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Green Roofs and Urban Biodiversity: Their Role as Invertebrate Habitat and the Effect of Design on Beetle Community

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Green Roofs and Urban Biodiversity: Their Role as Invertebrate Habitat and the Effect of Design on Beetle Community

by

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Abstract

With over half the world's population now living in cities, urban areas represent one of earth's few ecosystems that are increasing in extent, and are sites of altered biogeochemical cycles, habitat fragmentation, and changes in biodiversity. However, urban green spaces, including green roofs, can also provide important pools of biodiversity and contribute to regional gamma diversity, while novel species assemblages can enhance some ecosystem services. Green roofs may also mitigate species loss in urban areas and have been shown to support a surprising diversity of invertebrates, including rare and endangered species. In the first part of this study I reviewed the literature on urban invertebrate communities and diversity to better understand the role of green roofs in providing habitat in the context of the larger urban mosaic. My review concluded that, while other factors such as surrounding land use and connectivity are also important to specific invertebrate taxa, local habitat variables contribute substantially to the structure and diversity of urban invertebrate communities. The importance of local habitat variables in urban green spaces and strong support for the habitat complexity hypothesis in a number of other ecosystems has led to proposals that "biodiverse" roofs— those intentionally designed with varied substrate depth, greater plant diversity, or added elements such as logs or stones—would support greater invertebrate diversity, but there is currently limited peer reviewed data to support this. In order to address the habitat complexity hypothesis in the context of green roofs, in the second part of this study I surveyed three roofs designed primarily for stormwater management, three biodiverse roofs, and five ground-level green spaces, from March until September of 2014 in the Portland metropolitan area. Beetles (Coleoptera) were sampled bi-weekly as representatives of total species diversity. Biodiverse roofs had greater richness, abundance, and diversity of beetle species compared to stormwater roofs, but were not more diverse than ground sites. Both biodiverse roofs and ground sites had approximately 20% native beetle species while stormwater roofs had only 5%. Functional diversity was also higher on biodiverse roofs with an average of seven trophic groups represented, while stormwater roofs averaged only three. Ground sites, biodiverse roofs, and stormwater roofs each grouped distinctively in terms of beetle community composition and biodiverse roof communities were found to be positively correlated with roof age, percent plant cover, average plant height, and plant species richness. These results support the findings of previous studies on the importance of local variables in structuring urban invertebrate communities and suggest that biodiverse design can reliably increase greenroof diversity, with the caution that they remain no replacement for ground level conservation.

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Chapter 1: The role of green roofs as invertebrate habitat in the context of the urban mosaic: a review

By 2008 over half the world's human population lived in urban areas and this number is expected to increase to seventy percent by mid-century (UN Habitats 2012). 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) which has led to a loss of biodiversity (Tillman et al. 1994, Rosenzweig 2003). Human activities facilitate the introduction of generalist exotic species into urban areas causing a decline in native and specialist species in what McKinney (2002, 2006) terms biotic homogenization. Invertebrates are one group of organisms found to decline in diversity and body size along a rural to urban gradient, but this trend is not universal (Jones and Leather 2012). In fact, urban areas can often harbor important pockets of native diversity, and dominance by exotic species is spatially heterogeneous (Pickett et al. 2008).

Small ground-level urban green spaces like gardens and lawns, parks, brownfields, and historic land cover remnants have been shown to be an important refuge for native biodiversity (Croci 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 (Gedge and Kadas

2006, Cook-Patton and Bauerle 2012, toronto.ca/greenroofs). Low impact designs like green roofs have been shown to help ameliorate other ecosystem alterations in cities such as the urban heat island, an increase in local temperature compared to rural areas, and urban stream syndrome, a degradation of riparian and stream habitat (Mentens et al. 2006, Lundholm et al. 2010). However, developing a comprehensive understanding of how the built environment, including green roofs and other low impact development, might affect or determine biodiversity, community structure, and connectivity remains a major challenge in urban ecology (Pataki 2015).

Invertebrate diversity is especially important in the urban area because, although small and regarded with distaste by many human inhabitants (Hunter and Hunter 2008), EO Wilson (1987) reminds us that invertebrates are the “little things that run the world”. Insects alone perform services such as pollination, decomposition, pest control, and wildlife nutrition that have been estimated at nearly sixty billion dollars annually in the US (Losey and Vaughan 2006). In addition, insects and other invertebrates are small enough that small urban patches may be able to provide the needed resources for survival and reproduction (Hunter and Hunter 2008).

The ability of ground-level urban green spaces to support invertebrates and patterns in diversity, richness, and community composition depends on the interplay between the region, habitat type, and level of urbanization. On a global scale, a meta-analysis of nine cities across several European countries, Japan, and Canada, found that carabid community was always more similar within countries rather than across the same urbanization level in different cities (Magura et al. 2010). A study of urban green spaces within three Swiss cities found that arthropods of different functional types can be affected differently by age, percent surrounding impervious surface, and management intensity (Sattler et al. 2010a). A model showed that all species functional groups were positively sensitive to age of green space and negatively sensitive to impervious surface, while only low mobility species were negatively sensitive to management intensity (Sattler et al. 2010a). When considered alone, low mobility species were insensitive to age of green space. In this same study urban arthropod species richness was comparable to published data from nearby semi-natural forest and farmland, but the three cities were highly similar in terms of functional group composition, perhaps suggesting a trend towards biotic homogenization though this was not confirmed to species level (Sattler et al. 2010a). Two other studies on ground arthropods (McIntyre et al. 2001) and carabids (Angold et al. 2006) in Phoenix, Arizona, USA and Birmingham, England respectively, both found distinct communities among urban brownfield, park, and remnant ecosystem patches. The study in Phoenix found comparable richness in all patch types, while the Birmingham study found a distinct reduction in richness with increasing urbanization, but only in remnant woodland patches (McIntyre et al. 2001, Angold et al. 2006). In order to better understand if cities contribute to landscape biodiversity, one study looked at 45 sites in a single city on an urbanization gradient of forest, agriculture, and urban green patches and confirmed that, in Switzerland at least, urban sites did increase landscape gamma diversity (Sattler et al. 2011).

Research on green roofs is slowly catching up with the urban research on invertebrates at ground level and several recent studies have helped shed light on the role of green roofs in the urban mosaic. Studies comparing green roofs to nearby ground sites have found a trend toward lower diversity and abundance of invertebrates on roofs. In Nova Scotia, Canada, 14% fewer morphospecies of insects were collected from roofs sites than ground sites, with roofs having an average of 12 fewer species per site, though no statistically significant differences in richness, abundance, evenness, or diversity indices were found ($p>0.29$ for all; MacIvor and Lunholm 2011). Other studies of green roofs that included ground sites have found an average of 35% fewer bee species per year over three years (Colla et al. 2009), 52% lower bee abundance in one year (Ksiazek et al. 2012), and an average of 36% fewer spider species on roofs compared ground sites (Brenneisen and Hanggi 2006), though no statistical tests were performed in these cases. Differences between ground and roof sites may also depend on the type of ground site habitat. One study found green roofs had higher abundance but lower diversity of invertebrates than brownfields (Kadas 2006), while another study caught significantly fewer bees on green roofs compared to remnant prairie, but not compared to parks (Tonietto et al 2011).

