If You Build It, Will They Come? Plant and Arthropod Diversity on Urban Green Roofs Over Time

Kelly Ksiazek-Mikenas[1,2,*], John Herrmann[3], Sean B. Menke[4], and
Manfred Köhler[5]

Abstract - Cities can support biodiversity and provide the ecosystem services upon which life depends. Green roofs are increasingly common in cities and could be designed to increase biodiversity, but community assembly and succession patterns on green roofs are poorly documented. We used long-term vegetation surveys at 6 extensive green roofs and sampled a 1–93-year chronosequence at 13 extensive green roofs in northeast Germany to determine if plant and arthropod diversity increased over time in a deterministic pattern. We also explored abiotic factors that may contribute to community diversity on green roofs. We found that vegetation cover increased over time, but beyond the first 2 years, vegetation richness and diversity did not. There is no evidence for broadly applicable patterns of succession of plant communities on green roofs. Although the abundance, richness, and diversity of arthropods increased slightly over time, this trend was not statistically significant for ants, bees, beetles, or spiders. The size of the vegetated area of the roof, the conditions of the growing substrate, species richness and diversity of the vegetation, and the proportion of ground-level green space surrounding the roof at 0.5-km and 1.0-km radii were associated with increased arthropod abundance, richness, and diversity. We conclude that community diversity on green roofs is highly variable and dependent on several biotic and abiotic factors that are not consistent among extensive green roofs. Community successional patterns are not conserved; thus, each green roof may support a novel community and contribute to urban biodiversity.

Introduction

Rich biological diversity increases ecosystem function and stability (Hooper et al. 2005, Loreau et al. 2001). However, global changes in land use are predicted to negatively impact already impoverished biodiversity worldwide (McDonald et al. 2013, Millennium Ecosystem Assessment 2005, Sala et al. 2000, Seto et al. 2011). Traditional approaches to support biodiversity conservation have focused on preserving ecosystems in their unaltered state, but increasingly include restoration and conservation in urban areas, particularly as cities continue to expand (Ellis et al. 2010). Many urban and suburban environments contain novel ecosystems (Hobbs et

[1]Northwestern University, Department of Plant Biology and Conservation, Evanston, IL 60208, USA. [2]Chicago Botanic Garden, Department of Plant Conservation Science, Glencoe, IL 60022, USA. [3]University of Kiel, Department of Landscape Ecology, Kiel, Germany. [4]Lake Forest College, Department of Biology, Lake Forest, IL 60045, USA. [5]Hochschule Neubrandenburg University of Applied Science, Department of Landscape Planning and Geomatics, Neubrandenburg, Germany. [*]Corresponding author - kellyksiazek2011@u.northwestern.edu.

al. 2006), which are human-influenced habitats containing previously undocumented species combinations. The diversity of plants, animals, fungi, and microorganisms supported by novel ecosystems contributes to resilient ecological communities and supports global conservation goals (Kowarik 2011, Pickett and Zhou 2015).

Due to the novelty and variety of engineered urban habitats, it may be difficult to determine how biodiversity will change under different management scenarios. Typical natural patterns of succession show initial growth in species richness and diversity followed by a decline or plateau over very long periods of time (Johnson and Miyanishi 2008). In highly stochastic and environmentally stressful ecosystems like sand dunes and dry rocky grasslands, the sequential replacement of plant species and increase in species diversity, species evenness, and trophic-level complexity may proceed slowly as certain species die out and get replaced (succession; Odum 1969, Prach and Walker 2011, Walker and Chapin 1987). Predictable patterns of increased species richness and diversity following planting can also be observed in urban habitats, although patterns are more difficult to discern due to confounding effects of initial planting design, fragmentation, human disturbance, environmental stress, and a lack of large source populations for colonizing propagules (Niemelä 1999, Sattler et al. 2010). Urban vegetation and faunal assemblages undergo dramatic changes after establishment as the species respond to repeated disturbance and stress (Odum 1969, Palmer et al. 1997, Sterling et al. 1984). Thus, patterns of species richness, diversity, and composition tend to be site-dependent in human-altered habitats (Johnson and Miyanishi 2008, Palmer et al. 1997). Site characteristics, therefore, may play an important role in the biodiversity supported in cities.

Green roofs can serve as habitat for many plants and animals (Baumann 2006, Brenneisen 2006, Grant 2006, Kadas 2006, Köhler 2006). These novel habitats are now touted as supporting biodiversity (Cook-Patton and Bauerle 2012, Ksiazek 2014, Lundholm 2015, Oberndorfer et al. 2007, Thuring and Grant 2015, Williams et al. 2014) and some cities, such as Basel, Switzerland, have regulations which require biodiversity provisions on green roofs (Brenneisen 2015). As in other habitats, greater biodiversity provisions can increase diversity of both flora and fauna. Several rare and endangered animal species have been found to use intentionally designed "biodiverse roofs", which are green roofs specifically designed to attract diverse fauna (Brenneisen 2006; Brenneisen and Hänggi 2006; Dunnett 2015; Grant 2006; Kadas 2006, 2010; Mann 1998). However, the most common type of green roof, called extensive, consists of homogenous, shallow, rocky substrates <20 cm deep, with no additional provisions to enhance biodiversity. Extensive green roofs (hereafter referred to as green roofs) are typically planted with succulent *Sedum* or *Phedimus* spp. (stonecrops) and require minimal watering and maintenance due to the growth constraints of the shallow, nutrient-poor substrate (Dunnett and Kingsbury 2004, Oberndorfer et al. 2007, Snodgrass and Snodgrass 2006). Although the list of plant species suitable for green roofs is limited and biodiversity is not typically a design focus, if management is designed to enhance plant diversity to increase over time, the green roofs might host increasingly diverse organisms. The extent to which green roofs can support high biological diversity and continue to do so for generations remains unknown.

Just as natural systems go through successional transitions (Turner et al. 1998), plant and animal communities on green roofs are expected to become more diverse after installation as organisms colonize and communities assemble. Other urban habitats, such as vacant lots, that experience environmental stresses similar to green roofs, including high light-intensity and drought-prone soil, exhibit somewhat predictable patterns of community assembly (Kardol et al. 2012). On green roofs, seed-dispersing annual plants spontaneously colonize, germinate, and spread (Nagase et al. 2013). Arthropods and microorganisms begin to colonize these sites almost immediately, and are often brought in with the planting material or growing substrate (MacIvor and Ksiazek 2015, Molineux et al. 2014). To date, most studies of biota on green roofs have been carried out for very short time periods (Rowe 2015) and long-term monitoring is rare. Community assembly and diversity patterns on green roofs may resemble other urban habitats or may lack comparable reference sites (Dunnett 2015), and exhibit unique patterns due to their highly engineered state. Additional factors that may influence patterns of diversity and succession include availability of food and nesting resources in the surrounding environment, characteristics of the substrate, properties of the building itself, or interactions between these variables (Gabrych et al. 2016). Green roofs are more isolated than other urban habitats because they are separated from the ground and rarely visited by people and non-flying animals. Colonization under high stress but low disturbance may result in communities that increase in cover, richness, and diversity over time. Empirical research to support these expectations is lacking due to the relatively nascent state of ecological research on green roofs (Francis and Lorimer 2011).

Germany is one of the only countries with green roof sites older than a decade on which to study long-term successional patterns. Building guidelines that have been in place for more than 30 years require all green roofs to be built following similar practices (FLL 2006). We looked at patterns of plant diversity using both repeated surveys and a chronosequence, which is a space-for-time substitution that can be used to study plant succession to determine if the sites are following the same trajectory (Walker et al. 2010). We first compiled long-term vegetation surveys (a minimum of 12 consecutive years) from 6 green roofs in northeastern Germany. We then performed vegetation and arthropod surveys on a chronosequence of 13 green roofs ranging in age from 1 to 93 years in the same cities. Using these data, we explored the changes in vegetation cover, arthropod abundance, and vegetation and arthropod species richness and diversity on green roofs over time. We also generated hypotheses for future green-roof studies by testing the effect of site-specific variables (such as water retention, depth of substrate, surrounding green space, and roof size) on plant and arthropod colonization.

