The effect of urban green roof design on beetle biodiversity

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Abstract

The value of urban green spaces to biodiversity conservation depends on the design and management. The importance of habitat quality and complexity to species diversity has led to the suggestion that habitat design elements—varied substrate depth, greater plant diversity, logs or stones—would support invertebrate diversity on green roofs. To evaluate this possibility, we conducted pit-fall trap sampling on three green roofs of simple design (intended primarily for stormwater management), three habitat roofs, and five ground-level green spaces, in the Portland, Oregon metropolitan area. Beetles (Coleoptera) were sampled as representatives of total invertebrate diversity. Diversity was compared using sample coverage and Hill numbers to account for differences in sample intensity and fundamental differences in species diversity. Both habitat roofs and ground sites consisted of just over 20% native species, while stormwater roofs had about 5% native species, all of which were considered pests. We collected a greater abundance of beetles on the ground compared to roof sites like others have shown. However, when sample completeness is taken into account, habitat roofs had greater Shannon diversity compared to both ground and stormwater roof sites. Habitat roofs had the fewest dominant species representing 5% or more of total abundance, but also the lowest percent of species represented by singletons (27%). These results indicate that green roofs can support different beetle communities compared to those present at ground-level urban green spaces; our results also support previous findings that biodiverse design can reliably increase green roof diversity compared to more simply designed roofs.

Introduction

Urban areas represent one of earth's few ecosystems that are increasing in extent while other types of habitat continue to be lost through degradation, fragmentation, and land-use conversion (Pickett et al. 2011; Pataki 2015; UN 2016). Globally, this has resulted in species loss on every scale from large mammals to insects to microbes (Burkepile and Thurber 2019; Klink et al. 2020). Urban areas are often perceived as disturbed areas of little ecological value, but in fact are a unique type of ecosystem that can support important pools of biodiversity, including rare and endangered native species (Pickett et al. 2008; Kowarik 2011; Grimm et al. 2017). The value of urban green spaces to biodiversity conservation often depends on the design and management of such spaces (Aronson et al. 2017).

Small ground-level urban green spaces like gardens, lawns, parks, brownfields, and historic land cover remnants have been shown to be important refuges for native species (Crocini et al. 2008; Lorimer 2008; Pickett et al. 2008; Goddard et al. 2011). The ability of ground-level green spaces to provide habitat has fueled speculation by researchers and municipalities that green roofs may also help conserve and restore biodiversity in urban areas (Landolt 2001; Brenneisen 2003; Brenneisen 2006a; Gedge and Kadas 2006; Cook-Patton and Bauerle 2012; Williams et al. 2014). A comparative study of spider communities of near-natural managed railroad areas with species-rich ruderal vegetation and structure-rich green roofs with different vegetation showed comparable species numbers in both habitat types (Brenneisen 2006b). Independent of the differences between roof and ground locations, it could be shown, however, that green roofs can also be permanently populated by stenocious and Red Data Book listed species, which proves their possible suitability in principle as compensation habitats for urban biodiversity promotion and conservation aspects (Brenneisen 2003; Pétremand et al. 2017; Pétremand et al. 2018). However, in comparisons of green roofs to nearby ground-level urban green spaces, other studies found invertebrate species richness and abundance tended to be greater on the ground (MacIvor and Lundholm 2011; Tonietto et al. 2011; Ksaizek et al. 2012).

As habitat, green roofs can suffer markedly from the characteristics of habitat fragmentation: (1) isolation, (2) small area, and (3) poor habitat quality. These characteristics are known to be negatively related to species biodiversity (McArthur and Wilson 1967; Tschamtker et al. 2002). For example, green roofs on higher buildings were less likely to be nested on by bees and wasps (MacIvor 2015). A review of urban invertebrates found that the species-area relationship generally held for a variety of green spaces and locales (Jones and Leather 2012), though at least one study has found that green roof area did not strongly influence arthropod community (Braakar et al. 2014).

Of the three aforementioned characteristics of habitat fragmentation, green roof design has the most potential to improve habitat quality, which could help mitigate the negative effects of isolation and small area on species diversity (Rosenzweig 1995; Tschamtker et al. 2002). The potential benefits of greater habitat quality have led green roof organizations and local governments to publish guidelines for "biodiverse" or "habitat" roof designs in hopes of provisioning rare, native, and specialist species (Nikles et al. 2020; City of Toronto 2020). In this paper we refer to green roofs that incorporate design elements aimed at improving habitat quality as "habitat roofs". These elements could include planting native vegetation of multiple functional groups, the use of native soil as substrate, variation in substrate thickness, and the addition of elements such as logs and stones (Brenneisen 2003, 2006a; Gedge and Kadas 2005). In contrast, we define "stormwater roofs" as those whose primary function is to retain or detain stormwater; these are often thinner roofs planted with a variety of succulent species. Understanding how habitat quality can increase green roof species diversity is important to maintaining and creating critical patches of biodiversity in the face of increasing urbanization (Williams et al. 2014; Pickett et al. 2008; Sattler et al. 2011).

