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Vegetation management and benthic macroinvertebrate communities in urban stormwater ponds: implications for regional biodiversity

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Abstract

Designed ecosystems (e.g., gardens or engineered ponds) are increasingly common components of urban landscapes and contribute valuable ecosystem services. However, management of designed ecosystems is typically vegetation-centric and often does not consider associated fauna. Urban ponds typify this relationship as their vegetation is managed to improve ecosystem services, such as aesthetics and stormwater runoff mitigation, but it is unclear how pond management affects associated organisms. Here, we used urban stormwater ponds as a study system to determine how vegetation management related to benthic macroinvertebrate communities in these systems. We compared macroinvertebrates across a range of actively managed to unmanaged stormwater ponds and differentiated direct relationships with vegetation structure from indirect relationships of vegetation modulating pond chemistry. Pond vegetation and chemistry had little influence on macroinvertebrate abundance or diversity but did explain substantial variability in community composition (34%). Actively managed stormwater ponds with simpler vegetation structure were dominated by Amphipoda (scuds) and Diptera (primarily midges), unmanaged ponds with more complex structure were dominated by Oligochaeta (worms), and ponds with intermediate structure were dominated by a variety of macroinvertebrates. These community associations with vegetation management primarily occurred indirectly via changes in pond chemistry, such as unmanaged ponds with higher tree and shrub cover harboring macroinvertebrates characteristic of low oxygen environments. Additionally, variation in management maximized community differences because different macroinvertebrate orders dominated at different management intensities. Variability in the management intensity of plant communities in stormwater ponds may therefore be a feasible strategy to enhance regional benthic macroinvertebrate biodiversity in urban landscapes.

Keywords Urban biodiversity · Designed ecosystem · Stormwater pond · Macroinvertebrate · Vegetation management · Community turnover

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Introduction

Urbanization in the modern era has progressed at the fastest rate in human history (Seto et al. 2010), driving associated habitat loss and declines in global biodiversity (McKinney 2002). However, the expansion of urban land cover also drives the creation of designed ecosystems, such as gardens, lawns, parks, and engineered waterbodies (Gaston et al. 2005; Milesi et al. 2005; Sinclair et al. 2020). These ecosystems can provide a suite of associated services, such as improvements to urban aesthetics and air quality (Haase et al. 2014), and can help to mitigate the negative impacts of urbanization by providing habitat and improving the biodiversity and connectivity of ecological communities (Haase et al. 2014; Hassall 2014).

Unfortunately, the ecological mitigation potentially provided by designed ecosystems can be compromised by common management practices employed by urban residents. Many designed ecosystems are managed primarily for aesthetics to maintain a highly manicured look via chemical and fertilizer inputs, and by controlling vegetation diversity and structure through mowing, weeding, and purposeful plantings (Özgüner and Kendle 2006; Kendal et al. 2012). Consequently, these actively managed systems tend to have lower overall community diversity compared to those that are less intensively managed (Goertzen and Suhling 2013; Threlfall et al. 2016). Additionally, this type of vegetation-centric management ignores the unintended effects that altering vegetation can have on any associated fauna (e.g., Goddard et al. 2013; Hill et al. 2017), which provide their own ecological benefits such as increased biodiversity and food for higher trophic levels (Kozlov et al. 2017). Further improving urban biodiversity, and mitigating the impacts of urbanization, therefore requires a better understanding of how vegetation management affects the ecology of designed ecosystems, and particularly associated faunal communities.

To help address this knowledge gap, we surveyed the composition of benthic macroinvertebrate communities within urban stormwater ponds. Stormwater ponds are a prime example of common designed ecosystems built and managed primarily for anthropogenic functions, such as hydrologic control and pollutant mitigation (Collins et al. 2010), but whose associated fauna still provide ecological benefits. For example, stormwater ponds can harbor macroinvertebrate communities that are as, or even more, diverse than those of natural ponds (e.g., Le Viol et al. 2009; Hassall and Anderson 2015), and may also provide additional ecological functions such as organic matter processing (Kuntz and Tyler 2018). Furthermore, the vegetation in stormwater ponds varies considerably depending upon management intensity (Bean and Dukes 2016; Sinclair et al. in press). Ponds in more affluent or visible areas can be carefully managed and manicured to improve aesthetics, whereas other ponds can be completely unmanaged if pond owners cannot afford maintenance or if a more natural appearance is desired. These management-driven differences in the vegetation within and surrounding stormwater ponds (i.e., macrophytes and riparian plants) could subsequently directly and indirectly affect their associated benthic macroinvertebrate communities. In terms of direct effects, variation in macrophytes and riparian plants in freshwater ecosystems can affect habitat and food resources for benthic macroinvertebrates (Sweeney 1993; Cummins et al. 2008; Bakker et al. 2016). Differences in vegetation can also indirectly affect freshwater communities by altering dissolved oxygen (DO; Sand-Jensen and Staehr 2007), pH (Stoler and Relyea 2011), and sediment organic matter (Thorp and Covich 2015). Stormwater ponds and their associated vegetation therefore provide an opportunity to better understand the direct and indirect linkages between urban plant management and faunal ecology in designed ecosystems, subsequently aiding efforts to improve urban biodiversity.

