A Global Comparison of Beetle Community Composition on Green Roofs and the Potential for Homogenization

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Abstract - Globalization may confer a competitive advantage to species that are urban exploiters and result in homogenization of communities in cities. We tested the application of this hypothesis to green roofs. Using body size as a proxy for life-history strategy, we compared small-bodied and large-bodied subsets of beetle communities from 5 cities in Europe and North America. We found that city was an important organizer of both subsets, though more so for the large-bodied one. This result suggests either resilience against homogenization or simply that not enough time has occurred for it to develop. A majority of the 10 most-abundant species found in the North American cities were non-native, in contrast to those found in European cities, a majority of which were native. These findings signal that more research is needed to track drivers of homogenization, such as functional composition, on rooftops as well as in other urban green spaces.

Introduction

As we consider the social and political impacts of globalization (Sassen 1991), it is important to understand the ecological effects of rapid urban expansion, increasing interconnectedness, and domestication on urban environments (Kareiva et al. 2007, Liu et al. 2007). According to the biotic homogenization hypothesis, if rapid urban growth continues along its current trajectory, ecological diversity, especially with respect to urban fauna, will decline, leading to increased community similarity in the urban centers of global cities (McKinney and Lockwood 1999). Homogenization can be explained by physical changes to the environment including changing climate (Oke 1995) and habitat loss (Liu et al. 2007) along a rural-to-urban gradient (Pouyat et al. 1997) that make it either impossible or unfavorable for species (i.e., urban avoiders) to succeed in urban areas. These changes leave only urban adapters and the much more common and abundant generalist urban exploiters that are able to take advantage of the resources cities have to offer (Banaszak-Cibicka and Zmihorski 2012, Blair 2001, McKinney 2002).

In addition to the changes in environmental conditions that drive homogenization, trophic interactions, such as competitive exclusion of potential urban adapters

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by invasive species (Shochat et al. 2006, Turrini et al. 2016), may explain the decline in biodiversity in urban areas. Traits assumed to predict urban success of some species over others include high dispersal ability, adaptability to urban areas, and having a short life cycle (Baker 1965, Moller 2009). However, the issue should not be oversimplified; although Vazquez and Simberloff (2001) found that certain insect families had a greater potential to invade, they cautioned against premature generalizations outside of the importance of human transport as a mechanism of biotic invasions. Similarly, though they found a clear relationship between the body size of different insect orders and probability of establishment on the British Isles (Lawton et al. 1986), other authors do not support connecting these findings to assumed relationships between body size and life-history strategy. Nevertheless, a gradient of life-history strategies is known to exist. Species that invest more energy in reproduction, termed r-selected species, are predicted to have smaller body sizes compared to K-selected organisms that invest more energy into gathering environmental resources (Pianka 1970).

The relative proportions of r-selected colonizing species and K-selected competitor species may influence overall diversity, depending also on the frequency of disturbance (Bohn et al. 2014). Disturbance frequency is the main explanation of the intermediate-disturbance hypothesis (Connell and Slayter 1977), which predicts the greatest community diversity at intermediate levels of disturbance. More frequent disturbance would shift the community towards colonizers, of which there are generally fewer species in a community, thus lowering local community diversity, and less frequent disturbance would favor competitors, to some extent increasing local community diversity. Less is known about the effects of these trade-offs regionally (Cadotte 2007).

Several approaches to mitigating the effects of urbanization on declines in species diversity (McKinney 2002) apply to invertebrates. One strategy is to protect existing habitat such as urban forest remnants and other novel ecosystems (Kowarik 2011). Another strategy is to encourage habitat restoration (Schaefer 2009). Outreach and education can also foster appreciation of urban wildlife in order to promote a conservation ethic that could change the way in which future urban expansion proceeds (Dearborn and Kark 2010). This last approach emphasizing the role of human behavior is not trivial considering recent findings that the microclimates of human-regulated urban lawns from several cities across the US, such as Phoenix and Portland, were more similar to each other than to other local ecosystems (Hall et al. 2015). This global convergence of abiotic conditions has also been shown for urban soils (Pouyat et al. 2015). Remediation strategies for invertebrates vary according to the species of concern (Jones and Leather 2012) and how urbanization is defined (Sattler et al. 2011).