Improved habitat quality can combat the effects of small fragment size if it results in increased habitat complexity (Tschamtker et al. 2002; Kovalenko et al. 2012). Greater habitat complexity is thought to increase species diversity because it provides more micro-habitats and therefore more niches for species to occupy (MacArthur and MacArthur 1961; Tews et al. 2004; Kovalenko et al. 2012). In terrestrial systems, habitat complexity is often defined by plant community (Tews et al. 2004; McAbendroth et al. 2006; Srivastava 2006), but it may also be defined by topography, substrate variation, or the presence of animal species that alter or provide physical structure (Kovalenko et al. 2012). Habitat complexity can also be provided by man-made structures that provide shade, overhanging features, or attachment points for organisms (Ido and Shimrit 2015). On green roofs, these structures include air conditioning units, solar panels, and railings.

Some studies have previously evaluated the effect of green roof habitat complexity on invertebrate diversity. A study in Switzerland found that while green roofs designed with elements like vegetation of multiple height layers, woody debris, and topographic variation had greater colonization rates of beetles and spiders, the number of rare and endangered species was similar across roof types (Brenneisen 2006a). In London, habitat roofs have been designed to mimic

derelict industrial land, since ground-level brownfields are known to be hotspots of invertebrate biodiversity in England (Gedge and Kadas 2005; Kadas 2006; Bates et al. 2009, 2013). When compared with *Sedum* genus mat planted roofs, so called “brown roofs” (term related to the brownfield) had lower invertebrate species richness and diversity; however, the result was confounded by the younger age of the brown roofs (Kadas 2006). Most studies of green roofs include only a small number of sites. However, one unique study used a quick survey method (10 minute per roof) to sample 115 green roofs across a wide swath of northern France (Madre et al. 2013). While this study did not aim to fully document roof arthropod richness, it allowed for important intra-roof comparison showing that roofs with more vegetation layers (i.e., more complexity) had greater total arthropod abundance and richness (Madre et al. 2013).

In addition to abundance and richness, measures of relative abundance, community similarity, functional groups, and the presence of specialized or native species are important for describing overall biodiversity. On roofs, local characteristics like percent herbaceous cover, number of flowering plants, or amount of bare ground may help explain community composition of arthropod groups (Braakar et al. 2014). At ground-level, urban arthropod community similarity may be more strongly associated with land-use and vegetation type than physical distance between communities (McIntyre et al. 2001; Angold et al. 2006). A study in Basel (Switzerland) showed that local and landscape variables are playing a role in structuring beetle communities on green roofs, while at the individual species level, local roof variables were more important than characteristics of the surrounding urban landscape (Kyrö et al. 2017).

However, for invertebrate groups with greater mobility, physical proximity between roof and ground-level green spaces may be more important for community similarity (Braakar et al. 2014). Isolated and disturbed sites are associated with smaller body size species (Ksiazek et al. 2012; Jones and Leather 2012) and, while native species are found on green roofs, there may be fewer than at nearby ground-level green spaces (Tonietto et al. 2011).

In this study, we examine beetle (Coleoptera) communities on green roofs of two different designs (habitat roofs and stormwater roofs) and nearby ground-level urban green spaces in Portland, Oregon. We use this evaluation to answer the following questions: (1) Do habitat roofs, which were designed with habitat quality and complexity in mind, have greater beetle species diversity than stormwater roofs and green spaces on the ground? (2) Are differences in species diversity between habitat roofs, stormwater roofs, and the ground reflected in beetle community composition, presence of native or rare species, or proportions of body sizes represented?

Methods

Site Description

The sampled roof sites were chosen based on access availability and description in the City of Portland Ecoroof Database (Starry 2020). Ground sites were chosen based on accessibility and proximity to green roofs. Descriptive characteristics of the sites are summarized in Table 1. Three stormwater roofs were located in downtown Portland and were retrofits on existing buildings (Fig 1). These three stormwater roofs had an average substrate depth of $7.5\text{cm} \pm 1.7\text{cm}$ (Mean $\pm$ SD) and an average substrate organic content of $8.7\% \pm 1.0\%$. Two of the SW roofs were planted with low-growing, drought resistant plant species of the *Sedum* genus only. The third roof was planted predominantly with Sedums but had two small areas (<10% of total vegetated area) of herbaceous ornamental plants near the access points. The stormwater roofs were 3 to 5 years in age with vegetated areas ranging from 227-873m². All three stormwater roofs had railings and partial overhangs from higher parts of the building and two had solar panels.

Two habitat roofs were located downtown and were retrofits while the third habitat roof was located just north of downtown in an industrial area. The habitat roofs had an average substrate thickness of $10.1\text{cm} \pm 1.8\text{cm}$. Additionally, all three had purposely varied substrate depth to create spatial heterogeneity. The habitat roofs had an average substrate organic content of $12.4\% \pm 6.6\%$ and were planted with a mix of herbaceous, shrubby, and drought tolerant native and non-native species. Two of the habitat roofs also had woody debris to further increase habitat complexity. The habitat roofs were 4 to 16 years in age with vegetated areas ranging from 194-1,858m². All of the habitat roofs had railings, two of the roofs had air conditioner units, and one roof had sky-lights.