Our study was designed to: (1) determine how variation in stormwater pond vegetation management relates to the total abundance, taxa richness, community composition, and community variability of benthic macroinvertebrates; (2) identify which benthic macroinvertebrates tend to dominate across a vegetation management gradient; and (3) determine the relative degree to which variation in macroinvertebrate communities relates to variation in vegetation management directly via differences in vegetation structure versus indirectly via differences in pond soil and water chemistry. We predicted that actively managed stormwater ponds will contain a lower diversity and abundance of macroinvertebrates than less managed stormwater ponds. Actively managed ponds tend to have simpler plant communities (Fig. 1). Thus, managed ponds may lack riparian vegetation and macrophytes that provide important habitat and resources for benthic macroinvertebrates (Sweeney 1993; Bakker et al. 2016), and that indirectly modulate the chemistry of the water and sediments in which these benthic organisms live (Thorp and Covich 2015). We also predicted that macroinvertebrates indicative of more degraded or polluted urban waterbodies (e.g., Oligochaeta and Chironomidae; Walsh et al. 2005) will dominate in actively managed ponds because aesthetic plant management typically utilizes supplemental fertilizers and pesticides, which can degrade urban aquatic habitats and water quality (Khatri and Tyagi 2015).

Methods

Pond selection

We conducted our study using the stormwater ponds within the city of Gainesville, FL, USA, and surrounding urbanized areas, which encompasses about 740 stormwater ponds. The survey was designed to compare macroinvertebrate communities among 15 stormwater ponds ($N = 15$) that spanned a gradient of vegetation management intensities from heavily to never managed. Ponds were selected for inclusion in our survey following methods detailed in Sinclair et al. 2020. To summarize, we categorized ponds across a gradient of vegetation management intensities by grouping ponds into three management categories: 'low', 'medium', and 'high' (see examples in Fig. 1). These categorizations were based on the frequency and effects of management in pond 'outer' (upland and bank slope) and 'inner' (permanently inundated) sections. We placed three additional restrictions on pond inclusion: (i) only one pond could be included per city residential, commercial, or industrial neighborhood to avoid spatial autocorrelation; (ii) ponds had to be designed for permanent inundation to reduce the influence of periodic drying on macroinvertebrate communities; and (iii) only ponds with a total area less than 10,000m^2 (~90% of ponds in the city) could be included to reduce the influence of

Fig. 1 Examples of visually evident differences in vegetation among (**a**) low, (**b**) medium, and (**c**) high management stormwater ponds. Low management ponds have a more complex vegetation structure of woody trees, shrubs, vines, leaf litter, and woody debris, along with a variety of floating and submerged macrophytes. High management ponds, which are primarily dominated by turfgrass, have less dense tree, shrub, and vine vegetation along their banks, and in our study region are also often equipped with aeration systems, such as fountains, that can affect macroinvertebrates via increasing DO. The vegetation complexity of medium managed ponds falls between that of low and high management ponds, usually exhibiting unmanaged inner sections with mowed and/or consistently maintained outer sections (red arrow). Pond photographs were all provided by James Sinclair

atypically large ponds. Five ponds were selected that fit into each of the low, medium, and high management categories and we also ensured the ponds in each management category approximately evenly ranged from 11 to 38 years old (i.e., built between 1980 and 2007) to control for the effects of pond age on the macroinvertebrate community.

Vegetation and invertebrate surveys

We surveyed vegetation structure and benthic macroinvertebrates in the 15 selected ponds between 13-July-2018 and 10-Aug-2018, which is the period of peak plant biomass in this sub-tropical region. We measured the maximum depth (m) and total surface area (m^2) of each pond using, respectively, pond construction records and satellite maps. Most ponds were shallow (depth of 1.7 ± 0.8 m; mean ± SD), small (area of 2842 ± 1546 m^2), and designed with direct contact between pond water and the soil substrate. Additional details on pond locations and characteristics are provided in Online Resource 1.

The surface area of the inner and outer sections of each pond was divided into four equal areas and the total percent area covered by five different vegetation vertical strata was recorded for each quarter following the US National Vegetation Classification System (Jennings et al. 2009): (i) tree cover (measured using a densitometer); (ii) shrub cover; (iii) field cover (woody plants <0.5 m and all non-turf herbaceous plants); (iv) floating aquatic plant cover; and (v) submerged aquatic plant cover. We also quantified the cover of leaf litter, woody debris, bareground, and turfgrasses, which could be indicative of differences in pond vegetation management. Cover values were estimated from 0 to 100% in 10% intervals and all plants within 2 m of the upland edge of each pond were included. A preliminary Principal Components Analysis (PCA) of this vegetation strata cover data confirmed that our initial categorizations of pond management intensity (low, medium, and high) successfully captured a gradient in vegetation structure (Online Resource 2).

