



Optimization of bioretention systems through application of ecological theory

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Current design of bioretention systems is intended to intercept and retain stormwater, enhance infiltration, and remove organic particulates, nutrients, pathogens, metals, and other contaminants using natural processes that derive from the interactions of water, soil, microbes, plants, and animals. Most bioretention systems function as isolated patches of various shapes and sizes surrounded by impervious surface. A significant body of ecological theory has been developed that addresses the relationships among species composition, diversity, and ecosystem function, and how these vary with spatial structure. Here we highlight how such theories may be applied to improve the efficiency or effectiveness of bioretention systems. We consider (1) the role of plant and animal species that function as ecosystem engineers, (2) biodiversity–ecosystem function relationships, (3) complexity and stability, (4) disturbance and succession, and (5) spatial theory. Future testing of the utility of these theories may occur through incorporation of experiments into the design of bioretention systems or through meta-analysis of systems that span a range of configurations and biotic features. © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

How Can Ecological Theory Form Guiding Principles for ‘Built’ Ecosystems?

Human activities have a broad influence on the ecological function of systems, through alteration of land use and habitats, consumption of resources, hydrological disruption, modification of nutrient cycles and energy flow, influence on microclimate and release of contaminants. Yet until recently these activities have been largely excluded in both the development and application of ecological concepts.¹ The growing field of urban ecology strives to understand how ecological processes govern dynamics of urban ecosystems. These often consist of highly

heterogeneous, often novel, and sometimes heavily disturbed habitats, with green spaces that exist as isolated patches within a matrix of built environments. Urban ecologists have considered how ecological theory developed for natural systems might apply in urban settings² and whether a distinct theory is required to explain ecological patterns in such systems.³ Landscape ecology in particular has provided approaches and methods for understanding the dynamics of urban green spaces. Classic theories of island biogeography, metapopulations and invasion seem ideally suited to understanding the mosaic of patchy green spaces.²

Ecological engineering, in which humans are the engineers, has emerged as a subset of urban ecology that attempts to restore ecosystems that have been disturbed by human activities or create sustainable ecosystems with human and ecological value.⁴ Here we focus on the growing class of built ecosystems aimed at restoring hydrologic and water purification functions in urban settings through natural treatment processes.

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Bioretention Systems as Ecosystems Built to Achieve Water Services

Human efforts to manipulate natural systems to achieve desired ecosystem services date back at least to before 10,000 BC, to the advent of agriculture. Increases in population growth have led to expansion of agriculture, industry and urbanization that place pressure on water resources, and create growing demand for a class of ecosystem services related to water purification. The use of natural and artificial soils and natural biota to purify stormwater and wastewater, provide habitat, enhance biodiversity, and provide aesthetic benefits in urban settings has been called water sensitive urban design (WSUD), low impact development (LID), sustainable urban drainage systems (SUDS),⁵ or natural treatment systems (NTS), but here we summarize these built ecosystems as *terrestrial* bioretention systems. Often these are built habitats consisting of soil and filter media, plants, and associated naturally colonizing fauna. They are specifically designed to pond and retain water, reduce flooding, promote infiltration and remove nutrients such as nitrogen and phosphorus, metals, pathogens, pharmaceuticals, and pesticides.^{6–8}

An ultimate goal of terrestrial bioretention systems is the improved water quality of ground and surface waters entering streams, rivers, and ultimately the ocean. Common plant forms include rushes, sedges, grasses, and shrubs.^{9,10} Characteristic soil biota include oligochaetes (earthworms), millipedes, collembolans (spring tails), beetles, isopods, mites, spiders, and centipedes.¹¹ These systems, also called rain gardens, biofilters or bioswales, have become a common tool for stormwater management. They integrate knowledge from engineering, hydrology, soil science, horticulture, and landscape architecture.¹² Design criteria focus largely on hydrodynamics, filtration media including soils, and to a lesser extent on selection of plants, with limited to no attention to associated fauna.^{11,12}

Here we consider bioretention systems as ‘built’ ecosystems designed to clean and retain water. Such built systems exist in other contexts to provide similar services, for example, as reservoirs to provide potable water,¹³ and restored or constructed wetlands to provide habitat, shoreline protection, and water purification functions.¹⁴ For these, there is a literature that examines how ecological theory may guide practice,^{15,16} and in fact whole fields have arisen around such endeavors—i.e., restoration ecology.^{17,18} For wetlands in particular, a suite of theories associated with biodiversity, disturbance, succession, dispersal, facilitation, trophic structure, niche theory,

invasion, and spatial structure have proven useful in promoting restoration success.^{15,16} In fact, nearly every ecological theory has application to restoration practice,¹⁹ and the construction of bioretention systems can be considered a type of restoration activity. This paper examines how application of ecological theory can make stormwater and runoff bioretention systems more effective and efficient. We discuss the relevant guidance that can emerge from specific ecological theories or paradigms including the broad themes of (1) ecosystem engineering by biota, (2) diversity–function relationships, (3) complexity and stability, (4) disturbance and succession, and (5) spatial ecology including patch dynamics, dispersal, metapopulation, metacommunity, and landscape ecology (Table 1).

