha diversity. Alternatively, if urbanization facilitates nonnative species introductions and generalist taxa, alpha diversity may remain unchanged or increase, while beta diversity could decline due to the homogenization of community structure. Wetlands and ponds provide critical ecosystem services and support diverse communities, making them important systems in which to understand the consequences of urbanization. To determine how urban development shapes pond community structure, we surveyed 68 ponds around Madison, Wisconsin, USA, which were classified as urban, greenspace, or rural based on surrounding land use. We evaluated how landscape and local pond factors were correlated with the alpha diversity of aquatic plants, macroinvertebrates, and aquatic vertebrates. We also analyzed whether surrounding land use was associated with changes in community composition and the presence of specific taxa. We found a 23% decrease in mean richness (alpha diversity) from rural to urban pond sites and a 15% decrease from rural to greenspace pond sites. Among landscape factors, adjacent developed land, mowed lawn cover, and greater distances to other waterbodies were negatively correlated with observed pond richness. Among pond level factors, habitat complexity was associated with increased richness, while nonnative fishes were associated with decreased richness. Beta diversity was relatively high for all ponds due to turnover in composition between sites. Urban ponds supported more nonnative species, lacked a subset of native species found in rural ponds, and had slightly higher beta diversity than greenspace and rural ponds. Our results suggest that integrating ponds into connected greenspaces, maintaining riparian vegetation, preventing nonnative fish introductions, and promoting habitat complexity may mitigate the negative effects of urbanization on aquatic richness. While ponds are small in size and rarely incorporated

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into urban conservation planning, the high beta diversity of distinct pond communities emphasizes their importance for supporting urban biodiversity.

**KEYWORDS**
biodiversity, greenspace, homogenization, nonnative fish, ponds, stormwater, urbanization

## INTRODUCTION

While anthropogenic environmental change is causing decreases in global species diversity (Hooper et al., 2012), patterns of community change at the local scale are often more variable (Sax & Gaines, 2003). For instance, local species richness (i.e., alpha diversity) has been reported to decline, remain the same, or increase in response to anthropogenic change (Dornelas et al., 2014; McCune & Vellend, 2013; Newbold et al., 2015). When alpha diversity does not decrease, this result can sometimes stem from the introduction of nonnative species and colonization by disturbance-tolerant generalist taxa offsetting local declines of specialists (McCune & Vellend, 2013; Sax & Gaines, 2003). Beta diversity, or the change in community composition between sites, can also respond to anthropogenic disturbance in multiple ways (Socolar et al., 2016). Anthropogenic species introductions can increase community similarity (and decrease beta diversity) at the landscape scale (Groffman et al., 2014; McKinney & Lockwood, 1999). If anthropogenic disturbances are patchy in time or space, however, they may also increase beta diversity as more niches become available (Socolar et al., 2016).

Urbanization represents a widespread form of anthropogenic change that can have significant effects on aquatic community structure. In general, urbanization is expected to homogenize aquatic communities (Marchetti et al., 2006; Petsch, 2016; Rahel, 2000). Nonnative species are common in urban aquatic ecosystems due to accidental introductions (Padayachee et al., 2017), intentional stocking (Magnuson & Lathrop, 1992), and aquarium releases (Preston et al., 2022), leading to expectations of more similar community structure in urban environments. That said, in some cases beta diversity in aquatic ecosystems has increased after the anthropogenic change (Hawkins et al., 2015), leading to the potential for variable responses in community structure, which may be mediated by environmental context, species interactions, or stochastic factors (Leibold & Chase, 2017).

Pond ecosystems, which are small, discrete, and often well replicated on the landscape, provide an informative study system to explore changes in community structure due to urbanization. Small lentic waterbodies in urban environments perform important ecological functions and can support high levels of biodiversity (Hassall & Anderson, 2015; Oertli & Parris, 2019). For instance, wetlands and ponds are important for floodwater management, improving downstream water quality, sequestering carbon, and enhancing livability in urban areas (Moore & Hunt, 2012). In addition, wetlands and ponds are complex habitats that tend to support higher richness and more rare species than other waterbody types (Davies et al., 2008; Williams et al., 2004) and they can facilitate aquatic connectivity by acting as stepping-stones between larger waterbodies (Hassall, 2014). Despite their value to both humans and wildlife, small lentic waterbodies are frequently underrepresented in conservation planning and are often drained, filled, or developed into stormwater retention ponds during urban expansion (Hill et al., 2018; Rooney et al., 2015).

Ponds in urban environments may have unique characteristics that affect their community structure and function relative to ponds in undeveloped areas. Urban ponds are often developed for stormwater retention and are managed to maintain a minimum water level that is punctuated by sharp increases following storm events. Urban stormwater ponds generally have steep banks, and relatively homogenous substrate and vegetation structures (Rooney et al., 2015). In contrast, natural ponds typically have gentler slopes, more heterogenous substrate and vegetation, and continuous drawdown throughout months with low precipitation (Oertli & Parris, 2019; Rooney et al., 2015). Urban ponds can also act as sinks for heavy metals, pesticides, road salts, and nutrients due to runoff over impervious surfaces in developed environments (Campbell, 1994; Hintz & Relyea, 2019). Furthermore, urban impervious surfaces may reduce connectivity between aquatic habitats by acting as a barrier to dispersal for some semiaquatic species (Gledhill et al., 2008).

Although urban ponds may differ from natural ponds, the heterogeneity of land cover in the urban environment may cause large variations in pond characteristics. For instance, urban greenspaces (i.e., open areas within the urban environment with managed and natural vegetation) may mitigate some of the undesirable effects of development on pond communities (Taylor & Hochuli, 2017). Urban greenspaces such as public parks, green belts, and nature preserves have reduced impervious surfaces, higher heterogeneity of riparian habitats, and potentially higher connectivity to other aquatic and terrestrial natural habitats (Hyseni et al., 2021). As a result, urban greenspace ponds may retain some characteristics of ponds outside of developed areas, including elevated alpha or beta diversity, but the degree to which they differ from ponds surrounded by impervious surfaces has not been well studied.