Benthic macroinvertebrate surveys were conducted on the same days as the vegetation surveys. Invertebrates were collected from areas shallow enough to contain vegetation, i.e., littoral zones, of two of the four inner section pond quarters by sweep sampling the substrate. Isolated macroinvertebrates were preserved in 70% ethanol and classified to the family level, except for Amphipoda (identified to order), Ostracoda (identified to class), and Oligochaeta, Hydrachnidia, and Hirudinea (identified to subclass). All reported abundances approximate macroinvertebrates per $0.125m^2$ (further detail on sampling and identification methodology is provided in Online Resource 3).

Pond chemistry

The soil and sediment chemistry of each stormwater pond was assessed on the same days as the vegetation surveys using a 2.5 cm diameter soil probe. We collected 15 cm deep soil cores from the center of each pond outer section quarter (4 total cores) and 5 cm deep sediment cores from each pond inner section quarter (4 total cores). Additionally, water chemistry was assessed by collecting 250 mL grab samples from the upper 10 cm of the water column within each pond inner section quarter (4 total grab samples). Samples were then homogenized at the pond-level to produce one soil, sediment, and water sample for each pond. Percent organic matter was measured in soil and sediment samples via loss on ignition, and pH was measured in soil sediments and water samples by UF|IFAS Analytical Services Laboratories. Dissolved oxygen levels (DO; mg L^{-1}) were measured in each pond quarter using a YSI ProODO probe (YSI Incorporated, Yellow Springs, OH) and averaged across quarters.

Statistical analyses

All analyses of the benthic macroinvertebrate community data were initially performed at two levels, the lowest taxonomic level identified (termed ‘family’) and a higher-level taxonomic classification based on grouping taxa with similar functions at the level of order or above (termed ‘order’). Our results were robust across both family- and order-level analyses, therefore all further methods, results, and discussion use the order data for simplicity of interpretation. Family-level results are provided in Online Resource 4. Macroinvertebrate family and order data were also tested for spatial autocorrelation among geographically proximate ponds using Mantel correlograms (Oden and Sokal 1986), with no significant spatial relationships found (range of Mantel correlations: −0.09–0.04; range of *P*-values: 0.38–0.80).

To determine how stormwater pond vegetation management related to the benthic macroinvertebrate community (Objectives 1 and 2), we used six total Redundancy Analyses (RDAs). The first group of three RDAs determined the relationship between overall benthic macroinvertebrate abundance/diversity and pond vegetation structure, chemistry, and morphometric characteristics. These RDAs modeled a response matrix containing the total number of individual benthic macroinvertebrates (i.e., abundance), the total number of different orders (i.e., order richness), and the Shannon index of diversity (a combined measure of richness and evenness) in response to one of three predictor data matrices of either pond vegetation structure, chemistry, or morphometric characteristics. The vegetation structure data matrix included the percent cover of each vegetation strata (i.e., tree, shrub, field, floating aquatic plants, and submerged aquatic plants) in both the outer and inner sections of each pond. The chemistry data matrix included values for pond soil and sediment organic matter, soil and sediment pH, water pH, and water DO. The morphometric data matrix included values for pond maximum depth, total surface area, and pond age, which was calculated as the years elapsed between initial construction and the year of survey, i.e., 2018.

The second group of three RDAs determined the relationship between benthic macroinvertebrate community composition and pond vegetation structure, chemistry, and morphometric characteristics. These RDAs modeled a response matrix containing the Hellinger transformed (Legendre and Gallagher 2001) abundances of each benthic macroinvertebrate order in relation to the three predictor matrices of vegetation structure, chemistry, or morphometrics described above. In order to compare the relative contribution of variables measured in different units, we centered the variables in the community abundance/diversity, pond chemistry, and pond morphometric datasets to their respective means and standard deviations (i.e., z-scores).

To assess the significance of each predictor matrix in the above RDAs, we first removed highly co-linear variables (based on variance inflation factors >10) and those variables whose exclusion improved the adjusted R^2 (R^2_{adj}) of the model. The overall statistical significance ($P < 0.05$) of remaining predictors was then determined using global permutation tests (GPTs) with 10,000 permutations (Legendre and Legendre 2012).

To assess how pond management affects similarity in community composition (Objective 1), we calculated Simpson’s dissimilarity index among ponds within low, medium, and high management categories. This metric measures the degree of change in composition across communities, i.e., β-diversity, and has values ranging from 0, indicating no compositional differences, to 1, indicating entirely different communities.

We used variation partitioning (Legendre and Legendre 2012) to assess the degree to which variation in community composition was independently related to pond vegetation, independently related to pond chemistry, and related to covariation between both vegetation and chemistry. Community variability that was explained by both factors was interpreted as evidence of an indirect influence of vegetation via pond chemistry (and not an influence of chemistry on vegetation) because vegetation structure in these ponds is likely affected by management more so than by soil or water chemistry. Only the predictor variables retained in the final vegetation and chemistry RDAs were used for this analysis. We further examined community relationships to the independent influences of individual vegetation or chemistry variables by controlling for covariation between these factors using partial RDA (Legendre and Legendre 2012).

Results

Community abundance, richness, and diversity (objective 1)

At the community level, benthic macroinvertebrate abundance, richness, and Shannon diversity were not affected by pond vegetation structure (GPT, $F_{7,14} = 1.3$, $P = 0.3$), chemistry (GPT, $F_{6,14} = 1.7$, $P = 0.13$), or morphometric characteristics (GPT, $F_{2,14} = 1.8$, $P = 0.14$).

