Linking management to biodiversity in built ponds using metacommunity simulations

Eric R. Sokol [a],[*], Bryan L. Brown [a], Cayelan C. Carey [a], Brett M. Tornwall [a], Christopher M. Swan [b], J.E. Barrett [a]

[a] Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24061-0406, United States
[b] Geography and Environmental Studies, University of Maryland, Baltimore County, Baltimore, MD 21250, United States

ABSTRACT

In urban and other built environments, management decisions serve as a prominent feedback between biodiversity patterns and human-controlled environmental variables. In this study, we used the metacommunity concept to assess the mechanisms that link zooplankton biodiversity to different management regimes in urban water bodies associated with the Baltimore Ecosystem Study Long-Term Ecological Research site (USA). In the summer of 2011, we sampled zooplankton in 21 ponds built for stormwater management. Ponds were classified as either unmanaged ($n = 9$) or actively managed ($n = 12$) for recreation and aesthetic value, where managed ponds received multiple chemical and algaecide applications to improve water clarity. We found managed ponds had higher local (alpha) diversity and lower spatial turnover in community composition (beta-diversity), and thus greater biotic homogenization than ponds that were unmanaged. We developed a lottery-based metacommunity simulation (MCSim) to assess how niche and dispersal dynamics could create the observed biodiversity patterns, and to assess whether biotic homogenization was related to management. A comparison of empirical and simulated diversity patterns suggests the zooplankton pond metacommunity was influenced by both dispersal and niche-based community assembly dynamics. Simulations showed that the observed biotic homogenization effect was expected based on the spatially aggregated distribution of managed ponds, but pond management was not likely exacerbating biotic homogenization in this system. Such insight is essential to understand how environmental management can affect biodiversity at local and regional scales.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Humans have managed natural ecosystems for 40–50 millennia (Bird et al., 2008), yet strategies of ecosystem management continue to evolve as a rapidly growing human population places accumulating demands on natural systems (Wilkinson et al., 2013). Fortunately, our understanding of the functioning of communities and ecosystems is also evolving, allowing for more effective management of natural systems (Farber et al., 2006). One recent advance in our understanding of the structure and dynamics of ecological communities is the multi-scale perspective of metacommunity theory (Leibold et al., 2004). As a result, modern community ecology acknowledges that the movement of organisms across landscapes may have as large an effect on community

structure and dynamics as environmental tolerances and species interactions (Leibold et al., 2004).

Urbanization is a leading cause of biotic homogenization (McKinney, 2006), which describes a pattern of increasing similarity (or decline in beta diversity) among ecological communities across a region, or even globally (McKinney and Lockwood, 1999). This trend is caused by both local extirpations of indigenous taxa and the increased dispersal and introduction of "winner" taxa that become widely established (McKinney and Lockwood, 1999; Olden, 2006). A growing recognition among land managers and policy makers of the value of ecosystem services associated with biodiversity is reflected in municipal sustainability plans that guide conservation and natural resource management in U.S. towns and cities (e.g., Baltimore City, 2009). Therefore, it is important that we understand links between management and biodiversity in the built ecosystems that make up human dominated landscapes.

A rapid expansion of the human presence on the landscape has resulted in the increase of built ecosystems (Alig et al., 2004),

including stormwater detention basins (Fairchild et al., 2012). Built ponds collect stormwater and reduce the impact of a flashy hydrograph resulting from high impervious surface cover that is characteristic of urban landscapes (Plumb et al., 2013). Some detention ponds are also actively managed for recreational and aesthetic purposes when they occur in green spaces set aside for recreational use (Ferguson, 1991). Alternatively, unmanaged built ponds (e.g., Bishop et al., 2000) are relatively free from human alteration following construction except for routine structural maintenance.

Ponds represent sentinel ecosystems that integrate the landscape and are closely tied to local land use decisions (Céréghino et al., 2008; De Meester et al., 2005), and thus may provide a multi-scale perspective on how management practices affect biodiversity. Here, we focus on zooplankton biodiversity because zooplankton represent an intermediate trophic guild and zooplankton community composition integrates a suite of abiotic and biotic influences, including local physiological constraints, bottom-up and top-down trophic interactions, and pond trophic status (Jeppesen et al., 2011).

Our aim was to address the following two questions regarding built ponds in the Baltimore Ecosystem Study (BES), Long Term Ecological Research (LTER) site (Baltimore, Maryland, USA): does management for common aesthetic and recreational purposes throughout the region result in a homogenization of local habitats, and thus biodiversity? How important are local niche-based and regional inter-pond dispersal dynamics for understanding how biodiversity will respond to management decisions?

The first step in addressing the above questions was to assess whether we could detect a difference in zooplankton biodiversity between actively managed and unmanaged built ponds using field survey methods. We performed these surveys in collaboration with the local homeowners' association (Columbia Association, Columbia, Maryland, USA), which is responsible for management of both stormwater runoff and water quality of these detention features.

Following the field survey of BES ponds, our second step was to test hypotheses about how observed biodiversity patterns could be linked to metacommunity and hydroscape (i.e., a "landscape" of aquatic features) characteristics using process-based metacommunity simulations (Gravel et al., 2006; Hubbell, 2001; Mouquet and Loreau, 2003; Sokol et al., 2011). Specifically, we designed simulations to identify a set of metacommunity characteristics that could effectively reproduce *in situ* biodiversity patterns *in silico*. This approach can be used to identify a best-fit simulation scenario that represents a well-informed hypothesis describing zooplankton metacommunity dynamics in the built-pond hydroscape of the BES based on our current understanding of metacommunity theory and the empirical characteristics of the system (Fig. 1). We then used the best-fit simulation scenario as a reference for null model hypothesis testing to determine if observed differences in biodiversity between managed and unmanaged ponds could be explained by exogenous factors, i.e., properties of the hydroscape not affected by management (e.g., pond size and spatial connectivity, Frisch et al., 2012; Steiner et al., 2013), or if biodiversity patterns should be attributed to active pond management.

2. Methods

2.1. Empirical data collection and analysis

We chose 21 stormwater detention ponds in and around the cities of Columbia and Baltimore, Maryland, USA within the BES LTER for sampling. Site selection was based on pond proximity, management history, and accessibility. Unlike naturally occurring ponds, managers often restrict human access to private built ponds for safety and/ or privacy concerns (e.g., by building fences around the ponds). Therefore, we were only able to sample ponds that were unfenced or where we had permission to visit from the local homeowners' association. We designated ponds as either "managed" ($n = 12$) or "unmanaged" ($n = 9$) based on whether algal management was taking place (Table A1). Management classification was based on information acquired by the Columbia Association Department of Open Space Management, which actively manages algal blooms in built ponds with Aquashade© (pers. comm.). Aquashade© is an acid-based, light-attenuating dye designed to inhibit the wavelengths of light necessary for photosynthesis.

