



The interaction between spatial variation in habitat heterogeneity and dispersal on biodiversity in a zooplankton metacommunity



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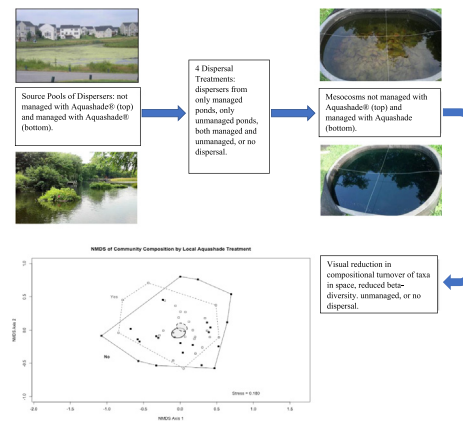
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HIGHLIGHTS

- Source pool of dispersers was important to explaining community composition.
- Local management marginally reduced compositional turnover among ponds.
- Management practices may act as environmental filters, reducing beta diversity.
- Management plans may have complex effects on biodiversity.

GRAPHICAL ABSTRACT



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ABSTRACT

It is hypothesized that biodiversity is maintained by interactions at local and regional spatial scales. Many sustainability plans and management practices reflect the need to conserve biodiversity, yet once these plans are implemented, the ecological consequences are not well understood. By learning how management practices affect local environmental factors and dispersal in a region, ecologists and natural resource managers can better understand the implications of management choices. We investigated the interaction of local and regional scale processes in the built environment, where human-impacts are known to influence both. Our goal was to determine how the interaction between spatial variation in habitat heterogeneity in algal management of urban ponds and dispersal shape biodiversity at local and regional spatial scales. A twelve-week mesocosm study was conducted where pond management and dispersal were manipulated to determine how spatial variation in habitat and dispersal from various source pools influence zooplankton metacommunities in urban stormwater ponds. We hypothesized that dispersal from managed or unmanaged source pools will lead to community divergence and local management practices will act as an environmental filter, both reducing beta diversity between managed ponds and driving compositional divergence. Our results suggest that zooplankton dispersal from managed or unmanaged source pools was important to explaining divergence in community composition. Furthermore, local management of algae marginally reduced compositional turnover of zooplankton among ponds but did not lead to significant divergence in community composition. Management practices

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may act as strong environmental filters by reducing beta diversity between ponds. As hypothesized, source pool constraints led to compositional divergence and local management practices resulted in reduced compositional turnover between ponds. The results of this study suggest that sustainability and management plans may have complex effects on biodiversity both within and across spatial scales.

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1. Introduction

It is hypothesized that biodiversity is maintained by interactions at local and regional spatial scales, and increasingly community ecologists are embracing a metacommunity approach when investigating biodiversity patterns and their underlying processes (Cottenie et al., 2003; Leibold et al., 2004; Leibold et al., 2010; Logue et al., 2011; Shurin and Allen, 2001; Swan et al., 2013). As such, dispersal from the regional species pool has increasingly been shown to be important not only in explaining community composition locally, but also among local assemblages and regionally (eg. Belyea and Lancaster, 1999; Brown and Swan, 2010; Cadotte, 2006; Havel and Shurin, 2004; Howeth and Leibold, 2010; Jenkins and Buikema, 1998; Leibold et al., 2004; Leibold et al., 2017; MacArthur and Wilson, 1963; Shurin, 2001; Urban, 2004). While dispersal is increasingly considered, constraints on species pool composition and any interactions with local environmental factors is less explored. The goal of this study was to address this gap in knowledge by independently and interactively manipulating two aspects of regional effects - source pool constraints and dispersal - along with a local environmental constraint to estimate how local and between habitat biodiversity emerge.

Source pool composition can influence local community structure, as local communities assemble given both dispersal and environmental constraints (Leibold et al., 2004). In undisturbed landscapes, colonization process proceeds from an intact regional pool. However, where disturbance or local degradation is widespread, the regional species pool can become depleted, comprised of highly tolerant species and/or habitat generalists (Lake et al., 2007; Sundermann et al., 2011). Urban environments are a prime example and ideal context to study this, as the harsh geophysical template can impose widespread depletion of the regional species pool (Groffman et al., 2014; Hassall, 2014; McKinney, 2006; Olden et al., 2006). But, as many cities and other built environments move to adopt more sustainable habitat management practices, such as restoration and water quality management, there is often a goal to support more desirable species assemblages. But, if the regional species pool is diminished at a larger scale, this outcome is unlikely. This "Field of Dreams" hypothesis, ie., build it and they will come, is a central problem in the field of restoration ecology and natural resource management in general (Lake et al., 2007; Palmer et al., 1997; Sundermann et al., 2011). Here, we contend that when different management practices are imposed on a landscape, regional species pool constraints result in divergent outcomes for how biodiversity patterns emerge locally and between habitats.

Dispersal or the rate of colonization and establishment can determine if local or regional processes will structure a community (Cohen and Shurin, 2003). If the rate of dispersal is low compared to the local extinction rate, then it is predicted that local community structure is shaped more by local environmental constraints and inter- and intra-specific interactions (Cohen and Shurin, 2003). This can lead to divergent patterns in local species richness, community divergence between habitats exhibiting different environmental conditions, and thus, ultimately, high compositional turnover (beta diversity). However, if the dispersal rate is high compared to the local extinction rate, then regional processes are predicted to structure local species composition. Local communities become homogenized, and local diversity can decline as competitively superior and/or habitat generalists dominate regionally. Community divergence is expected to decline, reducing beta

diversity. Such "biotic homogenization" is an often cited phenomenon in urban ecosystems (Groffman et al., 2014; Hassall, 2014; McKinney, 2006; McKinney and Lockwood, 1999; Olden et al., 2006).