More research is needed to determine the extent to which green roofs mitigate invertebrate habitat loss in urban environments (Williams et al. 2014). In contrast to earlier European studies that found higher numbers of mites and springtails on roofs compared to ground sites (Buttschardt 2001, Darius and Drepper 1983, Thuring and Grant 2015), both species richness and abundance of invertebrates were

found to be lower on green roofs compared to ground-level sites (MacIvor and Lundholm 2011), and these differences were significant for species richness when the study focus was narrowed to beetles (Gonsalves 2016). Excluding roofs with habitat elements such as substrate mounds, logs, or native vegetation, beetle species abundance and functional diversity were also significantly lower on roof sites compared to ground sites (Gonsalves 2016).

Green-roof design strategies, such as increased substrate depth or habitat complexity, have been linked to increased species diversity and abundance (Brenneisen 2006, Madre et al. 2014). Nevertheless, when measures of spider and beetle abundance, diversity, and rareness were tabulated into a score, these scores were correlated with those for ground-level sites (Brenneisen 2003). Green-roof invertebrate community composition may also be explained by the connectivity of green roof and ground-level sites, at least for highly mobile species (Braaker et al. 2014, Brenneisen 2003). Lack of appropriate habitat and resources in the built environment may preclude many invertebrate species from getting to and using a green roof. If this is the case, they may only be able to support generalist urban-exploiter species.

Beetles comprise an insect order that is especially useful for understanding the factors that affect urban community composition on green roofs and other urban habitats. This order includes a wide variety of abundant and taxonomically stable species from various trophic, mobility, and body-size classes that are easily sampled (Rainio and Niemela 2003, Sunderland et al. 1995). The number of beetle species is positively correlated with the number of total species in an ecosystem, including vertebrates, invertebrates, and plants (Duelli and Obrist 1998). Global studies of ground beetle (Carabidae) communities along urban-to-rural gradients attribute community dissimilarity in these different locations to the extent to which the communities became dominated by opportunistic species and specialists (Magura et al. 2010, Niemela et al. 2002).

A growing interest in and understanding of green-roof arthropod diversity and associated ecological functions (MacIvor and Ksiazek 2015) over the past 10 years since the publication of the original *Urban Habitats* series on biodiversity provides the chance to compare species found on green roofs in cities around the world. An international dataset characterizing green-roof beetle inhabitants allows us to test whether the biotic homogenization hypothesis might apply to green roofs, just as it has been tested in other urban patches such as lawns, or whether green roofs support regionally distinct communities. In this paper, we compare beetle communities from 5 cities in Europe and North America known for their effective green-roof implementation: Portland, OR, USA; Halifax, NS, Canada; Basel, Switzerland; Berlin, Germany; and Neubrandenberg, Germany. Typically, studies of homogenization compare similarities between urban and rural locations across global cities. Unfortunately, data from rural green roofs or even urban ground sites for comparison were not available for all the cities in our study. Therefore, instead of comparing urban and rural data across cities, we identified different body-size subsets of the beetle communities in our dataset, as a proxy for different life-history strategy, and

compared these. Consistent with the biotic homogenization hypothesis, we predicted that city would be a weak organizer of green-roof beetle communities and that the smaller and potentially r-selected colonizers of these green-roof communities would be more similar to each other than their larger, potentially K-selected competitor counterparts. We also predicted that there would be a high proportion of non-native species present in all cities, and that species most common to all cities would be would be generalists. From a practical standpoint, this global comparison of green-roof beetle communities allows managers to assess the role of green roofs in urban invertebrate biodiversity conservation and to identify both widespread and rare species of ecological and economic importance.