Our objective was to investigate the influence of urbanization on pond community structure and explore how local and landscape-level factors contribute to observed differences in local richness and composition. We sampled the physical, chemical, and biological conditions of ponds along a development gradient centered in Madison, Wisconsin, USA, with ponds categorized as urban, greenspace, or rural based on surrounding land use. We quantified local richness (alpha diversity) across several taxonomic groups: aquatic plants, macroinvertebrates, and aquatic vertebrates (fish, amphibians, and turtles). We further examined the difference in community composition (beta diversity) between urban, greenspace and rural ponds to test whether urban communities are more homogeneous (Knop, 2016; Lougheed et al., 2008). At the landscape level, we expected that human-modified land cover (i.e., impervious surfaces and lawn) and increasing distances to other waterbodies would both be associated with reduced taxonomic richness. In contrast, we expected the presence of adjacent wetlands to cause increases in taxonomic richness due to greater connectivity and colonization opportunities (Knutson et al., 1999). At the local level, we predicted that increases in the pond area and habitat complexity would be associated with increased taxonomic richness, while increases in chloride, pH, and presence of nonnative fishes, would correlate with decreased richness. Last, we expected urban ponds to have greater variation in community composition (higher beta diversity) than rural ponds due to heterogeneity in urban pond design and surrounding land cover.

## MATERIALS AND METHODS

### Site selection

Using aerial imagery, we selected 68 ponds within 25 km of the Madison, WI city center (Figure 1). Survey ponds

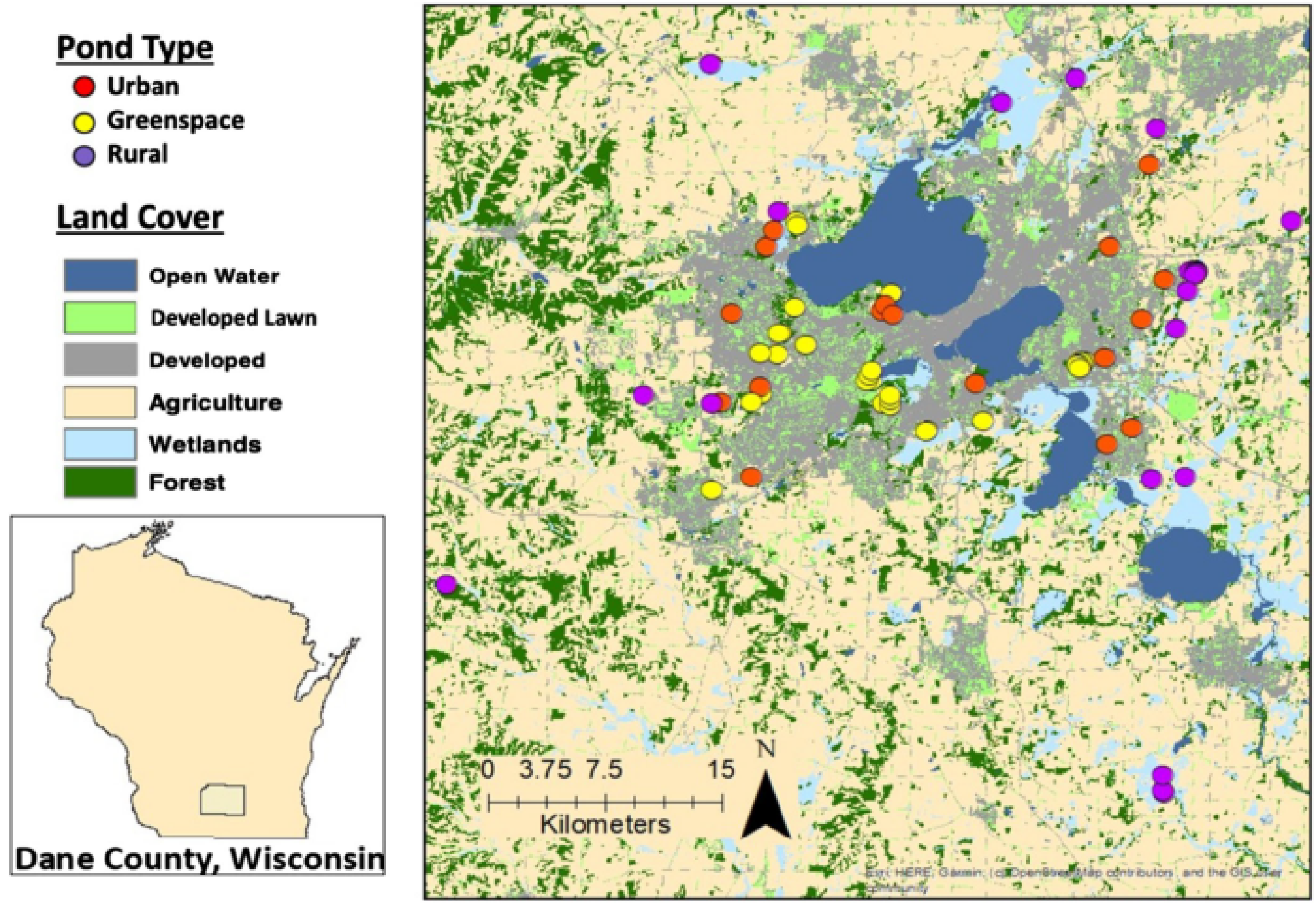

**FIGURE 1** Map of the study area and surrounding land cover, with each point representing a pond site. Pond types are represented by each color with urban sites in red ($n$ = 17), greenspace sites in yellow ($n$ = 29), and rural sites in purple ($n$ = 22). All pond sites were located in Dane County, Wisconsin, USA. The city of Madison is located in between Lake Mendota and Lake Monona, the two most northern lakes shown in the Yahara Chain.

had standing water year round and a surface area of less than 12,000 $m^2$. Most of the survey ponds were artificially constructed (88%) although, historically, many of these sites were wetlands that had been altered due to development. The ponds were selected to span multiple land cover types, including: (1) urban environments dominated by impervious surfaces (hereafter "urban ponds"), (2) urban green spaces, including parks and natural areas within highly developed areas ("greenspace ponds"), and (3) rural areas outside the urban environment, generally in protected wildlife areas ("rural ponds"). Ponds were assigned into these three categories based on their location and adjacent land use (for a complete summary of pond type characteristics see Appendix S1: Table S1).

