

# Plant species richness enhances nitrogen retention in green roof plots

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**Abstract.** Vegetated (green) roofs have become common in many cities and are projected to continue to increase in coverage, but little is known about the ecological properties of these engineered ecosystems. In this study, we tested the biodiversity–ecosystem function hypothesis using commercially available green roof trays as replicated plots with varying levels of plant species richness (0, 1, 3, or 6 common green roof species per plot, using plants with different functional characteristics). We estimated accumulated plant biomass near the peak of the first full growing season (July 2013) and measured runoff volume after nearly every rain event from September 2012 to September 2013 (33 events) and runoff fluxes of inorganic nutrients ammonium, nitrate, and phosphate from a subset of 10 events. We found that (1) total plant biomass increased with increasing species richness, (2) green roof plots were effective at reducing storm runoff, with vegetation increasing water retention more than soil-like substrate alone, but there was no significant effect of plant species identity or richness on runoff volume, (3) green roof substrate was a significant source of phosphate, regardless of presence/absence of plants, and (4) dissolved inorganic nitrogen (DIN = nitrate + ammonium) runoff fluxes were different among plant species and decreased significantly with increasing plant species richness. The variation in N retention was positively related to variation in plant biomass. Notably, the increased biomass and N retention with species richness in this engineered ecosystem are similar to patterns observed in published studies from grasslands and other well-studied ecosystems. We suggest that more diverse plantings on vegetated roofs may enhance the retention capacity for reactive nitrogen. This is of importance for the sustained health of vegetated roof ecosystems, which over time often experience nitrogen limitation, and is also relevant for water quality in receiving waters downstream of green roofs.

*Key words:* biodiversity–ecosystem function; green infrastructure; nitrogen; nutrient fluxes; phosphorus; stormwater runoff; vegetated roof.

## INTRODUCTION

Green (vegetated) roofs are a component of urban green infrastructure growing in popularity and implementation, with up to 20% coverage of flat roofs in some European cities and plans for rapid expansion in many North American cities (Deutsch et al. 2005, Carter and Fowler 2008, Kazmierczak and Carter 2010). As engineered ecosystems like green roofs grow in number and areal coverage, there is an increasing need to understand if and how ecological theories apply to these systems, particularly since they are designed in large part to replace functions lost when natural ecosystems are removed for urban development (Lundholm et al. 2010).

One such ecological theory with particular relevance to management and conservation of ecosystems is the biodiversity–ecosystem function (BEF) hypothesis, which suggests that there is a link between biological diversity and ecosystem functioning. A common expression of this relationship is an increase in productivity and resource use

(including nutrient use) as plant species richness increases in a given ecosystem, when other environmental factors are held constant (Tilman et al. 1996, Cardinale 2011, Latta et al. 2011). Commonly cited mechanisms for positive relationships between plant diversity and function (increased productivity and resource utilization) include increased complementarity among species (and therefore more complete niche utilization), the sampling or selection effect (increased likelihood of including a highly productive species), or some combination of the two (Hooper et al. 2005, Scherer-Lorenzen 2005, Cardinale et al. 2007). The net effect of species richness on any given ecosystem function depends on many factors, including the degree of dominance of species lost or gained, the degree to which the species interact with one another, the functional traits of each species, and other biotic and abiotic factors affecting the ecosystem (Lawton 1994, Naeem 1998, Hector et al. 1999, Hooper et al. 2005, Cadotte et al. 2011).

Relationships between plant diversity and ecosystem function have been examined for natural ecosystems (Tilman et al. 1996, Hooper et al. 2005, Scherer-Lorenzen 2005), but it is not known whether these relationships translate to engineered ecosystems like green roofs. In

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grassland ecosystems where much of the foundational BEF research has taken place, experimental increases in plant-species richness commonly result in an increase in primary productivity and an increase in nutrient retention (thus decrease in nutrient efflux; e.g., Tilman et al. 1996, Tilman 1999). More recent experiments with tree species have generally followed a similar pattern with higher species richness corresponding to higher productivity and nutrient retention (e.g., Scherer-Lorenzen 2005, Ewel and Bigelow 2011). Green roofs, however, as engineered ecosystems, have soil types and vegetation communities that have not co-evolved or co-adapted like natural systems, and the plants and soils are not necessarily well-tuned to one another, particularly in terms of nutrient supply vs. demand (Buffam and Mitchell 2015). Harsh environmental conditions and relatively thin soil layers on green roofs limit potential plant diversity, but may also influence species interactions (e.g., Dimitrakopoulos and Schmid 2004). Thus, these systems may respond differently to changes in diversity than do more well-studied natural ecosystems.

A green roof can be simply defined as vegetation that partially or completely covers a built structure, with the vegetation typically planted in a soil-like engineered growing medium (Oberndorfer et al. 2007). The most common type of modern green roofs, the so-called “extensive” green roofs, consist of a thin (<10 cm) layer of lightweight nutrient-rich growing medium and a relatively simple plant community, typically a species-poor mix of succulents of the genus *Sedum* (stonecrops), which have been selected for their ability to survive under conditions of periodic drought (Oberndorfer et al. 2007). Green roofs are designed, in part, to lessen the strain on water treatment plants and reduce combined sewer overflows because of their ability to retain storm water (e.g., Mentens et al. 2006, Carter and Jackson 2007, Dietz 2007, Hilten et al. 2008, Gaffin et al. 2009) and their perceived ability to retain nutrients and other pollutants (e.g., Berndtsson et al. 2009, Aitkenhead-Peterson et al. 2011, Buffam and Mitchell 2015). Green roofs thus have the capacity to make a significant difference in urban water and nutrient retention, which are important ecosystem services that reduce environmental pollution. Contribution of green roofs to ecosystem services could be particularly high in dense urban settings, where roof area accounts for up to 30% of the total impervious area (Carter and Jackson 2007).

However, despite their ability to reduce runoff water amount, green roofs may actually degrade local water quality by leaching out nutrients during larger storm events. Previous studies have identified green roofs as sources of phosphorus (P), nitrogen (N), and organic carbon (Berndtsson et al. 2006, Teemusk and Mander 2007). The dynamics of N and particularly P in runoff are of concern, since excess loading of these nutrients to receiving water bodies can result in eutrophication (Carpenter et al. 1998). Understanding of the nutrient retention properties and mechanisms at work in green roofs remains limited (Berndtsson 2010, Rowe 2011,

Buffam and Mitchell 2015), but green roofs have been repeatedly found to leach out phosphate in runoff, with levels often similar to that in wastewater, enough to contribute to eutrophication in downstream waterways (reviewed in Buffam and Mitchell 2015). The source–sink dynamics of nitrogen on green roofs are not well understood or easily predictable. Some studies have shown that nitrate is retained (Berndtsson et al. 2006), while others found no significant difference between precipitation and runoff (Teemusk and Mander 2007), and some green roofs can be a source of nitrate (Buffam et al. 2016). The frequently high levels of N and P leached from green roofs results in an ecosystem disservice, which offsets some of the benefits of green roofs and highlights the need to understand, and ideally limit, nutrient losses from these ecosystems.