Community composition (objectives 1 and 2)

When focusing on individual benthic macroinvertebrate taxa, rather than the total abundance or diversity of each community, there was a significant relationship between vegetation structure and community composition (GPT, $R^2_{adj} = 20.0\%$, $F_{3,14} = 2.2$, $P = 0.005$). Stormwater ponds with more complex vegetation structure, such as higher cover of trees, shrubs, and herbaceous plants in pond outer and inner sections, tended to be dominated by Oligochaeta, while ponds with a simpler structure, such as those consisting of mostly turfgrasses in the outer section and floating and submerged plants in the inner section, were dominated by Amphipoda and Diptera (Fig. 2). Ponds with intermediate levels of vegetation structure

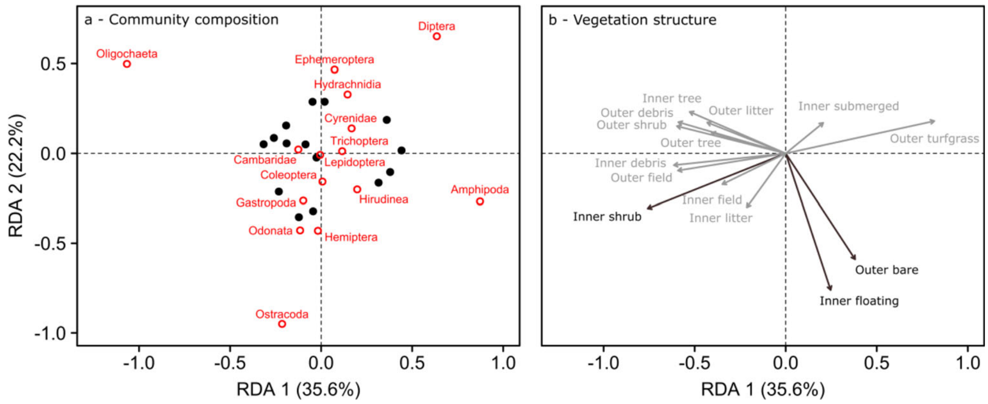

Fig. 2 Relationship between (**a**) benthic macroinvertebrate community composition and (**b**) stormwater pond vegetation structure based on Redundancy Analysis (RDA). Ponds with more outer and inner section woody and herbaceous vegetation (i.e., primarily low management ponds) were dominated by Oligochaeta, while ponds with more outer section turfgrass (i.e., high management) were dominated by Diptera and Amphipoda. Ponds with more inner section floating aquatic plants and outer section bareground also tended to be dominated by Ostracoda. Black points in (**a**) represent overall community composition and red points and text indicate the positions of individual orders. Associated vegetation predictors are shown in (**b**), with black text and arrows indicating predictors retained in the final RDA model

were dominated by a variety of different macroinvertebrate orders, including Odonata, Gastropoda, and Ostracoda.

Soil and water chemistry were also significantly related to macroinvertebrate community composition (GPT, R^2_{adj} = 28.7%, $F_{4,14} = 2.4$, $P = 0.001$). Stormwater ponds with higher organic matter and higher pH tended to have a benthic macroinvertebrate community dominated by Oligochaeta, while ponds with less organic matter and lower pH were dominated by Amphipoda (Fig. 3). Additionally, ponds with higher DO tended to be dominated by Diptera, Ephemeroptera, and Hydrachnidia, while ponds with lower DO tended to be dominated by Ostracoda.

Unlike vegetation structure and soil and water chemistry, pond age, depth, and size had no detected effects on macroinvertebrate community composition (GPT, $F_{2,14} = 1.4$, $P = 0.18$).

Community dissimilarity (objective 1)

Dissimilarity in benthic macroinvertebrate community composition among low, medium, or high management ponds was not monotonically related to management intensity. Instead, dissimilarity was highest at medium management intensities (Simpson's index = Low: 0.27; Medium: 0.46; High: 0.33). Furthermore, dissimilarity across all ponds was considerably higher than any one individual management level (0.62), indicating that variability in vegetation management occurring across all management styles contributed to maximizing community variability across all ponds.

Independent and covarying components of vegetation structure (objective 3)

Variation partitioning revealed that vegetation structure and chemistry together explained about 34% of the variation in benthic macroinvertebrate composition across ponds. The majority of this variation was approximately equally explained by the covarying vegetation-chemistry component (14.6%) and the independent chemistry component (14.0%), whereas the independent vegetation component explained a comparatively lower amount of variation (5.6%).

The covarying vegetation-chemistry relationship occurred because ponds with more tree and shrub cover tended to exhibit higher soil and sediment organic matter and lower DO. Conversely, ponds with more floating and submerged aquatic vegetation and less tree and shrub cover exhibited lower soil and sediment organic matter and higher DO (Fig. 4). Ponds with greater tree and shrub cover, which also had more organic matter and lower DO, were dominated by Oligochaeta, while ponds with lower tree and shrub cover and more aquatic vegetation, which also had less organic matter and higher DO, were dominated by Diptera and Amphipoda (these same patterns are also evident in Figs. 2 and 3).