The arthropod community on green roofs, however, is not simply a subset of that on the ground. For example, MacIvor and Lundholm (2011) found that 25% of the species caught were unique to the ground, while 18% were only found on the roof. One community analysis found that green roofs grouped separately from the ground sites (Colla et al. 2009), while a second (Tonietto et al. 2011) found that park, prairie, and green roof bee communities each grouped distinctively. One explanation for such habitat-specific communities is that there are fewer or no brachypterous species (ones with only rudimentary wings), and more macropterous and wing-dimorphic species in urban green areas like street margins, roundabouts, and parks than in remnant green patches (Jones and Leather 2012). Green roofs would likely fall into this category being both relatively young and hard to reach, though no green roof studies have reported wing type by species. Conversely, brachypterous species and individuals are common in urban forest and other unmanaged patches, suggesting these may be remnant populations (Jones and Leather 2012). Additionally, the community proportion of small, medium, and large bodied bee species was found to differ between the ground and roof sites, with medium bodied bee species making up a larger proportion of bees caught on roofs (Ksiazek 2012). In beetles, increasing disturbance along the urbanization gradient is known to be negatively correlated with body size since large species have lower dispersal ability and require more stable resources (Jones and Leather 2012). Based on these green roof bee and ground-level beetle studies, green roof beetle communities are likely to consist of small to medium bodied and large-winged species.

The above findings that green roof arthropod communities are often more similar to other green roofs than to nearby park or landscaped green spaces, all of which are distinct from nearby remnant habitat, supports the trends found from ground-level urban arthropod research of the importance of patch type in structuring arthropod community (McIntyre et al. 2001, Vanbergen et al. 2005, Angold et al. 2006, Sattler et al. 2011). Patches of different habitat type in close proximity were not more similar in their composition of urban arthropods than patches of the same type that were futher away, leading to the conclusion that local habitat variables were of more importance than connectivity (McIntyre et al. 2001). Similarly, patch spatial location was of little or secondary importance to the composition of ground level urban beetle community (Angold et al. 2006). Interestingly, this conclusion also extended to highly mobile butterfly species, which had no significant relationship between geographic and genetic distance: populations along intended habitat corridors were no more similar than other populations in the urban area (Angold et al. 2006).

Other ground level studies have also supported the conclusion that carabid beetles (Vanbergen et al. 2005, Small et al. 2006) and whole urban arthropod communities (Sattler et al. 2011) are explained primarily by local habitat variables rather than location in the landscape. One study attempted to dissect the influence of local environmental variables (such as site age, management intensity, and green cover) and purely spatial variables and found that very little variation in urban spider community (~3%) was explained by spatial variation, while 15-29% was explained by environmental variables (Sattler et al. 2010b). The authors therefore concluded that neutral processes play little role in urban meta-communities, instead speculating that a species sorting model, which emphasizes niche processes (Leibold et al. 2004), as well as stochastic population events may be important (Sattler et al. 2010b). Therefore, results of both green roof and ground level studies indicate that more work should be done to better understand the origin and role of green roof invertebrate communities in the urban mosaic.

An understanding of how green roofs might fit into meta-community theory is important since their isolated nature lends itself to the analogy of “stepping stones” (Kim 2004, Hopkins and Goodwin 2011, greenroofs.com). To this end, a recent study was the first to include green roofs in an urban meta-community analysis of green patches by separating out the importance of local variables (such as age, area, and number of flowering plants), land use, and connectivity on community composition of four arthropod groups (Braaker et al. 2013). In this study connectivity was defined by the arrangement of green spaces and purely spatial variables. When looking only at the green roof sites, local variables alone explained about half of the variation in carabid and spider communities, while connectivity and the interaction between connectivity and land use explained over 80% of the variation in the weevil and bee communities (Braaker et al.

2013). The pattern of community variation for all arthropod groups became much less distinct when roof and ground sites were combined and analyzed together. When only ground sites were considered, connectivity was least important which, for beetles, may be related to the observation that some ground sites are highly characterized by brachypterous species with limited dispersal ability (Jones and Leather 2012). Overall, both the mass-effect and species sorting theories of meta-community were found to be consistent with variation in community composition, depending on organism mobility. That there was some degree of spatial autocorrelation between nearby roof and ground sites indicates that neutral process may also play some role, since random movements would cause closer sites to be more similar than far sites. However, although previous research discussed above has found green roof invertebrate communities to be different from the ground, the lack of spatial autocorrelation between communities on the roofs themselves indicates that the roofs are not being used as “stepping stones” across the urban area. A study of bee nesting on green roofs also tested for spatial autocorrelation among roofs and found none (MacIvor 2015), while another study found little influence of surrounding land cover on beetle, bee, spider, and true bugs (Madre et al. 2013). For green roofs then, the species sorting model, which stresses the importance of patch quality and dispersal to track local environmental conditions (Leibold et al. 2004), appears influential to structuring invertebrate communities and warrants further investigation.

An important conclusion to draw from studies of urban arthropods is that local variables, such as type and amount of vegetation and management of site, greatly influence community composition and diversity and should be considered in roof design. Predictions for the potential of green roof habitat value have often been made based on the habitat heterogeneity hypothesis (Gedge and Kadas 2005, Brenneisen 2006, Kadas 2006, Cook-Patton and Bauerle 2012), which says that more structurally complex habitats will have more niches thus increasing resource exploitation and species diversity (MacArthur and MacArthur 1961, Tews et al. 2004, Kovalenko et al. 2012). A review of the literature found that there was generally a positive correlation between habitat heterogeneity and animal diversity, but that this relationship was drastically biased by the number of studies on vertebrates (Tews et al. 2004). However, experimental tests in ground level plots found a significant correlation between plant functional diversity and arthropod diversity (Siemann et al. 1998, Haddad et al. 2002). Similarly, a study of forest beetles found that more structurally complex sites had greater beetle species richness than less complex sites (Lassau et al. 2005).

Although there is strong support for the habitat heterogeneity hypothesis in a variety of systems, caution should be taken in universal application of this principal because the underlying mechanisms are not well understood (Kovalenko et al. 2012). Furthermore, determining the appropriate spatial and temporal scales for applying the hypothesis to planning and management, especially in constructed ecosystems, may be difficult (Kovalenko et al. 2012). A meta-analysis of 78 river restorations found that increasing habitat heterogeneity did not result in increased macroinvertebrate diversity (Palmer et al. 2010). Whether this was due to inappropriate spatial scale of restoration, too short a time period before monitoring data was collected, or lack of nearby colonizing organisms is unknown (Palmer et al. 2010). Like river restorations, increasing structural complexity on green roofs through varying substrate depth, adding elements such logs or stones, including multiple plant functional types, or even attempting to replicate whole ecosystem types (Gedge and Kadas 2005, Brenneisen 2006, Kadas 2006) has become increasingly popular (thegreenroofcentr.co.uk, toronto.ca/greenroofs), yet there remains relatively little published data to confirm the effectiveness of these designs in increasing biodiversity (but see Baumann 2006, Brenneisen 2006, Kadas 2006, and Madre et al. 2013).