RELEVANT THEORY

Ecosystem Engineering and Foundation Species

Although understanding that organisms modify their abiotic environment and that of other species has a long history, the ecological concept of ecosystem engineering (Figure 1) was formally introduced in 1994 by Jones et al.²⁰ Allogenic engineering, which modifies attributes external to the organism (e.g., soils, organic matter, light, moisture) is distinguished from autogenic engineering, where the biota’s physical presence (live or dead) creates habitat. When the engineering effects are disproportionately large and influence community structure, the engineering species is often considered to be a *foundation* species. Note we distinguish the concept of ecosystem engineering in ecology where organisms physically change the environment, with feedbacks to biota,⁴³ from the broader field of ecological engineering, in which humans endeavor to employ technological design that utilizes ecological systems and their self-organization in order to solve problems.^{4,44,45} Of course the two are linked when human engineers employ plants and animals to modify the environment.

In bioretention systems, humans are the ultimate ecosystem engineers, but we can identify abiotic modifications or attributes that enhance functional efficiency and seek key plant or animal species that ‘engineer’ the system appropriately. This is already standard practice for plant uptake of contaminants. Research targets plant species that remove the largest quantities of nutrients,¹⁰ the most metals,^{46,47} or in the case of *Melaleuca ericifolia*, enhance infiltration and hydraulic conductivity with deep roots (Figure 1(a)).⁴⁸ In a test of 20 plant species native to

TABLE 1 | Summary of Ecological Theories that Could Be Applied to Optimize Bioretention System Function

Theory	Representative References	Conceptual Summary	Potential Application to Bioretention Systems
Ecosystem engineers	Jones et al. ²⁰ ; Crain and Bertness ⁴⁸	Ecosystem engineers are species that modify the abiotic environment with consequences for other species.	Optimize system by selection of ecosystem engineering species that produce abiotic modifications that promote desired functions (e.g., plant roots or earthworms that promote infiltration).
Biodiversity–ecosystem function	Tillman et al. ²² ; Loreau et al. ²³ ; Duffey et al. ²⁴ ; Cardinale ²⁵	Enhanced biodiversity should promote one or multiple ecosystem functions through (a) sampling effect (b) complementarity (c) facilitation or (d) insurance effect	(a) Introduction of multiple plant species increases the probability that the best-performing (or best-surviving) species will be present. (b) Different plant species are likely to perform different desired functions best (infiltration, nutrient removal, metal uptake etc.) or perform the same function in different ways; together they maximize performance of the desired functions. (c) Multiple species increase the likelihood of species interactions that benefit some and improve performance. (d) Different species will perform best during different stages of bioretention system life or during changing weather conditions; increasing the number of species will improve time-integrated function of the system.
Complexity–stability	May ²⁶ ; McCann ²⁷ ; Tilman and Downing ²⁸ ; Huston ²⁹	The presence of multiple species increases the number of food–web interactions and promotes stability of the ecosystem.	Increasing biodiversity may promote stability of the bioretention system, thereby prolonging life and requiring less management. Such systems may also be more resistant to invasion.
Intermediate disturbance	Grime ³⁰ ; Horn ³¹ ; Connell ³² ; Dayton ³³ ; Sousa ³⁴	Intermediate levels of disturbance yield the most diverse assemblages.	Moderate disruption of bioretention systems (through harvest, scraping etc.) may maximize plant and animal diversity, accruing the benefits of biodiversity addressed in other theories above.
Succession	Clements, ³⁵ Gleason ³⁶ ; Whittaker ³⁷ ; Connell and Slayter ³⁸	Newly established communities change in a directed fashion, in part by modifying conditions that affect later colonizers.	As bioretention systems develop they clog and there is increased plant growth and soil faunal activity. Thus early stage systems may be better at some functions (e.g., infiltration) while late stages may be better at others (e.g., nutrient removal). Creating a mosaic of systems in different successional stages may promote overall function.
Spatial theory		Dynamics of habitat patches within an unsuitable matrix are influenced by immigration, emigration, size, and spatial arrangement.	Consider area, configuration, proximity, and other spatial features that may influence colonization, assemblage structure and function.

TABLE 1 | Continued

Theory	Representative References	Conceptual Summary	Potential Application to Bioretention Systems
Island biogeography	MacArthur and Wilson ³⁹	Large patches, and those nearest sources of migrants support more species.	Bioretention system area and proximity to colonists may affect plant and animal diversity, and thus function.
Metapopulation theory	Levins ⁴⁰	Dynamics are dictated by exchange between patches (immigration and emigration).	Recognizing interactions between bioretention systems in terms of water, contaminant and species exchange may maximize function.
Metacommunity theory	Liebold et al. ⁴¹	Mass effects, random drift, species niche requirements, and species interactions dictate assemblage structure.	By treating them as a network rather than individually, bioretention systems can be constructed with attributes that promote colonization, maximize biodiversity, and enhance persistence of desired species with desired functions.
Landscape ecology	Turner ⁴²	Patterns of fragmentation, boundaries, edges, and spatial arrangement control dynamics.	Wildlife habitat functions and species persistence may be maximized by considering landscape attributes such as area, configuration, corridors, and proximity to nearby systems.

south eastern Australia, *Carex appressa*, for example, by virtue of its longer, deeper and larger roots, exhibited superior nutrient removal.¹⁰ Other plant features to promote might include (1) architecture that slows water movement during high flow periods or (2) shading or litter production that reduces evaporation and maintains soil moisture, lower temperatures, and lower salinities, thereby promoting the wellbeing of other plants and soil invertebrates, particularly during dry seasons in arid settings.^{49,50} The harshness of conditions may dictate the mode of action for plant and animal ecosystem engineers. Environmental amelioration should be greatest under stressful conditions, as associated with new system construction, periodic harvest/scraping, high flows, or intense contamination.²¹