All ponds were sampled once during 6–15 June 2011. An 11 cm diameter, 63 μm mesh plankton net was used to collect a sample from the littoral zone in a 30 m long horizontal tow at 1 m depth. Samples were concentrated on a 63 μm sieve, then immediately preserved in 70% ethanol. To estimate zooplankton density (Table A2, A3), samples were brought to a total volume of 500 ml using distilled water, homogenized by stirring with a plastic pipette, and 10 subsamples (2 ml each) were viewed from each sample with a compound microscope using a $1\,mm^2$ gridded Sedgewick Rafter at $40 \times$ magnification. A total of 200–400 zooplankton were identified to the lowest practical taxonomic level for each sample.

Phytoplankton biomass and conductivity were used to characterize environmental variation among ponds. Phytoplankton biomass was estimated as chlorophyll *a* by collecting a 500 ml surface grab sample from the littoral zone of each pond. We filtered the sample onto a 47 mm Whatman GF/F, and froze the filters until they were analyzed via ethanol extraction and absorbance via spectrophotometry (ISO, 1992; Sartory et al., 1984). Conductivity was measured at the water's surface in the field with a YSI Model 30 M Conductivity Probe (YSI Inc., Yellow Springs, Ohio, USA). Dissolved oxygen ($mg\,l^{-1}$) and temperature were measured on site with a YSI Model 700 A Probe (YSI Inc., Yellow Springs, Ohio, USA). The concentrations of phosphorus (PO_4, $mg\,l^{-1}$) and nitrate ($NO_3\,mg\,l^{-1}$) were measured via ion chromotography following filtration through 47 mm Whatman GF/F filters. We used Welch's two-sample *t*-test to compare means and the robust Brown–Forsythe Levene-type test in the lawstat package (Gastwirth et al., 2013) to compare variances. All analyses were conducted using R v3.1.1 (R Core Team, 2014)

For all estimates of biodiversity in this study, we focused on occurrence rather than relative abundance because occurrence-based metrics will be less sensitive to seasonal fluctuations in zooplankton abundances, which reflect local dynamics that are beyond the scope of this study. We used the vegetarian package (Charney and Record, 2012) to conduct multiplicative diversity partitioning based on order $q = 0$ Hill numbers (Jost, 2007) to estimate D_α, D_β, and D_γ for managed and unmanaged ponds, where D_α, D_β, and D_γ represent alpha, beta, and gamma diversity, respectively. For diversity partitions based on order $q = 0$ Hill numbers, D_α and D_γ represent local and regional richness, respectively, and D_β represents the number of "distinct" communities in the metacommunity.

The difference in diversity between managed and unmanaged ponds (dD) was estimated by subtracting Hill number diversity estimates for the unmanaged group of ponds from the managed group (e.g., $dD_\alpha = D_{a,\ managed} - D_{\alpha,\ unmanaged}$). To test if shifts in diversity were significant, we calculated a null-distribution of dD_α, dD_β, and dD_γ for 10,000 random permutations of the observed data set (see Appendix). This test provided an estimate of the distributions of dD_α, dD_β, and dD_γ that would be expected if ponds were randomly assigned to a management group (managed vs. unmanaged). Estimates of dD for alpha, beta, and gamma diversities were considered significantly different than 0 if they were outside the 95% CI of their respective null distributions.
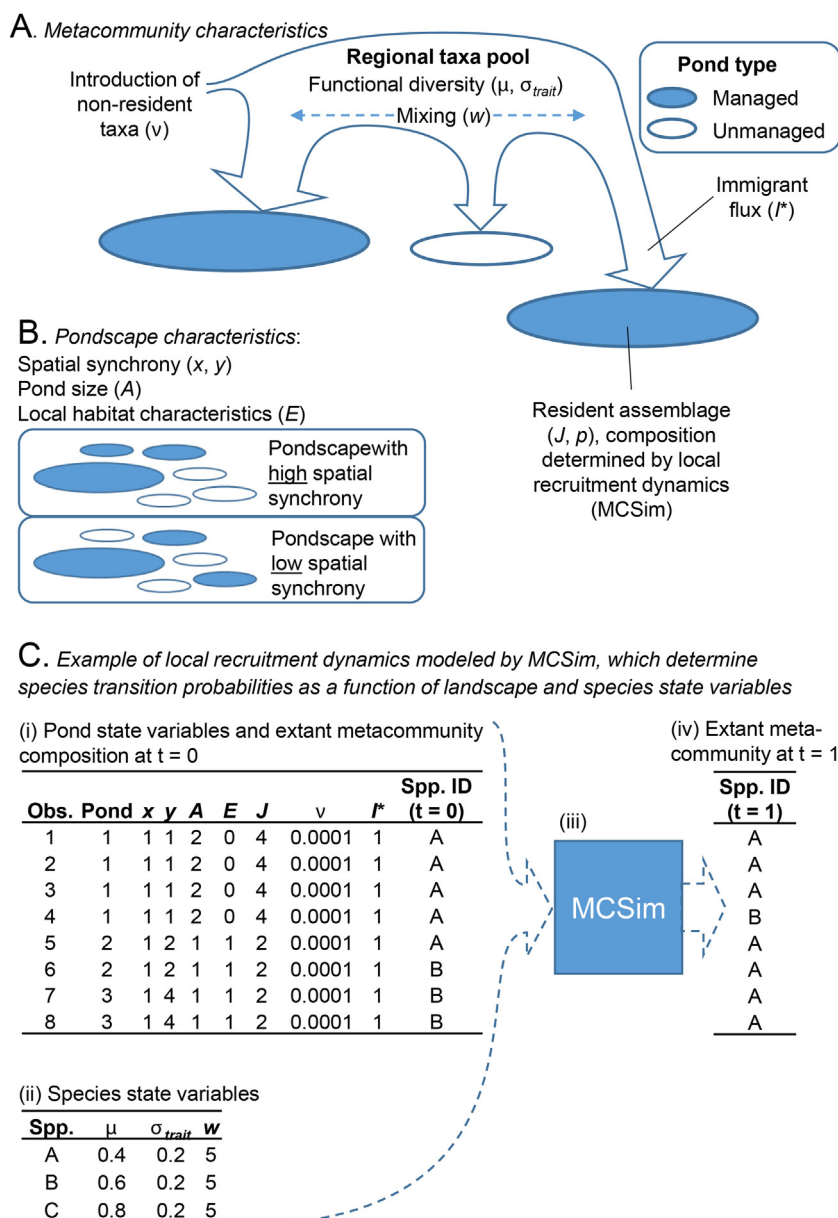
Fig. 1. Metacommunity (A) and landscape (B) characteristics are hypothesized to interact to produce emergent biodiversity patterns. An example MCSim scenario (C) uses pond (i) and species (ii Spp. C represents a potential, non-resident, invader) state variables to estimate recruitment probabilities (iii, Eqs. (1)–(6), see Table A4 for example calculations) that are then used in the lottery process that determines species transitions from one generation to the next (iv). See Table 1 for state variable descriptions.