There is evidence for both strong roles of dispersal and local environmental factors in structuring local communities. For example, in studies experimentally manipulating dispersal rates, many have found dispersal to play a dominant role in structuring local communities, exemplifying the importance of understanding species dispersal rates and resulting community dynamics (Cadotte et al., 2006; Hanly and Mittelbach, 2017; Howeth and Leibold, 2010; Kneitel and Miller, 2003). However in some cases, if local environmental factors are strong enough to select for distinct assemblages and heterogeneous across space, homogenization may be prevented through elevated dispersal rates (Cottenie et al., 2003; Howeth and Leibold, 2010). For instance, in a study of zooplankton metacommunities, Cottenie et al. (2003) found environmental factors at the local level were significantly related to local community structure, despite high dispersal rates in the highly interconnected pond system studied. In this case, strong local environmental factors related to community structure were alternate equilibria within the shallow lake system, demonstrating how local environmental constraints may be strong enough to select for distinct assemblages despite elevated dispersal rates (Cottenie et al., 2003).

The same regional and local processes known to play a role in shaping community structure in natural environments can become modified in built environments. Humans alter local scale processes, with habitat management activities, which can change local species interactions and compositional responses to environmental gradients (eg. Dormann et al., 2007; Ekroos et al., 2010; Loughheed et al., 2008; Maloney et al., 2011; Passy and Blanchet, 2007). Humans facilitate the movement of organisms, build corridors between habitats, and create spatially homogeneous habitats from management practices (Swan et al., 2013). Environmental management practices can impose new environmental gradients by altering disturbance regimes, and through the addition of pollutants and other stressors into the system (eg. Van Meter et al., 2011). The combined effects of altered dispersal patterns coupled with the degree to which management activity is spatially heterogeneous have implications for regional pool composition. For example, in regions that exhibit homogeneity in management or disturbance regime, lack of undisturbed refuge habitats should constrain the regional pool of colonists (Steiner et al., 2011). If the regional pool of colonists becomes constrained, the number and composition of species available to disperse into local communities can then become reduced or less compositionally divergent between local habitats.

Our overarching question is what are the independent and interactive effects between local environmental factors and regional influences on biodiversity patterns of the zooplankton metacommunity? We extend the now well-studied conclusion that dispersal can matter to local assembly by exploring different regional species pool constraints explicitly. We hypothesize that: (1) local environmental variables, here specific algal management in urban water bodies, will shift community composition and patterns of beta diversity, and (2) source pool constraints, from management with the product, Aqushade®, will lead to local community divergence. We predict (1) local algal management practices will act as an environmental filter, thereby reducing beta diversity, and (2) colonists from specific source pools will lead to diverging community composition.

2. Methods

2.1. Study system

Stormwater retention ponds in urban ecosystems are an ideal system for this study because they are widespread, support ecological communities, and increasingly serve as environmental amenities in green spaces. Although stormwater retention ponds are designed to regulate flow regimes and sediment loads into receiving streams, various aquatic and semi-aquatic organisms have been documented to use stormwater ponds as habitat (eg. Gallagher et al., 2011; Hansson et al., 2005; Hassall and Anderson, 2015; Le Viol et al., 2009; de Paggi et al., 2008; Spieles et al., 2006; Stanczak and Keiper, 2004; Van Meter et al., 2011; Woodcock et al., 2010).

Zooplankton in stormwater retention ponds were chosen as the community of focus because they readily disperse, many share similar modes of passive dispersal (such as wind and animal vectors), and many have rapid generation times, which allow ecological interactions to be measured over relatively short time spans (Cohen and Shurin, 2003; Hanly and Mittelbach, 2017; Havel and Shurin, 2004; Kristiansen, 1996). Evidence is mounting that invertebrate community composition, including the zooplankton studied here, is explained by both dispersal-driven effects, as well as human-mediated environmental gradients.

2.2. Survey design

To address hypothesis 1, zooplankton communities from six stormwater ponds in Columbia, MD were surveyed bi-weekly from May through July of 2014. The Columbia Association Open Space Management, a local nonprofit community services corporation, treated three of the six ponds with Aquashade® in order to manage algal blooms, while the other three ponds were not managed with Aquashade®. The three ponds managed with Aquashade® by the Columbia Association Open Space Management were Dannon Garth, Jackson Pond, and Waiting Spring. Aquashade® contains erioglaucine (Acid Blue 9 or FD&C Blue No. 1) and tartrazine (Acid Yellow 23 or FD&C Yellow No.5) dyes designed to inhibit algal and submerged aquatic vegetation growth by absorbing photosynthetically-active radiation (550–650 nm range) (Suski et al., 2018; U.S. EPA, 2005). Aquashade® is a preferred management method within this study area, as it has been labelled as practically non-toxic to mammals (U.S. EPA, 2005).

Within each stormwater pond, a zooplankton net (Wildco® Fieldmaster mini plankton net, 63 µm) was deployed and pulled for a total of 26 m, resulting in 78 L of pond water filtered through the net, following the methods from Suski et al. (2018) (di Bernardi, 1984). The 26 m pull was concentrated and brought up to 13 L with sieved pond water. From the 13 L sample, a 500 mL subsample was collected. The 500 mL sub-sample was concentrated into a 10 mL sample. The first 200 individual zooplankton from the sub-samples were identified to the lowest possible taxonomic resolution using a compound microscope at 40–100× magnification (Suski et al., 2018). Zooplankton were identified using taxonomic keys developed by Haney et al. (2013) and Balcer et al. (1984). Taxa accumulation curves were created to satisfy that enough individuals were identified per sample to reach an asymptote between number of new taxa identified and sampling effort. Individuals were usually identified to genus or species, except for Copepoda and Ostracoda. Identification of zooplankton to family or genus resolution has been documented as adequate to replace identification to species without a substantial loss of information (Machado et al., 2015). The zooplankton net was thoroughly rinsed with distilled water after sampling each pond, in order to prevent the dispersal of zooplankton on the net between ponds.