The independent chemistry contribution was primarily due to pH, which was evidenced by a significant partial RDA (GPT, R^2_{adj} = 14.5%, $F_{3,8} = 1.8$, $P = 0.045$). Oligochaeta and Odonata dominated ponds with higher pH, whereas Diptera dominated in ponds with lower pH (Fig. 5). Unlike the covarying vegetation-chemistry component and the independent chemistry component, the independent vegetation component did not explain significant variability in macroinvertebrate composition, which was evidenced by a non-significant partial RDA (GPT, $F_{3,7} = 1.3$, $P = 0.22$).

Discussion

Management of stormwater pond vegetation structure had little influence on benthic macroinvertebrate abundance, richness, or diversity. However, community dissimilarity (i.e.,

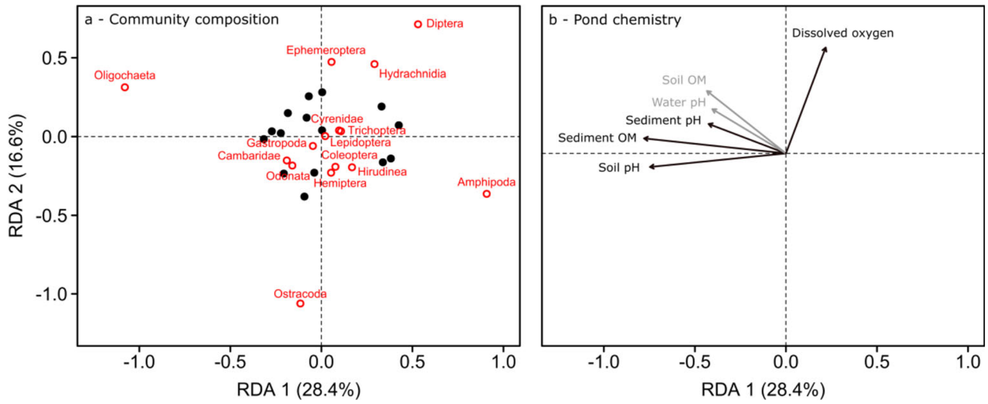

Fig. 3 Relationship between (**a**) benthic macroinvertebrate community composition and (**b**) stormwater pond chemistry based on Redundancy Analysis (RDA). Ponds with higher soil and sediment pH and organic matter (OM; %), and higher water pH, were dominated by Oligochaeta, while ponds with lower values of these chemistry variables were dominated by Diptera and Amphipoda. Additionally, ponds with higher DO (mg L^{-1}) were dominated by Diptera, while ponds with lower DO were dominated by Ostracoda. Black points in (**a**) represent overall community composition and red points and text indicate the positions of individual orders. Associated chemistry predictors are shown in (**b**), with black text and arrows indicating predictors retained in the final RDA model

β-diversity) was maximized by variation in vegetation management intensity. Additionally, our measured vegetation and chemistry variables explained substantial variability (34%) in benthic macroinvertebrate community composition despite our relatively small sample size (environmental variables explaining between 10 and 20% is common; Cottenie et al. 2003; Beisner et al. 2006). Differences in macroinvertebrate community composition that related to pond vegetation structure primarily occurred via associations between vegetation and soil and water chemistry, with further evidence for an influence of chemistry that was independent of any vegetation effects. These results indicate that the diversity of vegetation management practices utilized across the stormwater ponds of our study region, and the subsequent association between this management and the pond environments, were related to local benthic macroinvertebrate community composition within each pond and compositional dissimilarity across ponds.

The strongest relationship between vegetation structure and benthic macroinvertebrate composition emerged from the association between vegetation and pond chemistry. The abundance of trees, shrubs, and herbaceous plants in the inner section of ponds was positively related to the organic content of soil and sediment, likely reflecting the contribution of this vegetation to the detritus. Vegetation in pond inner sections was also inversely related to DO concentrations. Reduced DO in more vegetated ponds was likely due to the combined effect of shading reducing primary production and detritus from vegetation promoting high rates of respiration (Sand-Jensen and Staehr 2007). This relationship can substantially affect macroinvertebrates communities as low DO is limiting for many macroinvertebrate taxa (e.g., Tarr et al. 2005). In addition, ponds with the highest levels of vegetation management were also equipped with fountains that aerate the water, which undoubtedly further increased DO concentrations in these