Field Site Description

Long-term vegetation data were available for 6 green-roof sites (hereafter, long-term sites) in northeastern Germany built between 1986 and 2001 (Table 1). Four sites (B1–B4) are located in Berlin (4000 inhabitants per km^2) and 2 (N1–N2) in Neubrandenburg (740 inhabitants per km^2). These 2 temperate cities lie within 135 km

of each other and have similar average precipitation and temperature. All green roof sites had minimal to no watering, fertilizing, or weeding regimes, with the exception of removing tree seedlings to prevent roof damage from mature woody roots.

To compare results from the long-term sites to a chronosequence, we selected 13 green roofs (hereafter, chronosequence sites) in the same cities that varied in age from the time of construction (Table 1). Eight of these green roofs (B4–B11) were located in Berlin and 5 (N1–N5) were in Neubrandenburg. Sites varied in size (50–3040 m^2), roof height (2.9–24.7 m), and amount of green space in the vicinity (11–97% surrounding green space within 1 km). All sites had minimal to no maintenance schedules (Table 2).

Methods

Vegetation

At the long-term sites, we identified all plant species and estimated cover to the nearest percent once or twice per year following a complete search of each site. We conducted vegetation surveys at these sites after initial planting and then annually for 12–27 y; we followed the nomenclature of the Rothmaler field guide (Jäger et al. 2013). At sites with biannual surveys, we averaged values from the 2 surveys to estimate total annual cover. We determined separate cover values of overlapping species, thus it was possible for the total cover of the roofs to exceed 100%. Köhler (2006) and Köhler and Poll (2010) presented more-detailed methods of vegetation surveys at some of these locations.

At the chronosequence sites, we surveyed the vegetation in late June 2013 at the peak of the flowering season. We identified all flowering and non-flowering vascular plants on the roof to species, following the nomenclature in the Rothmaler field guide (Jäger et al. 2013). We estimated the percent cover of each species for

Table 1. Green roof sites used for long-term data collection (L) and chronosequence studies (C) in northeast Germany.

Site name	Site ID	City	Collection period/ years present	Study type
Paul-Linke Ufer Housing Complex	B1	Berlin	1986–2012	L
Ufa Fabrik Café	B2	Berlin	1992–2012	L
Ufa Fabrik Saal	B3	Berlin	1992–2012	L
Ufa Fabrik Schule	B4	Berlin	1992–2012/27	L/C
Ufa Fabrik, new building	B5	Berlin	1	C
Mensa Nord, Humboldt University	B6	Berlin	5	C
Block 6 Water Filtration Plant	B7	Berlin	6	C
Heinrich Roller Schule	B8	Berlin	7	C
Berliner Wasserbetriebe, East	B9	Berlin	13	C
Berliner Wasserbetriebe, West	B10	Berlin	15	C
Ökowerk Nature Center	B11	Berlin	93	C
Hochschule Neubrandenburg, Haus 2	N1	Neubrandenburg	1999–2012/14	L/C
Hochschule Neubrandenburg, Haus 3	N2	Neubrandenburg	2001–2012/12	L/C
Neubrandenburg Social Court	N3	Neubrandenburg	9	C
Haus des Sports	N4	Neubrandenburg	14	C
Marktplatz Center	N5	Neubrandenburg	16	C

the entire roof and for a 25-m^2 plot area (survey plot) centered on each roof, in which we collected additional arthropod and substrate data.

Arthropods

We collected arthropods from the chronosequence sites using pitfall traps. Traps were constructed from 200-ml glass jars with 56-mm diameter openings and screwon lids. Each trap contained a plastic insert coated with 1 of 3 colors of UV-reflective spray paint to attract bees: yellow, blue, or white (LeBuhn et al. 2003). We spaced 3 traps of each color (9 total) 5 m apart, in a 3 x 3 grid pattern centered on the survey plot except at N3, where a rectangular shape accommodated the small size of the 5 m x 10 m roof. In early April, we buried traps with closed lids flush with the substrate surface. Vegetation was short enough in these spots that flying insects could see the traps. After allowing the substrate to settle for 2 weeks, we filled the traps with a 5%-formaldehyde solution and removed the lids for ~96 h. We collected arthropods on the same days for all sites, with a ±1-day difference between Neubrandenburg and Berlin. We drained trap contents through a 1-mm sieve and stored the samples in 70% ethanol until identification. We repeated this collection procedure once per month, April–September (576 collection-hours on each roof), to accommodate for seasonal variation in arthropod activity throughout the flowering season (Ramirez et al. 2015).

We identified all collected arthropods to class, and individuals from Arachnida and Insecta to order. We chose 4 guilds from Arachnida and Insecta for further taxonomic resolution and species identifications: ants (Insecta, Hymenoptera, Formicidae), bees (Insecta, Hymenoptera, Apoidea), beetles (Insecta, Coleoptera), and spiders (Arachnida, Araneae). We identified Formicidae using Seifert (2007) and Arachnida using Roberts (1987) and Roberts (1999); we followed the

Table 2. Measured site properties, vegetation species richness (S) and Shannon-Wiener diversity (*H'*) on 13 green roofs along a chronosequence in northeastern Germany. Percent green refers to the amount of green space in the area within a circular radius measured from the center of the roof.

Site ID	Age (y)	Height (m)	Size (m^2)	1 km % green	500 m % green	250 m % green	% cover	Mean vegetation height (cm)	Mean substrate depth (cm)	S	*H'*
B5	1	4.3	140	52	35	13	80	37.8	10.3	21	2.344
B6	5	6.6	2510	13	16	9	95	7.9	9.2	22	1.758
B7	6	3.7	230	28	25	13	85	7.4	6.2	15	2.699
B8	7	12.5	70	17	12	11	95	24.9	11.0	24	1.876
N3	9	2.9	50	45	32	44	93	6.9	5.8	4	1.247
N2	12	16.7	1050	53	68	47	98	15.4	7.3	21	1.993
B9	13	24.7	1410	11	12	5	96	18.8	11.3	15	2.447
N4	14	14.5	270	42	43	53	98	21.6	11.4	22	2.331
N1	14	15.7	1030	46	44	42	90	10.3	7.3	11	2.441
B10	15	24.7	1470	12	7	3	97	12.9	11.4	16	1.719
N5	16	14.7	3040	50	31	17	97	7.5	6.7	6	1.914
B4	27	5.8	330	46	43	22	95	17.4	10.5	27	2.531
B11	93	3.4	620	97	97	89	94	6.4	9.2	30	2.539

nomenclature of Platnick (2013). Species identifications for remaining Apoidea were completed by J.C. Kornmilch, Universität Greifswald Zoologisches Institut und Museum, Greifswald, Germany, and Coleoptera were identified by Dr. K.-H. Kielhorn, BioM and independent consultant, Berlin, Germany. We assigned morphospecies when identification to species was not possible.

Site properties

We measured the size of each chronosequence site as total substrate area available for colonization and calculated roof height from calibrated digital photographs (Table 2). We obtained roof age from building managers at each site. We devised a method to estimate percent green space surrounding the building using CorelDraw Ex 3 (Corel Corporation, Ottawa, ON, Canada) to clip satellite images from Google Earth at 250-m, 500-m, and 1000-m radii from the center of each site. Clipped images were viewed in Adobe Photoshop, in which we employed the color-range selection tool to select all pixels within the yellow to green spectrum, using a fuzziness setting of 8. To calculate the percent green space, we divided the number of green/yellow pixels representing vegetation by the total number of pixels (Table 2). We used Google satellite images to confirm that the pixels selected for green space did not include oxidized copper or other green-colored structures.

At each chronosequence site, we collected samples and measured substrate depth at 4 locations within the 25-m^2 plot and calculated mean substrate depth. The samples from each plot were mixed, oven-dried for 48 h at 110 °C, and mixed again with deionized water to measure substrate pH (McGuire et al. 2013). We calculated the proportion of particle-size classes in 500-g dried substrate samples with a Haver EML 200 digital N-test sieve shaker (Haver and Boecker, Oelde, Germany). We ran the shaker for 5 min at an intensity of 6 to separate the samples into 7 size classes: >8.00 mm, 4.00–8.00 mm, 3.15–4.00 mm, 2.00–3.15 mm, 1.25–2.00 mm, 0.25–1.25 mm, and <0.25 mm. Proportions of the substrate in each category were used to calculate mean particle size for substrate at each site. We measured the difference in weight between the oven-dried and saturated substrate in three 100-g samples and calculated mean water-holding capacity of substrate (g water/g substrate). We performed water-infiltration rate tests 3 times using a 20-cm diameter uniform sieve sleeve and 1-cm calibrated pin-apparatus to calculate mean infiltration rate (cm/sec) for each substrate sample.