## Pond surveys

Ponds were surveyed in early summer (May–June) and again in late summer (July–August) for 2 years, for a total of four visits per pond. Most surveys (62 ponds) occurred in 2019 and 2020, with six additional sites surveyed in 2020 and 2021. Surveys conducted in 2019 were performed by a team of four researchers, while follow-up surveys in 2020 and 2021 were performed by one or two people at a time. In total, we conducted 272 site surveys at 68 ponds (17 urban ponds, 29 green space ponds, and 22 rural ponds). The surveys were designed to characterize the overall pond community structure, focusing on aquatic plants, aquatic macroinvertebrates, aquatic reptiles (i.e., turtles), pond-breeding amphibians, and fishes. We used a combination of 5-min binocular surveys followed by a visual encounter survey along the entire pond perimeter to initially record the occurrence of any visible vertebrates at each pond. We then conducted eight evenly spaced dipnet sweeps around the pond perimeter (D-frame dipnet, 600 $cm^2$ net opening, 3 mm mesh, 1 m in length sweeps) and at least three seine net hauls (3 m drag length, 1 × 2 m net size, 4 mm mesh) in the deeper pond regions. On the first visit to each site, we preserved the macroinvertebrates from all eight sweeps in ethanol and later identified them in the laboratory, mostly to family (see Appendix S1: Figure S1 for species lists and taxonomic resolution of invertebrates). All vertebrates seen or captured were identified to species, recorded, and released immediately (Appendix S1: Figure S2). If a species of any life stage was detected at a pond site, it was considered present for the survey. We combined amphibian, fish, and turtle detections across the four site visits for richness counts. This approach was used because colonization/extirpation of vertebrate taxa were likely to be uncommon on the timescales of our surveys (2 years), and multiple visits increased our likelihood of observing less abundant taxa. We assessed the efficacy of our sampling methods using species accumulation curves, focusing on the number of pond sweeps for invertebrates and the number of site visits within a pond type as measures of sampling effort (Appendix S1: Figure S4). During each visit, we also measured pH, chloride (mg/L), and dissolved oxygen (%) using a YSI Pro Plus handheld meter (Yellow Springs, OH, USA) placed approximately 2–3 m from the shore at 0.5 m below the water's surface. Surveys were conducted between 8:00 a.m. and 4:00 p.m. each day.

In the second year of surveys, we quantified plant community structure and habitat complexity during both survey visits. While walking the perimeter and wading (up to 1 m) into the pond, each plant taxon encountered was identified as genus or species in the field or by taking a cutting and examining under a dissection scope in the laboratory (Appendix S1: Figure S3). Frequent dipnet sweeps were used to assess the presence of submerged plants in areas with extensive floating plants or high turbidity. We then visually estimated and recorded the extent of the emergent, floating-leaved, and submerged plants as a percentage of the wetted area of the pond (Biggs et al., 2005), which was used as one component of a habitat complexity index. To characterize pond habitat complexity, we assigned a score of 1 (low complexity) to 5 (high complexity) based on four factors: the variation in substrate types, woody debris, surface heterogeneity, and subsurface heterogeneity. Surface heterogeneity was calculated using the proportion of open water to floating and emergent vegetation and subsurface heterogeneity was calculated using the proportion of bare substrate to submerged vegetation. Each component was scored individually by the same observer and the sum was divided by four to get an average habitat complexity score (see Appendix S1: Section S1 and Appendix S1: Figure S5 for complete details of habitat complexity scoring).

## Remotely sensed data

Using Google Earth software (version 7.3, 2020) and historical imagery provided by the Dane County Land Information Office (DCiMap application), we estimated each pond's surface area and distance to the nearest waterbody (defined as the shortest linear distance between the edge of the pond and the next closest waterbody). We then used the 2016 National Landcover Database in ArcGIS (NLCD; 30 $m^2$ resolution, equal-area projection, WGS 84 datum surface) to obtain the percentages of five land cover types (forest, wetland, open water, lawn, and developed) within 1000 m of each pond (following Sauer et al., 2022) (see Appendix S1: Section S2 and

Appendix S1: Table S1 for details on land cover types and buffer size selection).

## Analyses

To first compare alpha diversity across the three categorical pond types, we used analysis of variance (ANOVA) followed by post hoc Bonferroni-corrected pairwise *t*-tests, with the richness of aquatic plants, macroinvertebrates, and vertebrates, as well as total combined richness, as the response variables. To describe the relative importance of local-level versus landscape-level factors and infer the direction and magnitude of effects for each covariate, we then fitted generalized linear mixed-effects models (GLMM) using the "glmer" function (*lme4* package; Bates et al., 2014) with observed total pond richness as the response, using a Poisson distribution. We standardized all predictor variables and compared a local, landscape, and full model (local + landscape) using corrected Akaike Information Criterion ($AIC_c$) scores (Burnham & Anderson, 2010). When predictors were highly correlated, we excluded the variable that was hypothesized to be less biologically important, resulting in the following local-scale variables: pH, chloride (in milligrams per liter), habitat complexity score (averaged across visits), pond area (in square meters), and presence of invasive fish (common carp [*Cyprinus carpio*] and goldfish [*Carassius auratus*]). The two nonnative fishes were excluded from counts of vertebrate and total richness in the response variables of the GLMMs because we hypothesized they would be an important predictor of pond richness. Landscape-level variables included percent development, percent wetlands, and percent lawn within a 1000 m buffer around each pond and distance to the nearest waterbody. In all models, we included the watershed identity (hydrologic unit code 10; $n = 8$ watersheds) as a random effect to account for possible spatial autocorrelation. To evaluate overall model fit, marginal $R^2_{\text{GLMM}}$ (variance explained by fixed effects) and conditional $R^2_{\text{GLMM}}$ (the proportion of total variance explained through both fixed and random effects) were calculated following Nakagawa and Schielzeth (2013). While our analysis focused primarily on total richness, we also applied this same model structure to observed macroinvertebrate richness, vertebrate richness, and plant richness to evaluate whether responses differed across taxonomic groups (Appendix S1: Figures S6–S8). Diagnostics for all models, including variance inflation factors, were tested using the *DHARMa* package (Hartig, 2022).