2.3. Mesocosm study

To address our hypotheses, we performed a full-factorial manipulation of local and regional constraints in a mesocosm experiment

designed to reflect stormwater pond habitats in the Mid-Atlantic, USA, and estimated how zooplankton communities assembled in response (Table 1). We manipulated regional factors as source pool composition and the presence/absence of dispersal, in combination with a local factor, algal management in the form of the addition of Aquashade®. Source pool treatments were created by dispersing zooplankton from three ponds managed with Aquashade®, three not managed with Aquashade®, a combination of both, or a no dispersal treatment (hereafter, managed, unmanaged, managed+unmanaged, and none, respectively) (Table 2). The four regional treatments were crossed in a full factorial design with two local treatments of pond management by the addition of Aquashade® to mesocosms, or no addition of Aquashade®. We allocated $n = 6$ mesocosms per treatment combination, for a total of forty-eight mesocosms.

An array of forty-eight, 600 L mesocosms were set up on the campus of the University of Maryland, Baltimore County in Baltimore, Maryland. Each mesocosm was separated by one meter and between March 22–30, 2014 filled with approximately 500 L of tap water, aged for more than one week to remove chlorine (Suski et al., 2018; Van Meter and Swan, 2014). As a source of nutrients, 95.0 g of dry leaf litter, a mostly American Beech leaf mix, was placed into each mesocosm (Suski et al., 2018; Van Meter and Swan, 2014). Mesocosms were secured with a cover of 70% shade cloth to prevent colonization by non-study organisms and zooplankton dispersal between mesocosms (Suski et al., 2018; Van Meter and Swan, 2014). On April 17, 2014, pond water, sediments, and zooplankton were gathered from the six study ponds and deposited into each mesocosm. Mesocosms were arranged and treatments were assigned in a randomized block design.

Zooplankton were collected from the same six stormwater ponds as in the zooplankton survey above, using the above stated zooplankton collection method from Suski et al. (2018). These six ponds were chosen because the ponds are within 10 km from each other, which is considered to be where the supply of colonizing zooplankton should not be limiting (Cohen and Shurin, 2003; Havel and Shurin, 2004).

Mesocosms were inoculated with a mixture of zooplankton and sediments from the regional species pool, or all six stormwater ponds. A total of 1.5 L of zooplankton inoculum was added into each mesocosm, equating to 250 mL of inoculum from each source pool. Five milliliters of sediments from each study pond was also added to each mesocosm, in order to inoculate the mesocosms with zooplankton resting stage eggs (Suski et al., 2018). On May 3, 2014, the local treatment of Aquashade® was added to half of the mesocosms at the maximum label rate application of 2.00 ppm, using a 1 mL micropipette (U.S. EPA, 2005). Aquashade® degradation was measured weekly using a water column sample read in a La Motte Smart 3 Colorimeter (Chestertown, Maryland) at 635 abs. Additions of Aquashade® were made to each mesocosm as necessary to maintain a 2.00 ppm concentration.

Experimental dispersal of the source pool treatments was carried out by collecting zooplankton from either three managed ponds, or three unmanaged ponds and combining them to create a source pool addition to individual mesocosms according to the regional treatments

Table 1
Experimental variables arranged by local and regional treatments.

	Local Treatments	
	Aquashade	No Aquashade
Regional Treatments	Dispersal from Managed Ponds (Managed)	Dispersal from Managed Ponds (Managed)
	Dispersal from Unmanaged Ponds (Unmanaged)	Dispersal from Unmanaged Ponds (Unmanaged)
	Dispersal from Both Managed and Unmanaged Ponds (Both)	Dispersal from Both Managed and Unmanaged Ponds (Both)
	No Dispersal	No Dispersal

described above. Dispersal was designed to introduce ~2% by volume bi-weekly (Suski et al., 2018). To obtain zooplankton dispersers, at each source pond a 26 m pull was taken with a zooplankton net. The 26 m pull was concentrated and brought up to 13 L with sieved pond water, as described in the survey design above. Bi-weekly, mesocosms received a total of 1.5 L or 500 mL of zooplankton and water from each of the three managed or unmanaged ponds for the managed and unmanaged treatments, and for the managed+unmanaged treatment, 250 mL from each pond was added into the mesocosms. For the no dispersal treatment, 250 mL from each source pond was combined, for a total of 1.5 L of zooplankton and pond water. Before addition to the mesocosm, the no dispersal treatment was heated to boiling for 5 min so as to eliminate any zooplankton, but still add any detritus or nutrients that may have been added during dispersal events.

Bi-weekly column samples of the zooplankton community were taken. Mesocosms were split into quarters and a fair coin was tossed. The outcome of the coin toss determined what quarter and diagonal quarter of the mesocosm were sampled. A PVC pipe (5 cm diameter) with a rubber stopper on one end was used to collect a sample from the entire water column (Suski et al., 2018). To prevent dispersal of zooplankton between mesocosms, each mesocosm was sampled with a unique PVC pipe, and shoulder length rubber gloves were worn and washed between sampling each mesocosm (Suski et al., 2018). From the column sample, 500 mL was poured over a 63 μ m sieve and preserved in a whirl pack with 70% ethanol. The 500 mL sub-sample was concentrated into a 10 mL sample. The first 200 individual zooplankton from the sub-sample were identified to the lowest possible taxonomic resolution using a compound microscope at 40–100 \times magnification (Suski et al., 2018).

