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Horizontal and vertical island biogeography of arthropods on green roofs: a review

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Abstract From an ecological perspective, urban green roofs can be viewed as green islands embedded in an urban matrix. Island biogeography theory suggests that species richness on an island is the outcome of dynamic equilibrium between immigration and extinction. Immigration is affected by the size of an island and distance of an island from a colonizing source. In the context of green roofs, building height and horizontal distance from green areas can potentially be a limiting factor for many species. Here, we considered two distance components of green roofs - vertical (building height) and horizontal (distance of building from open green areas). Based on island biogeography theory, we would expect species richness or community similarity to be negatively related to horizontal or vertical distances from colonizing sources. The green roof literature addressing such questions is currently sparse. In our review comprised of 10 studies, we were unable to identify consistent statistically significant richness-distance or community similarity-distance (vertical or horizontal) relationships. The absence of statistically significant relationships could be due in large part to low statistical power as a consequence of both the paucity of roofs and limited range of vertical distances in many of the existing studies. In addition, these roofs differ in numerous aspects (e.g. roof size, age, substrate type, plant composition and building height). The low number of replicates, combined with the lack of homogeneity among replicates combines to reduce statistical power and our ability to detect differences.

Keywords Colonization · Community similarity · Species assemblage · Species diversity · Urban ecology

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Introduction

Island biogeography theory, originally developed by MacArthur and Wilson (MacArthur and Wilson 1963; MacArthur and Wilson 1967), is a fundamental theory in ecology and is the basis of many of the concepts and research areas in ecology. The generalization of island biogeography from island to patches was the basis for the development of metapopulation models (Levins 1969) and landscape ecology (Haila 2002).

The theory of island biogeography predicts that the number of species inhabiting islands is the result of two main processes. First, island size affects species richness because: larger islands usually contain a greater diversity of habitats; larger islands will support larger populations, making the populations less vulnerable to extinction; and the probability of encountering a larger island is higher for both mobile species that select habitats as well as passive species (MacArthur and Wilson 1963; MacArthur and Wilson 1967). Second, island isolation directly reduces species diversity, because isolated islands experience lower rates of immigration from the mainland. Since it was developed, island biogeography theory has been manifested in other systems where each habitat patch is surrounded by an uncolonizable matrix - e.g., ponds (Ward and Blaustein 1994; Spencer et al. 1999), lakes (Lepère et al. 2013), forest fragments surrounded by agriculture (Goheen et al. 2003), urban (Godefroid and Koedam 2003) or other

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land-uses and on smaller scales such as an individual tree in scrubland (Haila 2002; Blank and Carmel 2012) and bryophyte micro-landscapes (Gonzalez 2000; Haila 2002).

Green roofs, which are roofs that are covered with growing substrate and vegetation, have been proposed to contribute to the goals of reconciliation ecology (Rosenzweig 2003; Francis and Lorimer 2011; Lundholm 2016; Rosenzweig 2016). Reconciliation ecology was coined and defined by Michael Rosenzweig as "the science of inventing, establishing, and maintaining new habitats to conserve species diversity in places where people live, work, or play" (Rosenzweig 2003). In this context, green roofs can play a role in supporting biodiversity by recreating habitats for fauna and flora (Blaustein et al. 2016; Rosenzweig 2016).

Island biogeography theory can be applied to green roofs to understand spatial patterns in species richness. The species richness-distance relationships should apply both horizontally (distance of building from green area) and vertically (distance from rooftop to ground level). In this context, green roofs may encompass considerable potential to study the relationships between richness and distance as they are isolated habitats, occupying areas within cities that are depauperate of natural ecological habitats.

The research emphasis on the ability of green roofs to serve as habitat for various species is a relatively new focus in green roof research (Blank et al. 2013; Blaustein et al. 2016). Understanding how island biogeography applies to green roofs can aid to understand how the number and spatial configuration of green roofs can contribute to urban biodiversity (Kim 2004; Pickett and Cadenasso 2008). Green roofs have unique characteristics compared to ground-level habitats. From a species conservation perspective, the advantage of green roofs is that they are less impacted by direct human disturbance as they are less accessible to humans. However, environmental conditions are more restrictive and generally harsher: substrate depth is usually shallow due largely to roof weight restrictions; the majority of green roofs are small (generally ranging from a few square meters to hundreds of square meters); roofs, having more exposure to sun and wind, are generally drier (Lundholm 2006). Yet, in addition to plants, studies have shown that green roofs can support a variety of organisms including arthropods, bats, fungi and birds (Coffman and Davis 2005; Baumann 2006; Brenneisen 2006; Kadas 2006; McGuire et al. 2013).