Ground locations were selected based on accessibility within 200 meters of a roof location. In downtown Portland, two ground locations were undeveloped grassy lots; one was a landscaped area with a mixture of horticultural species, one was a neglected industrial area dominated by weedy colonizers, and one was in a public park with a grassy area and an area planted with native Pacific Northwest species. Ground location details are shown with their nearest roof site in Table 1.

Beetle Sampling

Beetles were sampled using ten pitfall traps at each site filled with 10% acetic acid. They were emptied and refilled biweekly. The traps consisted of 125ml plastic cups with approximately 5cm diameter opening, along with a 5 cm diameter PVC holder sleeve installed in the ground. A plastic cover prevented the traps from being flooded with rainwater. A study of pitfall trapping (Ward et al. 2001) found that traps spaced less than 5m apart interfered with each other and reduced the number of beetle morphospecies caught. However, there was no difference in number of beetle morphospecies between traps spaced 5 to 10 meters apart. Therefore, we maintained a 5-10m inter-trap spacing, placing the ten traps in a 5 x 2 grid format. In cases where this placement was not possible due to the shape of vegetated area, the traps were placed at a diagonal to each other while maintaining inter-trap spacing. The use of pitfall traps has well known limitations that bias catches towards high activity, surface and soil dwelling organisms, and under-sample beetles that live in higher vegetation levels (Woodcock 2005). However, pitfall traps can be used to sample continuously and cause low levels of disturbance while sampling (Woodcock 2005).

In order to minimize trap disturbance, a wire enclosure was placed around the traps toward the end of the season. The influence of enclosures on trap catch was tested at one roof with low disturbance by deploying enclosures on half the traps for two weeks. No difference in total catch number or rough taxonomic distribution was noted. The enclosures were secured by garden staples or, if roof substrate was not deep enough, a brick was placed on top of the cage.

Because traps were sometimes still disturbed by crows and humans, creating an uneven sampling intensity across sites, samples were compared by completeness as described in more detail in the data analysis section (Chao et al. 2014).

Predominant invertebrate groups collected in the pitfall traps included earth worms (Class: Clitellata), spiders (Order: Araneae), mites (Order: Acari), springtails (Subclass: Collembola), and insects (Class: Insecta). Beetles were selected since they are shown to be good indicators total invertebrate diversity in multiple habitat types (Duelli and Obrist, 1998; Cameron and Leather 2012).

For this analysis, only beetles (Order: Coleoptera) were retained for identification to species level and stored in a 70% ethanol, 20% acetic acid mixture. In 13 cases, a species-level identification was not made for a sample and it was identified only to genus level. Beetles species were assigned to the following feeding groups for soil and low vegetation food webs in the Pacific Northwest: *generalist predator*, *parasitoid*, *omnivore*, *generalist herbivore*, *specialist herbivore* (i.e. granivore, root chewer, moss feeder, fungivore), and detritivore (Moldenke 1999). Feeding group assignments were based on best professional advice (Andrew Moldenke, personal communication 2014) and a species-specific literature review. If a species-level identification was not made for a sample, it was assigned to a feeding group based on genus-specific information. Each species was also assigned an invasiveness and a body size classification based on a species-specific literature review (see Supplemental Information). Invasiveness classifications were *native*, *native pest*, *non-native*, *invasive*, or *unknown* if the species level identification was not made. A species was classified as invasive if it was non-native and one or more references documented an expanding range, economic damage, detrimental effects on native species, or used the word “invasive” or “pest”. Body size classifications were <5mm, “Small”; 5-10mm, “Medium”, >10mm, “Large” (Fattorini et al. 2013).

Data Analyses

All data analyses were performed using R Statistical software (R Core Team 2018); see below regarding specific packages.

Estimation of Species Diversity

A challenge in determining how green roof design and habitat complexity contribute to invertebrate diversity is the wide range of biodiversity metrics available (Chao et al. 2014). Recently, an Ecological Society of America forum advised moving towards a “species equivalent” estimate of diversity (Ellison 2010; Jost et al. 2010). This means that estimated diversity is equivalent to that of a theoretical assemblage with n equally abundant species (Chao et al. 2014). One approach is to use Hill numbers— a family of diversity indices that are species equivalents of well-known diversity metrics: richness, Shannon entropy, and Simpson index (Hill 1973). Interpolation and extrapolation of Hill numbers allow samples of different sizes to be more easily compared (Chao et al. 2014).

Because habitat roofs, stormwater roofs, and ground sites may have fundamental differences in beetle abundance and diversity and experience different levels of disturbance during sampling, sample completeness (rather than sample size) was used as an unbiased measure for comparing samples. The method for determining reference sample completeness is adapted from numbers theory and is based on the observed frequency of singletons (f_1), doubletons (f_2), and the total number of individuals sampled (Chao and Jost 2012). Chao and Jost (2012) suggest that reference sample completeness should be at least 50%.