Environmental conditions in the mesocosms were monitored weekly, and included chlorophyll *a* concentrations, pH, turbidity, conductivity, dissolved oxygen, temperature, and Aquashade® concentration. Nitrate nitrogen and phosphate concentrations were measured on July 24, 2014. Nitrate nitrogen and phosphate samples from each mesocosm were collected by filtering a column sample of water through a Whatman Glass Microfiber Filter (GF/F 25 mm diameter) and analyzed using ion chromatography. Chlorophyll *a* concentration in-vivo was measured using a fluorometer and chlorophyll *a* biomass was measured using a spectrophotometer. For the in-vivo measurements, a column sample of water was taken with the coin method described above. From this column sample a cuvette was filled and read using a Trilogy Laboratory Spectrophotometer on the “RAW mode” (Turner Designs, 2010). The chlorophyll *a* biomass samples were also acquired through the coin method, and 500 mL of that sample was filtered through a Whatman Glass Microfiber Filter (GF/F 47 mm diameter) using a vacuum filter. Samples were immediately frozen and taken back to the lab for analysis using a spectrophotometer (Sartory and Grobbelaar, 1984). The pH was measured using a LaMotte Smart 3 Colorimeter and pH test kit (Chestertown, Maryland). Turbidity and Aquashade® concentration were measured with the LaMotte colorimeter. Conductivity and dissolved oxygen were measured using YSI® sondes (Yellow Springs, OH).

2.4. Survey analysis

All statistical analyses were conducted with R version 3.1.0, using the vegan package (Oksanen et al., 2014; R Core Team, 2014). Data used were from one sampling event, temporal data was not pooled for analyses. To address the prediction of decreased alpha diversity in communities from managed ponds compared to communities from unmanaged ponds, two-sample *t*-tests were used to learn if taxa richness and Shannon diversity are significantly different between pond management practices. To analyze the effect of management practice on community composition and beta diversity, a Bray–Curtis dissimilarity matrix was used to determine species dissimilarity between pond management practices. The variation of the dissimilarity matrix was evaluated using a permutational multivariate analysis of variance (MANOVA) via the

adonis function. To learn if management or source pool treatments resulted in dissimilar patterns of beta diversity, the *betadisper* function was used to find and test the multivariate homogeneity of variances. The *betadisper* function determines non-euclidean distances between objects and group centroids by reducing original distances to principle coordinates; this command is comparable to Levene’s test for homogeneity of variances (Anderson, 2006; Oksanen et al., 2014).

2.5. Experiment analysis

Analyses of the experimental portion of this study were similar to the analyses for the survey portion. Data presented are from the last sampling event ($n = 48$). All analyses of community composition were conducted with R version 3.1.0, using the vegan package (Oksanen et al., 2014; R Core Team, 2014). To address the prediction of decreased alpha diversity in communities from managed mesocosms compared to communities from unmanaged mesocosms, we tested for the main and interactive effects of source pool, dispersal, and local effects using a three-way analysis of variance (ANOVA). To analyze the effect of management on community divergence and beta diversity, the *adonis* and *betadisper* functions were used. In order to investigate divergence in community composition and beta diversity in response to the source pool of dispersers, the *adonis* and *betadisper* functions were used (Anderson, 2006; Oksanen et al., 2014). To visualize the effect of management on beta diversity and divergence in community composition in response to source pool of dispersers, we used non-metric multidimensional scaling (NMDS) plots. These plots revealed if zooplankton communities from managed source pools showed reduced beta-diversity and if the zooplankton community composition from managed and unmanaged source pools diverge significantly. Although the mesocosms were arranged in a randomized block design, the randomized block design was not used in the analyses, as it was not significant.

3. Results

3.1. Survey results

Zooplankton communities from six stormwater ponds in Columbia, MD were surveyed bi-weekly from May through July of 2014, the locations and approximate pond areas were identified (Table 2). We found that alpha diversity measured as taxa richness and Shannon diversity were not significantly different between ponds with different management practices ($t_{df=4} = 0, p = 1$; $t_{df=4} = -0.822, p = 0.457$, respectively). Our results suggest that there is no significant shift in community composition between managed or unmanaged source pools ($F_{df=1,4} = 0.478, p = 0.7$, Table 4). Analysis revealed no significant difference in community dispersion, or beta diversity, between managed or unmanaged source pools ($F_{df=1,4} = 0.573, p = 0.401$, Table 5).

3.2. Experiment results

To address the prediction of decreased alpha diversity in communities from managed mesocosms compared to communities from

Table 2
Stormwater pond locations (latitude/longitude) and approximate pond area. Pond area in meters squared.

Pond Name	Pond Location (Lat/Long)	Pond Area (m ²)
Sewell’s Orchard	39°11’57.3”N 76°49’47.7”W	5191.89
Waiting Spring	39°12’09.0”N 76°49’36.3”W	3596.88
Dannon Garth	39°12’25.9”N 76°49’39.6”W	4071.16
McDonalds	39°12’28.3”N 76°48’03.5”W	3442.58
Petco	39°11’57.5”N 76°48’41.3”W	4423.02
Jackson	39°12’57.9”N 76°49’10.7”W	13,029.67

unmanaged mesocosms, we tested for the main and interactive effects of source pool, dispersal, and local effects using a three-way ANOVA. We found that alpha diversity measured as taxa richness and Shannon diversity were not significantly different between source pool treatments ($F_{df} = 2,40 = 0.598, p = 0.555$; $F_{df} = 2,40 = 0.906, p = 0.412$, respectively), dispersal ($F_{df} = 1,40 = 0.256, p = 0.615$; $F_{df} = 1,40 = 1.233, p = 0.273$, respectively), or local effects ($F_{df} = 1,40 = 0.021, p = 0.885$; $F_{df} = 1,40 = 0.009, p = 0.925$, respectively). There were no significant interactive effects on taxa richness or Shannon diversity between dispersal and local effects ($F_{df} = 1,40 = 0.007, p = 0.933$; $F_{df} = 1,40 = 0.244, p = 0.624$, respectively) or between source pool and local effects ($F_{df} = 2,40 = 1.396, p = 0.259$; $F_{df} = 2,40 = 1.059, p = 0.356$, respectively) (Table 6- richness; Table 7- Shannon diversity).