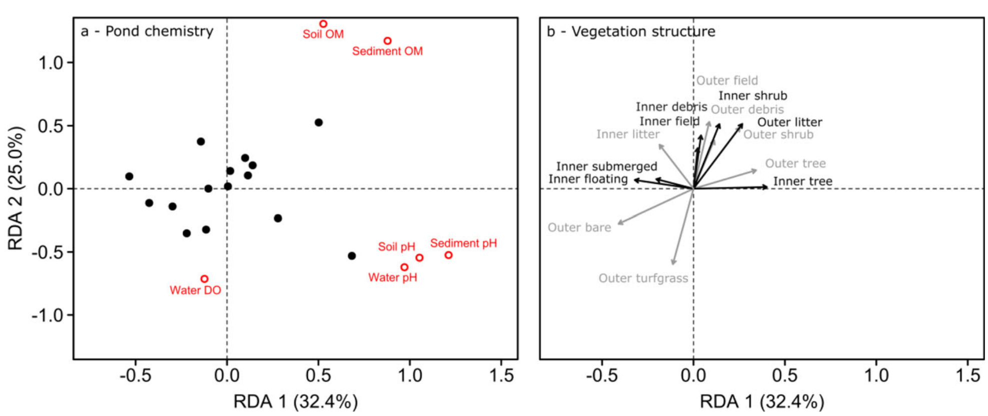

Fig. 4 Relationship between (**a**) stormwater pond chemistry and (**b**) vegetation structure based on Redundancy Analysis (RDA). Ponds with a more complex vegetation structure (e.g., more trees and shrubs) were primarily associated with higher soil and sediment organic matter (OM; %) and lower DO (mg L^{-1}), with the reverse true for ponds with less complex vegetation. Black points in (**a**) represent overall pond chemistry and red points and text indicate the positions of individual chemistry variables. Associated vegetation structure predictors are shown in (**b**), with black text and arrows indicating predictors retained in the final RDA model

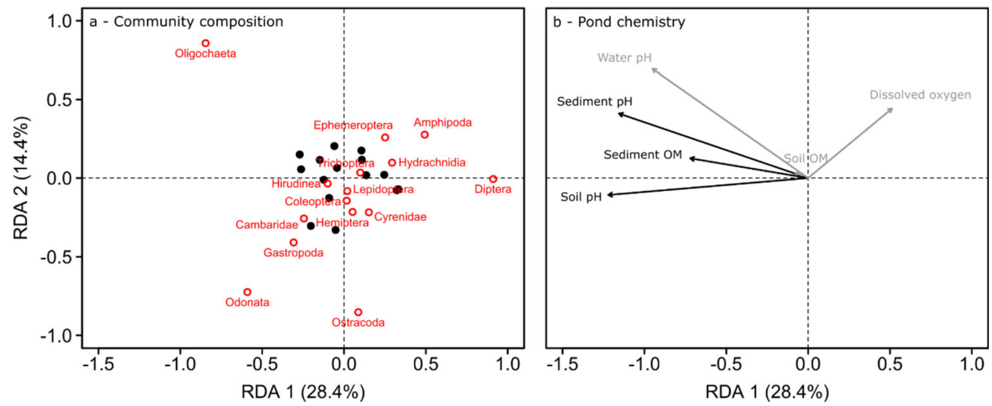

Fig. 5 Relationship between (**a**) macroinvertebrate community composition and its (**b**) independent relationship to stormwater pond chemistry. Ponds with higher soil, sediment, and water pH, and higher organic matter (OM; %), were dominated by Oligochaeta and Odonata, while ponds with lower values of these chemistry variables were dominated by Diptera and Amphipoda. Soil, sediment, and water pH exhibit the strongest loadings onto RDA axis 1 (the primary axis of variation), indicating that these variables are most related to variability in macroinvertebrate community composition. Black points in (**a**) represent overall community composition and red points and text indicate the positions of individual orders. Associated chemistry predictors are shown in (**b**), with black text and arrows indicating predictors retained in the final RDA model

ponds. Finally, ponds tended to become somewhat more acidic as floating and submerged macrophyte cover increased. This relationship could be driven by these macrophytes enhancing CO_2 concentrations by shading out primary producers, thereby promoting net heterotrophy and lower pH levels (Caraco et al. 2006). Overall, our data suggest that the relationship between stormwater pond vegetation and organic matter and DO were potentially important drivers of benthic macroinvertebrate community composition.

The lack of an effect of vegetation structure on benthic macroinvertebrate abundance or diversity, and the dominance of taxa indicative of more degraded ecosystems in both unmanaged and actively managed ponds, ran counter to our initial predictions. A possible explanation is that the low sample size of our survey did not provide the statistical power necessary to detect the effects of vegetation on abundance or diversity. However, an alternative explanation, which is supported by our chemistry results, is that both management extremes created potentially less suitable conditions for sensitive macroinvertebrates, thus there was no linear change in abundance or diversity as management increased. Ponds that experienced a low intensity of vegetation management were primarily dominated by Oligochaeta, while ponds at the highest management levels were dominated by Amphipoda and Diptera (95% of which were Chironomidae, i.e., nonbiting midges). Oligochaeta and Chironomidae commonly dominate macroinvertebrate assemblages in degraded freshwater ecosystems in urban landscapes because some species are highly tolerant of disturbed and polluted environments (Graves et al. 1998; Walsh et al. 2005; Carew et al. 2007). Such conditions may have occurred in lower management ponds due to low DO and higher organic matter, which may have favored Oligochaeta because several species of this taxon are tolerant of low oxygen (Chapman 2001) and can consume organic material. More actively managed ponds may also have been more disturbed or polluted due to their general lack of riparian vegetation, which reduces pollutant buffering (Tourbier 1994). More disturbed or polluted conditions may therefore have favored the Chironomidae because some species are notoriously tolerant to pollutants commonly found in urban runoff, including organic pollution, sediments, and heavy metals (Hilsenhoff 1987; Graves et al. 1998; Carew et al. 2007). Some species of Amphipoda are also tolerant of organic pollution (Hilsenhoff 1987), and several taxa are predators of Chironomidae (Taylor and Batzer 2010), and may thus have also dominated in some higher management ponds due to their higher tolerances and ability to exploit abundant food resources.