For green roofs, increasing “biodiversity” likely applies specifically to increasing abundance and diversity of invertebrates. One study looked at the ability of a green roof to provision ground nesting plovers and found 100% chick mortality (Baumann 2006). Even after several years of attempting to increase roof resources through changes to design, while length of chick survival increased, mortality remained at 100% before fledging (Baumann in Muller, Werner and Kelcey 2010). Invertebrates on the other hand, are small enough that a roof could provide many or all resource needs. A study in Switzerland (Brenneisen 2003, 2006) looked at a number of roofs, some of which had been designed to mimic threatened alluvial grassland habitat, and found that the habitat roofs had increased rates of colonization by beetles and spiders. A large-scale study of 115 green roofs across the entirety of northern France found a significant increase in abundance and richness of arthropods by increasing height of vegetation structure (Madre et al. 2013). One downside to this study was that in order to visit so many roofs in such a wide geographic range within two months, the authors were limited to sampling just ten minutes per roof. This meant that no arthropods were captured on 25% of the roofs, while just 290 individuals from 66 species were captured across the remaining roofs. While this presents an excellent snapshot in time, the average of just over 3 individuals and less than one species per roof likely substantially undersamples the roof communities. One other study (Kadas 2006) compared urban brownfields, roofs designed to mimic brownfields, and *Sedum*-mat green roofs and found that the brown roofs had the least arthropod diversity and abundance.

In determining the ability of spatially heterogeneous green roofs to promote and conserve invertebrate biodiversity in the urban area it is important to have multiple measures of diversity. For example, species diversity can sometimes be less important than functional diversity for ecosystem stability and function (Lefcheck et al. 2015). Relative abundance may also not be a good predictor of ecosystem importance (Hooper et al. 2005), especially in urban arthropod communities that are often characterized by a high abundance of mobile generalist predators such as carabid and staphylinid beetles and linyphiid spiders (McIntyre 200). Green roof studies have documented up to 10% of species as endangered or threatened (Brenneisen 2006, Kadas 2006) and these rare species could have a strong influence on energy and material flows (Hooper et al. 2005). In addition, some researchers (Kovalenko et al. 2012) hypothesize that the mechanism by which habitat heterogeneity increases diversity is through the alteration of species interactions, which are already altered in the urban area compared to the unbuilt environment (Schochat et al. 2006). From this perspective, increasing habitat heterogeneity would be the spatial equivalent of temporal uncoupling, increasing system stability and allowing for greater persistence of predator and prey (Kovalenko et al. 2012). Other studies have found that increased arthropod diversity and transition to species of greater body size was mediated by increased plant biomass that resulted from greater plant structural complexity (Borer et al. 2012). The mechanism by which habitat heterogeneity increases diversity may be different in different systems suggesting that multiple measures including diversity, abundance, body size distribution, and functional diversity may all be key in assessing ecosystem quality and should be included in determining green roof design success.

Because of the time, expense, and expertise required to identify invertebrates to species level most studies limit themselves to either one or two taxonomic orders (Brenneisen 2006, Tonietto et al. 2011, Ksiazek et al. 2012, MacIvor 2015) or do not identify to species level (McIntyre et al. 2001, Sattler et al. 2011). It may be important to identify to species level since allocation to coarser taxonomic groups may result in misclassification of functional traits (Sattler et al. 2011) or native species status. Therefore, in my assessment of the effect of heterogeneous green roof habitat design on arthropod diversity and community composition, beetles (Coleoptera), identified to species level, will be used as a measure of overall arthropod diversity. Beetles are a speciose and abundant, yet relatively taxonomically stable, order that comprise a wide variety of trophic, mobility, and body size classes and are easily sampled (Lovei and Sunderland 1996, Rainio and Nimela 2003). Beetles, in particular carabids, are also good as indicators of habitat quality since they are sensitive to environmental change and respond quickly to disturbance (McIntyre 2000, Rainio and Nimelä 2003, Jones and Leather 2012). Measures of beetle diversity have found the number of beetle species to have a positive 95% correlation with the number of total species in an ecosystem, including vertebrates, invertebrates, and plants (Duelli and Obrist 1998).

There are many motivations for wanting to conserve and better understand urban biodiversity, from the anthropocentric to ethical consideration of species intrinsic value (Dearborn and Kark 2009). Current conservation practices of restoration and setting aside land to preserve species diversity are dwarfed by the extent of land being converted to urban and agriculture use, leading some to argue that a solution must be developed for land to satisfy both human and conservation requirements (Rosenzweig 2003). The argument for land reconciliation hinges on the observation that the current practice of separating human and nature has not been beneficial for humans or nature (Diaz et al. 2006), that land will be converted to human uses regardless with some conservation value better than none (Rosenzweig 2003, Francis and Lorimer 2011), and that preserving species diversity in the areas where people live and work can affect perceptions and win support for traditional forms of conservation (Dearborn and Kark 2009). Yet, there are additional upfront costs, and possibly ongoing management costs, associated with designing green roofs to preserve species diversity, when simpler green roof designs might mitigate stormwater (Oberndorfer et al. 2007) or white roofs might reduce building heat load (Sproul et al. 2014) just as well. Some researchers argue that allowing “wild dynamics” to take over in constructed ecosystems will actually reduce management costs by allowing the system to reach a state of self-organization in which certain ecosystem services are enhanced (habitat provisioning, pollination) at the expense of more traditional roof services (stormwater and heat management) (Lundholm 2015).

The purpose of this review was to examine the less explored service of habitat provisioning to determine the role green roofs play for invertebrate species in the larger context of the urban ecosystem. The interaction between site type, management intensity, and age was found to be important: for example, whether the site is a new, highly managed roundabout or a little managed forest remnant can structure invertebrate community mobility and body size (Jones and Leather 2012, Ksiazek et al. 2012). Connectivity was found to have a strong influence on some taxa but not others (Braaker et al. 2013), indicating that many urban adapted invertebrate species may not be dispersal limited within the built environment (McIntrye et al. 2001, Angold et al. 2006). Finally, local habitat variables such as plant diversity (Madre et al. 2013), including number of flowering plants (Braaker et al. 2013, Tonietto et al. 2011), water availability (Angold et al. 2006), and total cover (Sattler et al. 2010a) were found to influence diversity and community composition, including the proportion of urban generalists. In order to further to elucidate the effect of local variables controlled by roof design, in the next chapter I test whether, as predicted by the habitat diversity hypothesis, spatially heterogeneous habitat roofs in Portland, Oregon provide for greater beetle (Coleoptera) diversity and abundance in comparison to spatially homogeneous *Sedum*-dominated stormwater roofs. I will also compare these roofs with ground-level sites to determine the extent to which the diversity of roofs complement or supplement habitat on the ground with regards to distinct beetle community composition and functional diversity. A recent review (Williams et al. 2014) cautioned proponents of green roofs to use restraint in claiming the benefits of green roof biodiversity conservation since the ability of green roofs to provision rare taxa or replicate desired biotic communities is poorly documented. However, a small group of studies do show a positive relationship between habitat complexity and biodiversity on green roofs, leading Williams et al. (2014) to call for more studies to confirm this trend. Hence, my study will shed light on whether spatially heterogeneous “biodiverse” designs of green roofs can reliably increase urban invertebrate diversity, and thereby green roof conservation value.