Statistical analyses

All statistical analyses were conducted in R, version 3.2.1 (R Development Core Team 2015). To incorporate species evenness and species richness into our diversity metrics (Morris et al 2014), we used vegetation species abundances at each site x year combination to calculate the Shannon–Wiener diversity index (H') at both the long-term and chronosequence sites. We chose the Shannon-Wiener diversity index because it takes into account rare species that may have been recent recruits to the sites. We conducted one-way ANOVAs to determine the significance of linear relationships between time and vegetation cover, richness, and diversity for the long-term sites. We used NMDS ordinations with the vegetation-cover data for both site

types to look for patterns of convergence toward a specific vegetation assemblage over time. We also grouped the chronosequence sites by age category (1–4 years, 5–10 years, 11–20 years, and >20 years) in addition to quantitative age to see if patterns emerged at a coarser level.

We used abundance of the arthropod guilds identified to species (ants, bees, beetles, and spiders) to calculate H' and characterize differences in arthropod communities between sites. We employed poisson generalized linear models for the analyses because ant abundance was not normally distributed. One of the chronosequence sites was more than 3 times older than the others (site B11: 93 years since construction); thus, we $\log_{10}$-transformed the age of the chronosequence sites for these analyses. We ran NMDS ordinations with abundance of each arthropod guild to look for patterns in arthropod diversity over time.

To determine the effect of substrate properties (depth, water-infiltration rate, water-holding capacity, mean particle size, and pH) on vegetation and arthropod diversity at the chronosequence sites, we performed a principal component analysis (PCA) using Euclidian distances. Due to non-normality of the data, we $\log_{10}$-transformed water infiltration rate and square-root–transformed water-holding capacity prior to the PCA. The resulting PC axis 1 (PC1) explained 86.3% of site variation and was heavily weighted by substrate depth and partially weighted by water-infiltration rate. PC axis 2 (PC2) explained an additional 7.9% of the variation and was heavily weighted by mean substrate-particle size with a lesser effect by water-infiltration rate. Together, PC1 and PC2 explained 94.1% of the between-site variation in substrate properties, and the axis values were used in subsequent regression analyses.

We employed backward elimination of linear models to test for the effects of the interaction between site age and each of the site properties (size; height; surrounding green space at 250 m, 500 m, and 1000 m; substrate PC1; and substrate PC2) on vegetation cover, richness, and diversity. The same procedure was used to test for the effects of interactions between age and the site properties in addition to the vegetation cover, species richness, and diversity on arthropod abundance, richness, and diversity.

To determine the effect of site properties on the community composition, we used the cover (vegetation) or abundance (arthropods) and relative frequency of the identified species to calculate importance values (IVs) at each chronosequence site. We used IVs to perform NMDS ordinations in the "vegan" package for the vegetation and each of the identified arthropod guilds. We excluded Formicidae (ants) from this analysis because we documented only 5 species during our surveys. Fitted environmental variables were plotted if they had a significant ($P < 0.05$) effect on structuring the community.

Results

Temporal changes in biodiversity

Vegetation. Species richness increased slightly after the initial planting at each of the 6 long-term sites. However, time was not a significant predictor of vegetation

cover, species richness, or diversity at any of these sites (Fig. 1). Vegetation composition remained relatively stable over time at 4 of the 6 sites but moved toward dominance by *Allium schoenoprasum* L. (Chives) at the other 2 long-term sites (Fig. 2).
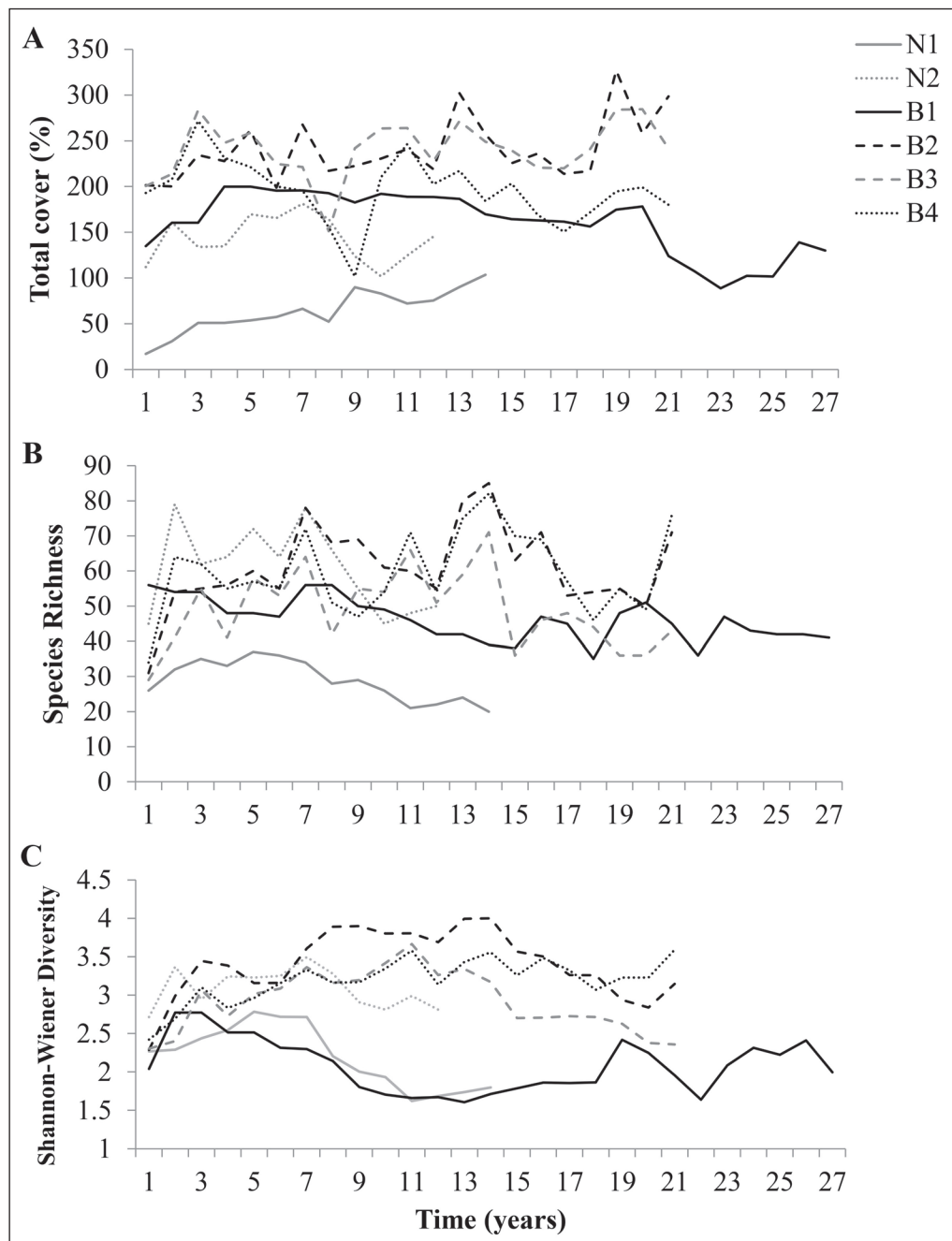

Figure 1. (A) Vegetation cover, (B) species richness, and (C) Shannon-Wiener diversity index at 6 long-term green-roof sites over time.

Plant species richness varied among the chronosequence sites from 4 to 30 species (Table 2). In contrast to the variable "time" for the long-term sites, age was a significant predictor of vegetation cover for the chronosequence sites ($P = 0.021$, $F = 7.17$, $R^2 = 0.340$); newer roofs had more open-substrate gaps following installation, but older roofs had few gaps and higher cover. Age was not a significant predictor of vegetation species richness or diversity (Fig. 3). The NMDS ordination of the chronosequence sites (not shown) revealed clustering of the sites by age group. However, no clear pattern of vegetation composition following a trajectory though time emerged when the quantitative age values of the sites were used rather than age categories.