Methods

Data assembly

We assembled data on beetle species diversity and abundance from 2 cities in North America (Halifax, NS, Canada; Portland, OR, USA) and 3 cities in Europe (Basel, Switzerland; Neubrandenburg, Germany; and Berlin, Germany; Fig. 1). A summary of the different studies compared in the present paper are provided in Table 1. In all 5 cities, beetles were collected using pitfall traps. We categorized roofs as intensive if they were over 20 cm in depth, extensive if they were under 20 cm in depth, and as extensive–varied if they were purposely designed with varied substrate-depth but where depth was ≤20 cm in all areas. Data from Portland (PDX) are from a 2014 (March–September) survey that included 8 roofs: 1 intensive, 2 extensive–varied, and 5 extensive roofs. Data from Halifax (HAL) came from a 2009 (May–October) study of 5 intensive roofs (MacIvor and Lundholm 2011). Our species lists from Berlin (BER), and Neubrandenburg (NEU), Germany are described in a separate article in this special issue (Ksiazek-Mikenas et al. 2018). Beetles were collected over 1 field season (April–September) in 2013 at 8 roofs in BER and 5 roofs in NEU; these roofs were all classified as extensive. Data from Basel (BSL) came from a 2013 (March–September) collection from 15 roofs: 6 extensive–varied and 9 extensive.

Figure 1. Map showing location of our study sites.

Table 1. Study sites and sampling techniques. Roofs types are classified by substrate depth as intensive (>20 cm), extensive (≤20 cm), or extensive–varied (purposely designed with varied substrate depth but depth ≤ 20 cm in all areas).

Reference	Study city	Study year	Sample period	# traps per roof	Estimated sample hrs per roof	Roof #	Average roof age (yrs)	Roof type (s)	Taxonomist
Brenneisen, S., unpubl. data	Basel, Switzerland	2013	April–September	10	3696	15	11.2	9 extensive, 6 varied	A.Szallies, Zurich University of Applied Sciences
Ksiazek-Mikenas et al. (2017)	Berlin, Germany	2013	April–September	9	576	8	20.5	Extensive	K.-H. Kielhorn, BioM, Berlin, Germany
MacIvor and Lundholm (2011)	Halifax, NS, Canada	2009	May–October	8	3360	5	19.2	Intensive	C. Majka, Natural History Museum of Nova Scotia
Ksiazek-Mikenas et al. (2017)	Neubrandenburg, Germany	2013	April–September	9	576	5	14.2	Extensive	K.-H. Kielhorn, BioM, Berlin, Germany
Gonsalves (2016)	Portland, OR, USA	2014	April–September	10	3696	8	6.8	1 Intensive, 5 extensive, 2 extensive–varied	A.Szallies, Zurich University of Applied Sciences

Community characterization, beetle size, and native ranges

All beetles were identified to species. We compared abundances and species composition across all 5 cities, focusing on the number of species that the cities shared, which we defined as the number of species found in any given city that were also found in at least 1 other city. We consulted several online clearinghouses to determine the average body size of a given species and whether a species was native to a given region (Agroatlas 2016, Beetle Fauna of Germany 2016, Bugguide 2016, Encyclopedia of Life 2016, Inaturalist 2016, Lompe 2016). The arrival of species such as *Amara communis* (Panzer) or *Chaetocnema concinna* (Marsham) (Brassy Flea Beetle) to North America were documented by peer-reviewed publications (Bousquet 1992, Lesage and Majka 2010). In order to determine to what degree the most commonly found green-roof beetles were native vs. invasive, we compared the relative proportions of invasive or non-native species for the top 10 most abundant species in each of our study cities. We assigned the most abundant species to functional feeding groups according to the aforementioned online databases as well as Arnett et al. (1992).