Rather than rarefy samples to the smallest sample completeness, sample interpolation and extrapolation was performed to allow for a range of comparison. Extrapolation was extended comparison up to two times the smallest numbers of equivalent sample sizes (Colwell et al. 2012; Chao et al. 2014). The first three Hill numbers ($q = 0, 1, 2$), which represent species richness, Shannon diversity, and Simpson diversity were used as diversity metrics and bootstrapped 95% confidence intervals were constructed over the range that metrics were estimated. Analysis was implemented using the *iNEXT* package in R (Hsieh et al. 2020).

Body Size Comparison

After sampled individuals were assigned to body size classifications, a Chi-Squared test was used to determine if the proportion of individuals of different sizes varied by site type. A false discovery rate method was used to correct for multiple comparisons during post-hoc testing (Benjamini and Hochberg 1995).

Indicator Species

An analysis to determine strongly associated species was performed using the *indicspecies* R package (De Cáceres and Legendre 2009). Indicator species may not be the most abundant species since the algorithm measures the association of a species to site type based on the product of specificity and sensitivity. Specificity is the likelihood a site belongs to the target site group given the fact that the species has been found, while sensitivity is the likelihood that the species will be found at one site type only (De Cáceres 2020). A maximum indicator value statistic of 1 would be calculate for a species that is found at all sites of a particular group and is only found at sites of that group. A p-value is then calculated to the association between species and site group using a bootstrap method ($n=10000$, $\alpha = 0.1$; De Cáceres 2020).

Community Similarity

Similarity of beetle community at each sampled location was evaluated using the Bray-Curtis (BC) dissimilarity index in the *vegan* package in R (Oksanen et al. 2019). A similarity tree was developed based on Ward’s minimum variance hierarchical clustering method. The Ward method defines groups in such a way

that the within-group sum of squares is minimized (Borcard et al. 2013).

Results

A total of 90 beetle species and 3,930 individuals were found within the Portland urban area. Fifty species were found only at ground sites and 11 were found only at green roof sites. Of species found only on green roofs, 9 were found only on habitat roofs, while two were found only on stormwater roofs. The most common beetle family at ground sites and stormwater roofs was Staphylinidae followed by Carabidae. On habitat roofs the pattern was reversed with Carabids being more common than Staphylinids.

Overall, both habitat roofs and ground sites consisted of just over 20% species native to North America, while stormwater roofs had about 5% native species, all of which were considered pests. One invasive species (*Nebria brevicollis*) was identified and was found at all ground sites, one habitat roof, and one stormwater roof.

Over half of all species found on habitat roofs (55.3%), 71.5% of ground site species, and 82.6% of stormwater roof species were classified as generalist predators. Only a small percent, 0.25% on habitat roofs and 0.06% at ground sites, were classified as parasitoids or specialist predators (mite eater). On habitat roofs, 36.7% of species were classified as facultative generalist herbivores or as omnivores. For stormwater roofs, 14.5% of species and at ground sites 14.0% of species were identified as such. Ground sites had the most species (13.0%) classified as specialist herbivore (granivore, moss eater, root eater, fungivore). Habitat roofs had the next most specialist herbivores (6.7%) followed by stormwater roofs (2.9%). Detritivore were the least represented feeding group, making up 1.4% of ground site species, 1% of habitat roof species, while none were found on stormwater roofs.

Species Diversity

Habitat roofs had 36 species among 403 individuals; the number of singletons was $f_1 = 10$ and the number of doubletons was $f_2 = 2$ (Fig 2a). The coverage estimate for the reference sample was 97.5% (SE = 1.4%). Stormwater roofs had 16 species among 69 individuals; the number of singletons was $f_1 = 7$ and the number of doubletons was $f_2 = 3$, yielding a sample coverage of 90.0% (SE = 6.7%). At the ground sites, we found 79 species among 3,458 individuals; the number of singletons was $f_1 = 25$ and the number of doubletons was $f_2 = 8$, yielding a sample coverage of 99.2% (SE = 0.25%). The top five most abundant species for each site type are shown in Table 2.

Doubling the number of individuals found is the maximum recommended for extrapolation (Chao and Jost 2012; Cowell et al. 2012). This allowed the lowest abundance stormwater roofs to be extrapolated to 138 individuals and for comparison of diversity up to 98% sample completeness (Fig 2b,c, and d).

For a Hill number of $q = 0$ (species richness), habitat roofs were estimated to be the most diverse for sample sizes up to approximately 88% sample coverage. When sample coverage was greater than 88%, ground sites had the greatest richness (Fig 2b). Non-overlapping 95% confidence intervals indicate that the differences were significant (Chao and Jost, 2012). At all sample coverages, stormwater roofs had the lowest species richness. Stormwater roofs had similar richness to ground sites until approximately 75% sample coverage. Above 75% coverage stormwater roofs had the lowest species richness, although confidence intervals for habitat roof and stormwater roof richness overlapped at coverages greater than 93%.

Habitat roofs had significantly greater Shannon diversity (Hill number $q = 1$) at all sample coverages (Fig 2c). Ground sites had greater Shannon diversity than stormwater roofs, but the difference was not statistically significant since the 95% confidence intervals were fully overlapping at all sample coverages.