Arthropods. We collected a total of 9797 arthropods from the chronosequence sites (Table 3), with a mean of 754 individuals per roof (sd ± 395, range = 327–1582). Diptera (flies) were the most abundant (5036 individuals, 51.4%), followed by Hemiptera (true bugs; 2542 individuals, 25.9%), Hymenoptera (bees, wasps, ants; 1080 individuals, 11.0%), Araneae (spiders; 682 individuals, 7.0%), Coleoptera (beetles; 295 individuals, 3.0%), and 1.7% other arthropod groups. We excluded 14 Coleoptera specimens from the analyses because they were larvae and could not be identified further. The arthropod collection is currently stored at the
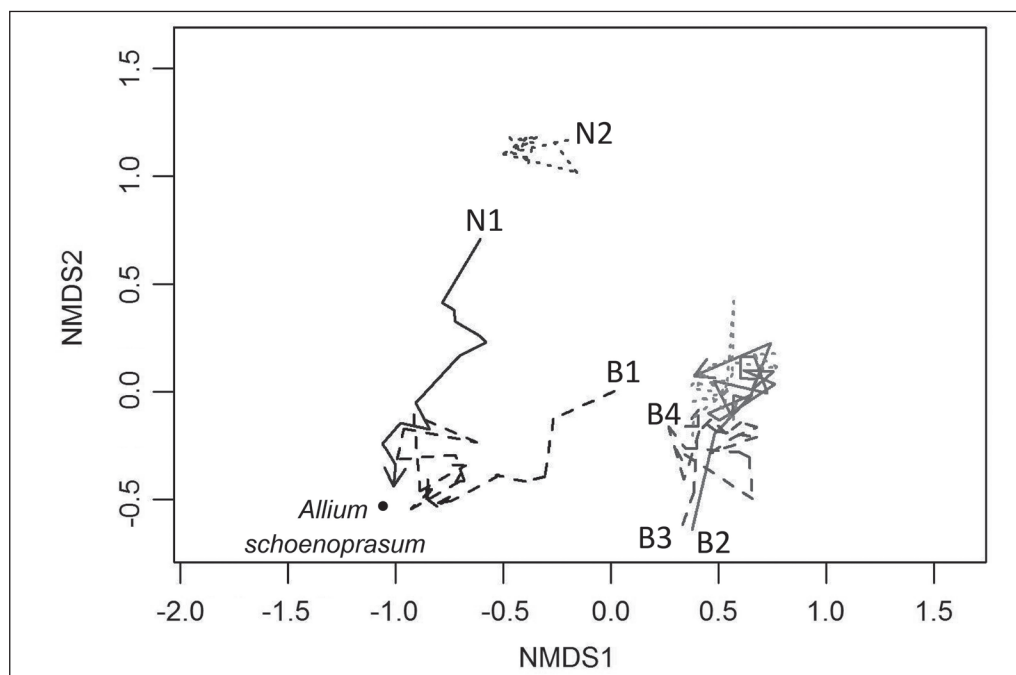

Figure 2. Non-metric multidimensional scaling ordination of vegetation coverage on 6 long-term green roofs sampled annually between 12 and 27 times. Site labels indicate the initial community composition, and solid, dotted, and dashed arrows connect the time-series data for each site, showing direction of vegetation-community composition progression over time. During the sampling period, vegetation assemblages at 2 of the 6 sites (N1 and B1) converged near the three-dimensional space where cover was dominated by *Allium schoenoprasum* (Chives).

Figure 3. (A) Vegetation cover significantly increases with green roof age on a chronosequence of extensive green roofs ($P = 0.021$, $R^2 = 0.34$). (B) Vegetation species richness and (C) Shannon-Wiener diversity index increase with green roof age but dashed slopes of the linear regressions are not significantly different from zero ($P > 0.05$).
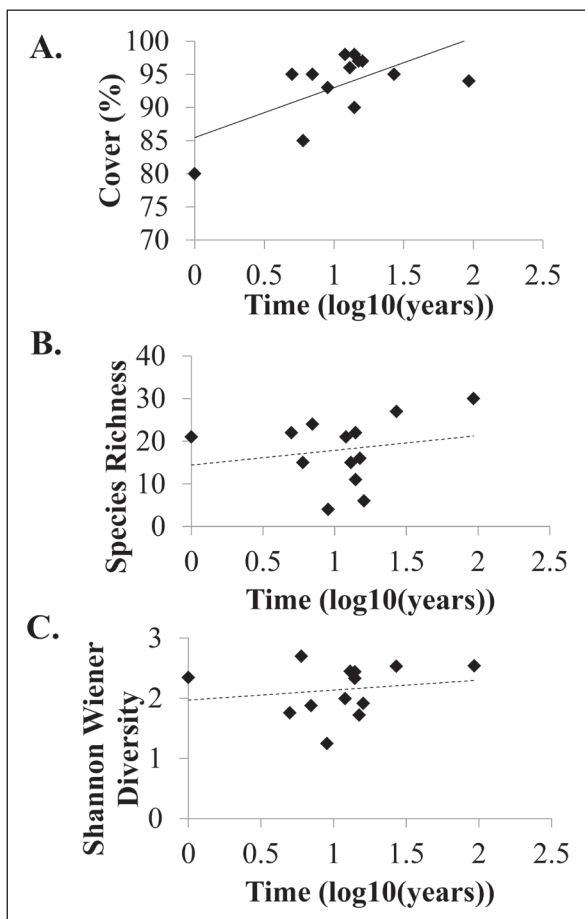
Table 3. Diversity indices for 4 arthropod groups collected from green roofs along a chronosequence. Indices are the number of individuals (n), species richness (S) and Shannon-Wiener diversity (H').

Site		Araneae (Spiders)			Apoidea (Bees)			Coleoptera (Beetles)			Formicidae (Ants)		
ID	Age (y)	n	S	H'	n	S	H'	n	S	H'	n	S	H'
B5	1	29	13	2.221	34	15	2.360	10	8	1.973	0	0	N/A
B6	5	20	13	2.773	28	11	1.921	9	6	1.735	2	1	0.000
B7	6	34	13	1.867	11	6	1.540	7	7	1.946	2	1	0.000
B8	7	19	9	1.936	3	3	1.099	5	3	0.950	167	1	0.000
N3	9	13	7	1.790	18	9	1.956	24	1	0.000	3	1	0.000
N2	12	69	16	2.690	19	12	2.361	12	7	1.699	44	1	0.000
B9	13	53	15	2.549	29	16	2.477	29	12	2.087	17	1	0.000
N4	14	303	30	2.921	20	10	2.086	53	26	2.750	203	2	0.031
N1	14	17	12	2.448	22	11	2.197	21	8	1.468	76	1	0.000
B10	15	33	18	2.752	26	11	2.087	37	12	1.916	140	2	0.042
N5	16	33	19	2.990	26	11	1.898	33	7	1.110	0	0	N/A
B4	27	26	14	2.530	104	21	2.491	13	6	1.411	6	3	0.868
B11	93	33	12	2.290	59	24	2.781	28	15	2.192	1	1	0.000
Overall		682	61	3.738	399	49	2.879	281	62	2.817	661	5	0.941

Chicago Botanic Garden, Glencoe, IL, USA (ants and spiders) and at the Hochschule Neubrandenburg, Neubrandenburg, Germany (all others).

Backward elimination of linear models revealed no significant effects ($P < 0.05$) of roof age on arthropod abundance, richness, or diversity for any of the 4 selected guilds (Fig. 4). According to the NMDS ordinations, only Formicidae assemblages clustered by age, with the 2 oldest roofs separate from the younger roofs, which contained 100% *Lasius niger* (L.) (Black Garden Ant).

Effects of site-specific variables on biodiversity

Vegetation. As shown in Table 4, there were significant additive effects of age and substrate properties on vegetation cover, with lower PC1 and PC2 values associated with greater cover over time. Decreasing substrate PC1 was also significantly correlated with higher vegetation species richness, and the additive models that included age and each PC axis explained more of the variation in the dataset than the models with age alone (Table 4). PC1 was also a significant variable in structuring the vegetation community (Fig. 5A). We found no significant effects of interactions between site age and any of the other site characteristics on vegetation diversity.