To evaluate whether community composition differed between the urban, greenspace, and rural ponds, we used nonmetric multidimensional scaling (NMDS) based on presence/absence data (Jaccard distance metric) with the "metaMDS" function (*vegan* package; Oksanen et al., 2020), with a stress cutoff value of 0.20 and three dimensions. We then conducted an analysis of similarity, again using Jaccard dissimilarity as the distance metric, and pond type as a categorical variable ("ANOSIM" function, *vegan* package). We next assessed the correlations of environmental variables with community structure, and which taxa contributed most to community dissimilarity using the "envfit" function and NMDS with 999 permutations (Oksanen et al., 2020). To evaluate which taxa may be lost or gained across the three pond types, we performed an indicator species analysis (Appendix S1: Table S3) (*indicspecies* package; De Caceres et al., 2016).

Finally, to evaluate whether urban and greenspace ponds were more homogenous in their community assemblages relative to rural ponds, we compared their beta diversity using the multisite method developed by Baselga (2012). For each of the three pond types, we quantified Jaccard dissimilarity ($\beta_{\text{jac}}$), which consists of two components: turnover in composition between sites ($\beta_{\text{jtu}}$) and nestedness ($\beta_{\text{jne}}$). Jaccard dissimilarity is the sum of turnover and nestedness ($\beta_{\text{jac}} = \beta_{\text{jtu}} + \beta_{\text{jne}}$). Because we had a varying number of sites within each pond type, and the multisite method of quantifying beta diversity is sensitive to the number of sites, we randomly sampled 10 sets of sites from each pond type 100 times to obtain distributions of values for Jaccard dissimilarity, turnover, and nestedness ("beta.sample" function, *betapart* package; Baselga & Orme, 2012). All analyses were completed using R 3.6.0 statistical software (R Core Team, 2021).

# RESULTS

Across all surveys, we detected 145 taxa consisting of 68 plant taxa (7 nonnative), 53 macroinvertebrate taxa (1 nonnative), 12 fish species (2 nonnative), 9 native amphibian species, and three native turtle species (Appendix S1: Figures S1–S3). In total, 105 taxa were detected at urban pond sites, 116 taxa at greenspace ponds, and 125 taxa at rural pond sites. Mean total richness differed between pond types (ANOVA; $F_{2,68}$, $p < 0.01$), with rural ponds having greater richness than urban ponds (pairwise comparison: $p < 0.01$) and greenspace ponds ($p = 0.04$), but no difference between greenspace and urban pond sites ($p = 0.47$; Figure 2). Compared with rural ponds, mean total observed richness was 23% lower in urban ponds and 15% lower in greenspace ponds. By taxonomic group, rural ponds had greater richness than urban ponds for both macroinvertebrates (pairwise comparison: $p = 0.03$), and vertebrates (pairwise comparison: $p < 0.01$), but there was no difference in plant richness across pond types (ANOVA; $F_{2,68}$, $p = 0.22$; Figure 2).

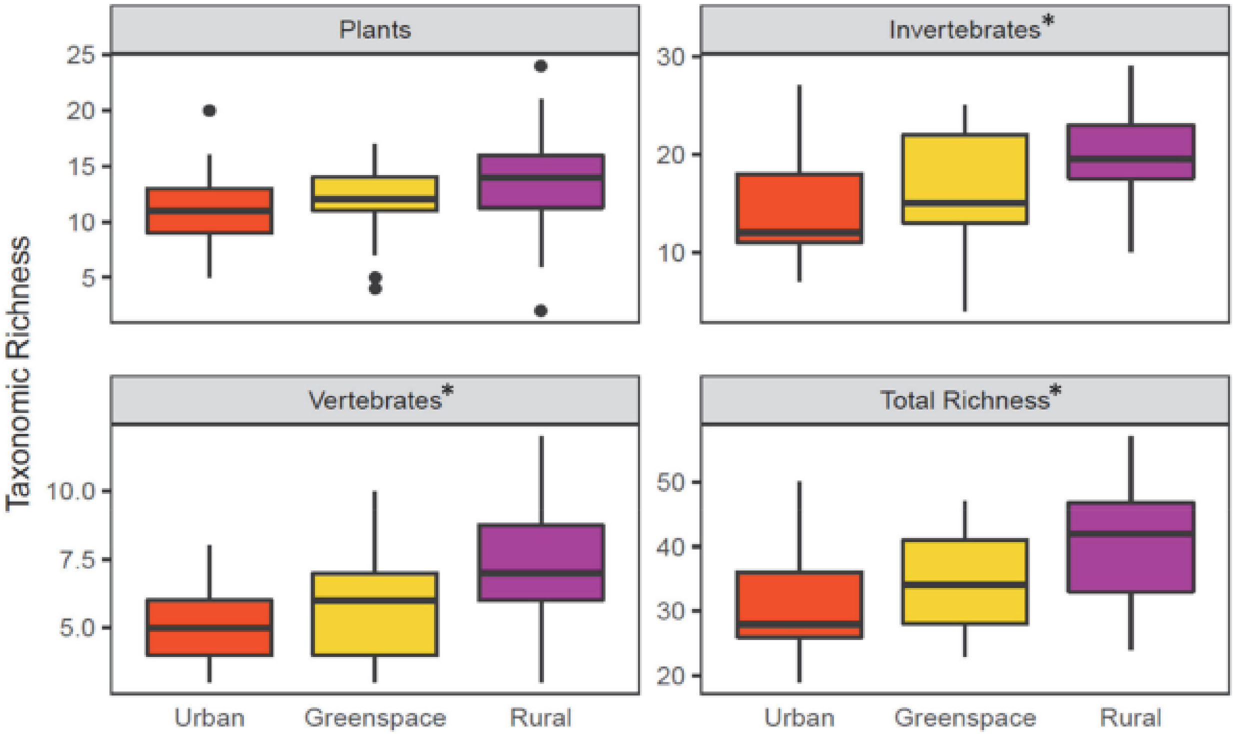

**FIGURE 2** Boxplots displaying the distribution of richness for each taxonomic group as well as total richness at urban, greenspace, and rural pond sites in Dane County, Wisconsin. Boxes visualize the median in bold and the first and third quartiles. Whiskers represent the minimum and maximum values. *Indicates statistical difference in richness (ANOVA with Bonferroni-corrected significance level; $p < 0.05$).