Earthworms were recognized by Darwin⁵¹ as major ecosystem engineers⁵² (Figure 1(b)), creating biogenic structures (burrows) that facilitate water and gas transport and may enhance drainage and reduce clogging.⁵³ They bioturbate minerals, litter, and contaminants, and break down organic matter, with casts and guts that are sites of enhanced denitrification.⁵⁴ Although some earthworm species, such as those that are geophageous, may be 'accidental' engineers,⁵⁵ others manipulate the environment by enhancing decomposition (e.g., endogeic or anecic earthworms that create casts). Earthworms enhance plant performance by mobilizing nutrients in the rhizosphere, controlling plant pests, facilitating mutualistic microbes, and producing hormone-like effects.⁵⁵

Other potential faunal engineers in biofilters include caterpillars, which can affect herbivore diversity.⁵⁶

Diversity–Function Relationships

Over the past quarter century, a large body of theory has accumulated regarding the importance of biodiversity for ecosystem function (BEF).^{23,57} Meta-analyses demonstrate positive diversity–function relationships for many attributes in terrestrial, aquatic, and marine systems,²⁵ both within and across trophic guilds.^{24,58} While there have been no explicit tests of this relationship for bioretention systems, it is reasonable to expect that the principles applied to natural systems would be relevant.

Multiple studies have shown that ecosystems with more species are more productive and are more efficient at removing nutrients from water and soil.^{22,25,59} A host of hypotheses highlight different mechanisms underlying a positive diversity–function relationship. Often the most important function (e.g., N uptake) is best performed by a single species or functional group. When the relative functional efficiency of different species or taxonomic groups is not known, introduction of multiple species improves the chance that the best performer will be present. This has been termed the *sampling effect* (Figure 2(a)), and can readily be applied to bioretention systems simply by planting multiple species likely to flourish regionally.

The *complementarity hypothesis* invokes niche partitioning, where different species carry out different

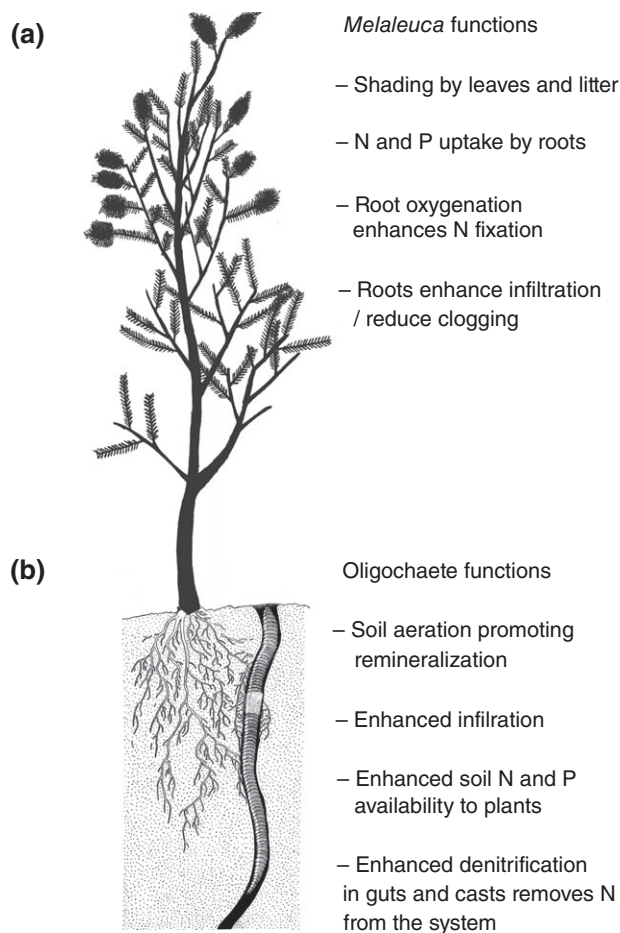


FIGURE 1 | Examples of plant and animal ecosystem engineers and their actions in natural treatment systems. (a) *Melaleuca* sp. (b) Oligochaeta Note: the oligochaete (earthworm) is not drawn to scale.

functions which, when performed together, enhance total function (Figure 2(b)).²³ In a restored California salt marsh, for example, experiments demonstrated that species-rich plantings enhance biomass and nitrogen accumulation, even in the presence of a dominant, highly productive species.⁶⁰ A compilation of Pacific coast wetland restoration results suggests that plant species diversity introduces varied architecture, recruitment capabilities, and expanded cover through vegetative growth, in addition to biomass and nutrient accumulation; thus all species are required to achieve maximal levels of all functions.⁶¹ Within bioretention systems we might identify different plant species that directly enhance system function by slowing horizontal flows, reducing erosion, maximizing vertical infiltration, physically trapping or flocculating particles or pathogens through chemical secretions, bioaccumulating metals, or rapidly removing nutrients. Appropriate species combinations can be targeted to achieve holistic function. For

example, two plants frequently used in Australian biofilters, *Carex appressa* and *Lomandra longifolia*, were shown to remove more nutrients when grown together compared with *L. longifolia* alone, independent of the proportion of *C. appressa*.⁶² Alternatively, different species may perform the same function (e.g., nutrient removal) in different ways, also enhancing efficiency. For nutrient uptake functions we may identify plants that preferentially remove different nutrients (N vs P), take up different forms of nitrogen (NO_3^- , NH_4 , or NO_2) from different sources (water, soil, air), or function best under different conditions (light, dark, wet, dry, saturated). Maximal nutrient removal would then be achieved by planting a suite of these species with complementary effects.