Arthropods. Our analyses revealed significant effects of the interaction between site age and the other site variables on some of the arthropod diversity metrics
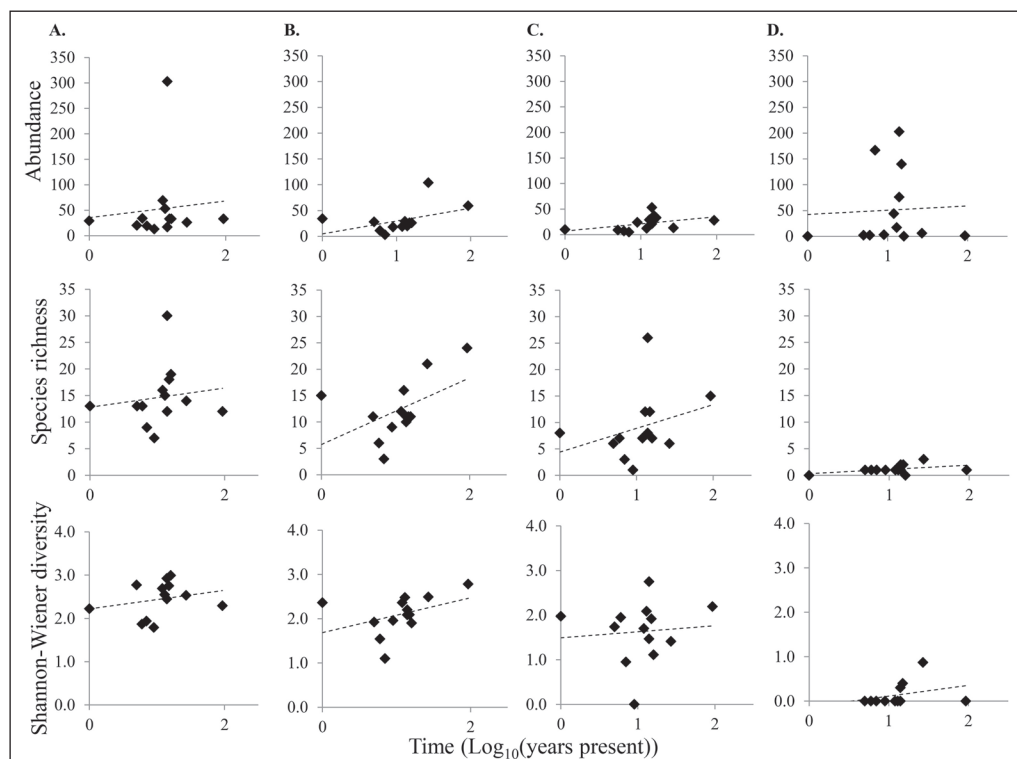

Figure 4. Abundance, species richness, and Shannon–Wiener diversity indices increase with green roof age from a chronosequence of sites but the slopes of the linear regressions are not significantly different from zero ($P < 0.05$): (A) spiders, (B) bees, (C) beetles, and (D) ants.

(Table 4). Specifically, spider diversity significantly increased with the interaction between age and vegetation species richness and the additive effect of age and roof size (Table 4). The interaction between increasing site age and decreasing substrate PC2 significantly increased abundance and species richness of bees. Bee species richness and diversity were also positively correlated to increased green space at both distances of 500 m and 1000 m from the roof (Table 4). Higher plant diversity had a significant positive effect on beetle diversity, and the interaction between age and decreasing substrate PC1 was positively correlated to increased species richness of ants (Table 4). Site age was not a significant variable in structuring the arthropod communities. Rather, the size of the roof (area) was a significant factor for both the spiders and bees and the composition of the spider community was additionally affected by the building height and vegetation diversity (Fig. 5B–D).

Discussion

Effects of time on green roof communities

The species richness and diversity of vegetation on green roofs was generally maintained over time. Both the long-term– and chronosequence-site analyses revealed no clear pattern of vegetation succession. Neither vegetation species richness nor species diversity increased significantly over time. Although species richness and diversity increased for some arthropods with roof age, we observed no statistically significant trends in fauna using the chronosequence sites. Our data suggest that green roof communities exhibit variable patterns of diversity, as seen in urban ecosystems on the ground (Pickett et al. 1999, Prach and Pysek

Table 4. Results of model selection and effects of age, site-level properties, and their interactions on vegetation cover, arthropod abundance (n) and vegetation and arthropod species richness (S) and Shannon-Wiener diversity (H'). Only models significant at $P < 0.05$ are shown.

		Best model	F	R^2	P
Vegetation	Cover	Age	7.171	0.340	0.0215
		Age + substrate PC1	3.663	0.307	0.0274
		Age + substrate PC2	5.491	0.282	0.0411
	S	Substrate PC1	6.641	0.377	0.0257
		Age + substrate PC1	6.166	0.287	0.0324
		Age * substrate PC2	6.058	0.338	0.0361
Arthropods					
Araneae (spiders)	H'	Age * vegetation S	8.593	0.358	0.0167
		Roof size	10.433	0.440	0.0080
		Age + roof size	9.352	0.416	0.0121
Apoidea (bees)	n	Age * substrate PC2	12.338	0.567	0.0057
	S	Green space 500	6.359	0.309	0.0284
		Green space 1000	6.039	0.296	0.0318
		Age * substrate PC2	21.055	0.701	0.0013
	H'	Green space 500	6.405	0.311	0.0279
		Green space 1000	4.883	0.245	0.0493
Coleoptera (beetles)	H'	Vegetation H'	7.484	0.319	0.0210
Formicidae (ants)	S	Age * substrate PC1	7.870	0.558	0.0205

1999, Zhang et al. 2013), where ecological succession can be altered, suppressed, or completely arrested (Collins et al. 2000). Our results support those of other green roof studies conducted over shorter time-frames (Bates 2013, Carlisle and Piana 2015, Dvorak and Volder 2010, Rowe 2015). It is possible that minimally maintained green roofs follow site-specific successional trajectories that are difficult to distinguish without additional replicates and longer observation periods (Matthews 2015, Prach et al. 2001). Conversely, the presence of an initial plant community on green roofs may preclude the detection of sharply increasing species diversity, as can be the case in more traditional studies of succession. This lack of an observed pattern of succession has also been found in other urban habitats (Gantes et al. 2014, Kopel et al. 2015) and has been attributed to the large heterogeneity in land-scape factors.

Vegetation cover was the only variable that significantly increased over time in our study. We drew this conclusion using the chronosequence sites but not when tracking individual long-term sites. Increasing cover on green roofs may indicate plant growth and appear advantageous to site managers, but greater plant cover may not, in fact, support greater biodiversity. For example, in abandoned lots in Berlin, Fischer et al. (2013) found that increasing vegetation cover was negatively correlated with target grassland species and that highly mobile and invasive species grew, spread, and increasingly contributed to cover over time. Cover and diversity may
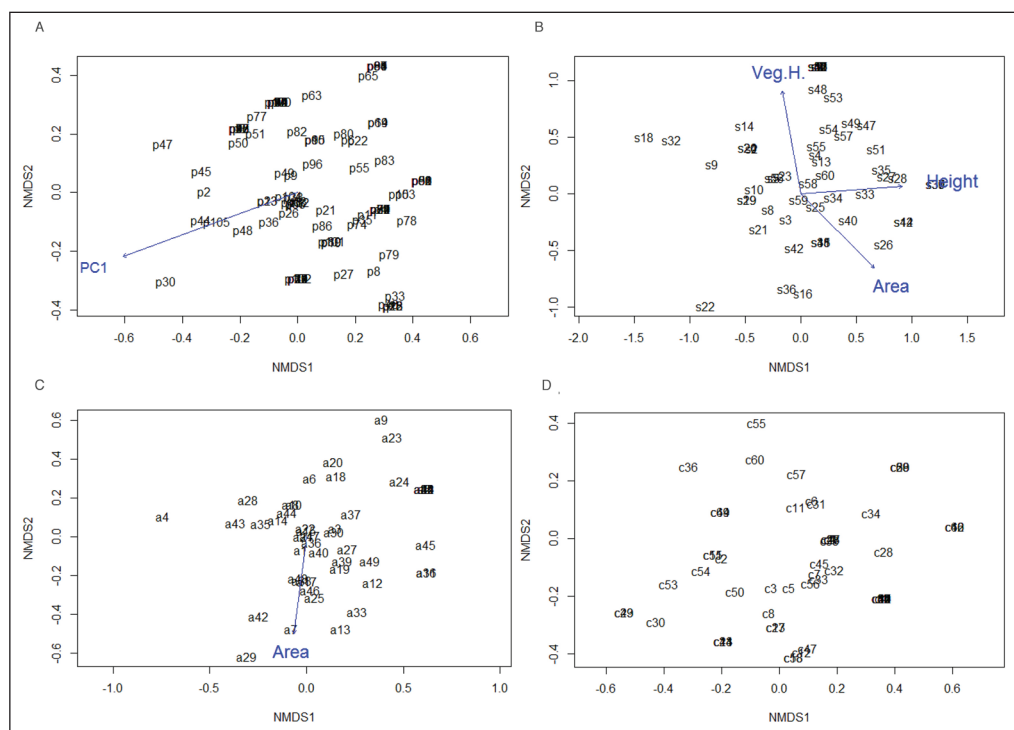