**TABLE 1** Model comparison of generalized mixed-effects models predicting total pond richness. Model selection was based on Akaike Information Criterion values with a correction for small samples sizes ($\text{AIC}_c$). Local variables included pH, chloride concentration, habitat complexity, pond area, and presence of invasive fish. Landscape variables included percent developed land, percent lawn cover, percent wetlands, and distance to the nearest waterbody.

| Model | Log(L) | $\text{AIC}_c$ | $\Delta\text{AIC}_c$ | Marginal $R^2_{\text{GLMM}}$ | Conditional $R^2_{\text{GLMM}}$ |
|---|---|---|---|---|---|
| Local + Landscape | −214.3 | 455 | … | 0.596 | 0.596 |
| Local | −228.1 | 472 | 17 | 0.335 | 0.542 |
| Landscape | −231.0 | 475 | 20 | 0.396 | 0.510 |

*Note*: The Local + Landscape model had the best performance, followed by Local, then Landscape models. To evaluate overall mixed-effects model fit, marginal $R^2_{\text{GLMM}}$ values (the variance explained by fixed effects) and conditional $R^2_{\text{GLMM}}$ values (the proportion of total variance explained through both fixed and random effects) were calculated.

Total pond taxonomic richness was best predicted by the model that included both local and landscape predictors, although local variables alone performed slightly better than landscape variables alone (Table 1, Appendix S1: Table S2). Total richness was negatively correlated with distance between waterbodies ($\beta = -0.089$, ±95% CI = 0.046), percentage lawn land cover ($\beta = -0.060$, ±95% CI = 0.051), percentage developed land cover ($\beta = -0.055$, ±95% CI = 0.057), and invasive fish presence ($\beta = -0.149$, ±95% CI = 0.138; Figure 3). Total richness was positively associated with habitat complexity ($\beta = 0.103$, ±95% CI = 0.043; Figure 3). The taxon-specific models showed that a subset of these same five predictor variables was most important for predicting the richness of plants, invertebrates, and vertebrates separately, but the directions of the effects remained consistent for each group (Appendix S1: Figures S6–S8).

Community composition differed between pond types (ANOSIM, $p = 0.004$, $R = 0.10$) however, the relatively low $R$-value suggests that differences were minor. Rural and urban communities slightly diverged from one another in composition, while green space communities had more overlap with both other pond types (NMDS; Figure 4A). Consistent with the generalized linear models, the NMDS indicated that sites with higher richness were

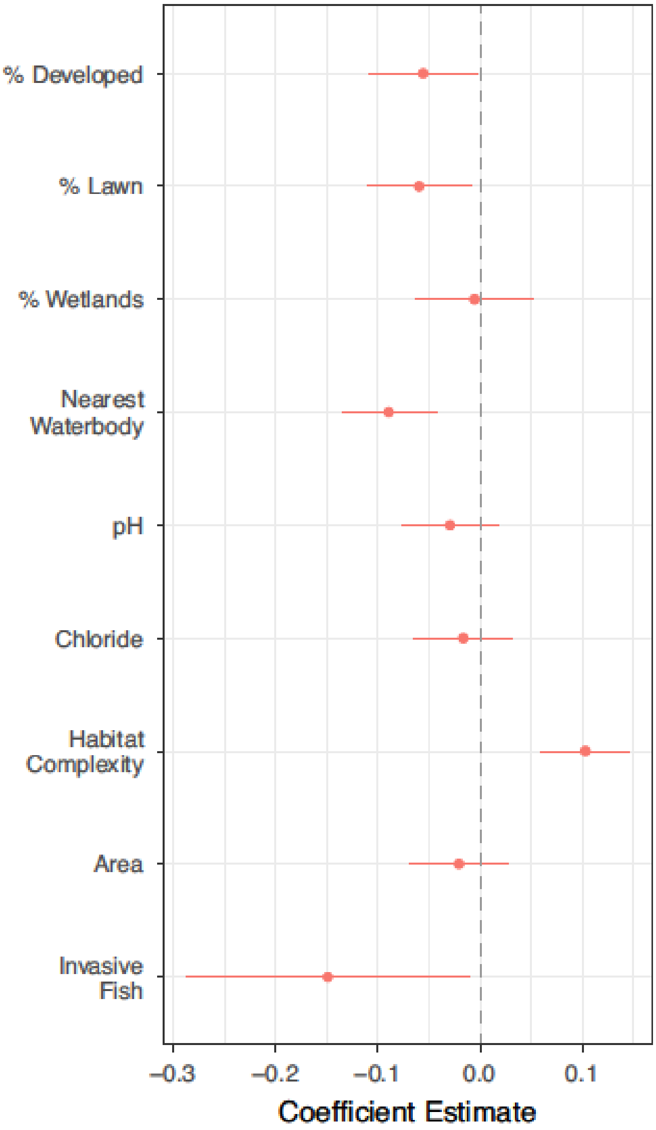

**FIGURE 3** Results from the full generalized mixed-effects model evaluating sources of variation in total richness of plants, macroinvertebrates, and vertebrates combined. Fixed effects included in the model are listed along the *y*-axis. Points represent the coefficient for each fixed effect included in the full model with 95% confidence intervals. The model also included watershed identity as a random intercept term.