In addition to the distance and size components proposed by island biogeography theory contributing to species richness, green roofs may contribute even more to overall species diversity in urban habitats if there is significant beta diversity or community dissimilarity – i.e., if the species composition on roofs is different from the composition in urban ground-level habitats. Geographical distance or ecological distance should be inversely related to community similarity (Whittaker 1960).

Horizontal and vertical components: Ecological analogs

Species diversity and community composition studies at ground level along urban-rural gradients (Niemelä et al. 2002; Weng 2007; McDonnell and Hahs 2008; van Heezik et al. 2008; Burton et al. 2009) suggest that the location of green roofs along this gradient will also influence largely the green roof ecological community. Urban areas are highly heterogeneous (Savard et al. 2000) and include mixtures of many habitats that can support many species. This gradient is generally characterized by densely human-populated and highly disturbed urban cores, to a less disturbed suburban zone and finally, least disturbed rural surroundings (McKinney 2002).

Some ground-level studies assessed evidence for how land cover (e.g., pasture, urban or forest) around gardens, parks or small fragments of natural habitat within cities affect arthropod species presence**.** Croci et al. (2008) studied the importance of urban areas for birds, carabid beetles and small mammals and found that urbanization affected these taxa differently according to their dispersal ability. Penone et al. (2013) found that urbanization had a negative effect on orthopteran species richness and abundance. Ortega-Álvarez and MacGregor-Fors (2009) showed that bird communities vary along different urban land-uses, showing reduced bird species richness with increasing urbanization intensity.

Natural analogs of the potential vertical component effects on green roofs might be for example, different tree canopy communities as a function of canopy height or differential use of the tree trunk at various heights, depending on species' preferences or mobility. For example, the mosquito *Aedes triseriatus* preferentially oviposits in lower water-filled containers or treeholes, while *Aedes hendersoni* shows an oviposition preference for higher elevation containers (Scholl and Defoliart 1977). Alencar et al. (2016), studying diversity of mosquitoes in the Atlantic Forest, Brazil, found strong negative correlations of richness and diversity with height above ground.

Classification of horizontal and vertical components in green roof studies

Here we consider the available literature on arthropod assemblages inhabiting green roofs to gather evidence of whether the horizontal and vertical distances from colonizing sources support island biogeography theory and community similarity-distance relationships. We searched for literature with ISI Web of Science (http://www.isiknowledge.com) through June 2016, using the search term set: ("green roof*" or "ecological roof*" or "roof garden*" or "living roof*") and (richness or diversity or ecolog* or biodiversity). We found only 10 papers that considered vertical and horizontal distances on arthropods. Given that these limited studies differed greatly with respect to distance components and other variations including green roof size, age, etc., plant community composition, and missing metrics, we deemed a meta-analysis for this data set not feasible. Instead, we describe the different kinds of studies and consider their support for the hypotheses recognizing that a nonsignificant effect in a particular study could still contribute to an overall significant tendency in a meta-analysis (Gurevitch et al. 2001).

We describe, from the literature, five different horizontal or vertical measures related to species richness or diversity or other community properties: (H1) horizontal distance from a green periphery along a city edge to a green roof located within an urban area; (H2) distance of a green roof to the closest green patch within urban area. This too is a horizontal component but is akin in island biogeography to distance from the nearest island or "stepping stone" rather than distance to the mainland (e.g., (Carvalho et al. 2015)); (V1) a range of vertical heights of building rooftops; (V2) a comparison between green roofs and adjacent yards; (H/V) amount of green area within a certain radius where the building green rooftop of interest is the midpoint. H/V can be considered as a hybrid of both horizontal and vertical components. When the radius is very small, or patches are next to the building, this is largely a vertical component. When lengthy radii are considered, this grades into horizontal distance.

Vertical and horizontal studies on green roofs

Based on the classifications described above, we found only one published study that considers differences in species richness or species composition as a function of horizontal distance from a colonizing source (categories H1 or H2; Table 1). Schindler et al. (2011) measured the diversity and abundance of insect families captured in pitfall traps on six green roofs with variable vegetation cover and found that the horizontal distance from ground-level vegetated areas did not significantly correlate with soil arthropod taxon richness on green roofs (Spearman's $r = 0.51$, $p = 0.30$). A second but unpublished study, Blank et al. (unpublished), also considered a horizontal component. Setting an array of flowering plants on 19 roofs of various heights and various distances from green areas in Haifa, Israel, they found that insect species richness and species diversity were significantly greater along the city edge than in the city core.