To address hypothesis (1) that local environmental variables, specifically algal management in urban water bodies, will shift community composition and patterns of beta biodiversity, we found that local management of algae with Aquashade® marginally reduced compositional turnover of zooplankton among mesocosms ($F_{df} = 1,46 = 3.314, p = 0.074$, Table 8), but did not lead to significant shifts in community composition ($F_{df} = 1,40 = 0.030, p = 0.158$, Table 9). To visualize this data, a NMDS plot was created (Fig. 1).

To address hypothesis (2) that source pool constraints will lead to local community divergence, we found that zooplankton dispersal from specific source pools led to significant shifts in community composition ($F_{df} = 3,40 = 0.098, p = 0.037$, Table 9), but did not lead to significantly reduced compositional turnover ($F_{df} = 3,44 = 0.912, p = 0.444$, Table 10). To visualize this data, a NMDS plot was created (Fig. 2).

Environmental conditions in the mesocosms were monitored weekly, and included chlorophyll *a* concentrations, pH, turbidity, conductivity, dissolved oxygen, temperature, and Aquashade® concentration (summarized in Table 3). Nitrate nitrogen and phosphate concentrations were measured once (Table 3).

4. Discussion

Community assembly results from processes operating at multiple spatial and temporal scales. Both local and regional scale processes are hypothesized to influence community assembly (Leibold et al., 2004). These processes are known to influence community assembly in both natural and built environments. However in built environments, a variety of human activities are altering biodiversity patterns at multiple spatial scales (eg. Dormann et al., 2007; Groffman et al., 2014; Hassall, 2014; Loughheed et al., 2008; Maloney et al., 2011; McGoff et al., 2013; McKinney, 2006; Olden et al., 2006; Passy and Blanchet, 2007; Van Meter and Swan, 2014).

In built environments, humans alter local scale processes with habitat management activities, which can alter local species interactions and compositional responses to environmental gradients (eg. Dormann et al., 2007; Ekroos et al., 2010; Loughheed et al., 2008; Maloney et al., 2011; Passy and Blanchet, 2007). Often management choices in urban landscapes reflect residents' interests and place wildlife diversity and enhanced ecosystem functioning as secondary concerns (Noble and Hassall, 2015). Examples of such management choices include the removal of vegetation and macrophytes, the addition of flowering plants, and the maintenance of "neat", highly-visible mown areas; however, these activities have been shown to reduce biodiversity in urban ponds (Chester and Robson, 2013; Hassall, 2014; Goertzen and Suhling, 2013; Noble and Hassall, 2015). In a survey of urban ponds with a variety of management intensities, Noble and Hassall (2015) found that "biodiversity" ponds (minimally managed, where most aquatic and terrestrial vegetation were left intact) were significantly richer, for both floral and invertebrate taxa, than "amenity" ponds (managed primarily for aesthetics, which involved removing all or most aquatic vegetation). Therefore, management choices and the driving interests behind these choices can have implications for aquatic diversity. Environmental management practices can impose new environmental gradients by altering disturbance regimes, for example, the herbicide for algal management used here. Humans can alter regional