Cook-Patton and Bauerle (2012) called attention to the potential importance of plant diversity for several key ecosystem services provided by green roofs, including temperature regulation, storm water runoff reduction, nutrient retention, habitat, and aesthetics. Three published studies have specifically addressed water-resource-related services as a function of plant species richness on green roofs. Lundholm et al. (2010) found that water retention was highest at an intermediate level of life-form diversity treatments in green roof plots, while Dunnett et al. (2008) found that water retention was highest in plots with tall plants (or high root biomass) but found no clear relationship between plant diversity and rain-water retention. They hypothesized that structural complexity was more important than diversity for water retention (Dunnett et al. 2008). Lundholm et al. (2015) predicted variation in six different green-roof-derived ecosystem services, including water and nutrient retention, based on plant functional characteristics (height, individual leaf area, specific leaf area, and leaf dry matter content). In that study, plant growth rate was correlated to a one-time measurement of soil N and P concentrations, and this was taken as an indication that plant uptake of nutrients could reduce nutrient leaching; however, a direct effect of species richness was not shown (Lundholm 2015, Lundholm et al. 2015). None of these studies measured nutrient retention vs. nutrient leaching directly, which is an important urban ecosystem service to help prevent eutrophication in downstream waterways (Smith et al. 1999).

### *Study objectives and hypotheses*

The main objective of this study was to test whether green roof ecosystems conform to commonly observed patterns from natural ecosystems, in terms of the relationship between plant species richness and ecosystem function. Specifically, we explored the influence of plant species richness on two water-quality-relevant ecosystem functions of green roofs: water retention and nutrient (N, P) retention, following rain events. Variation in plant biomass was also tested, as an increase in biomass

production is commonly observed as a consequence of experimentally increasing plant diversity (e.g., Hooper et al. 2005, Cardinale et al. 2007), and an additive partitioning method (Loreau and Hector 2001) was used to discriminate between complementarity and sampling related effects on changes in biomass. Using six different common green roof plant species with distinct morphology and life form, we varied plant species richness by testing plants in monoculture, mixtures of three species, and mixtures of six species in green roof test plots. Following a series of rain events over the course of one year, we measured stormwater runoff reduction (for 33 rain events) and the associated retention or loss of dissolved inorganic N and P (for a subset of 10 rain events, approximately monthly). We hypothesized that (1) nutrient and water retention would vary among different plant species in monoculture and (2) greater plant species richness would result in increased water and nutrient retention, i.e., decreased hydrologic leaching losses. These hypotheses were based on the understanding that species will vary with respect to their water and nutrient needs, and the expectation that richer mixtures of species will have higher productivity (thus greater demand for water and nutrients), as well as increased capacity to fully exploit available water and nutrients due to complementary resource use. This work represents a novel exploration of the relationship between biodiversity and ecosystem function in an engineered ecosystem. The research will also inform urban planners, landscape designers, and interested municipalities as to which species, or which mixture of species, will most effectively retain water and nutrients as part of stormwater management plans.

## METHODS

### *Experimental design and field setup*

Eighty-five green roof experimental plots were assembled and set up late in the growing season in July 2012 at the University of Cincinnati Center for Field Studies located in rural Harrison, Ohio, USA. Experimental treatments included each of six plant species in monoculture, combinations of three species, and combinations of six species (Appendix S1), as well as growing-medium only (plant-free) plots and atmospheric-deposition only control plots which contained neither growing medium nor plants (Table 1). The plots were installed in two south-facing rows at 60 cm height above the ground, with an 8% slope in a plowed, fenced area accessible from a country road. Each 0.186 m<sup>2</sup> (30.5 × 61 cm) green roof module consisted of a 100% recycled high density polyethylene (HDPE) plastic tray with drainage holes (Eco-Roofs, Berrien, Michigan, USA), a perforated root membrane (DeWitt Filter Fabric, Forestry Suppliers, Jackson, Mississippi, USA), 8 cm depth of green roof substrate (proprietary extensive green roof aggregate-based blend, Tremco

Roofing, Cincinnati, Ohio, USA), and 24 plants (Emory Knoll Farms, Street, Maryland, USA) in a regularly spaced 4 × 6 pattern. The modules were placed in a second identical tray lined with plastic sheeting (6mil Clear Construction Film, Model CFBH0620C, Blue Hawk, Mooresville, North Carolina, USA), which served as the drainage layer. An extra module containing growing medium was placed at each end of the two rows in order to diminish edge effects. Runoff water from each plot drained separately through 15.9 mm outer-diameter × 12.7 mm inner-diameter Tygon tubing into a covered plastic collection bin (16 quart boxes, Model 16448-3, Sterilite, Townsend, Massachusetts, USA). A separate 30 cm diameter high-density polyethylene reservoir (Encore Plastics, Byesville, Ohio, USA) was placed nearby to collect bulk atmospheric deposition.

The plots contained a uniform composition and depth (8 cm) of growing medium. The growing medium was analyzed at the Agricultural Analytical Services Laboratory (Pennsylvania State University, University Park, Pennsylvania, USA). The maximum water-holding capacity, measured at 28%, falls within the accepted range of the Forschungsgesellschaft Landschaftsentwicklung Landschaftsbau (FLL) guidelines for the planning, execution, and upkeep of green roof sites, specifically for single course extensive systems (FLL 2008). Water permeability (saturated hydraulic conductivity) measured 0.03 cm/s, slightly under FLL standards listed between 0.1 and 0.067 cm/s (2008). Total organic content accounted for 33.1 g/L, phosphorus for 218.5 mg/L, and nitrate and ammonium together accounted for 13.0 mg/L. These values were within FLL standards except for phosphorus, which was slightly above the standard listed as ≤200 mg/L (FLL 2008).

Six plant species were used in the study, selected from the Emory Knoll Farm plant catalog (Street, Maryland, USA). They were (1) *Allium schoenoprasum* (Wild chives), (2) *Sedum cauticola* (Showy stonecrop), (3) *Sedum ellacombianum* (Japanese stonecrop), (4) *Sedum middendorffianum* (Diffused stonecrop), (5) *Sesleria caerulea* (Blue moor grass), and (6) *Talinum calycinum* (Largeflower fumefflower). These species were chosen based on a USDA hardiness level of 6 or harder (withstands average annual minimum winter temperature of −17.8°C or

TABLE 1. Summary of experimental plots.

Treatment	Number of combinations	Number of replicates per combination	Number of plots
Empty control	1	5	5
Growing medium alone	1	5	5
1 species	6	5	30
3 species	10	3	30
6 species	1	15	15
Total			85

below) such that they can survive the winter climate of the Cincinnati region, as well as specific requirements for green roof plants: a shallow root depth such that they can grow in the shallow plots and a full sun requirement. *Sedum* species were chosen for this project because they are widely used on green roofs due to their ability to survive in harsh climates, their ability to survive shipping conditions, and their relatively low cost. *Sedum* species are compact succulents with relatively short, wide, thick leaves and are facultative CAM-photosynthesizers, making them drought tolerant. The other three species were chosen to cover a range of morphologies. *Allium schoenoprasum* is relatively tall C3 plant with long, narrow, thin leaves and also has a bulb that enables survival to the next growing season and may also serve for water storage (USFS 2015; Missouri Botanic Garden, data available online).<sup>4</sup> *Sesleria caerulea* is a C3 grass with short, narrow, thin leaves that typically spread out along the ground. *Talinum calycinum* is a shorter succulent with narrow, thick leaves and has a tap root which retains water and facilitates dormancy during the winter (see footnote 4). *T. calycinum* is also a facultative CAM photosynthesizer, making it drought tolerant (Martin and Zee 1983). Due to logistical constraints in our experiment, only 10 combinations of three species were included. In an attempt to include representative combinations, genera (*Sedum* and non-*Sedum*) were taken into account when making combinations (Table 2).