Figure 5. Environmental factors significantly structure the species composition of the (A) vegetation, (B) spider, and (C) bee communities but not the (D) beetle community on 13 extensive green roofs.

not be related on green roofs due to the initial predominance of succulent and grass species that reproduce vegetatively. As we observed in ⅓ of the long-term sites, a single planted species (Chives) dominated, making high cover an inaccurate proxy for measuring a green roof's diversity. Chives have also been found to dominate on older versus younger green roofs in Finland (Gabrych et al. 2016). This finding highlights the importance of distinguishing between cover and species richness and diversity, in addition to factors such as a plant species' origin, when evaluating a green roof's ability to support biodiversity.

Effects of site-specific variables on green roof communities

Site-level variables, such as those measured in this investigation, are considered important factors in structuring ground-level communities (Walker and Chapin 1987). Likewise, our results demonstrate the necessity of measuring these factors when determining how green roof communities develop, especially because shared patterns of vegetation and arthropod succession are lacking. In the chronosequence, properties of the substrate were the only variables found to have a significant relationship with vegetation species richness and community composition. The significant negative effects of PC1 and PC2 (representing substrate depth, particle size, and water infiltration rate) on vegetation cover and richness over time indicate that a greater cover and richness of plants may be achieved in substrates that hold more water (lower rates of water infiltration and substrate that contains more clay and sand than large rocks). This finding has been demonstrated on other German green roofs (Köhler and Poll 2010). The relationships between greater cover and species richness with decreased substrate depth is somewhat surprising and in contrast to what has been found in other green roof studies (Dunnett et al. 2008, Gabrych et al. 2016, Getter and Rowe 2009, Madre et al. 2014, Olly et al. 2011, Thuring et al. 2010). Deeper substrates are typically able to hold more water than shallow substrates (vanWoert et al. 2005) and can provide plants with increased root space. It is possible that these increased resources allow more-competitive species to dominate rather than creating niches for a larger variety of drought-tolerant species. Overall, our analyses indicate that substrate depth, particle size, and water retention are important factors to consider when designing green roofs for biodiversity purposes. Specific hypotheses to be tested in future experiments are outlined in Figure 6.

Our analyses confirm that effects of site-level variables differ between arthropod assemblages (Satler et al. 2010). The significant relationships between spider diversity and both green-roof area and plant species richness suggest that competition for space, resources, or limited microhabitat heterogeneity may limit spider diversity on small green roofs. These findings are supported by species-area curves in other habitats (Connor and McCoy 1979, Hooper, et al. 2005). In addition to area, the spider community was also affected by vegetation diversity and building height, suggesting that some species are not able to make it to the higher green roofs or, if they do, they may not find the necessary resources required to reside there and may move on. Availability of nesting and foraging resources may also help explain the positive relationship we found between beetle diversity and vegetation

diversity. For example, Haddad et al. (2009) showed that herbivores and predatory arthropods respond to plant diversity differently and, although not tested here, high plant-diversity may provide food for a greater diversity of herbivorous beetles that serve as prey upon which predatory beetle species feed. In ground-based systems, greater plant diversity typically supports more diverse arthropod communities (Siemann 1998). Thus, it is possible that greater plant diversity leads to more prey. Spiders and beetles were only affected by site-level factors, but bees responded to the availability of nearby vegetation surrounding the green roofs. Available nesting and food resources in the surrounding area most likely explain the significant relationship between bee-species richness and the percent of surrounding green space (Lonsdorf et al. 2009). Other studies have also demonstrated a significant relationship between both the richness and community composition of bees on green roofs and surrounding green space (Braaker et al. 2014, Tonietto et al. 2011). Smaller substrate particles may also have affected the abundance and richness of bees by influencing the suitability of nesting sites for solitary bee species that burrow into the substrate. This conclusion is supported by our finding that species diversity of ants was also affected by substrate depth. Furthermore, availability of nesting sites in the substrate may also be the reason for the significant effect of roof area on the composition of the bee community we found in our NMDS ordination. Together, these findings highlight the importance of substrate properties to soil-nesting arthropods. Overall, the fact that the arthropod guilds did not uniformly respond to the site-level variables suggests that green roofs do not provide a "one size fits all" habitat that ensures high support of biodiversity.

Future testable hypotheses

Data collected in our chronosequence study of 13 green roofs suggests that floral and arthropod guilds may respond differently to site-level variables. Future controlled experiments could test the generated hypotheses.

- *Spider diversity increases with age + green roof size.*
- *Spider diversity increases with vegetation species richness.*

- *Beetle diversity increases with increased vegetation diversity.*

- *Bee abundance and species richness increase with age * small particle size. Substrate infiltration may also play a role.*
- *Bee species richness and diversity increase with increasing surrounding green space.*

- *Ant species richness increases with age * substrate depth. Substrate infiltration may also play a role.*

- *Vegetation cover increases with age + shallow substrate depth, and age + small particle size. Substrate infiltration rate may also play a role.*
- *Vegetation species richness increases with age + shallow substrate depth , and age * small particle size. Substrate infiltration rate may also play a role.*

Figure 6. Hypotheses to be tested in future studies.

Recommendations for future green roof design

Our study shows that plant diversity is generally maintained on green roofs after an initial installation and colonization period, despite the expected annual fluctuations. Thus, diverse plant species should be selected at the onset of green roof design to maximize the support for diverse species assemblages over time. As with all engineered communities, green roofs may need maintenance efforts beyond establishment, such as weeding and replanting, to promote diverse communities and deliver ecosystem services. In the absence of management, fluctuations in the vegetation community on a green roof can be driven by the survival and dominance of a few specific species (Gabrych et al. 2016). Colonizing plants and arthropods can quickly alter the species assemblages on green roofs but once the community is established, dramatic changes in composition are unlikely, except in cases where a particularly successful species increasingly dominates available niches. Diverse ground-level habitats in highly engineered sites provide templates for communities with desirable successional trajectories when planted intentionally rather than relying on spontaneous colonization (Tischew et al. 2014). Green-roof planning could benefit from similar practices. Initial species composition must be intentional, especially for dispersal-limited species, if supporting biodiversity is a goal for a green roof (Fischer et al. 2013).

For green roofs where maintaining specific species assemblages is not a priority, increasing functional diversity (i.e., plants with varying roles in the community, such as C3 and C4 grasses, nitrogen-fixing forbs, and water-holding succulent species) may be a low-cost way to add value to these engineered habitats. Green-roof communities exhibit high variability in species abundance, richness, and diversity; thus, a focus on maintaining diverse vegetation and arthropod groups may be more appropriate than striving to establish certain species assemblages (Palmer et al. 1997). For example, designers could choose a wider diversity of species (such as early-flowering annuals and late-flowering perennials from different plant families) to bolster both plant and arthropod diversity. Designers could also create varied microhabitats to support both plant and animal taxa with varying abiotic requirements (Brenneisen 2006, MacIvor and Ksiazek 2015, Madre et al. 2014). Rather than supporting static communities in a type of arrested successional state through intensive management, building managers could moderately apply both stress and disturbance to discourage dominance of any one species or group (such as Chives or succulents) and maximize biological diversity on green roofs (Dunnett 2015).