In some cases species functionality varies under different conditions (e.g., dry vs wet weather),⁶³ adding a dynamic (temporal) context to the value of biodiversity. When knowledge exists of which species perform best at different seasons or under different flow regimes they can be planted in combination (or in sequence) to offer temporal insurance and continuity of function. This is termed the *insurance hypothesis* (Figure 2(c)).

Beyond water quality functions, different plant species may also offer a broader range of ecosystem services, providing wildlife habitat, food and refuge, carbon sequestration, or aesthetic and recreational value. Careful selection of plant species based on BEF principles, including those that promote desired fauna, can maximize the value of bioretention systems.

Facilitation, in which species interactions are positive, is another mechanism by which diversity can elevate function above that achieved by species alone.^{23,64} Facilitative interactions may involve different combinations of plants, animals and microbes. Use of nurse plants to ameliorate evaporation and hypersalinity of soils has been tested to promote seed germination and growth in newly restored southern California marshes.⁶⁵ This sort of facilitation could be applied to bioretention systems in arid settings. Although soil faunas are rarely (never?) manipulated in bioretention systems, plant diversity can facilitate development of animal communities.⁶⁶ Litter production or shading by plants will provide organic matter, enhance soil moisture, and ameliorate temperature extremes in arid settings, promoting earthworm development, which aerates soils and increases porosity (Figure 2(d)). Different types of litter arising from multiple plant species could promote different groups of detritivores, due to relative differences in palatability. Whether multiple soil taxa enhance water quality or infiltration in bioretention systems, perhaps through complementarity, remains to be tested. Nevertheless,

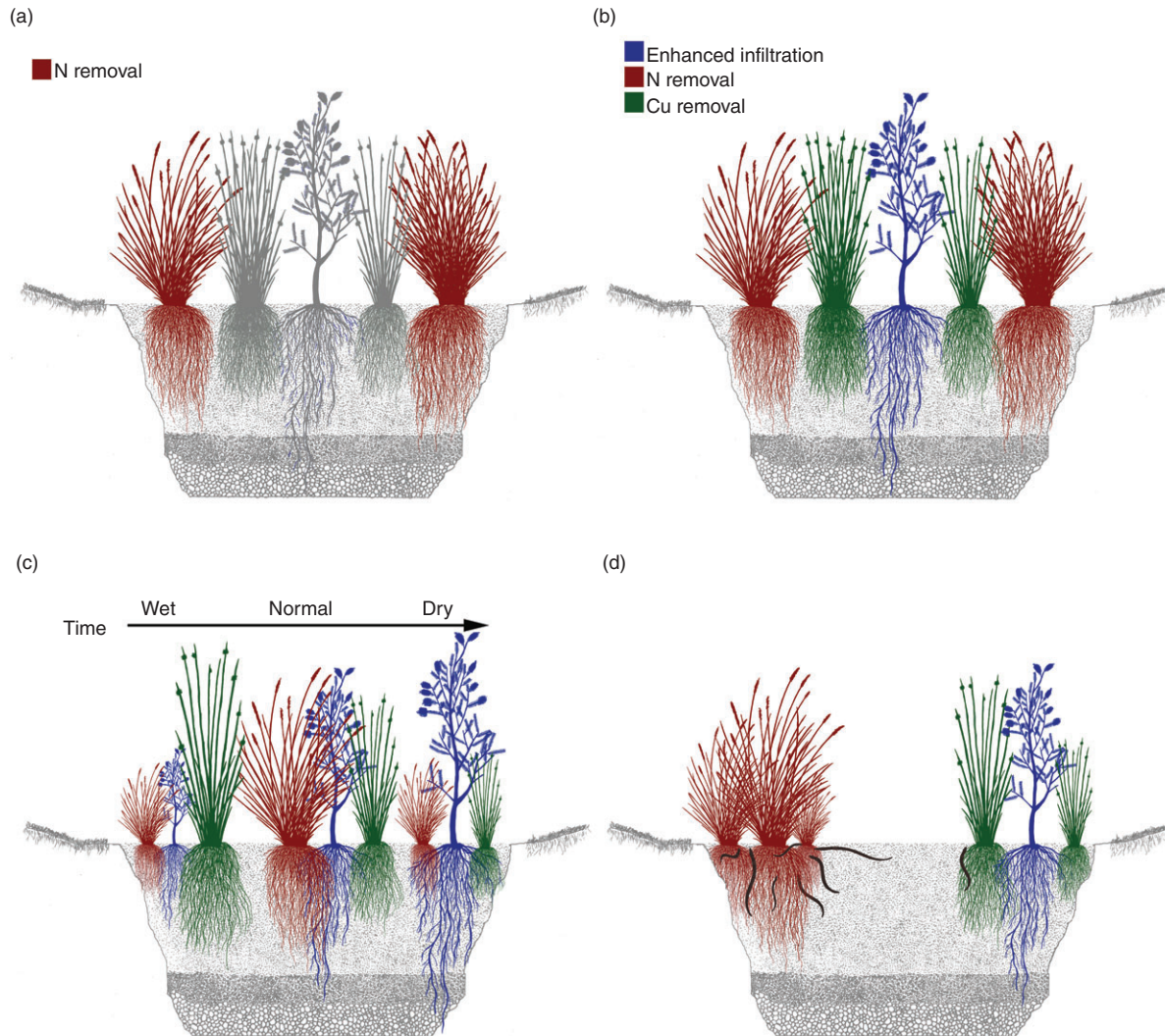


FIGURE 2 | Four hypotheses addressing mechanisms underlying biodiversity and function, applied to bioretention systems. (a) Sampling effect: when more species are present the probability of having the best functioning species (in this case for N removal) is greatest. (b) Complementarity: different vegetation taxa excel at different water purification functions; when they co-occur system performance is maximized. (c) Insurance hypotheses: different species survive and perform better at different times, for example, due to different climate tolerances. (d) Facilitation: specific species may promote the presence of others (in this example vegetation enhances oligochaetes), enhancing overall system function.

bioretention system designs and planting regimes may be developed that promote interspecific facilitation.