Habitat roofs had significantly greater Simpson diversity (Hill number $q = 2$) than stormwater roofs up to a sample coverage of approximately 65% and greater than ground sites up to a sample coverage of approximately 80% (Fig 2d). Above 65% sample coverage there is a large amount of overlap in the confidence intervals for Simpson diversity between habitat and stormwater roofs. Above 80% sample coverage, there is slight overlap in the 95% confidence intervals for Simpson diversity between habitat roofs and ground sites.

Habitat roofs had the fewest dominant species representing 5% or more of total abundance (3 species), but also the lowest percent of species represented by singletons (27%) and doubletons (5.5%). On the ground, six dominant species that represented 5% or more of individuals made up 75% of total abundance, while a larger number of species were represented as singletons (31%) and doubletons (10%) than habitat roofs. This is reflected in the greater richness on the ground as sample coverage approaches 100%. Stormwater roofs had the highest percent of species represented as singletons (43%) and doubletons (19%) but also had 5 dominant species that relatively evenly (9% – 28%) represented 77% of total abundance. This was reflected in the similar estimates of Simpson's diversity at all sample completeness levels for stormwater roofs compared to the ground (Fig 2d).

Body Size Comparison

We found that ground sites were composed primarily of large (53.4%) and medium-bodied species (36.2%), and relatively few small-bodied species (9.5%). Habitat roofs had the most medium (65.3%) and small-bodied species (23.1%) and the fewest large-bodied species (11.7%). Stormwater roofs had the most small-bodied species (36.2%), as well as the most even distribution of body sizes with 34.8% medium and 29.0% large-bodied species. Chi-squared testing showed that relative percentages of small, medium, and large bodied species were significantly different between site types ($\chi^2 = 57.6$, $df = 4$, $p\text{-value} = 9.3e-12$). Post-hoc testing indicated that habitat roofs had a significantly different distribution of body sizes compared to stormwater roofs and ground sites (habitat-stormwater: $p\text{-adj} = 1.30e-05$, habitat-ground: $p\text{-adj} = 2.90e-09$). Stormwater roofs and ground sites were significantly different from each other (stormwater-ground: $p\text{-adj} = 1.30e-05$).

Indicator Species

On habitat roofs, none of the 4 most highly abundant species were selected as indicator species (Table 2). This is likely because three of these species were also common at SW roofs (*Harpalus affinis*, *Xantholinus linearis*, *Gabrius appendiculatus*), while the fourth species (*Trechus obtusus*) was found at 4 of 5 ground sites. Instead, species ranked 5 and 11 were found to have high specificity (i.e., found primarily at habitat roof sites) and sensitivity (i.e., found at all habitat roof sites). The most strongly associated species with habitat roofs was a carabid *Stenolophus conjunctus*, (Indicator Value [IndVal] = 0.98, $p = 0.008$). A second indicator species for habitat roofs was the “ladybird” beetle *Hippodamia convergens* (Indicator Value [IndVal] = 0.93, $p = 0.066$).

On stormwater roofs, the most abundant species, carabid *Elaphropus parvulus*, was the only indicator species (IndVal = 1, $p = 0.012$). This small carabid represented 27.5% of total individuals sampled on SW roofs and was present only at SW roof sites.

On the ground, the first and second most abundant species were also indicator species. These species were large bodied staphylinid *Philonthus cognatus* (IndVal = 0.89, $p = 0.038$) and carabid *Nebria brevicollis* (IndVal = 0.99, $p = 0.009$). When combined, these species account for 42.9% of individuals sampled. *Philonthus cognatus* was not found on roofs in Portland, while *Nebria brevicollis* was found in small numbers (3 individuals) on study roofs. Both species have been found in greater abundance on a rural-suburban roof outside Portland (Gonsalves and Starry, unpublished data). Four other less abundant species were also strongly associated with the ground. One Nitidulidae species, *Carpophilus lugubris* (IndVal = 0.91, $p = 0.060$); two Curculionidae species *Sphenophorus parvulus* and *Sitona cylindricollis* (IndVal = 0.89, $p = 0.046$ and IndVal = 0.78, $p = 0.075$); and one Staphylinidae species, *Atheta fungi* (IV = 0.86, $p = 0.090$).

Community Similarity

Overall, all sites were relatively dissimilar from each other, with an average BC dissimilarity index of 0.76. The stormwater roofs clustered together in the hierarchical tree which minimized within-group variance (Fig 3), but the community at one of the stormwater roofs had strong dissimilarity (0.90 and 0.94) to the communities at the other two stormwater roofs, which were more similar to each other (0.66). Two of the habitat roofs clustered with one of the ground locations ((HAB2, HAB3, and GND2; Fig 3). These two habitat roofs in this cluster had the lowest dissimilarity of any pair of locations (0.40). Community dissimilarity between HAB2 and GND2 was 0.67, while dissimilarity was slightly lower (0.58) between HAB3 and GND2. A third cluster was made up of one of habitat roofs and the other four ground locations (HAB1, GND1,3, 4, and 5). Community dissimilarity in this cluster ranged from 0.52 between GND1 and GND4 to 0.73 between GND5 and both HAB3 and GND1.