associated with greater habitat complexity and higher percentages of adjacent wetlands, while sites with invasive fish, lower connectivity, and greater areas of mowed grass and development were associated with reduced taxonomic richness (Figure 4A,B). Indicator species analysis revealed that specific native taxa were indicative of rural pond sites including stoneworts (*Chara* spp.), forked duckweed (*Lemna trisulca*), aquatic moths (*Pyralidae* spp.), Northern leopard frogs (*Lithobates pipiens*), Blanding's turtles (*Emydoidea blandingii*), brook stickleback (*Culaea inconstans*), and mudminnows (*Umbra limi*), while invasive Eurasian milfoil (*Myriophyllum spicatum*) was affiliated with urban ponds (for a complete species list see Appendix S1: Table S3). Additionally, nonnative goldfish (*C. auratus*) and Chinese mystery snails (*Cipangopaludina chinensis*) were only found in urban and greenspace ponds and were absent from rural ponds. Last, mean beta diversity was slightly higher for urban ponds ($\beta_{\text{jac}} = 0.87$; SD = 0.005), relative to greenspace ($\beta_{\text{jac}} = 0.86$; SD = 0.008) or rural ponds ($\beta_{\text{jac}} = 0.85$; SE = 0.01; Figure 5A). The majority of the beta diversity in all pond types was due to turnover (Figure 5B), rather than nestedness components (Figure 5C).

## DISCUSSION

Identifying how and why variation in alpha and beta diversity occur over land cover gradients remains a conservation priority (Shochat et al., 2010). We found that connectivity, habitat complexity, adjacent land cover, and the presence of invasive fish played important roles in shaping community structure. Furthermore, our results display a clear negative relationship between urbanization and pond richness, with relatively consistent decreases in richness from rural to urban pond sites observed across multiple distinct taxa. However, we found that ponds within urban greenspaces tend to support higher richness than urban ponds surrounded by impervious surfaces. Development had only a minor influence on total richness in our multivariate models, indicating that urbanization influences diversity in pond communities, but the mechanisms driving change go beyond land cover alone.

Among landscape-scale covariates, the percentages of developed land and lawn cover, and the distance to the nearest waterbody, were each correlated with reduced total taxonomic richness, indicating that connectivity between aquatic habitats plays an important role in the urban environment. Many of the observed taxa have semiaquatic life stages and may disperse over land (e.g., amphibians and aquatic invertebrates), while others may disperse via intermittent aquatic connectivity during flooding events (Hassall, 2014). However, impervious surfaces and mowed grass can act as barriers to dispersal by reducing the cover necessary to prevent predation or desiccation, and by direct mortality from road collisions or mowing (Johnson et al., 2013; Knutson et al., 2018). These findings are consistent with previous studies attributing declines in richness to adjacent developed and mowed land cover and reduced connectivity in urban aquatic environments (Garbuzov et al., 2015; Gledhill et al., 2008; Johnson et al., 2013).

At the local scale, habitat complexity was particularly important, as it was the only variable that had a positive