Differences in species richness and species composition as a function of building height have received somewhat more attention than the horizontal component, but still, the number of studies is small (Table 1). Four studies considered how communities varied as a function of building height (V1 category). Kadas (2006) considered arthropod species diversity on five green roofs ranging in height from 5 to 66.7 m above ground level. From our own statistical analysis of the data available in this publication, we found that diversity tended to increase with building height rather than decrease, though the relationship was not statistically significant ($F_{1,3} = 2.75$, $R^2 = 0.478$, $p = 0.196$). This absence of a diversity-vertical distance relationship, and in fact, an opposite trend, can probably be explained by other variables – e.g. that the highest building also had the largest (800 m^2) and oldest (9 years) green roof while the lowest roof had the smallest (80 m^2) and youngest green roof (3 years). Schindler et al. (2011), considering the same six green roofs described above, also did not find an arthropod richness-vertical height relationship (*Spearman's* $r = 0.06$, $p = 0.91$). Again, other variables including differences in organic content, distance from a green space (ranging from 0 to 63 m), green roof size (14–326 m^2) and soil depth (7.5 to 75 cm) should make observing a richness-vertical distance relationship difficult to observe. MacIvor (2016) monitored cavity-nesting bees and wasps on 29 vegetated and non-vegetated roofs. He found that the relative abundance of bees and wasps declined significantly with increasing building height ($t = 3.240$, $p = 0.004$). Although species richness in trap nests tended to decrease with building height, the effect was not statistically significant ($t = 1.336$, $p = 0.195$). Madre et al. (2013) sampled several arthropod groups from buildings covered by green roofs in 115 sites across northern France and found a negative correlation between spider abundance and building height ($p < 0.01$), but did not find such correlations with abundances of other arthropod groups. In addition, Blank et al. (unpublished) found that a set of flowering plants placed in ground level yards attracted more arthropod species than an identical set of plants placed on roofs. However, in this study, a low level of community similarity between the plants placed on rooftops and adjacent yards supports the notion that green roofs can contribute significantly to urban biodiversity.

Six published studies compared communities on green roofs with adjacent ground level areas (category V2). Of these, three tended to have higher richness at ground level but two of these were not statistically assessed (Kadas 2006; Colla et al. 2009) and one was not statistically significant (MacIvor and Lundholm 2011). Colla et al. (2009) compared bee diversity and abundance between two green roofs and four non-green roof sites and found that diversity and richness were generally higher at ground-level but this was not statistically tested. In addition, they found that the green roofs support similar bee communities compared to the ground-level sites. MacIvor and Lundholm (2011) studied insect diversity and compared between five pairs of intensive green roofs and adjacent ground-level habitat in downtown Halifax, Nova Scotia and found no significant differences in richness ($p = 0.2923$), abundance ($p = 0.935$) or diversity (Shannon-Wiener and Simpson's indices, $p = 0.6747$ and $p = 0.4899$, respectively) were detected. However, MacIvor and Lundholm (2011) found that richness and abundance tended to be greater (but not significantly so) at

Table 1 Overview of the scientific literature on vertical and horizontal spatial components affecting species on green roofs