We used distance-based redundancy analysis (dbRDA) (Legendre and Anderson, 1999) using Sorensen dissimilarities for zooplankton occurrence data to assess the influence of environmental variables over differences in community composition among ponds (see Sokol et al., 2013 for a discussion on the interpretation of dbRDA using occurrence-based dissimilarities). We used a distance-based permutational MANOVA (Anderson et al., 2008) to test if overall community composition was different between pond management types. Data presented here represent cladoceran and rotifer families. Other zooplankton groups were excluded from analyses presented in this paper because either we were not able to practically reach a similar taxonomic resolution (e.g., copepods only identified to order) or they were not observed (e.g., Chaoboridae). However, analyses using all observed groups produced similar results (see Appendix). Pond characteristics used as predictors in dbRDA included pond surface area, temperature,

dissolved oxygen (DO), salinity, conductivity, and chloride, nitrate, phosphate, and chlorophyll *a* concentrations. Ponds were similar with respect to other characteristics (e.g., all ponds had similar hydrology, macrophytes in the littoral zone, and resident fish populations).

To assess the combined influence of environmental and spatial gradients over variation in community composition, we used variation partitioning (Borcard et al., 1992; Peres-Neto et al., 2006) using methods described in Sokol et al. (2013) and functions available in the vegan package (Oksanen et al., 2013) for R. Using dbRDA models, we partitioned the among-pond variation in zooplankton community composition between a matrix of environmental explanatory variables [E] and a matrix of spatial explanatory variables [S]. We used a two-step process to select the best environmental variables. We tested the significance of each environmental variable as a predictor of community composition

using a permutation test of a dbRDA model. All environmental variables that were significant predictors of community composition were used in forward, stepwise model selection (Blanchet et al., 2008). Selected environmental variables were included in matrix [E]. To estimate spatial filters that represent spatial heterogeneity at different scales, we used the eigenvectors from a Principal Coordinates of Neighbor Matrices (PCNM) analysis of a distance matrix calculated from the UTM coordinates of ponds included in the study (Dray et al., 2006). We used the same two-step process described for environmental variables to select important spatial variables and included them in the matrix [S]. We used the adjusted R^2 from dbRDA models for [E], [S], and all variables combined [ES] to calculate how much variation in community composition among ponds was linked to pure environmental variation [E|S], spatially structured environmental variation [E∩S], and pure spatial variation [S|E] (Peres-Neto et al., 2006). We conducted this analysis for all ponds combined and ponds grouped by management type.

2.2. Metacommunity simulation-based analyses

2.2.1. Model description

We created an individual oriented metacommunity simulation to examine how metacommunity (Fig. 1A) and hydroscape (Fig. 1B) characteristics could contribute to emergent biodiversity patterns. The simulation (modified from Sokol et al., 2011) was coded as a package for the R statistical environment (MCSim, maintained at https://github.com/sokole/MCSim v0.3 was used in this study) based on the lottery recruitment dynamics used in Hubbell's neutral model (Hubbell, 2001). The simulation was modified to add terms allowing for niche-based species sorting and spatially-explicit dispersal dynamics following Gravel et al. (2006). The model tracks the composition of assemblages at multiple sites through time (Fig. 1C, Table A4).

Here, metacommunity characteristics refer to the parameters that define the rules that govern regional (dispersal) and local (recruitment) community assembly dynamics as well as the general attributes of the simulated taxa that make up the metacommunity (Fig. 1). The parameter ν is Hubbell's speciation coefficient. Conceptually, ν could reflect any introduction of novel taxa, whether due to speciation or invasion from outside the extant metacommunity, such as recruitment of propagules from a pond outside the metacommunity, or recruitment from the dormant propagule "seed bank" in pond sediment. Therefore, we expand Hubbell's original use of the term and consider ν a term that represents metacommunity "openness".

The parameter σ_{trait} defines the niche-breadth of taxonomic groups, and thus the functional diversity in a metacommunity. When taxa have larger niche-breadth, there is more niche overlap along environmental gradients (E) (Gravel et al., 2006). The susceptibility of the metacommunity to species sorting by local environmental filters depends on functional diversity (Chase and Leibold, 2003). Very high niche overlap results in ecological equivalence among taxonomic groups, and will promote neutral metacommunity dynamics (Hubbell, 2001).

Mixing of the regional species pool was modeled using a dispersal kernel following Gravel et al. (2006), where

$$W(r) = \exp(-wr^2) \tag{1}$$

The dispersal kernel $W(r_{k,l})$ describes the influence of site l over the composition of the immigrant pool at site k, where $r_{k,l}$ is the Euclidean distance between sites k and l scaled to the maximum observed r. Overall, an increase in w corresponds with a steeper slope in the dispersal kernel (Fig. A1), and thus a metacommunity

in which close neighbors are more likely to contribute to each other's recruitment pools than far neighbors.

Metacommunity connectivity was determined by the coefficient m, which is the relative contribution of the immigrant pool to the local recruitment pool (Etienne, 2005; Hubbell, 2001), and can be estimated as

$$m = \frac{I}{I+J-1} \tag{2}$$

where I represents the immigration rate at a site (no. individuals site^{-1} generation^{-1}). Each simulation was parameterized using an immigration flux, I^* (no. individuals m^{-2} generation^{-1}), as a constant, and I was determined separately for each site as $I = I^* \times A$, where A represents pond surface area (m^2).

The immigrant pool (pM) at each site was determined from the composition of each neighboring site weighted by distance such that

$$p_{M,k,i} = \frac{\sum_{l \neq k} p_{i,l} W(r_{k,l})}{\sum_{j=1}^{s} \sum_{l \neq k} p_{j,l} W(r_{k,l})} \tag{3}$$

Local recruitment at a site was modeled as a lottery process for each time step, such that J individuals were selected from a local recruitment pool (p_R) at each site (Fig. 1C). Species interactions were implicit based on a competitive lottery among potential recruits for limited space (Mouquet and Loreau, 2003; Shmida and Ellner, 1984). At each site, J (i.e., local carrying capacity) was scaled to pond area so that all sites had the same density (no. individuals m^{-2}), however, the total size of the metacommunity was restricted to 10^6 individuals because of computational limitations. Local and regional metacommunity dynamics determined the composition of p_R at the beginning of each generation, such that

$$p_{R,i} = mp_{M,i} + (1-m)p_i \tag{4}$$

where $p_{R,i}$ is the relative abundance of taxon i in the recruitment pool, and $p_{M,i}$ and p_i represent the relative abundance of taxon i in the immigrant pool and local resident pool, respectively.