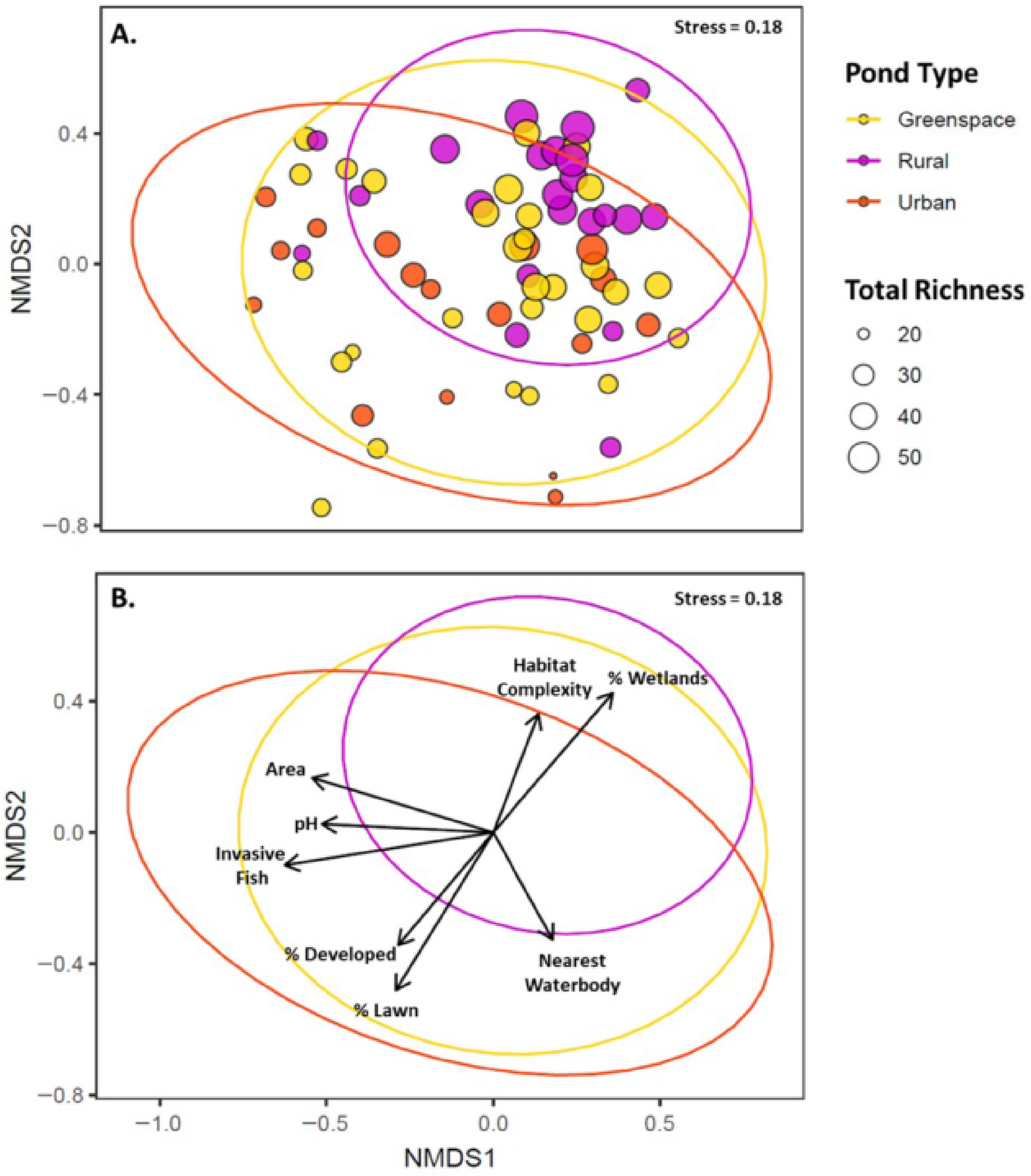

**FIGURE 4** Nonmetric multidimensional scaling (NMDS) plots depicting urban, greenspace, and rural pond communities. (A) Each pond is represented by a point with each color and shape indicating a pond type and the size of the respective shape is representative of the site-level taxonomic richness. Points plotted closer together are more similar in taxonomic composition while those further apart are less similar. (B) The weighted mean position of habitat variables and invasive fish presence in relation to pond communities. The amount of variation in the community explained by a particular variable is indicated by arrow length, while arrow angle indicates correlations between variables, with more obtuse angles being less correlated. Stress = 18.0 with 20 starts in three dimensions for both panels.

relationship with total richness and was the only variable that was a significant predictor for all individual taxonomic groups. Complex habitats increase microhabitat availability, protection from physical disturbance, and interception of organic matter, while mediating the strength of predator/prey interactions by providing refugia (Preston et al., 2017), leading to greater species richness and community stability (Kovalenko et al., 2012). Here we found that inputs of woody debris, greater variation in substrates, and high surface and subsurface heterogeneity

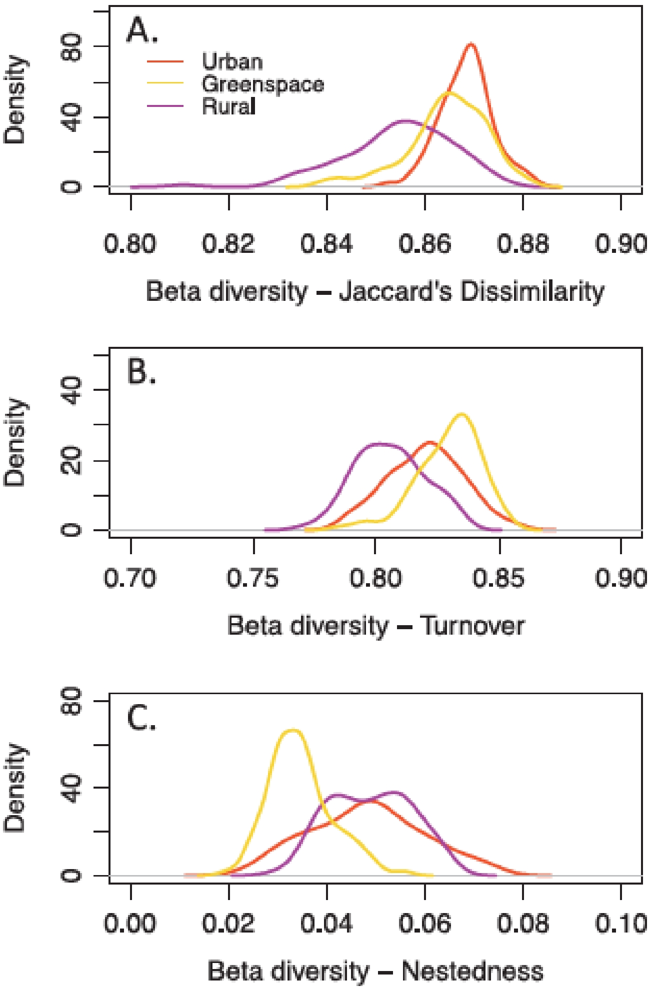

**FIGURE 5** Density plots of beta diversity, in terms of (A) Jaccard Dissimilarity, and its components of (B) turnover, and (C) nestedness. Each distribution shows the beta diversity values using the multisite method of Baselga (2012), from 100 random samples of 10 sites each within each pond type. Colors correspond to pond types as indicated in the legend of the top panel.

increased taxonomic richness across all taxonomic groups for all pond types. Urbanization often reduces habitat complexity, with stormwater ponds frequently designed with steep banks, uniform depths, and heterogeneous substrates (Rooney et al., 2015). This decreases emergent vegetation cover and the proportion of shallow water littoral zones, often used as refugia by macroinvertebrates, amphibians, and fish (Oertli & Parris, 2019; Yamaki & Yamamuro, 2013). These results demonstrate that subtle changes in retention pond design and management may be a cost-effective strategy to increase habitat value and support species-rich urban pond communities.

Other local pond variables that we measured did not have strong effects on the biotic responses in the survey, but this may reflect the range of variables measured. For instance, we did not incorporate measurements of urban pollutants that are associated with runoff from impervious surfaces (e.g., heavy metals or pesticides). Chemical pollutants have been shown to have strong effects on certain aquatic taxa in the urban environment, potentially creating "ecological traps" where some species are unable to reproduce (Sievers et al., 2018). Furthermore, it would be useful to quantify changes in dynamic water chemistry parameters over time (e.g., chloride; Helmueller et al., 2020), as temporal variation could possibly mask observed effects based on snapshot measurements in time. Hydrology was another variable that we did not robustly quantify, primarily because almost all of the surveyed ponds were permanent and many had consistent water levels over time due to controlled outflows. Cities in other regions with different climates (e.g., a dry summer period), may result in a significant effect of hydrology on aquatic community structure. In general, greater variation in hydrology, including ephemeral ponds, would lead to more sites without predatory fish and probably would promote higher beta diversity (Oertli & Parris, 2019).