Chapter 2: **The effect of green roof design on beetle diversity and community composition**

Introduction

As over half the world's population now live in cities (UN Habitats 2012), urban areas represent one of earth's few ecosystems that are increasing in extent (Ellis et al. 2010), but they are also sites of altered biogeochemical cycles, habitat fragmentation, and changes in biodiversity (Grimm et al. 2008, Pickett et al. 2011). Meta-analyses have found that the diversity of organisms tend to decrease along a rural to urban gradient (McKinney 2002, 2005; Magura et al. 2010), with few native and specialist species compared to the surrounding landscape (Grimm et al. 2008). However, urban patches can also be important pools of biodiversity and contribute to regional beta diversity (Pickett et al. 2008, Sattler et al. 2011). In addition, novel urban species assemblages can enhance some ecosystem services (Hansen and DeFries 2007).

Increasing the total area of available green space is a critical component in conserving urban biodiversity (Tilman et al. 1994), and use of green infrastructure is thought to be a way to simultaneously satisfy ecological needs and land development pressure (Rozenweig 2003, Francis and Lorimer 2011, EPA 2015). The design of infrastructure such that some aspects of the pre-development ecosystem remain intact is termed low-impact development (LID) (Davis 2005). Green roofs are LIDs that help maintain the hydrologic cycle by reducing stormwater runoff and mitigate local urban heat island effects

(Oberndorfer et al. 2007, Ranali and Lundholm 2015). Green roof biodiversity benefits, such as provisioning rare, native, and specialist species or increasing connectivity, are often promoted but have not been fully quantified (Williams et al. 2014). Given the importance of local habitat variables in determining arthropod community for both ground level and elevated green spaces (McIntyre et al. 2001, Angold et al. 2006, Sattler et al. 2010, Braaker et al. 2013) it is likely that different green roof designs will have varying influences on these communities.

Some green roof organizations and local governments have begun publishing guidelines for “biodiverse” roof designs that include planting native vegetation of multiple functional groups, using native soil as substrate, varying substrate thickness, and adding elements such as logs and stones to provide micro-habitats (thegreenroofcentr.co.uk, toronto.ca/greenroofs). The habitat diversity hypothesis in ecology is often used to support the biodiverse design model since it predicts that more complex habitats will provide more niches thus allowing a greater number of species and organisms to exploit available resources (MacArthur and MacArthur 1961; Tews et al. 2004, Kovalenko et al. 2012). In ground-level grassland plots, increasing the number of plant species and functional groups increased arthropod richness, biomass, and temporal stability (Siemann et al. 1998, Haddad et al. 2001, Borer et al. 2012), and in tropical reefs adding artificial reef elements increased the richness, abundance, and biomass of fish (Santos et al. 2011). However, theory has not always led to successful practice in constructed ecosystems; in a review of 78 stream restorations with added meanders, riffles, and boulders, only two had statistically significant increases in biodiversity (Palmer et al. 2010). For green roofs there remain few studies evaluating the habitat diversity hypothesis (but see Brenneisen 2003, 2006; Madre et al. 2013), so biodiverse roof design should be more fully studied before its benefits are promoted (MacIvor and Ksiazek 2015).

The metropolis of Portland, Oregon was one of the early adopters of green roof technology in North America, with approximately 93,000 square meters of green roof area implemented in large part by an incentive program that ran from 2008 to 2012 (City of Portland Ecoroof Incentive Program, portlandoregon.gov). In 2016 the City of Portland government will consider a green roof requirement as part of its 30-year downtown development plan. As more cities begin to adopt policies similar to the one being considered in Portland now, additional research and evidence will be imperative for demonstrating that green roofs perform all services ascribed to them. It is clear that green roofs can provide resources for a variety of organisms (Brenneisen 2006, Buanmann 2006, MacIvor and Lundholm 2011, Toneitto et al. 2011, MacIvor 2015), but it is difficult to draw clear conclusions about biodiverse roof design from studies to date (Cook-Patton and Baurele 2012, Williams et al. 2014). Roofs designed as habitat in Switzerland were found to have greater colonization rates of beetles and spiders, but the number of rare and endangered species was similar across roof types (Brenneisen 2006). In London, England roofs designed to mimic brownfield, derelict industrial land, are popular (Gedge and Kadas 2005; Kadas 2006; Bates et al. 2009, 2013), but a study comparing these “brown roofs” with *Sedum* planted roofs found they had lower invertebrate species richness and diversity (Kadas 2006). A large study of 115 green roofs in France showed significant increase in total arthropod abundance and richness with more vegetation levels, but was hampered by limited sample time (10 minutes) per roof (Madre et al. 2013).

The definition of biodiversity should also be considered when evaluating the quality of green roof habitat, since not all species contribute equally to ecosystem processes and services (Hooper et al. 2005, Stuart-Smith et al. 2013). Diversity of functional characteristics can be as important as species richness and abundance in determining how a constructed ecosystem will perform (Ranalli and Lundolm 2008) and should be considered in evaluating success of green roof design for biodiversity. For example, water retention and building cooling on green roofs is increased by facilitation among plants of different functional types more than by simply increasing plant species richness (Lundholm et al. 2010). Arthropods have the potential to perform a variety of human-desired services including pest control, decomposition, and pollination (Losey and Vaughn 2006), yet ground-level urban green space communities can be functionally homogenous, characterized by habitat generalists, predators, and cosmopolitan species (McIntyre 2000, McKinney 2005). Designing roofs to attract invertebrate communities that maximize ecosystem functions and services may contribute to the long-term resilience of the roof to disturbance (Hooper et al.

2005). Studies have shown that green roof arthropod communities have been found to differ in composition, have smaller body size, and increased mobility compared to ground sites (Colla et al. 2009, MacIvor and Lunholm 2011, Tonietto et al. 2011, Ksiazek et al. 2012, Braaker et al. 2013) though how this changes functional diversity and therefore affects roof processes and services remains unclear (Cook-Patton and Bauerle 2011).