Complexity and Stability

The BEF paradigm has its roots in work conducted by Elton,⁶⁷ May,²⁶ and others²⁷ on the relationship between *complexity and stability*, with much of the focus on foods webs. As originally developed the paradigm suggests that the presence of more species (predators, prey, parasites) generates more different types of interactions, but these are weaker, and thus less subject to disruption, thereby conferring stability. This stability can include

dampened population fluctuations, more rapid recovery from perturbation, resistance to invasion and increased persistence. Where consistency of plant and animal water purification functions is sought, a more diverse assemblage could achieve this. However, questions exist about whether diversity sometimes causes destabilization.^{68–70} A more recent manifestation of this debate suggests that population variation across species can sum to stable primary producer biomass at the community level.^{27,28} This occurs because plant species respond differently to varying environmental forcing. In some cases functional diversity is more correlated with plant production than species diversity.²⁹ The stability of plants

and animals in bioretention systems has yet to be studied. However, by maintaining vegetation diversity or by increasing numbers of consumer species to weaken food–web interactions²⁷ in bioretention systems it may be possible to stabilize biomass in a way that achieves hydrologic and contaminant removal goals.

Disturbance

Disturbance and stress have played a key role in ecological theory, largely due to the pioneering studies of ecologists such as Grime,³⁰ Horn,³¹ Connell,³² Dayton,³³ and Sousa.³⁴ The paradigm that diversity is maximal at intermediate disturbance levels has been applied to rain forests, coral reefs, and rocky shores. The theory is linked to concepts of succession, in which heavily disturbed systems host a few poor competitors that are opportunistic⁷¹ and undisturbed systems are dominated by few highly competitive species. Intermediate levels of disturbance may promote the most diverse assemblages by preventing competitive exclusion. How is this relevant to bioretention systems? Assuming that maximizing diversity is a means to promote desired functions, we may wish to design systems in which natural disturbances or stressors such as flood, drought, or storm surge act at moderate levels. Alternatively we may wish to impose moderate levels of disturbance (e.g., biomass harvest, soil aeration) to enhance both diversity and function. Biomass harvest has been tested in constructed wetlands with only modest improvements in nutrient uptake as a result, except when nutrient loading is low,⁷² which is the case in many bioretention systems. Therefore, this particular form of disturbance may lead to improvements in bioretention system function as well.

Another feature of disturbance is its potential to increase ecosystem susceptibility to invasion by exotic species.^{73–75} Invasion susceptibility may be greatest when the disturbance represents addition of unused resources (light, nutrients, or water).⁷⁶ The assumption is that an invasive species will be more successful if it does not encounter intense competition for these resources from resident species. Given that young bioretention systems represent physically disturbed settings, the potential for nonnative invaders must be recognized and possibly addressed through manual removal or design features.

Succession

It is unclear whether biological succession of plant species occurs as new bioretention systems develop, although increases in plant cover and root systems are likely to drive succession of soil fauna. There is also potential for increased clogging and contaminant

buildup over time. Many of the basic ideas about succession were developed by botanists Clements³⁵ Gleason,³⁶ and Whittaker³⁷ in terrestrial systems; with various mechanisms of species interaction proposed based on marine systems.³⁸ Animals or plants in soils can generate autogenic succession by modifying organic matter properties or pH. Shade-generating species can facilitate shade-tolerant species. Animals that disperse seeds, build mounds, or alter nutrient content can induce allogenic succession. Viewing the biota of bioretention systems as dynamic, it might be possible to identify a successional (dynamic) pattern to the ecosystem services provided, with certain water purification functions optimized in young systems and others in older systems. For example, water infiltration rates may be optimal in younger rain gardens while habitat provisioning or aesthetics take over in late stages. Indeed, a recommended practice to prevent clogging and heavy metal accumulation in rain gardens is to remove the top 2–5 cm of soil every 2 years,⁷⁷ which in essence reverts the rain garden to an earlier successional state with respect to the uppermost layers of soil.

Spatial Pattern

A host of ecological subdisciplines have evolved to address the consequences and dynamics of spatially resolved systems. Examples include metapopulation ecology,⁴⁰ metacommunity ecology,⁴¹ and landscape ecology, which often focuses on urban settings.⁴² Many of these have roots in the *theory of island biogeography*.³⁹ Fundamental is the recognition of multiple patches inhabited by populations, communities, or functioning as ecosystems that are situated within a matrix of unsuitable habitat (e.g., Figure 3). There is exchange of individuals, energy, or materials between patches, which may differ in size, configuration, quality (suitability), and occupancy. Larger systems hold more species (presumably due to potential heterogeneity creating niches) and increased immigration potential. There are competing forces of colonization and extinction as dictated by proximity to source populations, as well as stochastic processes.

While natural systems are often initially contiguous and become subject to fragmentation, constructed systems such as bioretention zones are nearly always patches within a dissimilar (often impervious) matrix. Those constructed patches that are closer to natural green spaces (forests, fields, wetlands) will experience greater colonization via seed and animal dispersal, and should therefore support greater biodiversity, potentially surpassing that of other built systems



FIGURE 3 | Google earth images showing a network of bioretention units at Elmer Avenue in Los Angeles. This is referred to as a green street. Shape and proximity to other bioretention units or vegetated areas may affect development of plant and animal species that promote desired functions.