In addition to receiving natural precipitation inputs, the plots were given supplemental water from a well on the property in a regime varying over time, particularly as the

plants established. Following planting, the plots were watered to saturation every 3 d for the first month to help establish the plugs. From late August to November 2012, the plots received only supplemental water every 5 rain-free days until the next rain event. No supplemental water was given in the winter. For the second year, the plots received supplemental water every rain-free 7 d during the spring/summer months (April–August 2013) and then were watered every rain-free 14 d during the autumn months (September–November 2013). For each irrigation, all plots were given the same amount of irrigation water.

### Plant biomass

Total plant biomass was estimated non-destructively for each of the experimental plots approximately 1 yr after planting, during the middle of the first full growing season (16–17 July 2013), using allometric equations to generate a biomass estimate for each plant. As allometric equations have not to our knowledge been published for these plant species, we first experimentally determined equations to relate aboveground and belowground plant biomass to easily-measurable non-destructive morphometry measurements (Appendix S2). Reliable allometric equations were generated for four of the six species, while the relationships for *Ses. caerulea* and *A. schoenoprasum* were weak, leading to higher uncertainty in biomass predictions for those two species (Appendix S2).

### Event runoff sampling

Following plant establishment in July–August 2012, the experimental monitoring period lasted from 1 September 2012 to 30 September 2013. After most rain events large enough to generate runoff from the plots, the amount of volume in the precipitation bucket and each runoff collection bin was measured by weight (CPWplus 35 Bench Scale, Adam Equipment, Oxford, CT, USA). Runoff was captured for 33 discrete events during the 13-month study period (Appendix S3), which included 73% of the total rain events of >10 mm precipitation and accounted for 72% of the total influent rain amount during that period. Snowfall in the region was minimal during this winter, and all 33 events were rain-driven rather than snowmelt-driven. Approximately once per month, immediately following a rain event of sufficient size to generate ample runoff for water chemistry analysis (typically >10 mm of precipitation), a sample of storm-water runoff was obtained from each of the 85 collection bins for chemical analysis ( $n = 10$  rain events; Appendix S3). Samples were collected in 500-mL clean acid-washed high-density polyethylene bottles, kept cool and dark, and transported to the lab for processing and analysis.

### Chemical analysis

For each sample immediately after collection, pH and conductivity (Orion 8102BNUWP ROSS Ultra

TABLE 2. Summary of three-species combinations.

Plant species content	Genera classification
<i>A. schoenoprasum</i> , <i>Ses. caerulea</i> , <i>T. calycinum</i>	NNN
<i>Sed. caudicola</i> , <i>Sed. ellacombianum</i> , <i>Sed. middendorffianum</i>	SSS
<i>T. calycinum</i> , <i>Sed. ellacombianum</i> , <i>Sed. middendorffianum</i>	NSS
<i>T. calycinum</i> , <i>Sed. caudicola</i> , <i>Sed. ellacombianum</i>	NSS
<i>Ses. caerulea</i> , <i>Sed. caudicola</i> , <i>Sed. middendorffianum</i>	NSS
<i>A. schoenoprasum</i> , <i>Sed. ellacombianum</i> , <i>Sed. middendorffianum</i>	NSS
<i>Ses. caerulea</i> , <i>Sed. middendorffianum</i> , <i>T. calycinum</i>	NSN
<i>A. schoenoprasum</i> , <i>Sed. caudicola</i> , <i>T. calycinum</i>	NSN
<i>A. schoenoprasum</i> , <i>Sed. middendorffianum</i> , <i>T. calycinum</i>	NSN
<i>A. schoenoprasum</i> , <i>Sed. caudicola</i> , <i>Ses. caerulea</i>	NSN

Note: N indicates non-*Sedum* and S indicates *Sedum*.

<sup>4</sup> <http://www.missouribotanicalgarden.org/PlantFinder/PlantFinderSearch.aspx>

Combination pH and Orion 013005MD Conductivity Cell, Thermo Scientific, Waltham, MA, USA) were measured. After filtering out particulates (EMD Millipore, Billerica, MA, USA), the samples were frozen for preservation until analysis of dissolved ammonium, nitrate, and phosphate concentrations. A microplate adaptation (Ringuet et al. 2010) was used for analyzing each dissolved nutrient, with the phenol-hypochlorite reaction method for ammonium (Weatherburn 1967), the vanadium reduction method for nitrate (Doane and Horwath 2003), and the molybdate method for phosphate (Lajtha et al. 1999). Samples were analyzed in quadruplicate, and quality control was assured using a quality assurance check standard (Ultra Scientific, North Kingstown, RI, USA). There were a small number of missing values (~1%) due to either collection bin malfunction in the field, loss of sample in the lab, or high analytical variability resulting in exclusion of sample from analysis. For statistical analyses, the data for these missing samples was gap-filled using the average value from the other replicates of the same event and treatment.

#### Calculations

Plant biomass was expressed in units of  $\text{g/m}^2$  by normalizing the calculated biomass to plot area ( $0.186 \text{ m}^2$ ). Runoff was calculated for each plot and event by normalizing runoff volume to plot area to give runoff in units of  $\text{L/m}^2$ . Nutrient fluxes ( $\text{mg/m}^2$  of N or P) were calculated by multiplying the runoff amount by concentration ( $\text{mg/L}$  of N or P) for each sample and normalizing to plot area. Runoff volume and nutrient fluxes were summed over all measured rain events to give a total flux value for each individual plot for each analyte.

#### Statistical analysis

Data distributions were examined with the help of histograms, Q-Q plots, and skew and kurtosis statistics, as well as the Shapiro–Wilk test for normality. Based on this information, to improve normality prior to statistical analysis, ammonium, nitrate, and DIN data were natural log transformed such that the absolute value of skew was  $<1$  and of kurtosis was  $<2$ . Runoff volume and phosphate data were already normally distributed based on the visual diagnostics and the Shapiro–Wilk test, and were left untransformed for analysis. The plant biomass data were left untransformed for the among-species ANOVA analysis but were natural log transformed for the ANOVA analysis of the effect of species richness, based on analysis of model diagnostics.

To test the hypothesis that water and nutrient retention varied among different plant species in monoculture, one-way ANOVA (JMP v. 10, SAS Institute, Cary, NC, USA) was used to test the effect of individual species on ammonium, nitrate, and phosphate fluxes and runoff

volume. The response variable used was the sum of fluxes over all measured rain events for the given analyte, with each plot as an individual replicate. The six individual species treatments (monocultures) had five replicates ( $n = 5$  each). The empty control and growing medium alone treatments were included in this analysis and were also replicated five times ( $n = 5$  each). Tukey's HSD post hoc test was administered for all pair-wise comparisons of treatments for any ANOVA that indicated significant differences among treatments ( $P < 0.05$ ).