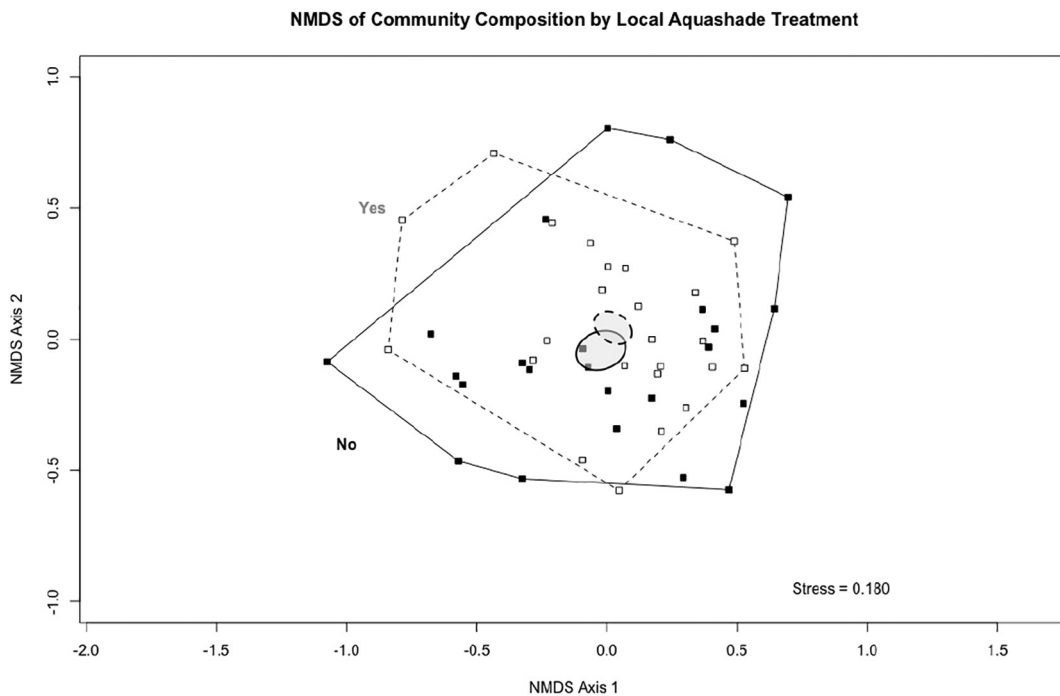


Fig. 1. Non-metric multidimensional scaling (NMDS) plot of zooplankton community composition among local Aquashade treatments. The solid boxes outlining the hulls represent communities from mesocosms and the centroids or median community compositions are represented by the hollow circles within each hull. The dashed lines and white boxes represent communities from mesocosms that received Aquashade, the solid lines and black boxes represent communities from mesocosms that did not receive Aquashade.

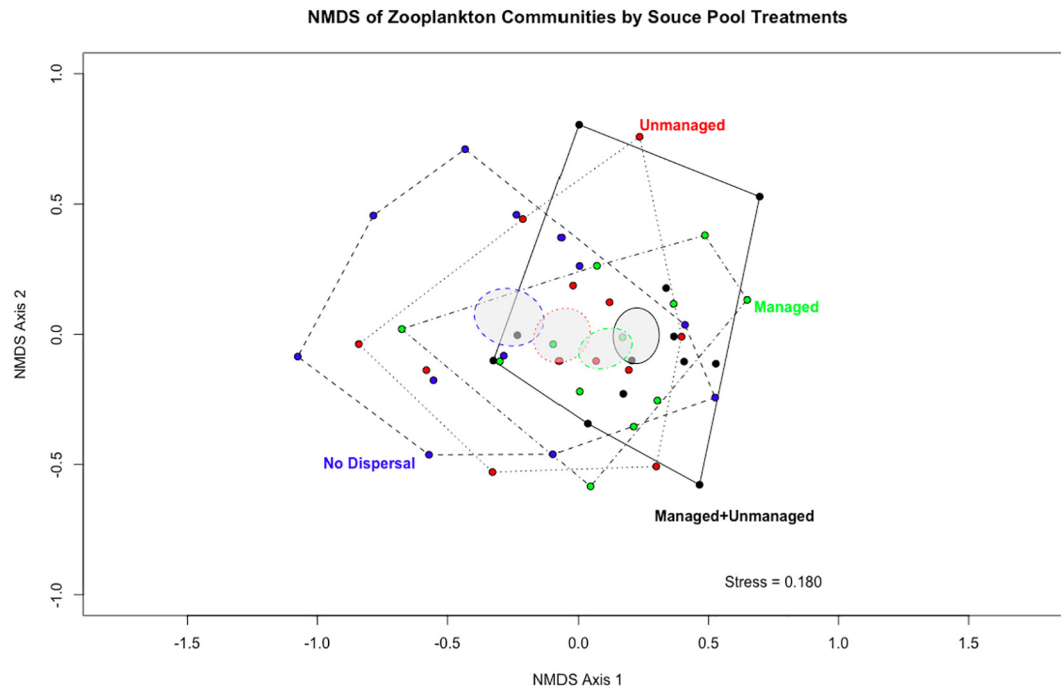


Fig. 2. Non-metric multidimensional scaling (NMDS) plot of zooplankton community composition among source pool treatments. Hulls represent communities from mesocosms and the centroids or median community compositions are represented by the small circles. The dashed hull line and dashed circle represent the communities and mean community composition from the no dispersal treatment. The dotted hull line and dotted circle represent the communities and mean community composition from the unmanaged source pool treatment. The dash-dot hull line and dash-dot circle represent the communities and mean community composition from the managed source pool treatments. The solid hull line and solid small circle represent the communities and mean community composition from the managed+unmanaged source pool treatment.

scale processes through facilitating the movement of organisms, building corridors between habitats, and creating spatially homogeneous habitats from management practices (Swan et al., 2013). The combined effects of altered dispersal patterns coupled with the degree to which management activity is spatially heterogeneous has implications for regional pool composition.

Species within a community are thought to be a reflection of the species within the larger regional species pool, who are able to disperse into

a local habitat and cope with local biotic and abiotic interactions (Belyea and Lancaster, 1999; Chase, 2003; Leibold et al., 2004). In built environments, where local degradation is widespread throughout the region, the regional species pool can become depleted or comprised of highly tolerant/generalist taxa (Lake et al., 2007). Built environments are an ideal context to study the implications of altered dispersal patterns and spatially homogeneous habitats from management practices, as the harsh geophysical template can impose widespread depletion of the regional species pool (Hassall, 2014; Groffman et al., 2014; McKinney, 2006; Olden et al., 2006). As many city management and conservation plans strive for sustainable habitat management practices,

Table 3

Environmental conditions assessed weekly for 12 weeks (May–July 2014) from all mesocosms, displayed as mean and standard error. * Refers to only treatments receiving Aquashade.

Environmental Condition	No Aquashade	Aquashade
Aquashade Concentration (ppm)*	n/a	1.47 (0.015)
Chlorophyll <i>a</i> In-Vivo (RFU)	97.56 (5.18)	130.16 (12.65)
Chlorophyll <i>a</i> Biomass	0 (0)	0.02 (0.02)
Conductivity ($\mu\text{S}/\text{cm}$)	163.86 (1.13)	166.31 (0.86)
Dissolved Oxygen (ppm)	6.03 (0.10)	5.54 (0.09)
pH	7.27 (0.02)	7.16 (0.02)
Temperature (C)	24.19 (1.08)	23.04 (0.31)
Turbidity (FAU)	5.05 (0.29)	6.51 (0.33)
Nitrate -N (mg/L)	<0.05	<0.05
Phosphate- PO4 (mg/L)	<0.05	<0.05

Table 4

Permutational multivariate analysis of variance using distance matrices on mean community composition between source pond management types.