For each simulation, the influence of environmental filters over local recruitment dynamics was a function of the local environment and niche overlap. The recruitment probability of each taxon i at a site was determined by how closely its habitat affinity (μ) matched the local environment (E), following (Gravel et al., 2006) (Fig. A2)

$$\lambda_i(E) = \exp\left(\frac{-(E-\mu_i)^2}{2\sigma_{trait}^2}\right) \tag{5}$$

Our objective was to compare metacommunity dynamics using niche versus neutral species pools, and an assessment of tradeoffs among functional types (e.g., generalists vs. specialists, etc.) was beyond the scope of this study. Therefore, σ_{trait} was a constant parameter for each simulation that determined the overall "neutrality" of the simulation. Because site environmental scores (E) were scaled to the interval [0,1], species affinities (μ) were randomly assigned a value in the interval [0,1]. Consequently, values of $\sigma_{trait} \gg 1$ effectively created ecological equivalence in the regional species pool and simulations with neutral metacommunity dynamics.

The probability (R_i) of recruiting species i from p_R during each lottery pick was

$$R_i = \frac{(1-\nu)\lambda_i p_{R,i}}{\nu\lambda_{novel} + (1-\nu)\sum_{j=1}^{S}\lambda_j p_{R,j}} \tag{6}$$

and the probability of recruiting a novel species was

$$R_{novel} = \frac{\nu\lambda_{novel}}{\nu\lambda_{novel} + (1-\nu)\sum_{j=1}^{S}\lambda_j p_{R,j}} \tag{7}$$

where ν is Hubbell's speciation coefficient, λ_i represents the influence of the local environmental filter over species i, $p_{R,i}$ is the relative abundance of taxon i in p_R.

2.2.2. Characterizing metacommunity dynamics

Simulation hydroscape characteristics (Fig. 1B) were constructed to approximate the empirical data set. Each simulation had 21 sites, where 12 were classified as "managed" and 9 were classified as "unmanaged". Simulations were spatially explicit, and the sites were mapped on an XY grid based on the UTM coordinates of ponds included in the survey (Fig. 2). Sites were assigned sizes based on surface area estimates (m^2) and environmental values (E), scaled to the interval [0,1], based on their scores for the first principal component of an ordination of environmental variables selected in the variation partitioning analysis described above.

Simulations were initialized using a regional species pool generated to reflect observed data. We used the untb package (Hankin, 2007) to fit α_{Fisher} of Fisher's log series (Fisher et al., 1943) to the regional rank-abundance curve for observed zooplankton diversity, and the estimate of α_{Fisher} was used to generate regional rank abundance curves to seed the metacommunity simulations. The value estimated for the rank abundance curve for cladoceran and rotifer families was 1.46, and this was used to seed simulations.

We found that the influence of model initial conditions disappeared after 10–20 generations, after which alpha, beta, and gamma diversity typically reached a steady state for the given metacommunity and hydroscape parameter settings (Fig. A3). Thus, we used 30 generations for all simulations (see Appendix for simulation R script).

Four model parameters that were needed to define regional metacommunity dynamics (Table 1, Fig. 1A) could not be estimated from observed data. These were Hubbell's speciation coefficient

(ν), average niche breadth in the regional species pool (σ_{trait}, determined the "neutrality" of a simulation), dispersal kernel slope (w, controls metacommunity mixing), and immigrant flux (I^*). We used 50 replicates each of 120 simulation scenarios (6000 total simulations, Table A5) to explore the emergent biodiversity patterns produced by a factorial combination of different levels for the four unknown metacommunity parameters (Table 1). Because our goal was to identify the scenario that best replicated observed estimates of dD for alpha, beta, and gamma diversity, we evaluated model fit by calculating a X^2 estimate of error for each metacommunity simulation as

$$X^2 = \sum_{i \in \{\alpha,\beta,\gamma\}} \frac{(dD_{i,\text{obs}} - dD_{i,\text{sim}})^2}{\sigma_{dD_{i,\text{obs}}}} \tag{8}$$

Squared differences between observed and simulated dD were normalized by an estimate of the standard deviation of the observed dD for alpha, beta, and gamma, respectively (see Appendix). The simulation scenario with the smallest X^2 error that also qualitatively produced a biotic homogenization effect in managed ponds ($dD_\alpha > 0$, $dD_\beta < 0$) was identified as the most plausible representation of the *in situ* zooplankton metacommunity (Fig. 3, Fig. A4).

2.2.3. Null model tests

The parameter settings from the most plausible (i.e., best-model) metacommunity scenario (Fig. 3) were used to create null hypothesis tests of four different factors that could potentially explain the disparities in diversity between managed and unmanaged ponds, represented by significant observed non-zero values for dD. We conducted replicated ($n = 1000$) null-model simulation scenarios for each factor to test if they influenced biodiversity. If a null-model simulation scenario produced biodiversity outcomes that consistently deviated from the observed data (and best-model outcomes), then we considered that as evidence that the factor being tested influenced the emergent biodiversity patterns observed in the BES urban pond metacommunity. Otherwise, we concluded the factor did not affect alpha, beta, or gamma diversity in this system. Three of these factors were hydroscape characteristics, including site location (XY coordinates), local habitat characteristics (E), and pond surface area (A). We recorded diversity outcomes for three separate sets of metacommunity simulation scenarios. In each null model scenario, we randomized either (1) site locations, (2) environmental scores for E, or (3) pond surface areas. The other factor was σ_{trait} (niche-breadth), which was inferred for the best-model based on exploratory simulations (Fig. 3). To assess the importance of niche-based species sorting in the best-model scenario, we compared best-model diversity outcomes against neutral simulations ($\sigma_{trait} = 20$), which otherwise had the same parameter settings as best-model scenarios. Here, neutral simulations provided a null-model test of whether niche-based species sorting was required to reproduce the biotic homogenization effect in managed ponds.

3. Results

3.1. Empirical results

Some local habitat characteristics varied between unmanaged and managed ponds (Table 2). Recreational ponds that were actively managed had larger surface areas and lower chloride concentrations, whereas unmanaged ponds had more variable conductivity, chloride concentrations, and salinity. Other environmental variables, including chlorophyll *a*, nitrate, phosphate,
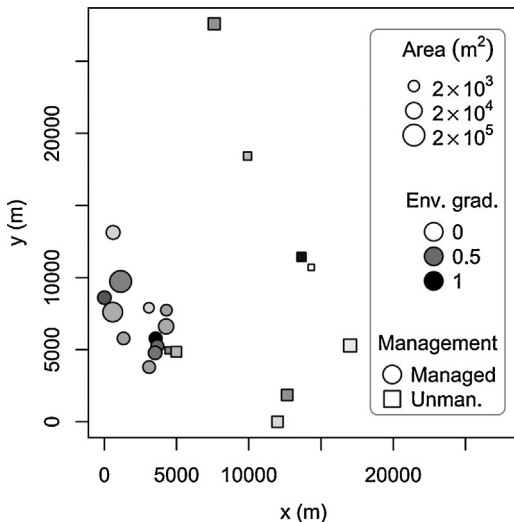

Fig. 2. Map of simulation hydroscape based on UTM coordinates using an arbitrary point of origin (See Table A1 for site coordinates).

Table 1
Metacommunity simulation (MCSim) state variables.