To test the hypothesis that greater plant species richness results in increased water and nutrient retention using one-way ANOVA (JMP v.10), the effect of richness was examined for ammonium, nitrate, and phosphate fluxes and normalized runoff volume. The richness treatments included each of the six monocultures in replicates of five ( $n = 30$ ), each of the 10 combinations of three species together in replicates of three ( $n = 30$ ), and the combination of all six species together replicated 15 times ( $n = 15$ ). Tukey's HSD post hoc test was administered for all pair-wise comparisons of treatments for any ANOVA that indicated significant differences among treatments ( $P < 0.05$ ).

To determine whether plant biomass varied as a function of plant species or richness, we carried out the same ANOVA analyses described previously, with total plant biomass as the response variable and using only the vegetated plots ( $n = 75$ ). For plant biomass, the relative contributions of selection (sampling) effects vs. complementarity effects among species were also calculated using the additive partitioning method of Loreau and Hector (2001), using data on biomass for individual species in monoculture vs. biomass of the respective species in the six-species mixtures.

Finally, to test the hypothesis that variation in water nutrient retention was related to variation in plant productivity and biomass for these green roof plots, we regressed the total fluxes of water, ammonium, nitrate, and phosphate against total plot plant biomass, with each plot as a replicate, excluding empty control plots but including the five plots with growing medium alone ( $n = 80$ ).

## RESULTS

### Plant biomass

Total plant biomass for the vegetated plots in mid-July 2013 ranged from 13 to  $323 \text{ g/m}^2$ , with an average of  $123 \text{ g/m}^2$ . Biomass varied substantially among the different species in monoculture (Table 3), with *Sedum ellacombianum* having the highest biomass, *Sedum middendorffianum* second highest, and the other four species having low biomass (Fig. 1a). In the three-species and six-species mixtures, biomass of the individual plots was intermediate between the extremes observed for the monocultures. The six-species mixture had significantly higher biomass than the average of the monocultures

TABLE 3. Effect of plant species identity.

Analyte	<i>F</i>	df	<i>P</i>
Plant biomass	77.95	5,24	<0.0001*
Runoff volume	75.50	7,32	<0.0001*
Ammonium	11.80	7,32	<0.0001*
Nitrate	16.93	7,32	<0.0001*
DIN	26.73	7,32	<0.0001*
Phosphate	102.40	7,32	<0.0001*

Notes: Results of one-way ANOVA tests for differences in plant biomass, runoff volume, and nutrient fluxes as a function of plant species identity in monoculture. For plant biomass, only the vegetated treatments were included in the analysis, while for the water and nutrient runoff fluxes, all treatments including empty control and growing medium alone were included. DIN = ammonium + nitrate.

\* $P < 0.05$ .

(Table 4, Fig. 1b), indicating a positive net biodiversity effect on plant biomass. The net biodiversity effect was a mean increase of 23 g/m<sup>2</sup> (+21%) plant biomass for the six-species mixtures as compared to the arithmetic mean of the monocultures. The differences among treatments were even more pronounced for the geometric means (Fig. 1b), corresponding to the difference in distributions among log-transformed biomass data. Average biomass in the three-species mixture was intermediate between that of the average monocultures and the six-species mixture, and was not significantly different from either. The six-species mixture ( $131 \pm 22$  g/m<sup>2</sup>) was still much lower in biomass than *Sed. ellacombianum*

( $311 \pm 21$  g/m<sup>2</sup>), the most productive monoculture (Student's *t* test,  $P < 0.001$ ).

The four species with low biomass failed to flourish in the plots, and in fact, there were no experimental plots of *A. schoenoprasum*, *Ses. caerulea*, *Sed. cauticola*, or *T. calycinum* monocultures in which all of the plants survived the entire year, with overall mortality ranging from 21% to 37% for these species. The two more productive species, in contrast, had <2% mortality. There was no evidence that the mortality rate varied by richness treatment (one-way ANOVA,  $P > 0.2$  for all individual species and for the plots as a whole), with total plot mortality at 20–21% for all three richness levels.

There was no relationship between the productivity of species in monoculture and the relative change in productivity in the same species in the six-species mixture (data not shown). This suggests that the selection (sampling) effect was minimal (Loreau and Hector 2001, Cardinale et al. 2007). This was borne out by an analysis of the relative contributions of selection vs. complementarity effects using the additive partitioning method of Loreau and Hector (2001), which revealed that most of the change in biomass could be attributed to complementarity (+20.9 g/m<sup>2</sup>), while selection contributed much less (+2.6 g/m<sup>2</sup>). In short, *T. calycinum*, *Sed. ellacombianum*, *Sed. middendorffianum*, and *A. schoenoprasum* all had somewhat higher biomass in the six-species mixture than would be expected based on their monoculture performance, with the mean difference ranging from 23% to 58%. *Sed. cauticola*, which had the highest mortality of any species, decreased in biomass by a mean of 29% when

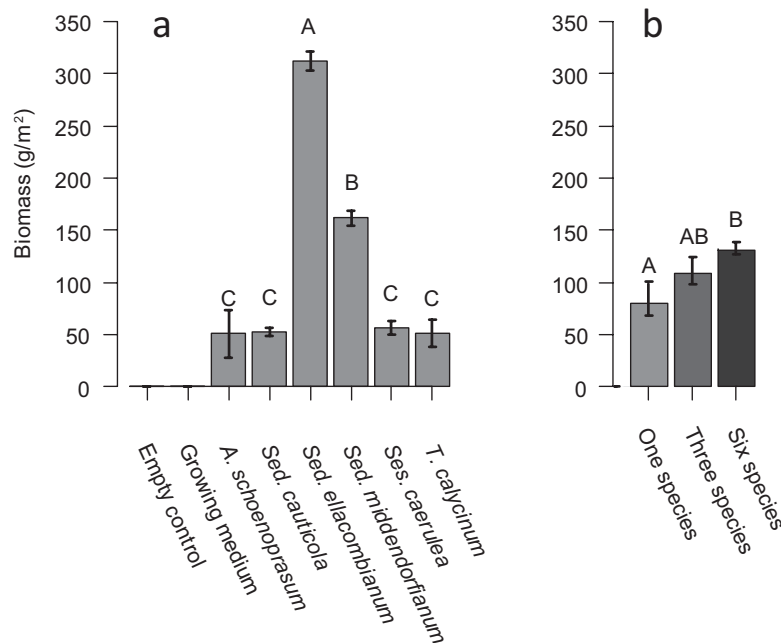


FIG. 1. Mean (error bars  $\pm 1$  SE) total plant biomass (16–17 July 2013) for (a) all individual species treatments and (b) species richness treatments. Within each panel, treatments not connected by the same letter are significantly different from one another. Note that for panel (b), the values shown are the geometric means, since the statistical analysis used log-transformed values.

TABLE 4. Effect of species richness.

Analyte	F	df	P
Plant biomass	3.35	2,72	0.041*
Runoff volume	0.85	2,72	0.431
Ammonium	2.89	2,72	0.062
Nitrate	4.43	2,72	0.015*
DIN	4.76	2,72	0.011*
Phosphate	0.44	2,72	0.644

Notes: Results of one-way ANOVA tests for differences in plant biomass, runoff volume, and nutrient fluxes as a function of plant species richness.