(lawns, gardens, parks, golf courses).⁷⁸ All of these built systems have boundaries and edges that may include ecotones (transitional zones) and human forcing which affect their function.

What do the space-based disciplines have to offer the study of bioretention systems? They allow us to consider bioretention systems as (1) a mosaic or network situated in a landscape that can influence their success and (2) dynamic assemblages whose composition and diversity reflect the interplay of different processes. Metacommunity models suggest competing influences of niche availability (the species sorting model), source-sink/dispersal dynamics (the mass effects model), succession and competition (the patch dynamics model) and stochastic processes (the neutral model) in shaping assemblages.^{41,79} While most bioretention systems are built as isolated entities designed to perform localized water services, there may be advantages to designing them with these models in mind. Such design elements could (1) promote connectivity (for example of colonizing soil biota, pollinating insects, birds, and reptiles) with other similar systems or green spaces, (2) introduce elements that promote architectural, landscape, or functional heterogeneity, and (3) allow different systems to specialize on different functions in space or time. Additional considerations for sustaining bioretention system plant services in a metacommunity context could include selection of perennial versus annual vegetation, maximizing dispersal potential, and seed bank development.

A WAY FORWARD

How Do We Operationalize the Concepts?

Most of the ecological concepts presented above (summarized in Table 1) have not been applied to bioretention systems, but could be examined relatively easily. In regions where the use of bioretention systems are widespread and their functions have been well studied in the field (e.g., Australia⁸⁰), it may be possible to conduct data-based meta-analyses to test the relevance of theories discussed here. Most amenable are relationships between bioretention system size, age, proximity to natural spaces, plant diversity, and various water purification functions (Figure 3).

Like restored ecosystems, bioretention systems are built environments highly conducive to experimentation. There is a long history of manipulating restored wetlands to test effects of soil amendments, planting, and genetic composition on wetland development and recovery.^{16,81} Best management practices such as bioretention systems are mandatory for new construction in many urban areas and near water bodies. These could be modified to include modules in which different filter media were tested, different numbers and functional types of plant species were introduced, and animals were seeded. Who might be interested in such designs? This could foster partnerships between developers, civil engineers, regulatory agencies, and biologists and ecologists knowledgeable about the relevant ecological processes. In many instances universities are taking the lead in implementing sustainable practices

and their own bioretention systems can serve as prime testing grounds.

Bioretention Systems as a Cup Half Full?

Restored ecosystems rarely recover full ecosystem function and this has led to warnings about use of restoration to justify further habitat degradation.^{82,83} However, where the implementation of bioretention systems replaces impervious surfaces or habitat with lesser function or value, the services provided can be considered a net gain. This is likely to be the case for bioretention systems in urban settings, surrounded by grass lawns or paved surfaces. Now that we recognize humans and their contaminants as critical elements in urban ecosystems, bioretention systems have become a valuable tool to achieve ecosystem-based management.⁸⁴ The application of ecological theories to improve bioretention systems, through experimentation and observation, can strengthen that arsenal.

Beyond the hydraulic and water purification functions highlighted in this paper, implementation of bioretention systems may promote a wide range of additional services of value in urban settings. Ecological theory can be applied to the functionality of bioretention services in order to maintain biodiversity, provide wildlife habitat and corridors, pollination services, carbon sequestration, aesthetic or recreational value, or even modulate microclimate. Tussock sedges such as *Carex* spp., which are commonly planted in bioretention systems, for example, are recognized not only for their superior nutrient uptake capabilities,¹⁰ but also for introducing structural complexity that promotes biodiversity and provides herbivore refugia²¹ and for their potential to sequester carbon.⁸⁵ A research agenda for bioretention systems that incorporates multiple types of ecosystem services, combined with stakeholder engagement in development planning,⁸⁶ could significantly advance the use of bioretention systems for sustainable urban management.

REFERENCES

- Alberti M, Marzluff JM, Shulenberg E, Bradley G, Ryan C, Zumbrunnen C. Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *Bioscience* 2003, 53:1169–1179.
- Breuste J, Niemela J, Snep RPH. Applying landscape ecological principles in urban environments. *Landsc Ecol* 2008, 23:1139–1142.
- Niemela J. Is there a need for a theory of urban ecology? *Urban Ecosyst* 1999, 3:57–65.
- Mitsch WJ, Jørgensen SE. *Ecological engineering and ecosystem restoration*. New York: John Wiley & Sons, Inc.; 2004, 411.
- BMT WBM. Evaluating options for water sensitive urban design – a national guide: prepared by the Joint Steering Committee for Water Sensitive Cities: In delivering Clause 92(ii) of the National Water Initiative, Joint Steering Committee, 2009.
- Roy-Poirier A, Champagne P, Filion Y. Review of bioretention system research and design: past, present, and future. *J Environ Eng* 2010, 136:878–889.
- Yang H, Dick WA, McCoy EL, Phelan PL, Grewal PS. Field evaluation of a new biphasic rain garden for stormwater flow management and pollutant removal. *Ecol Eng* 2013, 54:22–31.
- Payne EGL, Fletcher TD, Cook PLM, Deletic A, Hatt BE. Processes and drivers of nitrogen removal in stormwater biofiltration. *Crit Rev Environ Sci Technol* 2014, 44:796–846.
- Brisson J, Chazarenc F. Maximizing pollutant removal in constructed wetlands; should we pay more attention to macrophyte species selection. *Sci Total Environ* 2009, 407:3923–3939.
- Read J, Fletcher TD, Wevill T, Deletic A. Plant traits that enhance pollutant removal from stormwater in biofiltration systems. *Int J Phytoremediation* 2010, 12:34–53.
- Mehring AS, Levin LA. Can soil fauna improve the efficiency of rain gardens used as natural storm water treatment systems? *Journal of Applied Ecology* (In Review).
- Davis AP, Hunt WF, Traver RG, Clar M. Bioretention technology: overview of current practice and future needs. *J Environ Eng* 2009, 135:109–117.
- Lake PS, Bond N, Reich P. Linking ecological theory with stream restoration. *Freshw Biol* 2007, 52:597–615.
- Vymazal J. Emergent plants used in free water surface constructed wetlands: a review. *Ecol Eng* 2013, 61B:582–592.
- Palmer MA, Ambrose RF, Poff NL. Ecological theory and community restoration ecology. *Restor Ecol* 1997, 5:291–300.
- Zedler JB. Progress in wetland restoration ecology. *Trends Ecol Evol* 2000, 15:402–407.
- Young TP, Petersen DA, Clary JJ. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol Lett* 2005, 8:662–673.