While both lower and higher management intensity ponds were dominated by only a few, tolerant macroinvertebrate taxonomic groups, ponds that experienced intermediate management intensities were dominated by a variety of different macroinvertebrate taxa (i.e., higher community dissimilarity). A characteristic of medium management ponds in our survey region is a relatively unmanaged inner section combined with a more actively managed outer section. Several studies have found declines in Trichoptera, Ephemeroptera, Odonata, and Gastropoda species richness and/or abundance in wetlands impacted by agriculture or urbanization (Burton et al. 1999; Gernes and Helgen 1999; Lunde and Resh 2012). Thus, the association of these groups with medium management ponds suggests that intermediate levels of vegetation management may provide environmental conditions that are more similar to those in undisturbed ecosystems. Some vegetation management in the outer section may also increase suitability for more sensitive macroinvertebrate taxa by reducing vegetation inputs into the ponds, subsequently reducing hypoxia and preventing the dominance of Oligochaeta which occurred in low management ponds. Future research on the link between pond outer versus inner section vegetation management practices and environmental conditions, in addition to internal pond biogeochemical functioning (e.g., respiration and primary production), would help to identify the specific mechanisms by which pond plant management affects environmental quality, and whether this relationship varies seasonally.

There are a variety of environmental factors that could have driven the independent relationship between macroinvertebrate community composition and pond soil/sediment pH, such as surrounding land use and soil type. The density of buildings and infrastructure around urban ecosystems can affect their pH via alkaline refuse, construction materials, and leaching from asphalt and concrete (Godefroid and Koedam 2007; Wright et al. 2011). Similarly, the soil of urban areas is a complex mosaic of acidic to basic natural substrates combined with anthropogenic admixtures, which affects pH and subsequently the structure of associated ecological communities (Godefroid et al. 2007). While our survey design was focused on vegetation structure and chemistry, we conducted some post-hoc GIS analyses using Florida urban land use and soil type data, the results of which supported the idea that these factors may influence stormwater pond pH (Online Resource 5). We found that pond soil and sediment pH was potentially related to the soil order upon which or with which ponds were built (e.g., higher pH when built using alfisols) and tended to shift from acidic to basic as both building density and impervious surface increased. There are undoubtedly other, unmeasured environmental attributes or management practices affecting the pH of our surveyed ponds, such as liming. However, our land use and soil type results suggest that a combination of natural properties, such as soil type, and human activities, such as road construction, occurring in and around our surveyed ponds likely affected pond pH and subsequently the macroinvertebrate community.

Variability in macroinvertebrate community composition across ponds (i.e., dissimilarity) was maximized by variability in how vegetation was managed. Changes in pond vegetation structure had no strong influence on local macroinvertebrate abundance, taxonomic richness, or diversity, but instead shifted which macroinvertebrate orders dominated among communities. Medium management ponds were dominated by a variety of different macroinvertebrate orders, and hence exhibited the highest dissimilarity, while low and high management ponds were generally dominated by one or two highly abundant macroinvertebrate orders. Importantly, the macroinvertebrates that dominated communities differed across our surveyed vegetation management gradient (visually summarized in Fig. 6). These results suggest that variation in vegetation management among stormwater ponds could help to optimize regional benthic macroinvertebrate biodiversity, which is consistent with findings from other research on the ecological effects of environmental heterogeneity in urban aquatic systems (Goertzen and Suhling 2013; Hill et al. 2015, 2017). This effect may have occurred in our surveyed ponds because variation in vegetation management produced a gradient in vegetation that ranged from early (i.e., simpler vegetation structure) to late-successional (i.e., complex vegetation structure) plant communities (Sinclair et al. in press),