Entity	State variable	Description	Levels
Pond	Mgmt.	Management designation (managed or unmanaged)	Fixed
	x, y	Location based on UTM coordinates	Fixed
	J	Assemblage size (no. individuals in a pond). For pond k, $J_k = J_M \times A_k / \sum A$, where, J_M is the total metacommunity size	Fixed
	A	Surface area (m^2) estimated from Google Earth imagery	Fixed
	E	Environmental state variable, score from first axis of a PCA of habitat variables scaled to the interval [0, 1]	Fixed
	p	Vector of relative abundances of species occupying a pond	Response variable, initial state based on empirically observed rank abundance curve
	I^*	Immigrant flux (no. indiv. m^{-2} gen.$^{-1}$), levels comparable to those reported by Vancshoenwinkel et al. (2008)	10^{-1}, low propagule deposition rate $10^0 10^1 10^2 10^3$, high propagule deposition rate
	ν	Hubbell's (2001) speciation coefficient, a proportion representing the contribution of novel taxa to recruitment pool	10^{-6}, infrequent invasion ($\sim\sim 1$/generation) 10^{-4}, moderate invasion ($\sim\sim 100$/generation) 10^{-2}, frequent invasion ($\sim\sim 1\%$ of recruitment events)
Species	μ	Habitat affinity in the interval [0,1]	Random uniform distribution
	σ_{trait}	Niche breadth (Gravel et al. 2006), where high niche breadth creates a regional pool of ecologically equivalent (i.e., neutral) taxonomic groups (Hubbell, 2001)	0.01, low niche overlap 0.1, moderate niche overlap 0.5, high niche overlap 20, neutral
	w	Dispersal kernel slope (Gravel et al. 2006)	0, flat dispersal kernel, panmictic 300, steep dispersal kernel, limited mixing of the regional pool

dissolved oxygen, and temperature were not significantly different in managed and unmanaged ponds at the time samples were collected ($P > 0.05$).

Distance-based permutational MANOVA showed no difference in overall community composition ($F_{19,1} = 1.22$, $P = 0.25$) between unmanaged and actively managed ponds, and the occurrence frequencies for individual zooplankton families did not differ among management type (Table 3). However, zooplankton

Fig. 3. Rank order of simulated metacommunity scenarios based on mean simulation x^2 error for 50 replicate scenarios (error bars are estimates of 95% CI of the mean). The top 5 best fit simulations (lowest x^2 error) are shown in the inset. The arrow indicates the scenario that most closely reproduced values of dD_α, dD_β, and dD_γ observed for cladoceran and rotifer families in BES ponds (also see Fig. A4). Model parameter values are shown and described in Table 1.

community composition was related to environmental variation among ponds (Fig. 4A, Table 3).

Variation partitioning (Table 4) based on dbRDA outcomes from forward stepwise model selection showed that the relationship between zooplankton community composition and characteristics of the local habitat differed between managed and unmanaged ponds. In unmanaged ponds, zooplankton community composition was strongly linked to pure environmental variation [E|S] represented by salinity and DO concentrations (adj. $R^2 = 0.48$, $P < 0.001$). In contrast, no significant relationship between zooplankton community composition and environmental or spatial variables was observed in managed ponds. When managed and unmanaged ponds were pooled into a single analysis, salinity also represented the pure environmental gradient [E|S] with the strongest link to zooplankton community composition (adj. $R^2 = 0.30$, $P < 0.001$). Model selection indicated pure spatial variation [S|E] in community composition was represented by PCNM3 (adj. $R^2 = 0.162$, $P < 0.001$), which captured the spatial aggregation of managed ponds and spatial dispersion of unmanaged ponds (Fig. A6). Environmental variation measured in this study that was linked to zooplankton community composition did not correlate with any spatial variables.

Diversity partitioning showed a biotic homogenization effect was present in actively managed ponds, relative to unmanaged ponds. Actively managed ponds had higher richness ($dD_\alpha > 0$, Fig. 4B and C) and decreased beta diversity when compared to unmanaged ponds ($dD_\beta < 0$, Fig. 4B and C).

3.2. Simulation results

3.2.1. Characterizing best-model metacommunity dynamics

The simulation scenario that best reproduced zooplankton biodiversity patterns observed in BES ponds represented a metacommunity in which community assembly was influenced by both dispersal and niche-based dynamics. This scenario had a
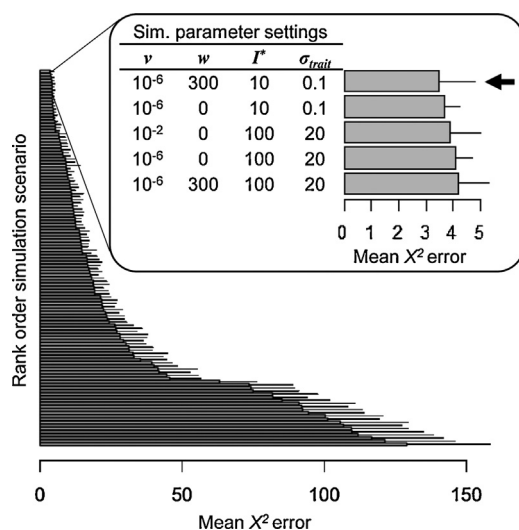
Table 2
Environmental characteristics of unmanaged and actively managed built ponds in the Baltimore Ecosystem Study (BES) at time of sampling.

Pond characteristic	Unmanaged (Mean (S.E.))	Managed (Mean (S.E.))	Compare means		Compare var.	
			Stat.	P value	Stat.	P value
Number Obs.	9	12				
Area (m2)[a]	3003 (909)	28700 (17800)	−2.4	0.025	0.010	0.931
Chlorophyll a (mg/L)[a]	19.97 (6.86)	20.29 (3.99)	−0.1	0.910	0.024	0.889
Conductivity (μS)[a]	3300 (2350)	377.4 (31.2)	2.2	0.056	9.64	0.008
Cl (mg/L)[a]	2650 (2140)	114.4 (23.7)	2.5	0.030	7.00	0.012
NO3 (mg/L)[a]	0.15 (0.071)	0.297 (0.134)	−0.9	0.356	0.37	0.587
PO4 (mg/L)[a]	0.127 (0.097)	0.121 (0.035)	−0.2	0.878	0.003	0.956
Temperature (°C)	26.5 (0.751)	24.7 (1.7)	1.0	0.351	1.19	0.320
DO (mg/L)[a]	7.75 (1.18)	9.67 (2.09)	−0.4	0.715	0.94	0.376
Salinity (PPT)[a]	1.93 (1.43)	0.183 (0.017)	1.7	0.123	5.44	0.009

Group means (unmanaged vs. managed) were compared using Welch's two-sample t-test and variances were compared using the robust Brown–Forsythe Levene-type test using group medians, P-value for the comparison of variances were estimated from 1000 bootstrap samples.
[a] Indicates comparisons were made using log $(x + 1)$ transformed data.

Table 3
Occurrence of cladoceran and rotifer families modeled as functions of pond management regime[a] and environmental variation[b].