The presence of introduced goldfish and common carp negatively affected total taxonomic richness and macroinvertebrate richness. Goldfish were found in urban and greenspace sites, likely to be from aquarium releases, but were not detected at any rural ponds. Invasive carp were detected in all three pond types and were stocked in Madison area lakes as a food fish starting in the 1880s (Magnuson & Lathrop, 1992). Both goldfish and common carp are benthic-feeding omnivores that disrupt sediments, increase turbidity, and have been associated with native species decline through direct predation and competition (Busst & Britton, 2017; Crone et al., 2023). Pond sites that contained carp or goldfish in our study area were observed to have greater turbidity and minimal free-floating and submerged vegetation. Our results are consistent with previous studies documenting the negative effects of introduced fish on native assemblages and highlighting the indirect biotic and abiotic influences urbanization can have on aquatic communities.

Urbanization was associated with reduced alpha diversity, but not beta diversity of pond communities. Urbanization is thought to be a major driver of the homogenization of communities due to the loss of native specialist species and the expansion of urban-adapted and introduced species (Groffman et al., 2014; McKinney, 2006). However, we hypothesized that urban pond communities would be less homogenous relative to rural ponds due to high heterogeneity in urban pond habitats and surrounding land cover (Hill et al., 2017), which may be a distinct feature of ponds relative to terrestrial habitats. In contrast with prior work in other ecosystems, we found relatively high and consistent beta diversity in urban, greenspace, and rural pond communities, with urban ponds having the highest beta diversity. Unlike larger and more highly connected ecosystems, ponds can have a wide range of environmental conditions over very short distances, leading to high heterogeneity and increased beta diversity (Hill et al., 2017). Interestingly, greenspace ponds had the highest turnover component of beta diversity, likely to be because they contained a mix of both introduced species not found in rural sites, as well as rare taxa not detected in urban pond sites. Indicator species analysis indicated a handful of native species that were only found in rural ponds, while several nonnatives were observed only in urban and greenspace ponds. This suggests that although urban and rural pond sites may have similar levels of beta diversity, some native species may be lost due to displacement by nonnatives and changes associated with urban development. Despite the increase in nonnative species, alpha diversity still declined with urbanization because the loss of native taxa exceeded the number of added nonnative taxa. Moving forward, surveys that quantify the change in pond composition over time in relation to changing urbanization would be useful to further evaluate homogenization effects (Olden & Rooney, 2006), as our study was focused on changes in space only. Additionally, the effects of beta diversity on ecosystem functioning and services warrant further study (Mori et al., 2018). Increased beta diversity has the potential to increase the rates of multiple ecosystem processes across a landscape (Grman et al., 2018). If a similar result occurs in ponds, enhanced beta diversity may result in desirable changes in valuable ecosystem services across urban areas. For instance, the beta diversity of pond macrophytes may be associated with changes in carbon storage or nutrient retention in urban ponds, providing a practical motivation to manage urban ponds for beta diversity.

Taken together, this study provides evidence that urbanization reduces richness across multiple freshwater taxa and identifies habitat complexity, connectivity, and the presence of invasive fish species as important drivers of community structure in pond habitats. Our results suggest that addressing the impacts of urbanization on freshwater communities will require management actions at multiple scales. At the local level, stormwater management that retains native riparian vegetation to increase leaf litter and woody debris inputs and enhances littoral habitat may increase habitat complexity with positive effects on species richness. Where feasible, constructed ponds may also be seasonally drained to eliminate invasive fish species, which has been shown to result in rapid colonization by taxa susceptible to predation (Walston & Mullin, 2007). More broadly, our results support the establishment of urban greenspaces, as they can promote a range of ecosystem services (e.g., water quality improvements) alongside enhancing aquatic habitat quality (Hamer, 2021; Stott et al., 2015). The study area had a relatively high number of urban greenspaces compared with many other cities. Variations in greenspace areas across different urban centers, and across neighborhoods within cities, should be carefully considered in future urban conservation planning that involves pond ecosystems. While freshwater management often focuses on larger lakes and rivers, our study highlights the potential of urban ponds to support biodiversity and serve as refugia for aquatic species, demonstrating the need for similar management attention directed toward pond ecosystems (Hill et al., 2017; Hyseni et al., 2021; Oertli & Parris, 2019).

## AUTHOR CONTRIBUTIONS

Daniel C. Trovillion, Erin L. Sauer, and Daniel L. Preston conceived the ideas and supervised the study; Daniel C. Trovillion, Erin L. Sauer, Gabrielle Shay, Erin R. Crone, and Daniel L. Preston collected the data; Daniel C. Trovillion and Daniel L. Preston performed statistical analyses; Daniel C. Trovillion and Daniel L. Preston led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data collected for this manuscript are freely available in Trovillion and Sauer (2023) in the EDI (Environmental Data Initiative) Data Portal at https://doi.org/10.6073/pasta/262866936bb8cffb3ff1d9faa9a04a93. Land cover data were obtained from the 2016 National Landcover Database in ArcGIS (NLCD; 30 $m^2$ resolution, equal-area projection, WGS 84 datum surface): NLCD 2016 Land Cover (CONUS)/Multi-Resolution Land Characteristics (MRLC) Consortium (https://www.mrlc.gov/data/nlcd-2016-land-cover-conus). Google Earth satellite imagery was downloaded from the Google Earth application (version 7.3, 2020) by searching for Dane County, Wisconsin: https://earth.google.com/web/search/Dane+County,+WI/@43.06961654,-89.42365127,272.84605913a,108746.11922398d,35y,0h,0t,0r/data=CnoaUBJKCiUweDg4MDZmNjU4MTY4MTRiNDc6MHgyYzU3YjU0ZjM5NGI0ZmNmGcJ7WLlhgkVAIdYi_VEvY1bAKg9EYW5lIENvdW50eSwgV0kYAiABIiYKJAnX6Icn7co0QBHW6Icn7co0wBld5pVYC95AQCGUnasAWDZRwA. Additional data on pond size and distance to the nearest waterbodies were extracted from maps available on the Dane County Land Information Office DCiMap application by searching for Dane County, Wisconsin (https://dcimapapps.countyofdane.com/dcmapviewer/).

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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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