Discussion

We found that green spaces on the ground have a richer beetle community with a greater number of both beetle species and individuals than green roofs, a finding consistent with other studies of insects on green roofs (MacIvor and Lundholm 2011; Toniello et al. 2011). However, when compared at equal sample coverage, habitat roofs had significantly greater Shannon diversity (Hill number $q = 1$) compared to the ground and to stormwater roofs. Stormwater roofs had the least number of individuals and lowest richness ($q = 0$) but had similar Shannon and Simpson diversity ($q = 2$) to ground sites. The finding that habitat roofs have greater Shannon diversity (although ground sites had nearly two times as many species) indicates that purposeful “biodiverse” design elements may increase green roof and urban biodiversity by supporting more even communities. Our finding that habitat roofs had greater richness and Shannon diversity than the more simply designed stormwater roofs supports the habitat complexity hypothesis, since habitat roofs had more layers of vegetations, varied substrate depth, and elements such as logs and stones.

We estimated diversity in terms of sample coverage, rather number of individual samples because this ensures that each community is sufficiently sampled and that comparisons are made between samples of equal completeness (Chao and Jost 2012). The use of sample coverage takes into account that ground and roof sites may be fundamentally different from each other in terms of abundance and richness. Based on smaller size, younger age, and lower accessibility, it is unlikely green roofs would have more species or more individuals than green spaces on the ground. However, green roofs generally experience less disturbance from public use or maintenance such as trimming and mowing and may provide refuge habitat for some more mobile species. This is supported by the finding of 11 species that were only on green roofs, 9 of which were found only on habitat roofs.

Additionally, we examined multiple metrics for diversity (Hill numbers $q = 0, 1$, and 2) to account for the fact that while older, larger ground sites had more species than roofs, they were also dominated by a few common species: on the ground just 6 species made up 75% of total abundance. Both Shannon and Simpson diversity take into account relative abundance of species and may be more reflective of roles in ecosystem function. Greater Shannon diversity on habitat roofs, as compared to both stormwater roofs and the ground, corresponded to more even representation in functional feeding groups, though some groups were represented by only one or two species. As Hill numbers increase, estimated diversity is less influenced by rare species. This effect explains why Simpson diversity on the ground was similar to that on stormwater roofs. At both site types a small number of dominant species made up over three-quarters of total abundance.

Consistent with other studies of invertebrates on green roofs compared to the ground, we found that the distribution of beetle body sizes was different between habitat roofs, stormwater roofs, and the ground (Ksiazek et al. 2012; Toniello et al. 2011). Habitat roofs had the greatest number of medium-bodied species, while ground sites had the greatest number of large-bodied species and relatively few small-bodied species. Stormwater roofs had the most even distribution of species by body size but had the greatest number of small-bodied species and the fewest large-bodied species. The greater presence of medium bodied species on the habitat roofs may reflect a more balanced system not dominated by small wind-delivered species or larger macro-predators (Starry et al. 2018). This pattern may also perhaps be due to the increased moisture capacity of habitat roofs that will support larger insects that would

otherwise need refuge at greater substrate depths to survive dryness, while a small body size offers more opportunities to escape from thinner and drier stormwater roofs.

Indicator species analysis showed that habitat roofs were characterized by the small native ground beetle *Stenolophus conjunctus* (Say), which often co-occurs and may compete with the non-native ground beetle *Elaphropus parvulus* (Dej.) that was characteristic of the stormwater roofs (LaBonte 1998). Habitat roofs were characterized by *Hippodamia convergens* (Guerin), an important pest predator. This native lady beetle, while not threatened, has been displaced in some areas by the introduced lady beetle *Coccinella septempunctata* L., which was also common at roof and ground sites (Alyokhin and Sewell 2004; Bahlai et al. 2014). Therefore, habitat roofs may also do a better job than stormwater roofs at provisioning desirable native insect species in the urban area. Ground sites, on the other hand, were characterized by the large-bodied generalist rove beetle, *Philonthus cognatus* and the invasive ground beetle, *Nebria brevicollis*, which is now found extensively throughout Oregon (LaBonte 2011). Though the neozoon *Nebria brevicollis* was strongly associated with ground sites, it was found on both habitat and stormwater roofs, confirming previous documentation of its ability to fly in the Pacific Northwest of North America (LaBonte 2011). To our knowledge, this species is not documented to fly in its native European range.

Clustering of beetle communities based on similarity resulted in three distinct clusters, one of which included only stormwater roofs. This result supports previous findings that urban arthropod community similarity is more related to local site characteristics such as land-use and vegetation, than to physical distance (Braaker et al. 2014; Kyrö et al. 2017). However, though stormwater roofs clustered together, indicating their uniqueness from habitat roofs and the ground, they were also relatively dissimilar to each other. One of the stormwater roofs in particular was unique compared to other two stormwater roofs. This may have been related to its larger size or greater amount of shading it received from other buildings, or it may indicate a more stochastic component to what species are found on the more simply designed stormwater roofs. In a spider study of 16 sites on the ground in urban ruderal locations and vegetated railroad areas with 6 green roofs in Basel (Switzerland), clear clustering was evident between the green roofs that were not structurally rich. One green roof site included in this study that was rich in structure clustered together with comparable vegetated sites on the ground in a similarity comparison (Brenneisen 2006b).