\* $P < 0.05$ .

in the six-species mixtures, while the grass (*Sesleria caerulea*) changed little.

#### Runoff volume

Runoff volume varied significantly among treatments (Table 3). Runoff from growing medium alone plots was significantly lower than empty control plots, with an average overall reduction of 22% relative to the controls. Vegetated plots had an even lower runoff volume, with an average overall reduction of 28% relative to empty control plots. All vegetated treatments had significantly reduced runoff volume relative to growing medium alone, except for the *Sed. ellacombianum* in monoculture (Fig. 2a). However, there was no difference in runoff amount among the different species in monoculture (Fig. 2a) or among the different levels of species richness (Table 4, Fig. 2b).

#### Dissolved inorganic nitrogen

Dissolved inorganic nitrogen ( $\text{DIN} = \text{NO}_3^- + \text{NH}_4^+$ ) fluxes varied substantially among species in monoculture. DIN flux was highest from the growing medium alone treatment and *Sed. cauticola* monoculture treatments, both significantly greater than the empty control plot (input) flux. The other monocultures had DIN flux between the values of the growing medium and empty control, with *Ses. caerulea* highest, *Sed. ellacombianum* lowest, and the other three species intermediate (Fig. 3a). Monocultures of *Sed. ellacombianum* and *Sed. middendorffianum* had significantly lower fluxes than did the empty control plots, i.e., showed a net retention of DIN. The high flux of DIN from plots containing growing medium alone and the decreased flux of DIN from those containing vegetation indicate that growing medium is a source of DIN but plants act to reduce this source, thus acting as a sink.

There was also a significant effect of species richness on DIN retention (Table 4). In summary, the higher the number of species, the greater the reduction of DIN flux, in accordance with our expectations based on the BEF hypothesis. Plots containing all six species presented a significantly lower flux of DIN than the mean of the plots containing monocultures, while the plots containing three species presented an intermediate DIN flux, though not significantly different than the other treatments (Fig. 3b). The biodiversity effect on N retention was substantial, with the DIN hydrologic leaching decreasing from an average of 91 mg N/m<sup>2</sup> in monoculture to an average of 53 mg N/m<sup>2</sup> in the six-species mixture. This corresponds to a shift from being approximately net

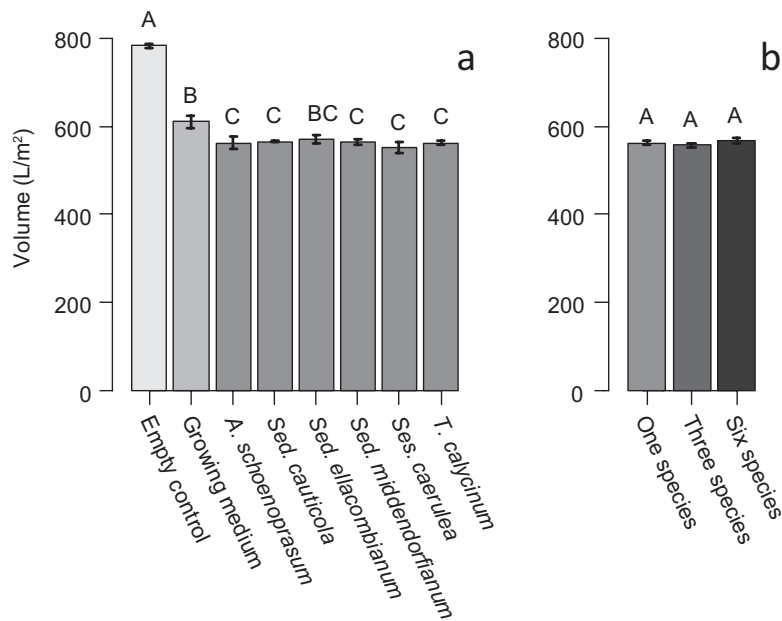


FIG. 2. Mean (error bars  $\pm 1$  SE) total summed runoff volume for (a) individual species treatments and (b) species richness treatments from entire duration of study (33 rain events). Within each panel, treatments not connected by the same letter are significantly different from one another.

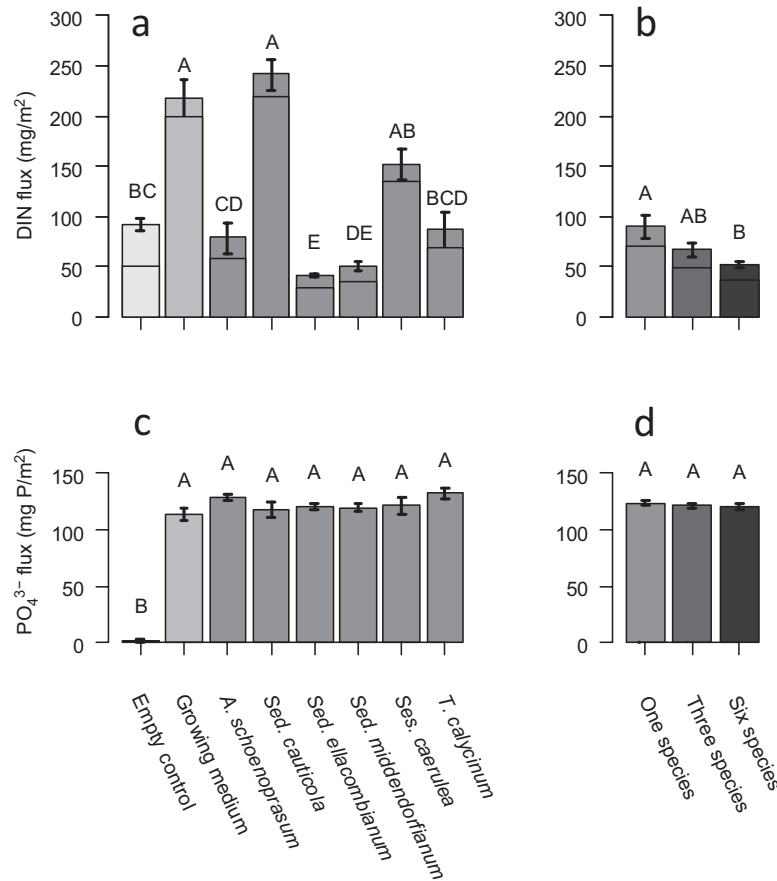


FIG. 3. Mean (error bars  $\pm 1$  SE) total summed flux of (a, b) DIN and (c, d)  $\text{PO}_4^{3-}$  for individual species treatments (left) and species richness treatments (right) from entire duration of study (10 events). The horizontal line in the DIN plots indicates division between mean  $\text{NO}_3^-$  flux (below the line) and mean  $\text{NH}_4^+$  flux (above the line). Within each panel, treatments not connected by the same letter are significantly different from one another. Note that for DIN, the values shown are the geometric means, since the statistical analyses used log-transformed values.

neutral with respect in DIN retention in monoculture to serving as a DIN sink with a net flux averaging  $-40 \text{ mg N/m}^2$  (relative to the average flux of  $93 \text{ mg N/m}^2$  in control plots). The DIN leaching from the six-species mixture ( $53 \pm 14 \text{ mg N/m}^2$ ) was not significantly different than the most productive monoculture (*Sed. ellacombianum*, DIN leaching =  $42 \pm 4 \text{ g N/m}^2$ ) though there was a trend (Student's  $t$  test,  $P = 0.10$ ) for the mixture to have lower N retention (greater N leaching).