The effect of city on beetle-community organization broken down by body size

We compared the communities observed at each site based on beetle body-size as a proxy for r- vs. K-selected species. Given that beetle size can vary within species, we calculated the average published size and divided the communities into 2 groups: ≤ or > the median size (4.5 mm) of all the species in our study. This median value is similar to the smallest-size–break descrbed in Fattorini et al. (2013). We did not include singletons in our calculations. Five roofs in the dataset did not have species >4.5 mm in length. To determine if beetle community composition differed by city, number of hours sampled, roof age, or roof design, we employed the 'adonis' function in the R package 'vegan' (Oksanen et al. 2015) to conduct a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, Anderson and Walsh 2013) for each community subset of large-bodied and small-bodied species. To reduce variance but to increase representation of rare species that might be important in defining each city's green-roof beetle community, we log+1-transformed the abundance community matrix (Wernberg et al. 2016) and set the algorithm to perform 999 permutations on the Bray–Curtis distance matrix. Analogous to an ANOVA, the 'adonis' function adds factors sequentially, checking for the significance of 1 factor by controlling for the previous factors. We thereby first accounted for differences in sample hours, before sequentially adding age, roof design, and city. When this analysis indicated a difference by city, we conducted a pair-wise test to determine which city-groups differed. For pair-wise testing, we applied a Bonferroni correction for 5 city-groups (10 tests) at the significance level, $\alpha = 0.05$, so that $\alpha_B = 0.005$. We excluded comparisons of Neubrandenburg and Berlin from this analysis due to contrast errors.

To better visualize differences in beetle community composition, we conducted a non-metric multidimensional scaling (NMDS) ordination on the between-site Bray–Curtis similarity coefficient in the 'vegan' package in R (Clarke 1993,

Oksanen et al. 2015). To achieve model convergence, we used 50 random starts to determine the appropriate number of axes, and checked the distortion in ordination space via the stress value and visually with a Shephard's diagram (Clarke 1993).

Results

Our datasets were comprised of 4759 individuals and 295 beetle species (Table 2; see Supplemental File 1, available online at https://www.eaglehill.us/URNAonline/suppl-files/U127e-Starry-s1). Overall, the proportion of species that were found to be unique to any given city was 0.83; this unique portion relative to the total number of species found varied by city (Table 2). Species occurring once at a single roof in a single city represented 34% of the total species observed in all studies ($n = 100$). When we removed these species from our analysis, the proportion of unique species overall was reduced to 0.74. This removal also reduced the proportion for the study cities, especially the ones in Germany where removing singletons reduced the proportion of unique species by greater than 50% (Table 2).

We predicted that the most common species in all cities would be non-native generalists. Only 1 species, *Amara aenea* (DeGeer), was found in all 5 cities. Four species were found in 3 cities: *Harpalus affinis* (Schrank) in PDX, HAL, and BER; *Harpalus rubripes* (Duftschmid) in all 3 European cities (BAS, BER, and NEU), and both *Sitona hispidulu*s (Fabricius) and *Cytilus sericeus* (Forster) in BER, NEU, and PDX. The most abundant species, of which 463 individuals were collected, was *Xanotholinus linearis* (Olivier); it was found in PDX and HAL.

In HAL and PDX, 5 and 8 out of 10 of the most abundant species were non-native, respectively (Fig. 2). For example, many palearctic species such as the Detrivore Rove Beetle, introduced on both the east and west coasts of North America, were found on PDX and HAL roofs in great abundance. Other species such as *Harpalus rubripes* (Duftschmid), which is known to prefer open, dry habitats and to have arrived in New Hampshire, USA, in the 1980s (Bell and Davidson 1987), have not yet appeared on the green roofs in HAL or PDX. All of the species found in Europe were native to the region in which they were found (Fig. 2).

We predicted that city would be a weak organizer of beetle communities and that the small-bodied subsets of the green-roof beetle communities would be more similar across cities compared to their larger counterparts. Even after accounting for the

Table 2. Summary statistics for beetle communities obtained from 41 green roofs in 5 cities.

Site code	# individuals identified	# species identified	# species shared with at least 1 other site	Proportion unique	Proportion unique (no singeltons)	Proportion of top 10 non-native
PDX	1406	60	22	0.63	0.49	0.80
HAL	1362	90	23	0.74	0.62	0.50
NEU	140	34	20	0.41	0.17	0.00
BER	134	38	22	0.41	0.15	0.00
BAS	1717	133	23	0.83	0.77	0.00

influence of different sampling efforts and roof types sampled in the different cities, the PERMANOVA analysis indicated a significant difference in beetle community by city for both body-size subsets of the communities investigated (Table 3). However, the effect of city was much greater for the portion of the communities comprised of larger beetles. Pair-wise comparisons showed a slightly opposite pattern in which fewer comparisons were significant when comparing the larger-bodied community subsets (Table 4). The NMDS procedure allowed us to visualize the separation of communities by city (Fig. 3).