These findings in Portland may be applicable in other locations: a global comparison of beetle species from 41 green roofs in 5 different cities indicated that, among other factors such as city, roof type was a significant predictor of community composition (Starry et al. 2018). A study of over 100 green roofs in France found a positive correlation between roofs types with more layers of vegetation and arthropod diversity. In Zurich, roof characteristics like the amount of herbaceous vegetation were more important than surrounding land cover or habitat connectivity metrics for determining community composition of lower mobility arthropods such as carabids and spiders (Madre et al. 2013; Braaker et al. 2014).

The majority of studies in a wide range of habitats have documented a positive correlation between various measures of habitat complexity and species richness, though this relationship is not universal (see reviews by Tews et al. 2004 and Kovalenko et al. 2012). Some authors have speculated that the lack of relationship between habitat complexity and species richness found in some studies could be due to a mismatch in attributes of complexity like size or spacing (Palmer et al.; 2009; St. Pierre and Kovalenko, 2014). Habitat complexity is thought to influence species richness independent of habitat area (Kovalenko et al. 2012; Kolusa et al. 2012). Our research and other studies of green roofs suggests that appropriately chosen vegetation and other efforts to increase green roof habitat complexity are effective in enhancing beetle and other arthropod community diversity. More work is needed to understand which specific components of habitat complexity on green roofs result in the greatest increases diversity for target taxa. Additionally, some elements that increase complexity such as areas of deeper substrate can also add substantial weight and therefore cost to a green roof design. Having a better understanding of what specific features and spatial scale of habitat complexity are most beneficial on green roofs would allow designers to incorporate those features. Future studies of green roofs could include quantitative metrics of habitat complexity such as have been used in studies of other types of habitats to shed light in this area.

Urbanization poses one of the greatest threats to global biodiversity, yet urban green spaces are now acknowledged as critical to conserving native biodiversity, including insect and other invertebrate biodiversity. Though most insect species are not well known or charismatic, they are critical to the basic functioning of ecosystems (Wilson 1987) and provide important ecosystem services in urban areas, including pollination, pest management, and decomposition (Gómez-Baggethun et al. 2013). Urban green spaces also perform the innate service of providing refuge and habitat for species affected by land-use change (Gómez-Baggethun et al. 2013; Aronson et al. 2017). Our study provides further evidence that, despite generally being small and more isolated, green roofs are an important part of the urban green infrastructure. However, as with other urban green spaces, design is a critical component for determining the overall value of green roofs for biodiversity conservation.

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Tables

Table 1 Details of study green roofs and ground-level green spaces. Green space ages are exact for green roofs and approximated based on historical aerial images for ground sites.

Site Type and Code	Neighborhood	Maintenance	Age	Average Substrate Depth ^b (mm)	Approximate Building Height (m)	Approximate Area (sq.m)	Average Vegetation Height ^a (cm)	Average Vegetation Cover	Vegetation Layers	Description
Habitat Roof (HAB1)	Central Eastside Commercial	Irrigation system not in use, limited maintenance	7	12	5.7	1858	14.2	73%	3	Native vegetation, soil depth variation
Habitat Roof (HAB2)	Northwest Industrial	Hand watering and maintenance as needed	4	10	5.3	194	15.2	64%	3	Native vegetation, woody material, soil depth variation
Habitat Roof (HAB3)	Downtown	Irrigation, maintenance as needed	16	8	28.7	543	13.0	84%	4	Native herbaceous vegetation, woody material, soil depth variation
SW Roof (SW1)	Pearl District	Routine irrigation and maintenance	5	8	12.4	604	1.8	36%	1	Low drought tolerant plants, solar panels
SW Roof (SW2)	Old Town/China Town	Hand watering and maintenance as needed	3	9	15.5	227	3.4	67%	1	Primarily low drought tolerant plants
SW Roof (SW3)	Old Town/China Town	Irrigation, maintenance as needed	3	6	14.1	873	2.0	43%	2	Primarily low drought tolerant plants, solar panels
Ground (GND1)	Central Eastside Commercial	Mowing	10	-	-	2361	-	100%	1	Grassy lot
Ground (GND2)	Old Town/China Town	Mowing	30	-	-	2340	-	100%	1	Grassy lot
Ground (GND3)	Pearl District	Mowing, landscaping	18	-	-	1025	-	95%	4	City park
Ground ^c (GND4)	Northwest Industrial	None	-	-	-	292	-	46%	2	Low use area of railyard
Ground (GND5)	Downtown	Landscaping	50	-	-	650	-	72%	4	University green space

1. Because of frequent mowing and landscaping vegetation height surveys were not performed at ground sites.
2. Substrate depth could not be determined at ground sites.
3. The age of the site was unclear from historical imagery.

Table 2 Indicator and five most common beetle species for habitat roofs, stormwater roofs, and ground-level green spaces. Feeding group assignment, native species status, body size group, and any additional notable descriptive information is provided.