Family	Freq. of occurrence associated with management of built ponds			Occurrence associated with Env. (dbRDA)	
	Unman.	Managed	P value	CA 1	CA 2
Bosminidae	0.78	1.00	0.997	0.55	0.12
Daphniidae	0.56	0.75	0.355	0.71	−0.24
Chydoridae	0.44	0.83	0.074	0.75	−0.35
Sididae	0.22	0.67	0.054	0.11	−0.13
Asplanchnidae	0.22	0.50	0.205	0.22	0.33
Brachionidae	0.67	1.00	0.997	-0.24	0.13
Notommatidae	0.33	0.33	1.000	0.06	0.23
Collothecidae	0.00	0.08	0.998	0.06	0.14
Dicranophoridae	0.22	0.08	0.384	0.16	−0.08
Filinidae	0.22	0.25	0.882	0.13	−0.08
Floscularidae	0.22	0.58	0.109	0.39	0.24
Lecanidae	0.56	0.42	0.530	0.39	−0.43
Mytilinidae	0.11	0.08	0.831	0.03	−0.19
Philodinidae	0.11	0.08	0.831	0.15	0.17
Synchaetidae	0.33	0.33	1.000	0.21	0.25
Trichocercidae	0.44	0.83	0.074	0.54	0.58

[a] Family occurrence modeled as a function of pond management using binomial family generalized linear model with a logit linking function (Venables and Ripley, 2002).
[b] Family occurrence associated with environmental variables was assessed using dbRDA (Fig. 4). Environmental variables strongly associated with CA (canonical axis) 1 include salinity (−0.92), conductivity (−0.83), chloride (−0.82), and chlorophyll a (−0.65); environmental variables strongly associated with CA 2 include phosphorus (0.66) and temperature (−0.37).

low rate of invasion by novel taxa ($\nu = 10^{-6}$ recruitment event^{-1}), a steep dispersal kernel ($w = 300$), a moderate immigrant flux ($I^* = 10$ propagules m^{-2} generation^{-1}), and moderate niche overlap among taxonomic groups ($\sigma_{trait} = 0.1$) (Table 1). While other scenarios had equally low estimates of x^2 error (Fig. 3), this scenario was the only one that qualitatively reproduced the in situ biotic homogenization effect (Fig. A4), which was characterized by $dD_\gamma \sim \sim 0$, $dD_\beta < 0$, and $dD_\alpha > 0$ (Fig. 4C).

3.2.2. Null model tests of the biotic homogenization effect

Null model tests of the best-model metacommunity scenario (Fig. 5) showed the biotic homogenization effect ($dD_\alpha > 0$ and $dD_\beta < 0$) in managed ponds disappeared when pond xy coordinates were randomized (Rand. XY sim. in Fig. 5 does not predict dD_α and dD_β are different from 0). The biotic homogenization effect was also eliminated in neutral model simulations (Fig. 5B, Neutral sim.), which overestimated total alpha diversity and underestimated total beta diversity (Fig. 5A, Neutral sim.). Alternatively, a biotic homogenization effect remained prominent in managed ponds in simulations with randomized environmental gradients (Fig. 5, Rand. env. sim.) or pond areas (Fig. 5, Rand. area sim.).

4. Discussion

Using field survey data, we detected biotic homogenization (decreased beta-diversity) of zooplankton among actively managed BES ponds, relative to unmanaged ponds. Without context, this outcome could lead the Columbia Association to conclude that their current management plan (i.e., application of Aquashade© dye to mitigate algal blooms) is homogenizing the zooplankton metacommunity, and in turn lead pond managers to modify their
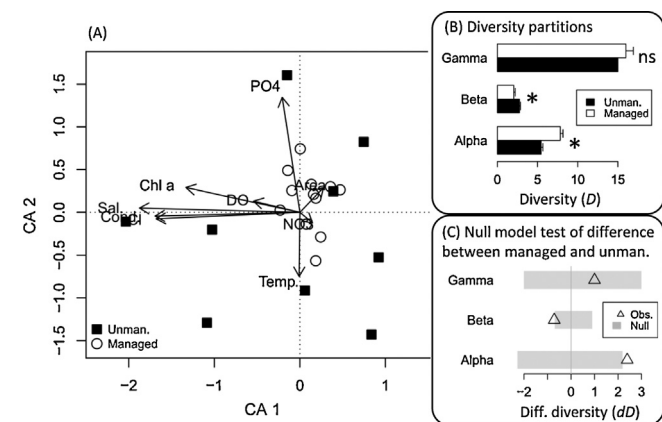

Fig. 4. Cladoceran and rotifer community composition and diversity (families) in unmanaged and managed BES ponds. A constrained ordination (A) shows environmental variation among ponds is associated with variation in community composition (also see Tables 3 and 4). Multiplicative diversity partitioning outcomes (B) based on occurrence (order $q = 0$) and a null model test (10,000 resamples) of differences (dD) in diversity partitions between pond types (C). Similar patterns are observed when these analyses are conducted using all observed zooplankton taxa (Fig. A5).

Table 4
Variation partitioning of zooplankton (cladoceran and rotifer) community composition in actively managed and unmanaged ponds.

| Group | N | Best fit env. variable(s) | Best fit spatial variable(s) | Adj. R^2 | | | Un-explained |
				[E|S]	[E∩S]	[S|E]	
Managed	12	ns	ns	NA	NA	NA	NA
Unmanaged	9	Salinity, DO	ns	0.478[*]	NA	NA	0.522
All	21	Salinity	PCNM3	0.285[*]	−0.058	0.162[*]	0.611

N is number of ponds represented in each group, ns indicates no variables were correlated with community composition using a cutoff of $P < 0.05$ (based on a permutational test), DO is dissolved oxygen, PCNM3 is the third eigenvector from the principal coordinate analysis of neighbor matrices (PCNM) used to calculate spatial variables from pond geospatial data, NA indicates no available R^2 value because no model was significant. [E\|S] is the pure environmental partition of beta-diversity, which represents variation in community composition that is related to environmental variation after factoring out spatial influences; [E∩S] is the spatially structured environmental partition; and [S\|E] is the pure spatial partition, which represents the relationship between beta-diversity and spatial variables after factoring out the influence of environmental variation.
[*] indicates an adj. R^2 significantly greater than 0 using a cutoff of $P < 0.05$.

management strategy because biotic homogenization contradicts Baltimore's municipal sustainability and conservation goals (Baltimore City, 2009; Duraiappah et al., 2005). However, further examination of empirical data suggests multiple explanations for biotic homogenization in managed ponds are possible. Consequently, the effectiveness of a change in Aquashade© use as a means of increasing zooplankton beta-diversity will depend on which metacommunity dynamic(s) is causing the observed biotic homogenization pattern.