Discussion

We found that city was a significant organizer of both large- and small-bodied subsets, though this influence was greater for the larger-bodied fraction, as was shown by PERMANOVA analysis. Pair-wise comparisons showed a slightly opposite pattern in which fewer comparisons were significant when comparing the larger-bodied community subsets, but we attribute this small difference to some outlier communities in the large subsets. The results of PERMANOVA analysis and tighter clustering amongst the larger-bodied community subset on the NMDS visualizations, despite the exception of the aforementioned outliers, implies that
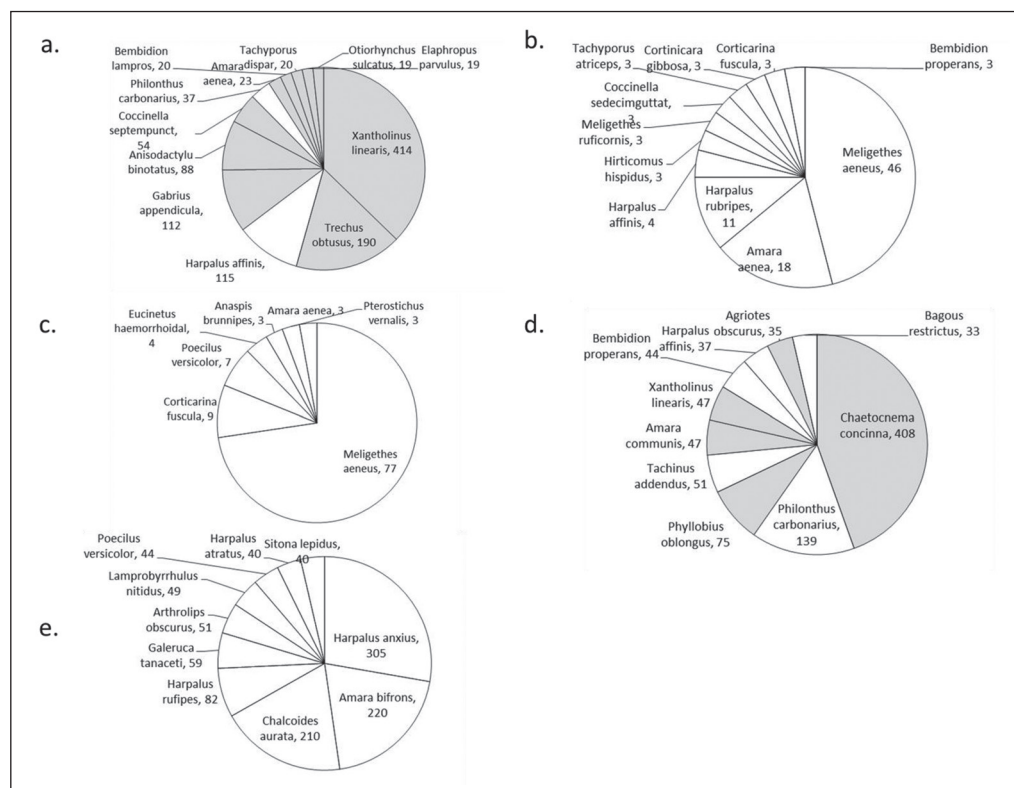

Figure 2. Relative proportion of the species of greatest abundance on green roofs in (a) Portland, (b) Neubrandenburg, (c) Berlin, (d) Halifax, and (e) Basel. Non-native species are shaded in gray.

Table 3. Results of PERMANOVA comparing the effect of different factors, including sample hours, roof type, roof design, and city on green-roof beetle community composition for small-bodied and large-bodied subsets of the communities studied. The abundance community matrix was log+1-transformed, and 999 permutations were performed per test. Significant effects ($P < 0.001$) are marked with an asterisk (*).