18. Wezel A, Bellon S, Doré T, Francis C, Vallod D, David C. Agroecology as a science, a movement, and a practice. *Agronomy for Sustainable Development* 2009, 29:503–515.
19. Zedler JB. Ecological restoration: guidance from theory. *San Francisco Estuary and Watershed Science* 2005, 3: Article 4.
20. Jones CG, Lawton JH, Shachak M. Organisms as ecosystem engineers. *Oikos* 1994, 69:373–386.
21. Crain CM, Bertness MD. Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* 2006, 56: 211–218.
22. Tilman D, Wedin D, Knops J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 1996, 379:718–720.
23. Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, et al. Biodiversity and ecosystem function: current knowledge and future challenges. *Science* 2001, 294:804–808.
24. Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thebault E, Loreau M. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecol Lett* 2007, 10:522–538.
25. Cardinale BJ. Biodiversity improves water quality through niche partitioning. *Nature* 2011, 472: 86–91.
26. May RM. Patterns of species abundance and diversity. In: Cody ML, Diamond JM, eds. *Ecology and Evolution of Communities*. Cambridge, MA: Harvard University Press; 1975, 81–120.
27. McCann KS. The diversity-stability debate. *Nature* 2000, 405:228–233.
28. Tilman D, Downing JA. Biodiversity and stability in grasslands. *Nature* 1994, 367:363–365.
29. Huston MA. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 1997, 110:449–460.
30. Grime JP. Competitive exclusion in herbaceous vegetation. *Nature* 1973, 242:344–347.
31. Horn HS. Markovian properties of forest succession. In: Cody ML, Diamond JM, eds. *Ecology and Evolution of Communities*. Cambridge, MA: Belknap Press; 1975, 196–211. ISBN 0-674-22444-2.
32. Connell JH. Diversity in tropical rain forests and coral reefs. *Science* 1978, 199:1302–1310.
33. Dayton PK. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr* 1971, 41:351–389.
34. Sousa WP. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 1979, 60:1225–1239.
35. Clements FE. *Research Methods in Ecology*. Lincoln: University Publishing Company; 1905, 334.
36. Gleason HA. The individualistic concept of the plant association. *Bull Torrey Bot Club* 1926, 53:7–26.
37. Whittaker RH. A consideration of climax theory: the climax as a population and pattern. *Ecol Monogr* 1953, 23:41–78.
38. Connell JH, Slayter RO. Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 1978, 111: 1119–1144.
39. MacArthur RH, Wilson EO. *The Theory of Island Biogeography*. Princeton: Princeton University Press; 1967, 203.
40. Levins R. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 1969, 15:237–240.
41. Leibold MA, Holyoak M, Moquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, et al. The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 2004, 7:601–613.
42. Turner MG. Landscape ecology: the effect of pattern on process. *Annu Rev Ecol Syst* 1989, 20:171–197.
43. Hasting A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG. Ecosystem engineering in space and time. *Ecol Lett* 2007, 10:153–164.
44. Odum HT, Odum B. Concepts and methods of ecological engineering. *Ecol Eng* 2003, 2003:339–361.
45. Kangas PC. *Ecological Engineering: Principles and Practice*. Boca Raton: CRC Press; 2004, 472.
46. Feng W, Hatt BE, McCarthy DT, Fletcher TD, Deletic A. Biofilters for stormwater harvesting: understanding the treatment performance of key metals that pose a risk for water use. *Environ Sci Technol* 2012, 46:5100–5108.
47. Yang X, Mei Y, He J, Jiang R, Li Y, Li J. Comprehensive assessment for removing multiple pollutants by plants in bioretention systems. *Chin Sci Bull* 2014, 59:1446–1453.
48. Le Coustumer SL, Fletcher TD, Deletic A, Barraud S, Poelsma P. The influence of design parameters on clogging of stormwater biofilters: a large-scale column study. *Water Res* 2012, 46:6743–6752.
49. Holmgren M, Gómez-Aparicio L, Quero JL, Valladares F. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. *Oecologia* 2012, 169:293–305.
50. Xu S, Liu LL, Sayer EJ. Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments. *Biogeosciences* 2013, 10:7423–7433.