Reference	Type	# Roofs	Location	Height or # floors	Community comparisons	
					Richness/α-Diversity	Other
Schindler et al. 2011	H2	6	Boston, MA, USA	0-60 m	Arthropod richness not correlated with horizontal distance to ground-level vegetated areas	Beta-diversity not checked
Kadas 2006	V1 & V2	5	London, UK	5–66.7 m	Arthropod richness not correlated with vertical height#	High community overlap between green roofs and yards
Colla et al. 2009	V2	2	Toronto, Canada	3 and 5 floors	Diversity and richness generally higher at ground-level but not statistically tested	High community overlap between bee species assemblages on green roofs and yards
MacIvor and Lundholm 2011	V2	5	Halifax, Canada	6-12 m	Insect richness and diversity tended to be higher at ground-level sites than green roofs, but no statistically significant differences	No significant differences for abundance or evenness
Schindler et al. 2011	V1	6	Boston, MA, USA	0-60 m	No effect of building height on arthropod richness	Not checked
Ksiazek et al. 2012	V2	4	Chicago, IL, USA	2–12 floors	Lower bee richness on green roofs compared to the ground level (Building height-richness correlation not tested)	Bee abundance and body size on green roofs was lower than on the ground
Quispe and Fenoglio 2015	V2	8	Cordoba, Venezuela	all 1 floor	Parasitoid richness lower on potted plants on roof than ground level	Leaf-miner abundance in potted plants was significantly higher in plants at the ground level than on the roof
Tonietto et al. 2011	H/V	6	Chicago, IL, USA	2–15 floors	Lower bee richness and diversity on green roofs than in prairies or parks. Bee richness on green roofs positively correlated with ground level green areas	Lower bee abundance on green roofs than in prairies or parks
Madre et al. 2013	V1 & H/V	115	Northern France	0-25 m	Negative correlation between building height and arthropod species richness; no significant correlation between green land cover and roof richness	Negative correlation between building height and spider abundance; No effect of land cover on arthropod composition and abundance on green roofs
MacIvor 2016	V1 and H/V	29	Toronto, Canada	1–9 floors	Species richness in trap nests was not affected by building height; green space area within a 600 m radius positively correlated with bee and wasp species richness	Building height was negatively correlated with bee/wasp abundance, and positively correlated with the number of unfinished bee nests; Decreasing abundance with decreasing proportion of green space surrounding the buildings
Braaker et al. 2014	V2 & H/V	40	Zurich, Switzerland	5-30 m*	Not Checked	Community composition on green roofs depends on species mobility

"Type" refers to the five criteria outlined in the text

H1 horizontal distance - rural/city periphery to building, *H2* horizontal distance - green patch within urban environment to building, *V1* Vertical distance: correlation as a function of building height, *V2* Vertical comparison: Adjacent yard versus green roof top; (5) H/V hybrid: amount of green area in a certain radius around the building

#Calculated from data in paper

*S. Braaker, personal communication

ground level for all orders except Heteroptera. This absence of building height effect might be explained by other variables that might mask the vertical effect such as differences in roof area (ranging from 985 to 2842 m^2) and differences in plant richness between roofs and the adjacent ground level sites (one of the lowest buildings was also the smallest in area and had the lowest number of species in the adjacent yard). Two other studies showed a statistically significant relationship with arthropod richness; adjacent green ground-level space harbored more species of bees (Ksiazek et al. 2012) and parasitoids (Quispe and Fenoglio 2015). Ksiazek et al. (2012) evaluated pollen limitation of nine native plant species on four green roofs and ground-level sites and found that bees on green roofs were represented by fewer species and individuals than on ground level habitats and that the composition on the green roofs was biased towards smaller bee species. As body size is positively correlated to foraging distance (Gathmann and Tscharntke 2002; Greenleaf et al. 2007), the large number of small-bodied genera found by Ksiazek et al. (2012) suggests these bees live within or in close proximity to these locations and generally do not travel from areas surrounding the city. Quispe and Fenoglio (2015) studied colonization of leaf-miner *L. commelinae* and its parasitoids on green roofs and found that species richness of parasitoids was significantly lower in plants on the roof than that at the ground level, that the leaf-miner abundance was significantly higher in plants situated at the ground level than on the roof, and that colonization rate of leaf-miners and parasitoids was lower on the roof than nearby ground even though the availability of resources was similar at both locations. In addition, no individual categorized as 'small' colonized roofs, and more individuals of this size than expected were associated with the leaf-miner at ground level. Conversely, more individuals of 'large' species were observed on roofs and less on the ground compared to that expected. Braaker et al. (2014) did not consider differences in richness between rooftops and ground level but investigated how local environmental conditions and dispersal processes affected arthropod community composition on 40 green roofs and 40 green sites on the ground. They found similarity and thus connectivity between nearby roof and ground sites suggesting considerable movement between green roofs and ground sites. In a seventh but unpublished study, Blank et al. (unpublished) found that sets of flowering plants placed in ground level yards attracted more arthropod species than identical sets of plants placed on roofs. However, a low level of community similarity between green roofs and ground-level yards demonstrated that green roofs can contribute significantly to urban biodiversity.