Factors	df	F	R^2	P
Small-bodied				
Sample hours	1	10.712	0.179	0.001*
Age	1	1.304	0.022	0.661
Roof type	2	3.165	0.106	0.001*
City	3	2.880	0.145	0.001*
Residuals	33		0.554	
Total	40		1.000	
Large-bodied				
Sample hours	1	7.398	0.138	0.001*
Age	1	0.616	0.011	0.933
Roof type	2	3.067	0.114	0.001*
City	3	3.865	0.216	0.001*
Residuals	28		0.521	
Total	35		1.000	

Table 4. Results of PERMANOVA pair-wise permutation test of beetle-species community-composition difference between cities for small-bodied and large-bodied subsets of the communities studied. A Bonferroni correction for 10 pair-wise tests (0.05/10) was applied to the significance criteria, α, and 999 permutations were performed per test. Significant differences ($P < 0.001$) in community comparisons by city pair are marked with an asterisk (*).

PERMANOVA group comparison	$α_B$	F	R^2	P
Small-bodied				
PDX–BER	0.005	5.653	0.288	<0.001*
PDX–NEU	0.005	5.796	0.345	<0.001*
PDX–HAL	0.005	4.294	0.281	<<0.001*
PDX–BAS	0.005	5.486	0.207	0.001*
BER–HAL	0.005	7.085	0.392	0.002
BER–BAS	0.005	7.050	0.251	<0.001*
NEU–HAL	0.005	9.242	0.536	0.009
NEU–BAS	0.005	6.648	0.270	<0.001*
HAL–BAS	0.005	6.072	0.252	<0.001*
Large–bodied				
PDX–BER	0.005	5.289	0.306	<0.001*
PDX–NEU	0.005	3.951	0.283	0.003
PDX–HAL	0.005	5.044	0.314	<0.001*
PDX–BAS	0.005	7.673	0.288	<0.001*
BER–HAL	0.005	8.544	0.487	0.005
BER–BAS	0.005	7.656	0.311	<0.001*
NEU–HAL	0.005	6.257	0.472	0.010
NEU–BAS	0.005	4.690	0.238	0.002
HAL–BAS	0.005	8.492	0.347	<0.001*

smaller species may be slightly more easily exchanged amongst roofs. Contrary to any concerns about balanced sampling effort, results from the PERMANOVA analysis demonstrate that sampling effort did not mask the effects of city or roof type. We chose this approach instead of correcting for sampling effort by rarefication, which would have resulted in a substantial loss of information from many of the sites. However, a larger, more intentional study with more sample sites, especially including either rural green-roof sites or possibly ground sites, would enable us to more thoroughly address the homogenization hypothesis. There is also some uncertainty around the some of our size assignments because it was not always clear how size was reported; we assumed it was based on the length of the elytra. Size is also not always a good predictor of life history or dispersal ability (Fattorini et al. 2013). However, there are at least 2 other aspects of our dataset that suggest potential for homogenization in the future.

First, the North American green-roof communities were comprised of a higher proportion of non-native species compared to the European ones. The extent to which homogenization is observed may be influenced by the relative proportion of newly-arrived, naturalized, and native species which one would expect to vary over space and time. For example, one might expect a higher invasion of non-native species in port cities such as PDX and HAL (Withers et al. 2012). Likewise, newly introduced invader species may differentiate communities over short time-scales, only beginning to homogenize them once they become more wide-spread. A study of European plant communities which classified species as native archaeophytes (Old World alien plants), and neophytes (modern alien plants), found neophytes differentiated the urban plant communities, and that these differences were driven primarily by rates of species turnover (Hahs and McDonnell 2016, Lososova et al. 2016).
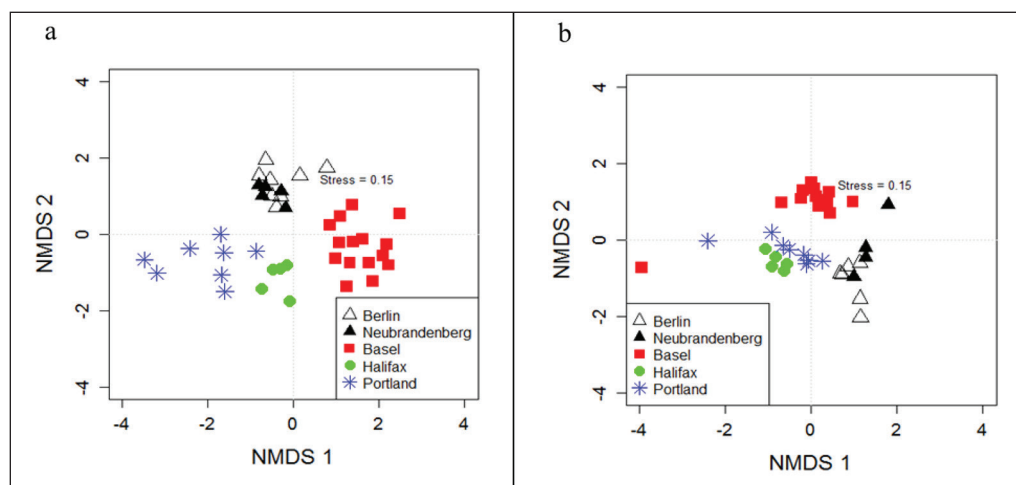