In the study reported here I evaluate in greater detail how green roof design might affect invertebrate diversity and community composition. I use beetles (Coleoptera) as a proxy for arthropod community since this order is easily sampled and is highly correlated with total ecosystem diversity in multiple habitat types (Duelli and Obrist 1998, Cameron and Leather 2012). I sampled three biodiverse green roofs, three *Sedum*-dominated stormwater roofs, and corresponding ground sites in Portland, Oregon to determine beetle diversity and abundance. In accordance with the habitat diversity hypothesis, I predict that biodiverse designed roofs will have greater beetle diversity than stormwater roofs and that both types of roof will be distinct from ground sites with regards to beetle community composition including the relative proportion of different functional feeding groups. I also assess the influence of local habitat and surrounding land use variables, and predict that local habitat variables characterizing roof type will have a greater influence on beetle community.

Methods

Site Description

The sampled roofs were chosen based on access availability. Descriptive characteristics of the roof sites are summarized in Table 1. Six of the eight roofs were in the downtown core, one roof was located just north of downtown in a heavy industrial area (site code GU), while one roof (site code TC) was located in the surrounding community of Oregon City, which is outside Portland city limits, but inside the metropolitan urban growth boundary (Metro 2016; Figure 1). Three of the roofs (ET, OC, and NH) in the downtown area were designed primarily with stormwater management in mind and were retrofits on existing buildings. These three stormwater roofs were extensive, with an average substrate depth of 7.5cm ± 1.7cm (Mean ± SD), and an average substrate organic content of 8.7% ± 1.0%. Two of the SW roofs (ET and NH) were planted with low-growing, drought resistant plant species of the *Sedum* genus only, while the third roof (OC) was planted predominantly with *Sedum* but had two small areas (<10% of total vegetated area) of herbaceous ornamental plants near the access points (City of Portland Ecoroof Incentive Program documentation, accessed 2015). The SW roofs were 3 to 5 years in age with vegetated areas ranging from 227-873m^2 (City of Portland Ecoroof Database, accessed 2015).

Two of the roofs in the downtown area (HW and CWW) were designed with urban biodiversity and stormwater management in mind and were retrofits (City of Portland Ecoroof Incentive Program documentation, accessed 2015), while a roof located just north of downtown (GU), was designed primarily to mitigate biodiversity loss at a superfund site (personal communication, Coleman LaFazio, Gunderson LLC, Environmental Group). The three roofs designed to encourage biodiversity (from here “habitat roofs”) had an average substrate thickness of 10.1cm ± 1.8cm; however, all three had purposely varied substrate depth to create spatial heterogeneity. The habitat roofs had an average substrate organic content of 12.4% ± 6.6% and were planted with a mix of plant functional types of native and non-native species. Two of the habitat roofs (HW and GU) also had added dead wood elements meant to further increase spatial heterogeneity. The habitat roofs were 4 to 16 years in age with vegetated areas ranging from 194-1,858m^2 (City of Portland Ecoroof Database, accessed 2015).

The stormwater roof and the nearby ground site in the suburban Oregon City (TC) were excluded from statistical hypothesis testing in order to provide a clearer picture of the effect of roof design on beetle diversity in the urban core after examination of the species accumulation curves indicated comparison would not be appropriate (Appendix A). This suburban site was much more speciose than the urban sites and was not fully sampled even after 13 biweekly sample periods, while the urban sites were fully sampled well before this time. An additional roof (NAC), and its associated ground site, were excluded from statistical hypothesis testing because its intensive design (>20cm substrate depth, vegetation including small trees) excluded it from either the habitat or SW design groups. Therefore, for statistical comparison of habitat roofs, SW roofs, and ground sites sample size was n=3, n=3, and n=5 respectively (Figure 1, inset). For exploratory analysis of community composition via clustering and ordination, all roofs (n=8) and ground sites (n=7), were used (Figure 1, main map).

The amount of irrigation on the roofs was known only qualitatively either from conversations with roof maintenance personnel or observation of the control box at roofs with irrigation systems. Irrigation levels of high (H), medium (M), low (L), or none (N) were assigned based on the following criteria: H = automated irrigation running 5-6 days per week for 5min or 3 days a week for >10 mins; M = automated irrigation running 3 days a week for 5 mins or 2 days a week for 5-10mins; L = automated irrigation only after set number of dry days or hand watering "as needed"; N = no watering.

Information on landuse type and determination of proportion non-impervious land cover in a 1km radius circle surrounding the roofs was determined in Esri ArcMap 10.2.2 software using the database Regional Land Information System, which is publically available from the METRO regional government. I used its layers for Zoning, Major Rivers, Vegetation Cover, Parks and Greenspaces, and Outdoor Recreation and Conservation Areas.

Ground sites were ground-level green spaces selected based on accessibility within 200 meters of a roof site. In the urban core two ground sites were undeveloped grassy lots, one was a landscaped areas with a mixture of horticulture species, one was a brownfield (unused industrial area dominated by weedy colonizers), and one was in a public park planted with native Oregon wetland species (n=5). One additional landscaped area near the intensive roof and one grassy lot in the suburbs were sampled. Ground site types are shown with their corresponding roof site in Table 1.

Beetle Sampling

Beetles were sampled using ten pitfall traps 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, while there was no difference between traps spaced 5 to 10 meters apart. Therefore, I maintained a 5-10m inter-trap spacing, placing the ten traps in a 5 x 2 grid format unless this was not possible due to the shape of vegetated area, in which case the traps were placed at a diagonal to each other while maintaining inter-trap spacing. Because traps were sometimes disturbed by crows and humans, which created an uneven sampling intensity across sites, species accumulation curves were constructed; all sites were determined to be fully sampled before data analysis (Appendix A). In order to minimize trap failure, a wire cage was placed around the traps toward the end of the season. The wire cages were secured by garden staples or, if roof substrate was not deep enough, a brick was place on top of the cage. The use of pitfall traps has well known limitations in biasing trap catches towards high activity, surface and soil dwelling organisms, and under-sampling beetles that live in higher vegetation levels (Woodcock 2005). However, advantages of the pitfall trap method are that it can be used to sample continuously for the entire season, rather than a brief snapshot in time, and in the low level of disturbance while sampling (Woodcock 2005).

Beetle samples were sorted from by-catch in the lab and stored in a 70% ethanol, 20% acetic acid mixture and shipped to taxonomist Alexander Szallies at the Zurich University of Applied Sciences in Switzerland where he identified them to species level. Beetle trophic groups were defined as megapredator (>12mm), predator, parasitoid, omnivore, herbivore, granivore, root chewer, moss predator, fungivore, and detritivore as suggested by Andrew Moldenke of Oregon State University (personal communication 2014). Assignment of individual species to trophic groups was based on advice given by Dr. Moldenke as well as a by-species literature review (full references in Appendix B). In 22 cases (13 in the urban core, 9 at the suburban site) a species-level identification was not made for a sample, and it was assigned to a trophic group based on genus-specific information. Each species was also assigned an invasiveness classification based on a species specific literature review (full references in Appendix B). Invasiveness classifications were native, native pest, non-native, non-native species of concern, or unknown if the species level identification was not made.