In conclusion, our results support the idea that if green roofs are built, plants and arthropods will use the resources provided. However, ecological succession and patterns of community diversity on green roofs are variable and not easily predicted but appear to fluctuate around the community that is established within the first couple of years. As in other highly engineered urban habitats, diverse plant and arthropod communities do not necessarily self-assemble, especially if biodiversity support is a low priority in the initial vegetation selected. Lack of consistent patterns in species abundance and diversity among green roofs reinforces the need

for more and continued long-term monitoring of sites and implementation of site-specific strategies to promote biodiversity. Additional factors such as roof size, surrounding landscape, and depth and water-holding capacity of the substrate are likely important for supporting diverse plant and arthropod assemblages. The hypotheses generated here should be tested to inform green roof designs that support urban biodiversity.

Acknowledgements

Literature Cited

Bates, A., J. Sadler, and R. Mackay. 2013. Vegetation development over 4 years on 2 green roofs in the UK. Urban Forestry and Urban Greening 12:98–108.

Baumann, N. 2006. Ground-nesting birds on green roofs in Switzerland: Preliminary observations. Urban Habitats 4:37–50.

Braaker, S., J. Ghazoul, M.K. Obrist, and M. Moretti. 2014. Habitat connectivity shapes urban arthropod communities: The key role of green roofs. Ecology 95(4):1010–1021.

Brenneisen, S. 2006. Space for urban wildlife: Designing green roofs as habitats in Switzerland. Urban Habitats 4:27–36.

Brenneisen, S. 2015. Begrünte Flachdächer, Norm SIA 312: Entsehung und Hintergrund der Norm SIA 312 "Begrünung von Dächern." [Green Roofs, Standard SIA 312: Origin and background of the standard SIA 312 "Green Roofs".] Anthos 3. Available online at http://www.nextroom.at/periodical.php?id=22537andinc=artikelandsid=39954. Accessed 11 December 2015.

Brenneisen, S., and A. Hänggi. 2006. Begrünte Dächer: Ökologische charakterisierung eines neuen habitattyps in siedlungsgebieten anhand eines vergleichs der spinnenfauna von dachbegrünungen mit naturschutzrelevanten bahnarealen in Basel (Schweiz) [Green roofs - ecological characterization of a new habitat type in urban areas based on a comparison of the spider fauna of green roofs with conservation-related railway areas in Basel (Switzerland).] Mitteilungen der Naturforschenden Gesellschaften beider Basel 9:99–122.

Carlisle, S.C., and M. Piana. 2015. Green roof plant assemblage and dynamics. Pp. 285–310, *In* R.K. Suton (Ed.). Green Roof Ecosystems. Springer International Publishing, Basel, Switzerland. 447 pp.

Collins, J.P., A. Kinzig, N.B. Grimm, W.F. Fagan, D. Hope, J. Wu, and E.T. Borer. 2000. A new urban ecology: Modeling human communities as integral parts of ecosystem poses special problems for the development and testing of ecological theory. American Scientist 88(5):416–425.

Connor, E.F., and E.D. McCoy. 1979. The statistics and biology of the species–area relationship. The American Naturalist 113(6):791–833.

Cook-Patton, S.C., and T.L. Bauerle. 2012. Potential benefits of plant diversity on vegetated roofs: A literature review. Journal of Environmental Management 106:85–92.

Dunnett, N. 2015. Ruderal green roofs. Pp. 233–255, *In* R.K. Suton (Ed.). Green Roof Ecosystems. Springer International Publishing Switzerland, Basel, Switzerland. 447 pp.

Dunnett, N., and N. Kingsbury. 2004. Planting Green Roofs and Living Walls, Timber Press, Portland, OR, USA. 336 pp.

Dunnett, N., A. Nagase, and A. Hallam. 2008. The dynamics of planted and colonising species on a green roof over six growing seasons 2001–2006: Influence of substrate depth. Urban Ecosystems 11(4):373–384.

Dvorak, B., and A. Volder. 2010. Green roof vegetation for North American ecoregions: A literature review. Landscape and Urban Planning 96(4):197–213.

Ellis, E.C., K.K. Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589–606.

Fischer, L.K., M. von der Lippe, M.C. Rillig, and I. Kowarik. 2013. Creating novel urban grasslands by reinforcing native species in wasteland vegetation. Biological Conservation 159:119–126.

Forschungsgesellschaft Landschaftsentwicklung Landschaftsbau (FLL) E.V. 2008. Guideline for the Planning, Execution, and Upkeep of Green-Roof Sites. The Landscaping and Landscape Development Research Society, Bonn, Germany.

Francis, R.A., and J. Lorimer. 2011. Urban reconciliation ecology: The potential of living roofs and walls. Journal of Environmental Management 92:1429–1437.

Gabrych, M., D.J. Kotze, and S. Lehvävirta. 2016. Substrate depth and roof age strongly affect plant abundance on sedum–moss and meadow green roofs in Helsinki, Finland. Ecological Engineering 86:95–104.

Gantes, P., L.B. Falco, C.E. Coviella, and A.S. Caro. 2014. Plant secondary sucession age-related changes in landfills. Urban Ecosystems 17:1209–1218.

Getter, K.L., and D.B. Rowe. 2009. Substrate depth influences *Sedum* plant community on a green roof. HortScience 44(2):401–407.

Grant, G. 2006. Extensive green roofs in London. Urban Habitats 4:51–65.

Haddad, M.N., G.M. Curtsinger, K. Gross, J. Haarstad, J.M.H. Knops, and D. Tilman. 2009. Plant-species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12:1029–1039.

Hobbs, R.J., S. Arico, J. Aronson, J.S. Baron, P. Bridgewater, V.A. Cramer, P.R. Epstein, J.J. Ewel, C.A. Klink, A.E. Lugo, D. Norton, D. Ojima, D.M. Richardson, E.W. Sanderson, F. Valladares, M. Vila, R. Zamora, and M. Zobel. 2006. Novel ecosystems: Theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15:1–7.

Hooper, D.U., F.S. Chapin III, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, s. Naeem, B. Schmid, H. Setälä, A.J.Symstad, J. Vandermeer. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75:3–35.

Jäger, E., K. Wesche, C. Ritz, F. Müller, and E. Welk (Eds.). 2013. Rothmaler: Exkursionsflora von Deutschland—Gefäßpflanzen: Grundband. [Wild Plants of Germany: Vascular Plants—Foundational Volume]. 20th Edition. Springer Spektrum, Heidelberg, Germany. 822 pp.ae

Johnson, E.A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters 11:419–431.

Kadas, G. 2006. Rare invertebrates colonizing green roofs in London. Urban Habitats 4:66–73.

Kadas, G. 2010. Green roofs and biodiversity: Can green roofs provide habitat for invertebrates in an urban environment? LAP LAMBERT Academic Publishing GmbH and Company KG, Saarbrücken, Germany.

Kardol, P., L. Souza, and A.T. Classen. 2012. Resources mediate the importance of priority effects in plant-community assembly and ecosystem function. Oikos 122:84–94.

Köhler, M. 2006. Long-term vegetation research on two extensive green roofs in Berlin. Urban Habitats 4:3–26.

Köhler, M. and P.H. Poll. 2010. Long-term performance of selected old Berlin greenroofs in comparison to younger extensive greenroofs in Berlin. Ecological Engineering 36:722–729.

Kopel, D., D. Malkinson, and L. Wittenberg. 2015. Characterization of vegetation–community dynamics in areas affected by construction waste along the urban fringe. Urban Ecosystems 18:133–150.

Kowarik, I. 2011. Novel urban ecosystems, biodiversity, and conservation. Environmental Pollution 159:1974–1983.

Ksiazek, K. 2014. The potential of green roofs to support urban biodiversity. Pp. 101–124, *In* J. Briz, M. Köhler, and I. de Felipe (Eds.). Green Cities in the World. Pronatur, Madrid, Spain. 358 pp.

LeBuhn, G., T. Griswold, R. Minckley, S. Droege, T. Roulston, J. Cane, F. Parker, S. Buchmann, V. Tepedino, N. Williams, C. Kremen, and O.J. Messinger. 2003. A standardized method for monitoring bee populations: The bee inventory (BI) plot. Available online at http://online.sfsu.edu/~beeplot/. Accessed February 2013.

Lonsdorf, E., C. Kremen, T.H. Ricketts, R. Winfree, S. Greenleaf, and N.M. Williams. 2009 Modeling pollination services across agricultural landscapes. Annals of Botany 103:1589–1600.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D.A. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804–808.

Lundholm, J.T. 2015. The ecology and evolution of constructed ecosystems as green infrastructure. Frontiers in Ecology and Evolution DOI:10.3389/fevo.2015.00106.