One hypothesis is that pond managers have common goals for their management outcomes based on aesthetic and recreational ecosystem services provided by ponds (Cooke et al., 2005). Thus, the active management of ponds may lead to habitat homogenization, and ultimately biotic homogenization, through niche-based species sorting dynamics. Surprisingly, chlorophyll a concentrations were not significantly different between unmanaged ponds and ponds that received applications of Aquashade© dye, suggesting this management activity was not contributing to habitat homogenization. However, managed ponds had lower and less variable conductivity, Cl, and salinity, which were linked to zooplankton community composition (Figs. 3 and S3, Table 4). These patterns suggest unmanaged ponds drain catchments with greater and more variable impervious surface cover, which creates a less predictable and more stressful local habitat for zooplankton (Kaushal et al., 2005; Van Meter et al., 2011). Therefore, relative to unmanaged ponds, managed ponds represent a more homogenous habitat with the potential for biotic homogenization via niche-based species sorting dynamics.

A second hypothesis is that the observed biotic homogenization effect is a product of limited dispersal in a spatially synchronous hydroscape, where managed ponds tend to be clustered together (e.g., spatial synchrony, Koenig, 1999; Liebhold

et al., 2004). While resource managers decide where to build ponds and which ponds to manage, this mechanism is independent from the effects of active management once the pond is constructed. Consistent with this hypothesis, variation partitioning showed a strong spatial component that was independent from environmental variation at a scale that corresponded with the spatial synchrony of management. A related hypothesis is that dispersal dynamics may also interact with pond size. Managed ponds in this study were larger than unmanaged ponds, and pond size could potentially affect local diversity based on a sampling effect (e.g., species-area relationships) or by changing immigration/colonization dynamics (Dodson, 1991; Frisch et al., 2012; Fryer, 1985).

Because metacommunities are inherently complex systems, a major goal in this study was to create a relatively simple parameterization scheme to allow us to relate state variables to meaningful metacommunity characteristics that could be used to link ecological hypotheses to simulation scenarios (Fig. 1). Given the assumptions outlined in the model description, we narrowed unparameterized metacommunity variables to include I^*, ν, σ_{trait}, and w (Table 1). Simulations allowed us to explore a range of parameter settings that represented different metacommunity concepts, including scenarios contrasting different levels of ecological equivalence in the regional taxonomic pool and different levels of metacommunity mixing. The best-model simulation scenario that explained the observed biotic homogenization pattern required both a steep dispersal kernel (dispersal limitation) and heterogeneity in habitat affinities among taxonomic groups (non-neutral). Therefore, given our assumptions about the system, the characteristics of the hydroscape (spatial arrangement, surface areas, environmental variation), and the observed emergent biodiversity patterns (biotic homogenization), we were able to identify the most likely metacommunity characteristics for zooplankton in BES ponds (Fig. 3).

The parameterized best-model representation of the zooplankton metacommunity in BES ponds provided a tool to test alternative hypotheses using a null model approach (Fig. 5). We found that the clustered arrangement (i.e., spatial synchrony, Fig. 1B) of managed ponds was necessary for the observed biotic homogenization effect to occur. We also found that niche-based species sorting was necessary for the biotic homogenization effect, but not because species sorting dynamics linked biotic homogenization to environmental homogenization. Rather, neutral models overestimated local pond diversity given the same regional richness as niche-based models (Fig. 5A). This result suggests that local niche-based processes were necessary to create sufficient heterogeneity in the metacommunity for dispersal dynamics to create observed biodiversity patterns. Thus, the biotic homogenization effect observed in managed ponds in this system appears to be an emergent pattern from a complex interaction between spatial and niche dynamics that could not be understood without a process-based model.
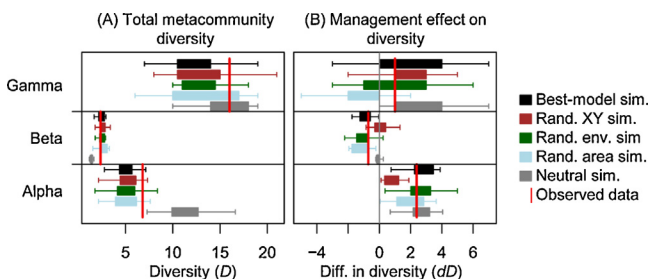

Fig. 5. Simulated metacommunity biodiversity outcomes (A) and management effects (B), estimated as $dD = D_{\mathrm{managed}} - D_{\mathrm{unmanaged}}$. Boxplots represent distribution of outcomes from 1000 replicated simulations. Black represents the best-model simulation; brown, green, and blue represent scenarios in which pond XY-coordinates, the environmental gradient (E), and pond surface area were randomized, respectively, to provide null model comparisons against the best-model; gray represents neutral model simulations. Red lines represent the estimates of D and dD based on the observed occurrences of cladoceran and rotifer families in BES ponds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Built and managed habitats, such as green spaces and retention ponds, are a rapidly expanding component of the human-dominated landscape (Céréghino et al., 2008; Fairchild et al., 2012). In this study, we demonstrated that a failure to account for metacommunity and hydroscape characteristics could lead investigators, managers, or land-owners to incorrectly attribute biotic homogenization to pond management activities. Moving forward, metacommunity theory will improve our ability to understand mechanisms linking management decisions to biodiversity in realistic landscapes. Failure to account for the complex dynamics that emerge based on metacommunity and landscape characteristics could potentially lead to management regimes having unintended consequences, such as decreased regional diversity (Noss, 1983). Approaches that allow a multi-scale understanding of the dynamics that organize biodiversity, such as the simulation-based approach presented here, can be implemented to better understand how biodiversity outcomes may or may not be associated with the choices of natural resource managers.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmo-del.2014.10.022.

References

Alig, R.J., Kline, J.D., Lichtenstein, M., 2004. Urbanization on the US landscape: looking ahead in the 21st century. Landsc. Urban Plan 69 219–234. doi:http://dx.doi.org/10.1016/j.landurbplan.2003.07.004.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods PRIMER-E. Plymouth, UK.

Baltimore City, 2009. The Baltimore sustainability plan. Baltim. City Sustain. Comm. Baltim MD .

Bird, R.B., Bird, D.W., Codding, B.F., Parker, C.H., Jones, J.H., 2008. The fire stick farming hypothesis: Australian aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. Proc. Natl. Acad. Sci. 105, 14796–14801. doi:http://dx.doi.org/10.1073/pnas.0804757105.

Bishop, C.A., Struger, J., Shirose, L.J., Dunn, L., Campbell, G.D., 2000. Contamination and wildlife communities in stormwater detention ponds in Guelph and the Greater Toronto Area Ontario, 1997, and 1998. Part 2. Contamination and biological effects of contamination. Water Qual. Res. J. Can. 35 437–434.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. Ecology 89, 2623–2632.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Céréghino, R., Biggs, J., Oertli, B., Declerck, S., 2008. The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. Hydrobiologia 597, 1–6. doi:http://dx.doi.org/10.1007/s10750-007-9225-8.

Charney N., Record S., 2012. Vegetarian: Jost Diversity Measures for Community Data.