A species was classified as a non-native species of concern if one or more references documented an expanding range, economic damage, detrimental effects on native species, or used the word “invasive” or “pest”. A key with trophic and invasiveness group definitions and a table of species names, assigned groups, and full references is given in Appendix B.

Vegetation and Substrate Sampling

Field assistants and I surveyed each roof three times to estimate vegetation height and cover, once each in April, June, August 2014, in 1m^2 plots. Either overhead satellite images (Google Earth) or installation drawings (City of Portland Ecoroof Incentive Program documentation, accessed 2015) were used to divide the vegetated area of each roof into a 1m grid and ten random quadrat placements were selected using the random number generator in R statistical software. For each survey, the same ten plots were used. For each plot a cross-section of vegetation height was measured and percent vegetative cover (including moss) was estimated using gridded lines. A running total of plant species and plant functional types (Moss, Sedum, Herbaceous, Grass, Woody Shrub, Tree, and Weedy Colonizer) was recorded. Weedy Colonizers were separated from the other plant types using the Oregon State University Department of Horticulture Pacific Northwest Weed Identification Module website (accessed 2015). Vegetation surveys were not conducted at ground sites since there was little temporal variability in cover, and vegetation height often changed abruptly due to intensive management.

Substrate samples were taken once from three randomly selected spots at each roof by inserting a 2.4cm sample core to a depth of 10cm or until the bottom of the substrate was reached. In the lab, samples were oven dried at 100°C for 1 day and then ashed in a muffle furnace at 440°C for 1 hour following ASTM D2874, with one change to this procedure: after drying the hot weigh method was used to determine dry weight (Windham 1986, NFTA Method 2.1.2). The difference between dry weight and ashed weight relative to dry weight was used to calculate substrate percent organic content and all three sub-samples were then averaged together for one value per roof.

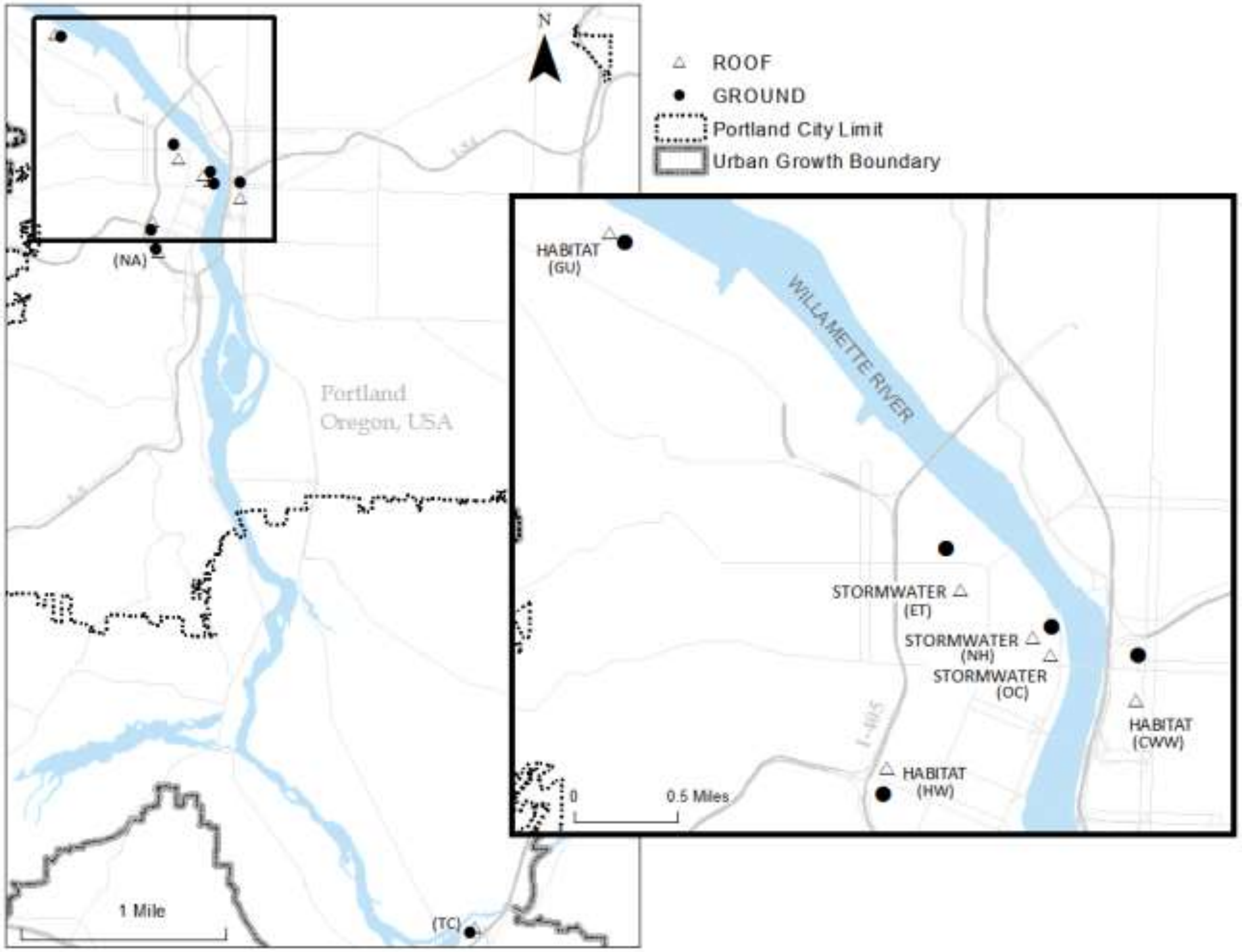

Figure 1: Map of all roof and ground sites. Sites shown in inset are those used for statistical hypothesis testing of habitat and stormwater roofs.

Table 1: Names, abbreviations, physical characteristics, and surrounding land cover of roof study sites. Irrigation (irrg.) levels are none (N), low (L), medium (M), and high (H). Land use zone are high-density mixed use (HIMX), heavy industrial (HIND), and light industrial (LIND). Ground sites are undeveloped grassy lot (UGL), brownfield (BF), native wetland park (NWP), and landscaped horticulture (LSH). Plant cover and height are average values, and substrate (subs.) depth and organic (org.) content are average values. Non-impervious (non-imp.) surface is in a 1km diameter surrounding area.