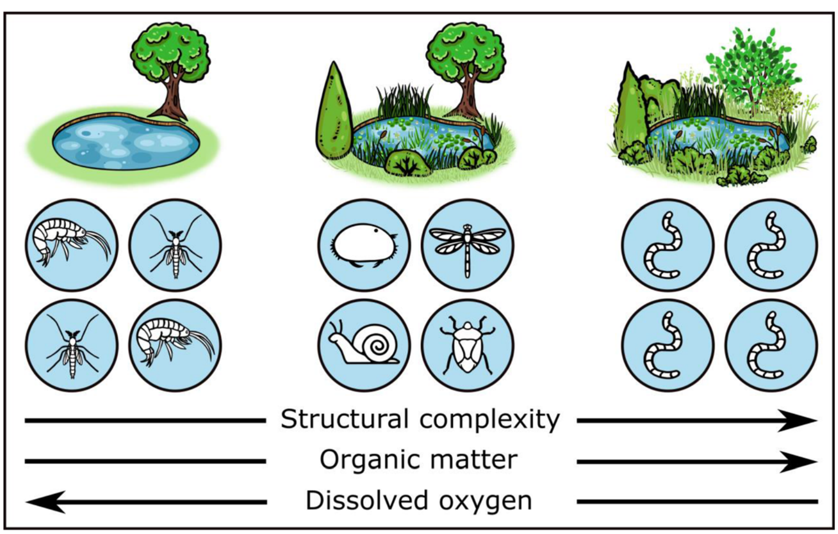

Fig. 6 Conceptual depiction of management-related differences among stormwater pond benthic macroinvertebrate communities. Differences in vegetation structure and pond chemistry helped to maximize differences among ponds in macroinvertebrate community composition (i.e., β-diversity). This relationship is visually represented as different macroinvertebrate orders (black and white illustrations) dominating in ponds (blue circles) that span a gradient of vegetation structural complexity (reflected in pond illustrations), organic matter, and DO. Ponds with simpler vegetation structure (left), which exhibited lower organic matter and higher DO, were dominated by Amphipoda and Diptera. Ponds with more complex structure (right), which exhibited higher organic matter and lower DO, were dominated by Oligochaeta. Ponds with intermediate structural complexity (middle) were dominated by a variety of macroinvertebrates, including Ostracoda, Odonata, Gastropoda, and Hemiptera. Illustrations for this figure were provided by Marie-Josée Létourneau

which resulted in unique community assemblages associated with different management intensities.

However, while having a range of unmanaged to actively managed pond ecosystems may improve regional benthic macroinvertebrate diversity, the broader ecological impacts of active pond management are still unclear. Highly managed ponds can appear as good-quality habitat to other organisms, such as amphibians, but may negatively affect survival or reproduction creating 'ecological traps' (McCarthy and Lathrop 2011), though this is not always the case (e.g., O'Brien 2015). Stormwater ponds can also accumulate pollutants, such as nutrients and metals (Vincent and Kirkwood 2014; Song et al. 2015), which could be further exacerbated by active vegetation management that utilizes fertilizers and pesticides resulting in negative impacts on water quality. Therefore, while a mixture of management regimes may benefit regional macroinvertebrate diversity and alleviate some of the ecological impacts of urbanization (McKinney 2006), these benefits could come with negative ecological tradeoffs from common pond management practices.

Conclusions

As we seek to improve the ecology of urban landscapes and designed ecosystems, like stormwater ponds, there will be necessary tradeoffs between intended functionality and biodiversity. Vegetation management is often necessary to ensure that designed ecosystems provide their intended, human-related functions. For example, vegetation in stormwater ponds is managed to improve hydrologic control, pollutant removal, and often aesthetics. Other designed ecosystems, such as green roofs, rain gardens, and community parks, would similarly not provide their primary intended ecosystem services without some management, even though such practices can come at the cost of reducing local biodiversity (e.g., Goertzen and Suhling 2013; Threlfall et al. 2016). Thus, there is a pressing need to determine how to build designed ecosystems to both provide human needs and support biodiversity (Haase et al. 2014; Hassall 2014), which is a conflict that is not unique to urban areas (e.g., similar questions arise in ecological restoration; Bullock et al. 2011).

Encouragingly, our results suggest that tradeoffs between primary functionality and biodiversity in a single pond could be partly resolved by adopting a regional management perspective, though this idea requires further exploration at broader scales. The macroinvertebrate diversity of one pond may be low, but a range of vegetation management regimes across the ponds within a given region could improve overall biodiversity of that region without compromising individual pond services. Adopting this regional perspective would require managers to tailor their practices to different areas across the urban landscape. Aesthetics are a strong driver of intense vegetation management in stormwater ponds (Monaghan et al. 2016), thus city areas for which aesthetics are desired will necessitate highly managed ecosystems. Conversely, ponds for which aesthetics are less important, such as those maintained solely for hydrologic functions, to mimic natural wetlands, or in secluded areas, could be managed less intensely to increase vegetation complexity. Creating regional heterogeneity in pond vegetation management may also benefit other urban faunal species, such as amphibians (e.g., McCarthy and Lathrop 2011), which may in turn also improve human welfare as stormwater ponds provide some of the only aquatic habitat to which urban residents are exposed (Warner et al. 2019) and can access (Wendel et al. 2011). Urban biodiversity depends on effective management of plant and animal populations (Aronson et al. 2017), and our study provides further evidence that vegetation management practices could be altered to enhance urban diversity by creating habitat variability within the urban matrix.

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Author's contributions This manuscript involved equal effort from the BVI (including JSS) and LSR labs. JSS collected the vegetation and chemistry data, conducted the analyses, and wrote portions of the manuscript. LSR collected the macroinvertebrate community data and wrote portions of the manuscript. CRA contributed to the vegetation survey design and edited the manuscript. EB contributed to pond selection study design and edited the manuscript. AJR supervised sediment and water quality analyses and edited the manuscript. BVI funded and supervised the study and wrote portions of the manuscript. All authors contributed to the design of the study and interpretation of results.

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Data availability Data is publicly available from the Institutional Repository at the University of Florida at https://ufdc.ufl.edu/l/IR00011298/00001.

Compliance with ethical standards

Conflicts of interest/competing interests Not applicable.

Code availability Not applicable.

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