Figure 3. Non-metric multidimensional scaling (NMDS) ordination on the Bray–Curtis similarity coefficient between sites (red = Basel, green = Halifax, blue = Portland, black = Berlin, and white = Neubrandenburg) for (a) small-bodied and (b) large-bodied subsets of the communities studied.

Second, many of the species that were shared amongst roofs internationally were generalists with respect to their feeding preference (Arnett et al. 1992). These results support those of other studies of homogenization of beetles on the ground, which found global communities to be distinct but also noted a high abundance of exploiter species in urban areas (Magura et al. 2010, Niemela et al. 2002). For example, *Amara aenea,* the only species found at all our study sites, is a generalist at the larval stage, but the adults feed specifically on grass seed; thus, it is not surprising that the most common beetle species on green roofs across cities would be associated with one of the most synanthropic plants commonly used in urban lawns.

Nevertheless, we found that city was an important organizer of both the large-bodied and small-bodied subsets of the beetle communities sampled from green roofs at 5 different locations globally; 84% of the species found were unique to the city in which they were located. These findings are similar to those of others who have suggested that the homogenization hypothesis is more applicable to species such as birds than insects (Magura et al. 2010, Niemela et al. 2002), whereby local factors such as climate or habitat have a greater influence on community organization than disturbance due to urbanization. Nevertheless, Aronson et al. (2014) found that the majority of bird and plant species were native to their respective cities globally, although the density of these native species had declined. The authors further noted that this decline in native species density was better explained by anthropogenic factors rather than non-anthropogenic factors such as geography or climate (Aronson et al. 2014).

We also provide further evidence that roof type was a major influence on community composition because it was a significant factor in our PERMANOVA analysis. This finding suggests that we can influence urban community composition with informed design and planning, as has been previously suggested (Brenneisen 2003, 2006; Gonsalves 2016). Additionally, 35% of the species were found only once in the dataset. This high number of singletons could be explained by, or used as evidence for, the establishment of would-be invaders being constrained by the harsh fluctuations in temperature, wind speed, and moisture availability on rooftop locations. Alternatively, another potential constraint to establishment may be the high proportion of predator species found on green roofs. Lawton et al. (1986) emphasized this possibility for different insect orders on the ground, and Starry (2016) noted a high proportion of predator beetles on Portland green roofs; their presence may deter invasion.

Our observation of regionally distinct beetle communities, independent of body size, could indicate the potential of green roofs to contribute to invertebrate conservation in cities (Hunter and Hunter 2008); however, more research is needed to understand the green-roof properties that can further sustain diverse invertebrate communities (MacIvor and Ksiazek 2015). Determining the degree to which the relatively newly arrived and common species in North America might lead to homogenization will require studies on diversity and ecosystem structure, barriers to dispersal, random species sorting, and ecological relationships such as trophic

interactions. Likewise, more research on the less-common constituents of the beetle communities should be conducted for conservation purposes. This research will become especially important in determining how resilient green-roof communities might be to disturbance and is applicable to similar urban green spaces such as parks or lawns.

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