SITES	Plant Functional Richness	Plant Species Richness	Plant Cover (%)	Plant Height (cm)	Roof Area (m^2)	Build. Height (m)	Subs. Depth (mm)	Subs. Org. Content	Roof Age	Ground Site Type	Land Use Zone	Non-Imp. Surface (%)	Irrg. Level
Habitat Roofs													
Southeast Commercial (CWW)	5	12	0.73	14.15	1858	5.69	11.7	0.106	7	UGL	HIMX	22	N
Northwest Industrial (GU)	5	12	0.64	15.21	194	5.26	10.45	0.069	4	BF	HIND	31	L
Downtown 1 (HW)	6	17	0.84	13.03	543	28.65	8.1	0.198	16	LSH	HIMX	23	M
Sedum Roofs													
Pearl District (ET)	3	10	0.36	1.78	604	12.37	8.2	0.098	5	NWP	HIMX	19	H
Old Town 1 (OC)	4	16	0.67	3.42	227	15.47	8.75	0.081	3	UGL	HIMX	20	L
Old Town 2 (NH)	4	18	0.43	2.03	873	14.07	5.5	0.082	3	UGL	HIMX	19	H
Other Roofs													
Downtown 2 (NAC)	4	14	0.98	69.66	165	4.57	23.4	0.255	12	LSH	HIMX	25	M
Suburban (TC)	4	13	0.67	8.88	1319	8.53	10.2	0.06	5	UGL	LIND	31	H

Data Analysis

All statistical analyses were conducted using R statistical software (version 2.15.2, R Development Core Team 2012).

To test the habitat diversity hypothesis, specifically whether complex habitat roofs provide greater number and abundance of organisms than less complex roof habitats (stormwater roofs) and how this compares to ground sites, I applied ANOVA to determine the difference in beetle abundance, species richness, Shannon-Weiner diversity, and trophic functional richness between the habitat roofs (n=3), stormwater roofs (n=3), and ground sites (n=5). Before ANOVA, abundance data was log transformed in order to reduce intergroup variance. A post-hoc Tukey's honest significant difference (HSD) test was conducted after each ANOVA to determine which groups were significantly different. A Bonferonni correction for multiple tests was not applied since, for small sample size, the probability of making a Type II error is already high (Nakagawa 2004).

To determine which beetle species were most important to each site type (species listed in Appendix B) an analysis to determine strongly associated species was performed using the function multipatt in the R package 'indicspecies' (De Caceres and Legendre 2009). Strongly associated species may reflect the biotic or abiotic conditions at a site and can possibly predict the presence or diversity of other species or taxa (De Caceres 2013). The algorithm measures the association of a species to site type based on the product of specificity, the likelihood that a species will be found at all sites of a certain type, and fidelity, the likelihood that the species will be found at one site type only (Dufrene and Legendre 1997). A statistical significance is then assigned to the association between species and site type using a permutation test (n=999, α = 0.1; Sattler et al. 2011, De Caceres 2013).

An exploratory analysis of beetle community composition was conducted by non-metric multidimensional scaling (NMDS) ordination on the Bray-Curtis similarity coefficient between sites using the 'vegan' package in R (Clark 1993). Beetle singletons, species represented only by a single individual throughout the study, were removed to avoid the influence of stochastic species occurrences (Legendre and Gallagher 2001; Sattler et al. 2011). To reduce variance but to increase representation of rare species that might be important in defining green roof beetle communities, the abundance community matrix was log transformed (Clarke 1993). After scaling, the distortion in ordination space was checked via the stress value and visually with a Shephard's diagram to confirm the appropriateness of using two axes (Clarke 1993). To further visualize the effect of representing the community data in two dimensions, a Wards minimum variance hierarchical clustering was performed and the groups overlaid on the NMDS plot (Clarke 1993, Borcard et al. 2011). In order to further evaluate differences in functional diversity by site type, a 'community' matrix of abundance by trophic group was constructed and log transformed before NMDS analysis.

The influence of local habitat variables and surrounding land cover (Table 1) on beetle community at the different site types was assessed using the function envfit in the R package ‘vegan’ (Oksanen et al. 2015). Envfit is an exploratory analysis that plots a vector in NMDS ordination space in the direction in which an environmental variable changes most rapidly and in which the variable has maximal correlation with the ordination coordinates (Oksanen, vegan package 1.16-32 documentation). Each environmental variable was analyzed independently in envfit and a permutation test ($p = 1000$) assessed the strength of the linear correlation (R^2) between each environmental variable and the NMDS coordinates. Since envfit employs a linear model, before analysis all quantitative variables were checked for normality using a Shapiro-Wilks test. If normality was not met, positively skewed variables were log transformed, proportion data were arcsine square-root transformed, and count data were square-root transformed (Gotelli and Ellison 2013). After transformation a second Shapiro-Wilks test showed the variables met the assumptions of normality. Any environmental variables found to have a significant correlation ($p < 0.05$) in NMDS space were remodeled using the lm function in the ‘stats’ R package so that the appropriateness of a linear model could be determined by examining the model residuals for homoscedasticity.

Results

Diversity

As predicted by the habitat diversity hypothesis, the habitat roofs averaged nearly six times higher beetle abundance, three times as many species, a higher mean Shannon-Weiner diversity index, and four more trophic groups than Sedum roofs (boxplots shown in Figure 2). The habitat roofs also had a higher mean Shannon-Wiener Diversity index than the ground sites though in all other measures, the ground sites had greater diversity than both types of roof sites, including significantly greater number of species than habitat roofs. A post hoc Tukey's HSD test showed that all three groups differed in richness (ANOVA $F_{2/7}$=30.92, p=0.0003), while only ground and stormwater roofs differed from each other in log transformed abundance ($F_{2/7}$=10.46, p=0.008). Habitat roof and ground sites had a greater number of trophic groups ($F_{2/7}$=14.89, p=0.003) but none of the groups significantly differed in Shannon-Wiener diversity ($F_{2/7}$=3.12, p=0.11).

Across all sites 125 species and 26 families of beetles were found. Roof and ground sites in Portland's urban core had 99 total species, and twenty-six species were found only at the light industrial roof and ground site (TC) outside city limits. Within the urban core, 51 beetle speces were found only at ground sites, 11 were found only on roofs, and 37 were found at both roof and ground sites. Of the 11 species found only on urban roofs, 9 were found only on habitat roofs, while two were found only on stormwater roofs. 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 (Figure 3).

Associated Species

Associated species analysis showed that habitat roofs were characterized by three native species and one introduced species (Table 2). The ladybird beetle, *Hippodamia convergens* (Guerin), a species important for pest control (Bahlai et al. 2015), and *Stenolophus conjunctus,* a native ground beetle, were both found to be indicative of habitat roofs (p=0.096 and p=0.008, respectively). A non-native moss eater, *Cytilus sericeus* (Forst.), and a native weevil, *Dryophthorus americanus*, also characterized the habitat roofs. The weevil is associated with dead wood (Empire State Forest Products Association 1914) and grasses (Arnett et al. 2002), so either of these elements could have attracted *D. americanus* to the habitat roofs.

The stormwater roofs were most strongly characterized by a small non-native ground beetle *Eplaphropus parvulus* (Dej.) (p=0.007) that is usually associated with riparian and lacustrine habitats (LaBonte and Nelson 1998). The intensive watering regime at the stormwater roofs may have attracted *E. parvulus*. Consistent with previous research on urban insect communities, ground sites were characterized by two large rove beetles and the invasive ground beetle *Nebria brevicollis* (LaBonte 2011). The ground sites were also characterized by two herbivorous weevil pests and the native detritivore *Carpophilus lugubris* Murray.