Number of Permutations:	df	Sum of squares	Mean square	F.Model	R2	Pr(>F)
719						
Management Type	1	0.175	0.175	0.478	0.107	0.7
Residuals	4	1.467	0.367		0.893	
Total	5	1.645			1.000	

Table 5

Analysis of multivariate homogeneity of group dispersions (variances) of communities between source pond management types.

Number of Permutations:	df	Sum of Squares	Mean Square	F	Pr(>F)
719					
Groups	1	0.007	0.007	0.573	0.401
Residuals	4	0.050	0.013		

Table 6

Factorial ANOVA for main and interactive effects of dispersal, source pool, and local Aquashade on taxa richness in mesocosms.

	df	Sum of Squares	Mean Square	F	Pr(>F)
Dispersal	1	1.00	1.000	0.256	0.615
Source Pool	2	4.67	2.333	0.598	0.555
Local Aquashade	1	0.08	0.083	0.021	0.885
Interaction (Dispersal:Local Aquashade)	1	0.03	0.028	0.007	0.933
Interaction (Source Pool: Local Aquashade)	2	10.89	5.444	1.396	0.259
Residuals	40	156.00	3.900		

Table 7

Factorial ANOVA for main and interactive effects of dispersal, source pool, and local Aquashade on Shannon diversity in mesocosms.

	df	Sum of Squares	Mean Square	F	Pr(>F)
Dispersal	1	0.262	0.262	1.233	0.273
Source Pool	2	0.385	0.193	0.906	0.412
Local Aquashade	1	0.002	0.002	0.009	0.925
Interaction (Dispersal:Local Aquashade)	1	0.052	0.052	0.244	0.624
Interaction (Source Pool: Local Aquashade)	2	0.450	0.225	1.059	0.356
Residuals	40	8.504	0.213		

there is a common theme to support more desirable species assemblages. However, this outcome is unlikely if the regional species pool of potential colonists is diminished at a larger spatial scale. The debated “Field of Dreams” hypothesis, ie., build it and they will come, is a central problem in the field of restoration ecology and natural resource management in general (Lake et al., 2007; Palmer et al., 1997).

Here, we found that when different management practices are imposed on a landscape, biodiversity patterns showed divergent outcomes as a result of regional species pool constraints (hypothesis 2; Table 9; Fig. 2). In this study, this outcome has implications for biodiversity patterns at multiple spatial scales. While we did not observe a significant effect of source pool on alpha diversity of communities from managed or unmanaged mesocosms (Tables 6; 7), we did find that the source pool of potential dispersers led to significant divergence in composition of experimental pond communities, regardless of local management treatment. Our results demonstrate the potentially critical role regional processes, such as source pool of dispersers, can play in shaping community composition. This result highlights a problem within the debated “Field of Dreams” hypothesis, as desired local species assemblages may not be available at the regional level to colonize restored habitats, if the regional pool becomes depleted or homogenized. Although we did not find a decrease in local diversity as a result of local management practices, we did observe a shift in the mean local composition of taxa, depending on the source pool of dispersers. While this may not necessarily result in a “depleted” regional species pool, the composition of local assemblages may not reflect the desired species assemblages, as more tolerant or generalist species may have been able to replace less tolerant species if all local habitats are managed similarly.

Sundermann et al. (2011) presented field results demonstrating that the presence of source populations of desired taxa in the areas surrounding river restoration sites were key contributors to the establishment of desired invertebrate communities within restored sites. The

Table 8

Analysis of multivariate homogeneity of group dispersions (variances) of communities between Aquashade treatments.

	df	Sum of Squares	Mean Square	F	N. Perm	Pr(>F)
Groups	1	0.052	0.052	3.314	999	0.074
Residuals	46	0.717	0.016	–	–	–

Table 9

Permutational multivariate analysis of variance using distance matrices on mean community composition between source pool treatments.

	df	Sum Of Squares	Mean Square	F	Pr(>F)
Local Aquashade	1	0.387	0.387	0.030	0.158
Source Pool	3	1.279	0.426	0.098	0.037 *
Interaction	3	0.599	0.200	0.046	0.869
Residuals	40	10.839	0.271	0.827	–
Total	47	13.104	–	1.000	–

* Indicates a statistically significant difference.

Table 10

Analysis of multivariate homogeneity of group dispersions (variances) of communities between source pool treatments.

	df	Sum of Squares	Mean Square	F	N. Perm	Pr(>F)
Groups	3	0.050	0.017	0.912	999	0.444
Residuals	44	0.804	0.018	–	–	–

implications of this for city management and conservation efforts are if local management practices that are impacting diversity at the local scale are applied throughout a region, it is likely that the regional pool will decrease, and consist mainly of opportunistic, highly tolerant generalists (Lake et al., 2007; Sundermann et al., 2011). It has been predicted that as a prerequisite for successful recolonization of a restored site, the existence of a diverse regional species pool is necessary, independent of the role of dispersal (Lake et al., 2007; Sundermann et al., 2011). If local species composition is a reflection of the species in the regional pool, then the more species available in the regional pool, the greater the chance that local species richness will increase in a restored site (Sundermann et al., 2011). Sundermann et al. (2011) were able to demonstrate this in their review of field studies, showing a positive relationship between the regional species pool size and the potential restoration outcome.