51. Darwin C. *The formation of vegetable mould through the action of worms with observation of their habits*. London: John Murray; 1881, 326.
52. Meysman FJR, Middelburg JJ, Heip CHR. Bioturbation: a fresh look at Darwin's last idea. *Trends Ecol Evol* 2006, 21:688–695.
53. Shipitalo MJ, Bayon R-CL. Quantifying the effects of earthworms on soil aggregation and porosity. In: Edwards CA, ed. *Earthworm Ecology*. Boca Raton: CRC Press; 2004, 183–194.
54. Horn MA, Mertel R, Gehre M, Kästner M, Drake HL. In vivo emission of dinitrogen by earthworms via denitrifying bacteria in the gut. *Appl Environ Microbiol* 2006, 72:1013–1018.
55. Jouquet P, Dauber J, Lagerlof J, Lavelle P, Lepage M. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Appl Soil Ecol* 2006, 32:153–164.
56. Lill JT, Marquis RJ. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology* 2003, 84:682–690.
57. Loreau M. Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philos Trans R Soc B* 2009, 365:49–60.
58. Duffy JE. Biodiversity and ecosystem function: the consumer connection. *Oikos* 2002, 99:201–219.
59. Zhang Y, Chen HYH, Reich PB. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J Ecol* 2012, 100:742–749.
60. Callaway JC, Sullivan G, Zedler JB. Species-rich plantings increase biomass and nitrogen accumulation in a wetland restoration experiment. *Ecol Appl* 2003, 13:1626–1639.
61. Zedler JB, Callaway JC, Sullivan G. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. *BioScience* 2001, 51:1005–1017.
62. Ellerton JP, Hatt BE, Fletcher TD. Mixed plantings of *Carex appressa* and *Lomandra longifolia* improve pollutant removal over a monoculture of *L. longifolia* in stormwater biofilters. In: Barton ACT, ed. *WSUD 2012: Water Sensitive Urban Design; Building the Water Sensitive Community; 7th International Conference on Water Sensitive Urban Design*. Melbourne, Australia: Engineers Australia; 2012, 164–170.
63. Payne EGI, Pham T, Cook PLM, Fletcher TD, Hatt BE, Deletic A. Biofilter design for effective nitrogen removal from stormwater – influence of plant species, inflow hydrology and use of a saturated zone. *Water Sci Technol* 2014, 69:1312–1319.
64. Bruno JF, Stachowica JJ, Bertness MD. Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 2003, 18:119–125.
65. Zedler JB, Morzaria-Luna H, Ward K. The challenge of restoring vegetation on tidal, hypersaline substrates. *Plant Soil* 2003, 253:259–273.
66. Whitcraft CR, Levin LA. Light-mediated regulation of the sediment ecosystem by salt marsh plants. *Ecology* 2007, 88:904–917.
67. Elton CS. *The Ecology of Invasions by Animals and Plants*. London: Methuen; 1958, 181.
68. Gardner MR, Ashby WR. Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature* 1970, 228:784.
69. Pimm SL, Lawton JH. On feeding on more than one trophic level. *Nature* 1978, 275:542–544.
70. Yodzis P. The stability of real ecosystems. *Nature* 1981, 289:674–676.
71. Gray JS. Effects of environmental stress on species rich assemblages. *Biol J Linn Soc* 1989, 37:19–32.
72. Vymazal J. Removal of nutrients in various types of constructed wetlands. *Sci Total Environ* 2007, 380:48–65.
73. Holzner W, Werger MJA, Ikusima I. *Man's impact on vegetation*. The Hague: W. Junk Publishers; 1983.
74. Mills EL, Leach JH, Carlton JT, Secor CL. Exotic species and the integrity of the Great Lakes. *BioScience* 1994, 44:666–676.
75. Altman S, Whitlatch RB. Effects of small-scale disturbance on invasion success in marine communities. *J Exp Marine Biol Ecol* 2007, 342:15–29.
76. Davis MA, Grime JP, Thompson K. Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 2000, 88:528–534.
77. Hatt BE, Fletcher TD, Deletic A. Hydraulic and pollutant removal performance of fine media stormwater filtration systems. *Environ Sci Tech* 2008, 42:2535–2541.
78. Kazemi F, Beecham S, Gibbs J. Streetscape biodiversity and the role of bioretention swales in an Australian urban environment. *Landsc Urban Plan* 2011, 101:139–148.
79. Logue JB, Mouquet N, Peter H, Hillebrand H. Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol Evol* 2011, 26:482–491.
80. Ambrose RF, Winfrey BK. Comparison of stormwater biofiltration systems in southern California and southeast Australia. *WIREs: Water*, This volume. In press. doi:10.1002/wat2.1064.
81. Levin LA, Talley T. Influences of vegetation and abiotic environmental factors on salt marsh benthos. In: Weinstein MP, Kreeger DA, eds. *Concepts and Controversies in Tidal Marsh Ecology*. Amsterdam: Kluwer Academic Publishers; 2000, 661–708.
82. Moreno-Mateos D, Power ME, Comín FA, Yockteng R. Structural and functional loss in restored wetland ecosystems. *PLoS Biol* 2012, 10:e1001247. doi:10.1371/journal.pbio.1001247.

83. Bernhardt ES, Palmer MA. River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecol Appl* 2011, 21:1926–1931.
84. Endreny TA. Storm water management for society and nature via service learning, ecological engineering and ecohydrology. *Int J Water Resour Dev* 2004, 20:445–462.
85. Lawrence BA, Zedler JB. Carbon storage by *Carex stricta* tussocks: a restorable ecosystem service? *Wetlands* 2013, 33:483–493.
86. Sitas N, Prozesky HE, Esler KJ, Reyers B. Exploring the gap between ecosystem service research and management in development planning. *Sustainability* 2014, 6:3802–3824.