The variation in DIN reflects treatment effects on both ammonium and nitrate (Table 4), but most of the variation in DIN was driven by variation in nitrate, which was the major part of the DIN in almost all cases. Interestingly, the green roof plots, regardless of treatment, were a sink for ammonium relative to empty control plots, with a significantly lower flux of ammonium in the runoff from vegetated and growing medium alone plots relative to the empty control plots (mean values shown on Fig. 3). However, the presence or absence of vegetation did not significantly affect ammonium fluxes. Nitrate, in contrast, was increased in runoff from growing medium alone plots

relative to empty controls, but the presence of plants decreased nitrate runoff to a varying degree, depending on species and richness level (mean values shown on Fig. 3).

#### Phosphate

All treatments exhibited high fluxes of phosphate relative to the empty control plots (Fig. 3c). The plots containing vegetation, either in monoculture or in varying levels of species richness, were not different from growing medium alone nor were they different from one another in their phosphate fluxes (Table 4, Fig. 3). The greater flux of phosphate from planted plots and growing medium alone plots indicate that these green roof systems, particularly the growing medium, are sources of phosphate.

#### Plant biomass vs. runoff fluxes

There was no relationship between plant biomass and runoff volume, flux of ammonium, or flux of phosphate



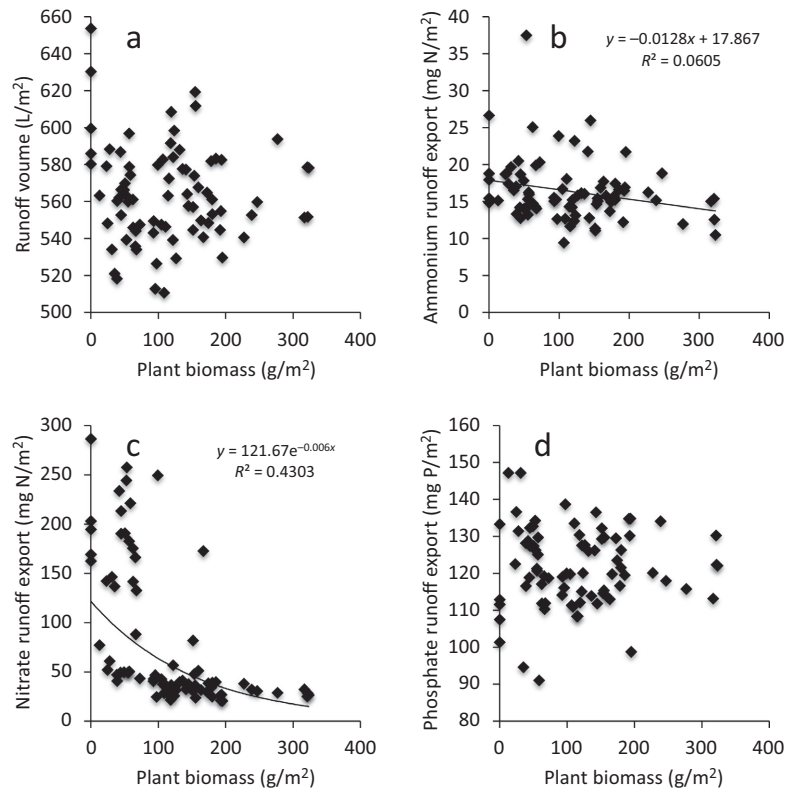


FIG. 4. Total runoff and nutrient fluxes from each experimental plot as a function of peak growing season plant biomass. (a) Runoff water volume from 33 events; (b) ammonium flux from 10 events; (c) nitrate flux from 10 events; (d) phosphate flux from 10 events. Best-fit regressions are shown, where significant.

(Fig. 4). However, there was a significant negative correlation between plant biomass and runoff of nitrate or DIN (which primarily consists of nitrate). The best-fit equation to the data was a negative exponential with an intercept (example for DIN shown in Fig. 5). The relationship was particularly strong ( $R^2 = 0.92$ ,  $P < 0.001$ ,  $n = 9$ ), when the values were expressed as means of each experimental treatment (Fig. 5b); the relationship was still highly significant, though noisier, with values expressed as data from individual plots ( $R^2 = 0.46$ ,  $P < 0.001$ ,  $n = 80$ ; Fig. 5a).

## DISCUSSION

### *Water and nutrient retention in green roof systems*

In the current investigation, the presence of vegetation significantly increased water retention relative to growing medium alone, presumably due to increased evapotranspiration between rain events. Transpiration loss in the vegetated plots was apparently greater than any decrease in evaporation from the growing medium due to shading from the plants. These findings contrast with two recent studies that found in some green roofs the presence of vegetation does not change water retention relative to growing medium alone, suggesting that in those studies

any increase in transpiration was similar to the decrease in evaporation (VanWoert et al. 2005, Lundholm et al. 2010). Lundholm et al. (2010) carried out a similarly designed experiment to ours, on extensive green roofs investigating the effects of monocultures and mixtures of one, three, and five life-form groups on the ecosystem functions of summer roof cooling and water retention. They found that intermediate levels of life-form diversity treatments captured significantly more water than monocultures but not more than growing medium alone treatments (Lundholm et al. 2010). In contrast, in the present study there was no difference in water retention among vegetation types or based on species richness.

The relative degree of plant cover, type of plants or growing medium, or climate conditions could contribute to the contrasting results between our study and the others in terms of the effect of vegetation on water balance. One potentially important difference between the present study and the Lundholm et al. (2010) study is that the present study allowed one month of establishment period while the Lundholm study allowed two years, and our vegetation coverage was somewhat lower. This allowed for growing medium exposure to solar radiation even in the vegetated plots, which would allow for relatively high evaporation rates. Based on our results relative to those of the other studies with more complete vegetation