We found that local management with the product Aquashade® led to marginally reduced compositional turnover of zooplankton between ponds (hypothesis 1; Table 8; Fig. 1). However, we found no significant effect on mean community composition (Table 9). Local management through the use of Aquashade® may have created an environmental filter, preventing the persistence of intolerant taxa, resulting in more similar communities than would be expected in habitats not experiencing this environmental filter. Our results demonstrate that communities receiving the local treatment of Aquashade® were more compositionally similar to each other (reduced beta diversity) than communities that

Table 11

Dominant taxa by percent abundance arranged by treatment. Taxa in bold are in common between treatments. (a) Dominant taxa by percent abundance by local management treatment (b) Dominant taxa by percent abundance by regional source pool treatment.

a.		
Local Treatment	Dominant Taxa	Abundance (%)
Managed	Polyarthra	0.16
	Keratella	0.04
	Diaphanosoma	0.03
	Testudinella	0.03
	Chydorus	0.03
Unmanaged	Keratella	0.14
	Polyarthra	0.10
	Cephalodella	0.05
	Chydorus	0.04
b.		
Regional Treatment	Dominant Taxa	Abundance (%)
Managed Only	Polyarthra	0.23
	Cephalodella	0.05
	Cyclopoid	0.03
	Diaphanosoma	0.02
	Chydorus	0.02
Unmanaged Only	Polyarthra	0.09
	Keratella	0.08
	Testudinella	0.04
	Diaphanosoma	0.03
	Chydorus	0.03
Managed + Unmanaged	Keratella	0.14
	Polyarthra	0.12
	Diaphanosoma	0.04
No Dispersal	Calanoid	0.02
	Keratella	0.11
	Polyarthra	0.07
	Chydorus	0.07
	Cephalodella	0.05

did not receive the local management treatment, although there were no significant differences in mean community composition or alpha diversity. We found zooplankton of the genera *Polyarthra* and *Keratella* to be dominant by percent abundance of total zooplankton per treatment for the local management treatment (Table 11a) and for most treatments in the regional source pool treatment (Table 11b). These two genera of opportunistic rotifers are often common in natural zooplankton communities (Allan, 1976; Gilbert and Williamson, 1978; Sendacz, 1984). This indicates that likely in managed mesocosms, generalist or tolerant taxa were better able to survive and become dominant, while intolerant taxa may not have been able to persist in the community. If this local management practice were spread throughout a region, the environment could become homogenized, as all available habitats are experiencing this particular environmental filter. This would in turn prevent the persistence of intolerant species, and deny a refuge habitat, thereby also homogenizing local communities and possibly depleting the regional species pool.

Biotic homogenization is a decrease in beta diversity, by means of an increase in similarity of assemblages through time. It has been well documented that as impact or proximity to an urban core increases, generally most assemblages experience biotic homogenization (eg. Declerck et al., 2013; Donohue et al., 2009; Lake et al., 2007; McGoff et al., 2013; McKinney, 2006; Pedruski and Arnott, 2011; Rahel, 2000; Shurin et al., 2009; Vogt and Beisner, 2011). Such "biotic homogenization" is an often cited phenomenon in urban ecosystems (eg. Groffman et al., 2014; Hassall, 2014; McKinney, 2006; Olden et al., 2006). Several authors have noted that increased environmental harshness contributes to decreased beta diversity by reducing the influence of stochastic processes in structuring communities, resulting in biotic homogenization (Donohue et al., 2009; McGoff et al., 2013). The biotic homogenization of ponds is concerning because of the large potential contribution of these freshwater habitats to landscape level (gamma) diversity (Céréghino et al., 2008; Hassall, 2014; Hassall and Anderson, 2015; Hassall et al., 2011; Le Viol et al., 2009; Williams et al., 2003). While individual ponds may not contain a large diversity of species (α -diversity), ponds can make a large contribution to gamma diversity because they are highly susceptible to stochastic environmental events and tend to have habitats with a high diversity of biotic and abiotic conditions, also resulting in potentially high beta diversity in the region (Hassall, 2014).

We found that both local and regional processes influenced the biodiversity patterns of the zooplankton metacommunity (Tables 8; 9, respectively). In the survey portion of this study, we did not find any significant differences in alpha or beta diversity, or divergence in community composition between pond management strategies. Over time Aquashade® concentration degrades in aquatic systems (Suski et al., 2018). The frequency and concentration of application by the Columbia Association Open Space Management was not documented. We suspect that if the frequency or concentration of application did not maintain the highest recommended concentration of Aquashade® in the ponds, it is possible that the communities quickly recovered or intolerant taxa were not completely excluded in such ponds.

In this study, we measured two components of biodiversity, alpha and beta. Alpha diversity was defined as the local composition of taxa in a community, and was measured as taxa richness and Shannon diversity (Chase, 2003). Here, we found that alpha diversity did not change with environmental pressure, or the presence of Aquashade®. However, patterns of beta diversity, defined here as the composition of taxa between communities (Chase, 2003), did shift with environmental pressure. In the experimental field manipulation, we demonstrated that pond management with the product Aquashade® can act as an environmental filter, marginally reducing beta-diversity, by creating more compositionally similar communities than would otherwise be predicted in unmanaged ponds (Table 8; Fig. 1). We may have observed this pattern if the presence of Aquashade prevented the persistence of intolerant taxa and allowed generalist or tolerant taxa to be better able to survive and become dominant in the community. Furthermore, dispersal from

managed or unmanaged source pools also had a significant effect on compositional divergence between communities (Table 9; Fig. 2). The results of this study suggest that sustainability and management plans may have complex effects on biodiversity both within and across spatial scales.

CRediT authorship contribution statement

NV and CS designed the study. NV carried out the experiment and data analysis. NV lead writing of the manuscript with input from CS.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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