Four studies considered how community assemblages on green roofs are a function of green areas within certain radii of a building (Category H/V). Madre et al. (2013) measured the percentage of habitats (i.e., Corine Land Cover classes) in a 2-km radius around each site and found that the surrounding environment exhibited a minor influence on the composition, abundance and richness of the arthropods. MacIvor (2016) found positive relationship between increase in green area proportion within a 600 m radius around each rooftop and increase in species richness ($t = 2.341$, $p = 0.029$) and abundance ($t = 3.035$, $p = 0.006$). Tonietto et al. (2011) investigated green roofs as habitat for native bees in the Chicago region by comparing them against a reference tallgrass prairie natural areas and ecologically managed areas in city parks. They tested the extent to which bee community patterns could be explained at landscape scale by quantifying land cover categories (urban, suburban, water, and green space) within a 500-m radius of each site and found that bee abundance ($r = 0.65$, $p = 0.04$) and species richness ($r = 0.55$, $p = 0.0004$) increased with greater proportions of green space surrounding the roofs. Braaker et al. (2014) investigated the relative importance of the surrounding land-cover composition, and habitat connectivity on arthropod community composition and found that community composition on green roofs depends on species mobility: highly mobile arthropod groups (bees and weevils) were mainly shaped by habitat connectivity whereas less mobile arthropod groups (carabids and spiders) were more influenced by local environmental conditions.

Discussion

There is a debate on whether green roofs can significantly add to biodiversity within the densely populated urban matrix (Colla et al. 2009; Lundholm 2016). The goal of many studies is to plan and design a roof that will be able to support a high diversity of species (Brenneisen 2006; Williams et al. 2014; Schindler et al. 2016; Vasl and Heim 2016). Apart from defining the suitable abiotic conditions (e.g. substrate type and depth, shade, low maintenance [extensive green roofs – i.e., not regularly irrigated or fertilized and not gardened] vs. high maintenance [intensive green roofs – i.e. irrigated, fertilized and weeded]), another fundamental requirement for a species to be able to colonize this newly formed habitat, is its ability to disperse to and among green roofs. Much like a continent serves as a species colonization source to islands, so do natural and agricultural areas surrounding the urban areas serve as a species source to parks, gardens and green roofs within cities.

The study of green roofs in the context of island biogeography theory and beta diversity -distance relationships is in its infancy although it encompasses much potential similarly to other systems that were studied extensively in this context such as forest fragments (Laurance 2008) or natural vegetation within an agricultural landscape (Giladi et al. 2011). While some green roof studies statistically supported, and other studies tended to support, the island biogeography theory and/or distance-similarity relationships, no studies demonstrated an opposite significant relationship inconsistent with these theories.

In assessing whether vertical and horizontal components of green roofs are consistent with island biogeography theory and a distance-community similarity relationship, we encountered a number of existing limitations in the literature. As constructing a reasonable number of green roofs for such studies is not trivial and is expensive, most studies surveyed existing green roofs. This might pose two potential problems: [1] the number of roofs in some of the works is limited; [2] these roofs differ in numerous aspects such as green roof size, age of the green roof, substrate type, plant composition, building height and potential shading by adjacent buildings. Thus, researchers are in a problematic position of either constructing a rather limited number of small green roofs or using a rather limited number of green roofs that usually are very different from each other (Blaustein et al. 2016). The low number of replicates, combined with the lack of homogeneity among replicates within a treatment combine to reduce statistical power and our ability to detect differences (Mason et al. 2003).

The low replicates problem is even more severe as urban areas are among the most heterogeneous landscapes (Rosenzweig 2003). This heterogeneity exists at multiple scales. For example, a local plant community can be very different even in very close yards due to land owners in urban habitats choosing different plants, adding to the overall heterogeneity. At broader scales, transportation, pollution and building density might be different in different parts of the city. Thus, it is important to note that despite the use of constant repetitive units, there are still small- and large-scale effects that could potentially affect species. In general, the limited number of studies, limited number of replicates per study, and the large heterogeneity among replicates do not yet give a clear picture of whether our hypotheses raised in this paper are generally supported.

Future directions

Ecology is a relatively new research area in the study of green roofs, where most of the original focus was understandably on design and engineering. Only recently has research started to address environmental and ecological issues (MacIvor and Lundholm 2011; Tonietto et al. 2011; Blank et al. 2013; McGuire et al. 2013; Sutton and Lambrinos 2015). In addition, urban areas are highly complex and heterogeneous. Therefore, in order to address fundamental issues in ecology such as island biogeography and beta diversity, more studies and thorough and systematic studies are needed in order to account for different factors that might affect habitat selection by species. With an increase in studies, meta-analysis can then be conducted to assess overall patterns. As green roofs are novel ecosystems, they can provide many opportunities for innovative ecological research in community assembly, spatial and temporal dynamics of species and individuals and habitat suitability. However, heterogeneity between green roofs should be taken into account.

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