Chase, J.M., Leibold, M.A., 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, Chicago, Ill.

Cooke, G.D., Welch, E.B., Peterson, S., Nichols, S.A., 2005. Restoration and Management of Lakes and Reservoirs. CRC press.

De Meester, L., Declerck, S., Stoks, R., Louette, G., Van De Meutter, F., De Bie, T., Michels, E., Brendonck, L., 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. Aquat. Conserv. Mar. Freshw Ecosyst. 15, 715–725. doi:http://dx.doi.org/10.1002/aqc.748.

Dodson, S., 1991. Species richness of crustacean zooplankton in European lakes of different sizes. Int. Ver. Fuer Theor. Angew. Limnol. Verhandlungen IVTLAP 24.

Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol. Model 196, 483–493.

Duraiappah, A.K., Naeem, S., Agardy, T., Assessment, M.E., 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. Island Press, Washington, DC.

Etienne, R.S., 2005. A new sampling formula for neutral biodiversity. Ecol. Lett. 8, 253–260. doi:http://dx.doi.org/10.1111/j.1461-0248.2004.00717.x.

Fairchild, G.W., Robinson, C., Brainard, A.S., Coutu, G.W., 2012. Historical changes in the distribution and abundance of constructed ponds in response to changing population density and land use. Landsc. Res. 0, 1–14. doi:http://dx.doi.org/10.1080/01426397.2012.672640.

Farber, S., Costanza, R., Childers, D.L., Erickson, J., Gross, K., Grove, M., Hopkinson, C. S., Kahn, J., Pincetl, S., Troy, A., 2006. Linking ecology and economics for ecosystem management. Bioscience 56, 121–133.

Ferguson, B.K., 1991. Taking advantage of stormwater control basins in urban landscapes. J. Soil Water Conserv. 46, 100–103.

Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. J. Anim. Ecol. 42–58.

Frisch, D., Cottenie, K., Badosa, A., Green, A.J., 2012. Strong spatial influence on colonization rates in a pioneer zooplankton metacommunity. PLos ONE 7, e40205. doi:http://dx.doi.org/10.1371/journal.pone.0040205.

Fryer, G., 1985. Crustacean diversity in relation to the size of water bodies: some facts and problems. Freshwater Biol. 15, 347–361. doi:http://dx.doi.org/10.1111/j1365-2427.1985.tb00206.x.

J.L. Gastwirth, Y.R. Gel, W.L.W. Hui, V. Lyubchich, W. Miao, K. Noguchi, Lawstat: an R package for biostatistics public policy and law, 2013.

Gravel, D., Canham, C.D., Beaudet, M., Messier, C., 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecol. Lett. 9, 399–409.

Hankin, R.K., 2007. Introducing untb, an R package for simulating ecological drift under the unified neutral theory of biodiversity. J. Stat. Softw. 22, 1–15.

Hubbell, S.P., 2001. A Unified Theory of Biodiversity and Biogeography. Princeton University Press.

ISO, 1992. Water Quality – Measurement of Biochemical Parameters. Spectrometric Determination of the Chlorophyll-a Concentrations (No. ISO 10260). International Organization for Standardization, Geneva.

Jeppesen, E., Nõges, P., Davidson, T.A., Haberman, J., Nõges, T., Blank, K., Lauridsen, T. L., Søndergaard, M., Sayer, C., Laugaste, R., Johansson, L.S., Bjerring, R., Amsinck, S.L., 2011. Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). Hydrobiologia 676, 279–297. doi:http://dx.doi.org/10.1007/s10750-011-0831-0.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439. doi:http://dx.doi.org/10.1890/06-1736.1.

Kaushal, S.S., Groffman, P.M., Likens, G.E., Belt, K.T., Stack, W.P., Kelly, V.R., Band, L.E., Fisher, G.T., 2005. Increased salinization of fresh water in the northeastern United States. Proc. Natl. Acad. Sci. U. S. A. 102, 13517–13520. doi:http://dx.doi.org/10.1073/pnas.0506414102.

Koenig, W.D., 1999. Spatial autocorrelation of ecological phenomena. Trends Ecol. Evol. 14, 22–26.

Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1–24.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613.

Liebhold, A., Koenig, W.D., Bjørnstad, O.N., 2004. Spatial synchrony in population dynamics. Annu. Rev. Ecol. Evol. Syst. 35, 467–490.

McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. Urbanization 127, 247–260. doi:http://dx.doi.org/10.1016/j.biocon.2005.09.005.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14, 450–453. doi:http://dx.doi.org/10.1016/S0169-5347(99)1679-1.

Mouquet, N., Loreau, M., 2003. Community patterns in source-sink metacommunities. Am. Nat. 162, 544–557.

Noss, R.F., 1983. A regional landscape approach to maintain diversity. BioScience 700–706.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. vegan: Commun. Ecol. Package R package version 2.0–10.

Olden, J.D., 2006. Biotic homogenization: a new research agenda for conservation biogeography. J. Biogeogr. 33, 2027–2039.

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices – estimation and comparison of fractions. Ecology 87, 2614–2625.

Plumb, P.B., Day, S.D., Wynn-Thompson, T.M., Seiler, J.R., 2013. Relationship between woody plant colonization and *Typha L.* Encroachment in stormwater detention basins. Environ. Manage. 52, 861–876.

R Core Team, 2014. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Sartory, D.P., Grobbelaar, J.U., 1984. Extraction of chlorophyll a from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114, 177–187. doi:http://dx.doi.org/10.1007/BF00031869.

Shmida, A., Ellner, S., 1984. Coexistence of plant species with similar niches. Plant Ecol. 58, 29–55.

Sokol, E.R., Benfield, E.F., Belden, L.K., Valett, H.M., 2011. The assembly of ecological communities inferred from taxonomic and functional composition. Am. Nat. 177, 630–644.

Sokol, E.R., Hoch, J.M., Gaiser, E., Trexler, J.C., 2013. Metacommunity structure along resource and disturbance gradients in everglades wetlands. Wetlands doi: http://dx.doi.org/10.1007/s13157-013-0413-1.

Steiner, C.F., Stockwell, R.D., Kalaimani, V., Aqel, Z., 2013. 2013. Population synchrony and stability in environmentally forced metacommunities 122, 1195–1206. doi:http://dx.doi.org/10.1111/j.1600-0706.2012.20936.x.

Van Meter, R.J., Swan, C.M., Snodgrass, J.W., 2011. Salinization alters ecosystem structure in urban stormwater detention ponds. Urban Ecosyst. 14, 723–736.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, fourth ed. New York, Springer.

Wilkinson, C., Sendstad, M., Parnell, S., Schewenius, M., 2013. Urban governance of biodiversity and ecosystem services. In: Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P.J., McDonald, R.I., Parnell, S., Schewenius, M., Sendstad, M., Seto, K.C., Wilkinson, C. (Eds.), Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities. Springer, Netherlands, pp. 539–587.