Family	Genus and Species	Number	Rank	Percent of Total Individuals	Indicator Species Statistic (IndVal)	Indicator Species p-value	Feeding Group	Native Species Status	Body Size Group	Additional notable description
Habitat Roofs (403 total individuals)										
Carabidae	<i>Harpalus affinis</i> (Schrk.)	107	1	26.6	-	-	Facultative herbivore, omnivore	Non-native	Large	Possibly play a beneficial biocontrol role in agricultural systems (Sunderland et al. 1995); synanthropic (Majka et al. 2007).
Staphylinidae	<i>Xantholinus linearis</i> (Ol.)	62	2	15.4	-	-	Predator	Non-native	Medium	
Staphylinidae	<i>Gabrius appendiculatus</i> Sharp	26	3	6.5	-	-	Predator, detritivore	Non-native	Large	
Carabidae	<i>Trechus obtusus</i> Er.	16	4	4	-	-	Predator	Non-native	Small	Oregon populations are documented to have a high frequency of macroptery (Liebherr & Takumi 2002).
Carabidae	<i>Stenolophus conjunctus</i> (Say)	15	5	3.7	0.98	0.008	Predator	Native	Small	
Coccinellidae	<i>Hippodamia convergens</i> Guerin	8	11	2	0.93	0.066	Pest predator	Native	Small	
Stormwater Roofs (69 total individuals)										
Carabidae	<i>Elaphropus parvulus</i> (Dej.)	19	1	27.5	1	0.012	Predator	Non-native	Small	Associated with lacustrine and riparian habitats (LaBonte and Nelson 1998).
Staphylinidae	<i>Gabrius appendiculatus</i> Sharp	10	2	14.5	-	-	Predator, detritivore	Non-native	Large	
Staphylinidae	<i>Xantholinus linearis</i> (Ol.)	10	3	14.5	-	-	Predator	Non-native	Medium	
Staphylinidae	<i>Ocypus aeneocephalus</i> (DeG.)	8	4	11.6	-	-	Megapredator	Non-native	Large	
Carabidae	<i>Harpalus affinis</i> (Schrk.)	6	5	8.7	-	-	Facultative herbivore, omnivore	Non-native	Large	Possibly play a beneficial biocontrol role in agricultural systems (Sunderland et al. 1995); synanthropic (Majka et al. 2007).
Ground-level (3458 total individuals)										
Staphylinidae	<i>Philonthus cognatus</i> Steph.	1074	1	31.1	0.89	0.038	Megapredator	Non-Native	Large	
Carabidae	<i>Nebria brevicollis</i> (F.)	409	2	11.8	0.99	0.009	Predator	Invasive	Large	Rapidly expanding range and present in a wide range of habitats and climates in Oregon (LaBonte 2011).
Tenebrionidae	<i>Blapstinus</i>	400	3	11.6	-	-	Granivore,	Native	Medium	

	<i>moestus</i> <i>Melsh.</i>						detritivore				
Carabidae	<i>Amara aenea</i> <i>(DeG.)</i>	307	4	8.9	-	-	Generalist	Non-Native	Medium	Considered synanthropic (Majka et al. 2007).	
Staphylinidae	<i>Philonthus carbonarius</i> <i>(Grav.)</i>	226	5	6.5	-	-	Megapredator	Non-Native	Large		
Nitidulidae	<i>Carpophilus lugubris</i> <i>Murray</i>	34	12	1	0.91	0.060	Detritivore	Native	Small		
Curculionidae	<i>Sphenophorus parvulus</i> Gyll.	20	17	0.6	0.89	0.046	Herbivore	Non-Native	Medium	Turf grass pest (Kindler and Spomer 1986).	
Staphylinidae	<i>Atheta fungi</i> <i>(Grav.)</i>	20	17	0.6	0.86	0.090	Generalist pest predator	Non-Native	Small		
Curculionidae	<i>Sitona cylindricollis</i> <i>(Fahrs.)</i>	5	28	0.1	0.78	0.075	Herbivorous	Non-Native	Small	Pest of sweet-clover, alfalfa, alsike clover, and black medic (Bright and Bouchard 2008)	

Figures

Figure 1

Map of Portland, Oregon, with locations of green roofs and ground-level green spaces.

Figure 2

(a) Species rank abundance curves for ground-level green spaces (GND; circles), habitat roofs (HAB; squares), and stormwater roofs (SW; triangles). (b) Sample completeness-based rarefaction (solid line) and extrapolation (dashed line) curves for species richness (Hill number $q = 0$). (c) Sample completeness-based curves for Shannon diversity (Hill number $q = 1$). (d) Sample completeness-based curves for Simpson diversity (Hill number $q = 2$). Reference samples are shown as points using the same symbology as in panel (a).

Figure 3

Ward's distance cluster tree on Bray-Curtis dissimilarity for sampled beetle communities. Shading indicates three major clustering groups. Notes: Fig 1 was created in ESRI ArcMap. Fig 2 and Fig 3 were created in R Statistical Software using the vegan, iNEXT, ggplot2, and gg dendro libraries. All figures were converted to .eps format using Adobe Editor.

Supplementary Files

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- [SupplementaryInformationGonsalvesetalSpeciesList.xlsx](#)
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