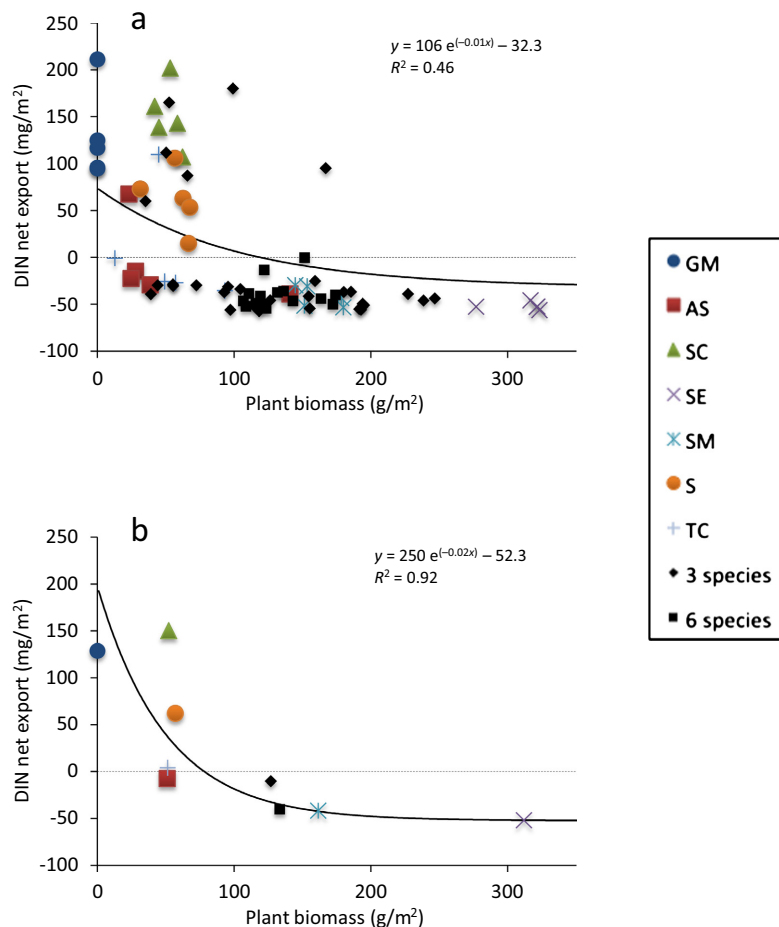


FIG. 5. (a) Total net DIN runoff flux as a function of total plant biomass, for each of 75 experimental plots containing various combinations of plants in monoculture, three-species, or six-species mixtures, and five plots containing growing medium alone without plants. The net flux is calculated by subtracting the average runoff flux for the empty control plots from the runoff flux for the given experimental plot, so that values above zero are net export, below zero net retention. The best-fit curve to the data is shown with a solid black line. (b) Identical figure but depicting the average value for each treatment. Abbreviations are GM, growing medium; AS, *Allium schoenoprasum*; SC, *Sedum cauticola*; SE, *Sedum ellacombianum*; SM, *Sedum middendorffianum*; S, *Sesleria caerulea*; and TC, *Talinum calycinum*.

coverage, we suggest that there is likely a non-linear relationship between plant cover and water retention in green roof ecosystems, with the highest retention occurring at an intermediate level of cover where both evaporation and transpiration can be substantial.

All of the treatments had lower ammonium flux than the empty control, indicating that these green roofs are a sink for ammonium. Other studies have also concluded that green roofs retain ammonium (Berndtsson et al. 2009, Wang et al. 2013). This seems to be a consistent pattern for green roofs. The decrease of ammonium may be attributable to nitrification (Berndtsson et al. 2009). Ammonium, a positively charged compound, may also decrease in the runoff as it binds to the growing medium, which typically has high cation-exchange capacity due to the presence of heat-expanded shale, slate, or clay with an abundance of negatively charged surfaces (e.g., Solano et al. 2012).

Nitrate runoff flux was significantly less in nearly all the vegetated treatments (as well as the empty control) than the growing medium alone treatment, indicating that growing medium is a source of nitrate while the plants provide a sink/removal mechanism. A range of results have been found in other recent green roof studies (reviewed in Buffam and Mitchell 2015), suggesting that green roofs can serve as a sink or a source or be neutral with respect to nitrate fluxes (Berndtsson et al. 2006, Teemusk and Mander 2007, Speak et al. 2014, Buffam et al. 2016). The varying results have been attributed to varying plant requirements for nitrate, differing types or depths of growing media, and the age of the roofs (Buffam and Mitchell 2015). The wide range of nitrate fluxes for the different treatments in our study confirm the influence on N balance of growing medium and a variable effect of the plant community depending on the species involved and their productivity. In our study, the

release of nitrate from growing medium is similar to that found in other studies of relatively young/new green roofs or newly created green roof plots, which have an abundant internal supply of available nitrogen in the growing medium.

The effect of plant presence on nitrate flux in our study confirms patterns seen in other recent controlled studies using green roof plots (reviewed in Buffam and Mitchell 2015). For instance, the efflux of nitrate from green roof plots can be reduced by about an order of magnitude by the presence of vegetation relative to growing medium alone (Beck et al. 2011, Vijayaraghavan et al. 2012) but that effect depends upon the type of vegetation, with, for instance, individual species in monoculture giving rise to different nitrate efflux (Aitkenhead-Peterson et al. 2011). The method of cultivation and density of plants also influences nitrate retention, with a few studies showing that more fully vegetated plots having higher nitrate retention, thus lower efflux (Emilsson et al. 2007, Wang et al. 2013). The increase of nitrate accompanied by the decrease in ammonium as water passes through the growing medium, may indicate that nitrification is occurring (Berndtsson et al. 2009, Buffam et al. 2016). The fluxes of nitrate cannot all be attributed to nitrification of precipitation-derived ammonium but could result from nitrification of mineralized organic nitrogen that is contained within the organic matter component of the growing medium.

Phosphate runoff flux was significantly greater in all treatments than in the empty control, indicating that these green roof systems are a source of phosphate. The lack of difference among growing medium alone vs. vegetated plots indicates that the source of phosphate is the growing medium, and the plants have little additional effect. Other studies in the literature support these results, finding that compost and/or fertilizing agents in the green roofs are responsible for the increased total phosphorus (Berndtsson et al. 2006, Teemusk and Mander 2007, Bliss et al. 2009, Wang et al. 2013, reviewed in Buffam and Mitchell 2015). In contrast, some studies have not found a release of phosphate in their green roof plots (Teemusk and Mander 2007, Berndtsson et al. 2009). Kohler et al. (2002) concluded that phosphate decreases over time as compost is lost from the system and fertilizer application ceases. The phosphate in the present study appears to come from the relatively fresh growing medium and is likely derived from mineralization of the organic material (Rowe 2011, Buffam and Mitchell 2015).

It is notable that there were significant effects of vegetation on fluxes of water and N, in spite of the fact that the experiment had only been running for one year, and the plots had not yet fully filled in. As a consequence of the low biomass of four of the six plant species (Fig. 1a) and the lack of full coverage after one year (see Appendix S1 for a picture), biomass in our experiment was low relative to typical ranges for fully established green roofs with close to 100% plant cover. For context, a survey of 12 established, fully vegetated extensive green roofs in

Michigan and Maryland, USA, indicated an average plant biomass of  $\sim 619 \text{ g/m}^2$  based on calculations from the carbon content of aboveground biomass (Getter et al. 2009). The vegetation-related effects will likely increase over time as plots fill in and are expected to be more pronounced for systems with more complete vegetation coverage (Buffam and Mitchell 2015).

#### *Biodiversity and ecosystem function in green roofs*

Our results indicate that the biodiversity–ecosystem function hypothesis holds for these green roof plots, with higher plant productivity and higher nitrate and DIN retention for more species-rich plots. The results are qualitatively similar to patterns reported for natural and restored ecosystems, with plant productivity and resource utilization commonly increasing with plant species richness (e.g., Tilman et al. 1996, Callaway et al. 2003, Balvanera et al. 2006). Much less information is available on BEF relationships in engineered ecosystems like green roofs, although Lundholm et al. (2010) carried out plot-scale green roof BEF experiments and found that mixtures of life-form groups outperformed monocultures for a number of green roof functions, while some monocultures performed other functions especially well. They suggested that when observing combinations of functions (multifunctionality), rather than single functions, the more diverse mixtures of life-form groups optimized performance (Lundholm et al. 2010, 2015). In a follow-up study, the researchers examined species mixture performance for changes to leachable nutrient content of green roof substrate over time, but did not find significant results for N or P and did not distinguish between leaching vs. incorporation into biomass for the fate of these nutrients (Lundholm 2015).