MacIvor, S., and K. Ksiazek. 2015. Invertebrates on green roofs. Pp. 333–355, *In* R.K. Suton (Ed.). Green Roof Ecosystems. Springer International Publishing, Basel, Switzerland. 447 pp.

Madre, F., N. Vergnes, N. Machon, and P. Clergeau. 2014. Green roofs as habitats for wild plant species in urban landscapes: First insights from a large-scale sampling. Landscape and Urban Planning, 122:100–107.

Mann, G. 1998. Vorkommen und Bedeutung von Bodentieren (Makrofauna) auf begrüten Dächern in Abhängigkeit von der Vegetationsform [Occurrence and significance of soil organisms (macrofauna) on green roofs in response to vegetation type]. Ph.D. Dissertation. Eberhand Karls Universität, Tübingen, Germany.

Matthews, J.W. 2015. Group-based modeling of ecological trajectories in restored wetlands. Ecological Applications 25:481–491.

McDonald, R.I., P.J. Marcotullio, and B. Güneralp. 2013. Urbanization and global trends in biodiversity and ecosystem services. Pp. 31–52, *In* Urbanization, Biodiversity, and Ecosystem Services: Challenges and Opportunities. Springer, Dordrecht, The Netherlands. 755 pp.

McGuire, K., S.G. Payne, M.I. Palmer, C.M. Gillikim, D. Keefe, S.J. Kim, S.M. Gedallovich, J. Discenza, R. Rangamannar, J.A. Kosner, A.L. Massmann, G. Orazi, A. Essene, J.W. Leff, N. Fiere. 2013. Digging in the New York skyline: Soil fungal communities in green roofs and city parks. PLoS ONE 8(3):e58020.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: Biodiversity synthesis. World Resources Institute, Washington, DC, USA. Available online at: http://www.millenniumassessment.org/en/Synthesis.html. Accessed 6 March 2016.

Molineux, C.J., S.P. Connop, and A.C. Gange. 2014. Manipulating soil microbial communities in extensive green roof substrates. Science of the Total Environment 493:632–638.

Morris, E.K., T. Caruso, F. Buscot, M. Fischer, C. Hancock, T.S. Maier, T. Meiners, C. Müller, E. Obermaier, D. Prati, S.A. Socher, I. Sonnemann, N. Wäschke, T Wubet, S. Wurst, and M.C. Rillig. 2014. Choosing and using diversity indices: Insights for ecological applications from the German biodiversity exploratories. Ecology and Evolution 4(18):3514–3524.

Nagase, A., N. Dunnett, and M. Choi. 2013. Investigation of weed phenology in an establishing semi-extensive green roof. Ecological Engineering 58:156–164.

Niemelä, Jari. 1999. Ecology and urban planning. Biodiversity and Conservation 8:119–131.

Oberndorfer, E., J. Lundholm, B. Bass, RR. Coffman, H. Doshi, N. Dunnett, S. Gaffin, M. Köhler, K.K.Y. Liu, and B. Rowe. 2007. Green roofs as urban ecosystems: Ecological structures, functions, and services. BioScience 57(10):823–834.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164(3877):262–270.

Olly, L.M., A.J. Bates, J.P. Sadler, and R. MacKay. 2011. An initial experimental assessment of the influence of substrate depth on vegetation assemblage for extensive green roofs. Urban Forestry and Urban Greening 10:311–316.

Palmer, M.A., R.F. Ambrose, and N.L. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology 5(4):291–300.

Pickett, S.T.A., and W. Zhou. 2015. Global urbanization as a shifting context for applying ecological science toward the sustainable city. Ecosystem Health and Sustainability 1(1):1–15. DOI:10.1890/EHS14-0014.1.

Pickett, S.T.A., J. Wu, and M.L. Cadenasso. 1999. Patch dynamics and the ecology of disturbed ground: A framework for synthesis. Pp. 707–722, *In* L.R. Walker (Ed.). Ecosystems of Disturbed Ground. Elsevier, Amsterdam, The Netherlands. 868 pp.

Platnick, N.I. 2013. The world spider catalog, version 9.0. American Museum of Natural History, New York, NY, USA. Available online at: http://research.amnh.org/entomology/spiders/catalog/index.html. Accessed June 2013.

Prach, P., and P. Pysek. 1999. How do species dominating in succession differ from others? Journal of Vegetation Science 10(3):383–392.

Prach, K., and L.R. Walker. 2011. Four opportunities for studies of ecological succession. Trends in Ecology and Evolution 26(3):119–123.

Prach, K., P. Pysek, and M. Bastl. 2001. Vegetation succession in human-disturbed habitats: A pattern across seres. Applied Vegetation Science, 4:83–88.

R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramirez, S.R., C. Hernandez, A. Link, and M.M. Lopez-Uribe. 2015. Seasonal cycles, phylogenetic assembly, and functional diversity of orchid bee communities. Ecology and Evolution 5(9):1896–1907.

Roberts, M.J. 1987. The Spiders of Great Britain and Ireland: Linyphiidae. Volume 2. Harley Books, Colchester, UK. 714 pp.

Roberts, M. 1999. Spiders of Britain and Europe (Collins Field Guide). Harpercollins Publishing, Ltd. Glasgow, Scotland. 384 pp.

Rowe, B. 2015. Long-term rooftop plant communities. Pp. 311–332, *In* R.K. Suton (Ed.). Green Roof Ecosystems. Springer International Publishing, Basal, Switzerland. 447 pp.

Sala, O., F. Chapin, J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanld, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Dodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker, and D.H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Sattler, T., D. Borcard, R. Arlettaz, F. Bontadina, P. Legendre, M.K. Obrist, and M. Moetti. 2010. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology 91:3343–3353.

Seifert, B. 2007. Die Ameisen Mittel und Nordeuropas [The ants of Central and Northern Europe.] Iutra Verlangs- und Vertriebsgesellschaft, Tauer, Germany.

Seto, K.C., M. Fragkias, B. Güneralp, and M.K. Reilly. 2011. A metaanalysis of global urban land expansion. PLoS ONE:6:e23777.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79(6):2057–2070.

Snodgrass, E.C., and L.L. Snodgrass. 2006. Green Roof Plants: A Resource and Planting Guide. Timber Press, Portland, OR, USA. 204 pp.

Sterling, A., B. Peco, M.A. Casado, E.F. Galiano, and F.D. Pineda. 1984. Influence of microtopography on floristic variation in the ecological succession in grassland. Oikos 42:334–342.

Thuring, C., and G. Grant. 2015. The biodiversity of temperate extensive green roofs: A review of research and practice. Israel Journal of Ecology and Evolution 62:44–57. DOI: 10.1080/15659801.2015.1091190.

Thuring, C., R. Berghage, and D. Beattie. 2010. Green roof plant responses to different substrate types and depths under various drought conditions. HortTechnology 20(2):395–401.

Tischew, S., A. Baasch, H. Grunert, and A. Kirmer. 2014. How to develop native plant communities in heavily altered ecosystems: Examples from large-scale surface mining in Germany. Applied Vegetation Science 17:288-301.

Tonietto, R., J. Fant, J. Ascher, K. Ellis, and D. Larkin. 2011. A comparison of bee communities of Chicago green roofs, parks, and prairies. Landscape and Urban Planning 103:102–108.

Turner, M., W.L. Baker, C.J. Peterson, and R.K. Peet. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.

VanWoert, N., D.B. Rowe, J.A. Anderson, C.L. Rugh, R.T. Fernandez, and L. Xiao. 2005. Green roof stormwater retention: Effects of roof surface, slope, and media depth. Journal of Environmental Quality 34:1036–1044.

Walker, L.R., and F.S. Chapin III. 1987. Interactions among processes controlling successional change. Oikos 50(1):131–135.

Walker, L.R., D.A. Wardle, R.D. Bardgett, and B.D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725–736.

Williams, N.S.G., J. Lundholm, and J.S. MacIvor. 2014. Do green roofs help urban biodiversity conservation? Journal of Applied Ecology 51(6):1643–1649.

Zhang, C., J. Wu, N.B .Grimm, M. McHale, A. Buyantuyev. 2013. A hierarchical patch mosaic ecosystem model for urban landscapes: Model development and evaluation. Ecological Modeling 250:81–100.