Observations from the patterns of DIN flux in our study suggest (1) the growing medium itself is a source of DIN in runoff and (2) the different plant species vary greatly in their effect on DIN, but on balance generally take up DIN and thus reduce DIN runoff, the one exception being *Sed. caudicola*, which was actually an additional net source of DIN. (3) The loss in N via runoff was correlated with plant biomass. Treatments with mean plant density above a threshold of about  $100 \text{ g/m}^2$  biomass were a net sink for DIN, while plots with lower plant biomass could either be net neutral or be a source of DIN. This relationship could be related to the incorporation of N into biomass by the plants that are actively growing (thus reducing leaching N loss in high biomass plots) or to the microbial mineralization of dead organic material from the plants that were failing to thrive (thus increasing leaching losses in low biomass plots). *Sed. caudicola* for instance did not fare well in the experiment under the harsh environmental conditions and had many plants dying, which could explain the N loss. (4) The mixtures of plant species, particularly the mixture of all six species, retained more DIN than would be expected based on the behavior of the six individual species.

A possible explanation for this is that the species that were thriving and growing (*Sed. middendorffianum* and particularly *Sed. ellacombianum*) were able to capture and use the excess DIN from the species which were faring poorly, particularly from *Sed. caudicola*, which suffered from mortality and was a net source for DIN.

Based on an analysis of the relative performance of the individual species in the six-species mixtures as compared to monocultures (Loreau and Hector 2001), the increase in production (biomass) with species richness in our study was driven primarily by complementarity effects rather than selection or sampling effects. This indicates that interactions among plant species are important in this system and the augmented performance in terms of increased biomass and nutrient retention is not simply due to the higher probability of the inclusion of highly productive species in the diverse mixture. Complementarity and sampling effects have been observed individually, concurrently, and sequentially in different studies (Aarssen 1997, Huston 1997, Hector et al. 1999, Huston et al. 2000, Hooper et al. 2005), but several reviews have found that commonly complementarity is the more important of the two (Loreau and Hector 2001, Cardinale et al. 2007), as found in this study.

There was a positive net biodiversity effect (Loreau and Hector 2001) for both biomass and N retention, with the mean value for the mixture greater than the mean of the monocultures. This overyielding of plant biomass in species-rich mixtures relative to the average of monocultures is common, observed, for instance, in 79% of biodiversity studies in a meta-analysis by Cardinale et al. (2007) and in the majority of studies analyzed by Balvanera et al. (2006). However, there was no evidence in our study of transgressive overyielding (Schmid et al. 2008), where the more species-rich plots would have higher overall productivity than any one monoculture. This lack of transgressive overyielding has also been a common observation when measured in other biodiversity experimental studies (Schmid et al. 2008), found for example in only 12% of the studies analyzed by Cardinale et al. (2007). Cardinale et al. (2007) suggested that transgressive overyielding is only likely to occur after substantial time has elapsed, estimated at about five years in that study. In that context, it is not surprising that our study found the most productive monoculture *Sed. ellacombianum* to still exceed the diverse mixture in terms of biomass after only one year of growth in our experiment.

More surprising was our finding that the species-rich plots were nearly as effective at retaining N as the most effective monoculture (*Sedum ellacombianum*). This is in spite of the fact that the *Sed. ellacombianum* monoculture has more than twice the biomass of the six-species mixture. The non-linearity in the relationship between biomass and N leaching and the variation among treatments even at similar biomass (Fig. 5) suggests that N retention is not simply a linear reflection

of variation in biomass or productivity. One plausible interpretation of the strong effect of richness on DIN retention is that there is more effective overall use of N with more diverse plant assemblages. In this case, increasing diversity could serve to increase resilience against N loss under difficult environmental conditions, when some species suffer or die off, as was the case in our study.

### Summary

In summary, this study revealed that for these newly established green roof plots (1) biomass varied among plant species and increased with species richness, (2) the presence of plants reduced the volume of runoff, but with no measurable effect of plant identity or species richness, (3) the plots were a sink for ammonium, with the greatest effect in the most species rich plots, (4) the soil-like substrate was a source of nitrate while plants were a sink for nitrate, with effect varying by plant species, (5) increasing plant species richness increased nitrate and DIN retention, and (6) green roof substrate was a source of phosphate, with the presence and identity of plant species having no measurable additional effect. These results generally align with published observations from full-scale green roofs, which have consistently exhibited retention of water and ammonium, leaching of phosphorus, and variable impact on nitrate (reviewed in Buffam and Mitchell 2015).

This study also provides strong evidence for the BEF hypothesis in engineered ecosystems as evidenced by the increased biomass and inorganic nitrogen retention with increased plant species richness. Results for biomass were similar to patterns commonly observed in diversity experiments (e.g., Loreau and Hector 2001, Cardinale et al. 2007), with the most species-rich treatment having greater biomass than the average of all monocultures, but not greater than the most productive monoculture. Tight internal cycling of N is a characteristic of many natural terrestrial ecosystems (Vitousek and Reiners 1975, Likens et al. 1977, Chapin et al. 2011), but the behavior of N in engineered ecosystems like green roofs has not been as well studied; this study provides some of the first clear evidence of the role of plant diversity in directing nutrient cycling within an engineered system. Interestingly, clear biodiversity effects were seen in this study of the first year after establishment, even though plots had not yet fully filled in. It is quite possible that among-species interactions, and thus effects of biodiversity, would further increase over time as has been observed in studies of natural ecosystems (Cardinale et al. 2007). Biodiversity effects might also be stronger in intensive green roofs (Oberndorfer et al. 2007), which have much deeper soils, larger biotope space in which distinct ecological niches can develop (Dimitrakopoulos and Schmid 2004), and more diverse plant assemblages as compared to those in our experiment.

### *Implications for green roof design*

We found that increasing plant species richness increased the capacity of the green roof plots to retain N and hold it tightly within the ecosystem, during the initial year after planting. The implication is that vegetated roofs with a mixture of species are likely to be more efficient at N retention, particularly if the different species are in close proximity to one another so that if some of the plants are failing to thrive or even dying off, the excess N can be used by other plant species within the roof, rather than being lost to hydrologic leaching during runoff events. This is an important feature since N fertilizer is expensive and leaching losses of N can be detrimental to downstream ecosystems. In this context, we encourage green roof designers to use diverse plantings, particularly functionally diverse plantings (Cadotte et al. 2011), to minimize loss of inorganic N.

This tight vegetation control of the cycling of N suggests that the vegetation may be N-limited in these ecosystems. This suggestion is supported by the observation that green roofs frequently develop into sinks for N, while in contrast P is often leached out in large excess for many years or decades (Buffam and Mitchell 2015). This pattern implies that the substrate mixtures currently used for the construction of green roofs could be designed to contain much lower P content, thus higher N:P. A decrease in P content has the potential to improve effluent water quality without sacrificing plant vitality, particularly if the ecosystems can be designed to hold N tightly. Thus, in addition to diverse roof plantings, we recommend substrate mixtures that contain available N:P ratios appropriate to plant needs.

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