Community Analysis

Further analysis of functional diversity through exploratory NMDS ordination of beetle community showed that habitat roofs tended to cluster with ground sites in the presence and composition of trophic groups (Figure 4). NMDS ordination of community abundance data showed that, consistent with previous green roof research, the roof and ground sites cluster distinctly from each other. The overlaid Ward hierarchical clustering groups show that, while stormwater roofs do not appear to cluster closely, they are still more similar to each other than to the habitat roofs. This may indicate some loss of information in the two-dimensional ordination though the stress value was low (stress = 0.14). The one intensive roof that was sampled (NAC) clustered closely with the habitat roofs, while the roof that was located outside city limits (TC) was the only site to be misclassified (Figure 3). For roofs in downtown Portland, linear fitting of local habitat and surrounding land cover variables (listed in Table 1) found mean vegetation height (R^2=0.81, p=0.047), mean vegetation cover (R^2=0.67, p=0.093), plant species richness (R^2=0.77, p=0.057), and roof age (R^2=0.74, p=0.063) were well correlated to NMDS ordination coordinates (Figure 6).

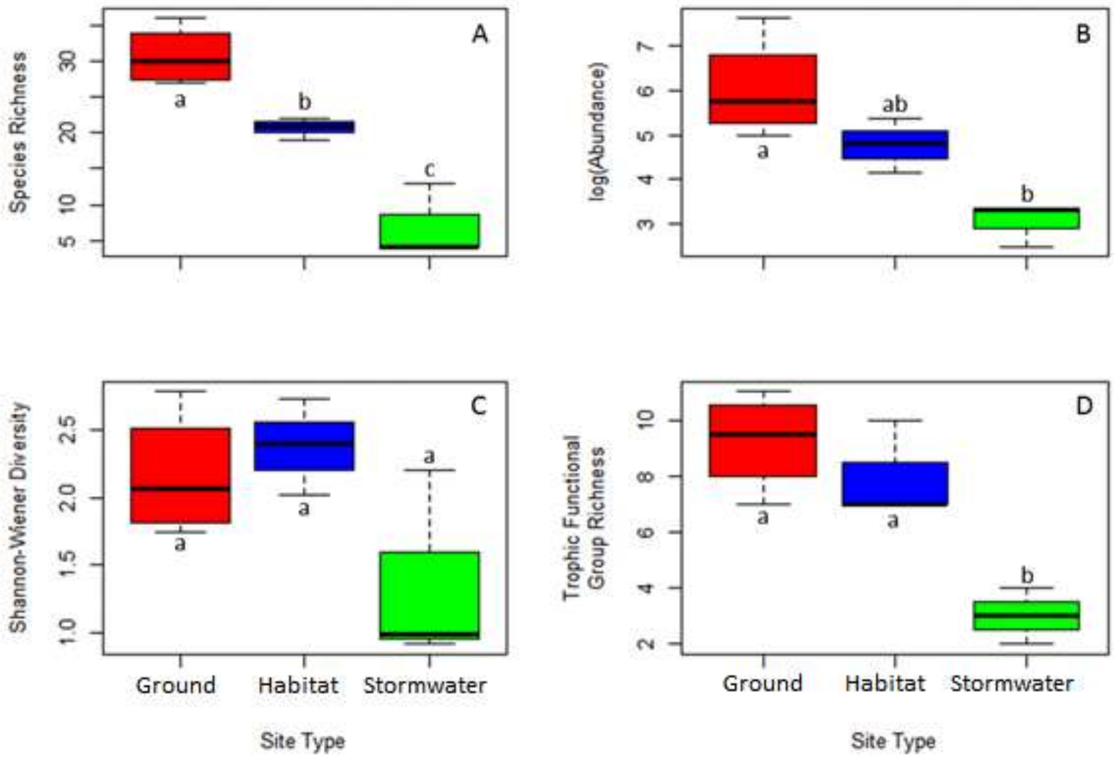

Figure 2: Boxplots comparing diversity at ground (red), habitat roof (blue), and stormwater roof (green) sites. Plots are (A) species richness, (B) log(abundance), (C) Shannon-Wiener Diversity index, and (D) trophic group richness. Groups that significantly differed are denoted with lower case letters.

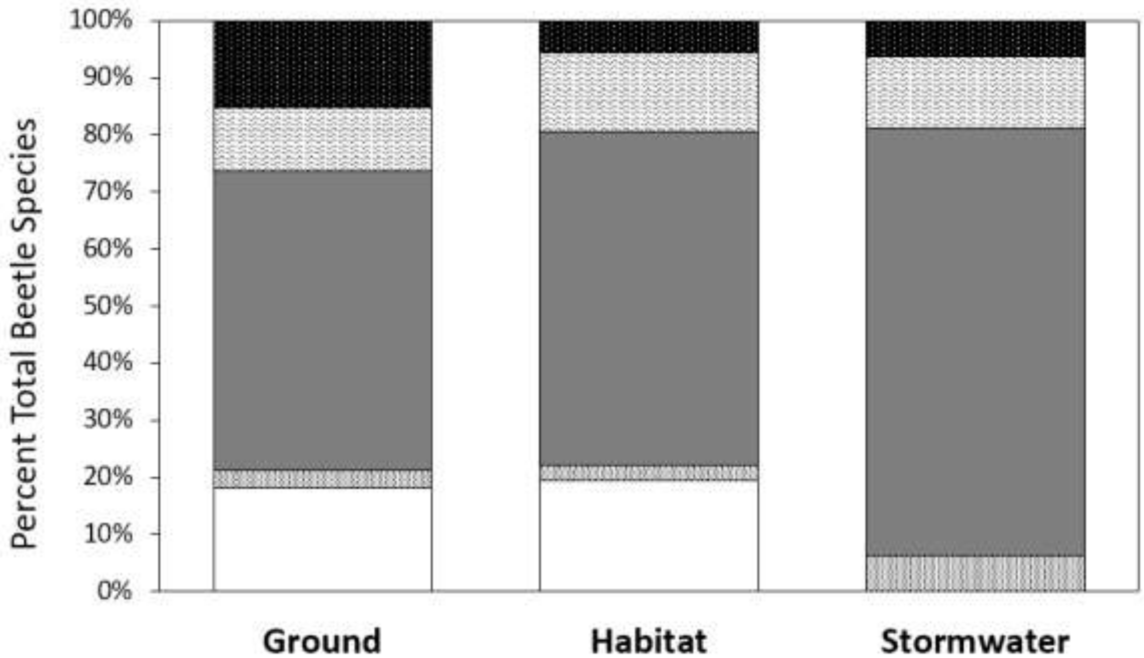

Figure 3: Bar chart shows percent of total beetle species found in terms of origin for habitat roofs, stormwater roofs, and ground sites. Categories are native (white), native pest (dotted grey), non-native (solid grey), non-native species of concern (variegated grey), and unknown (dotted black).

Table 2: Results of associated species analysis (n = 1000, α = 0.1) showing which species are most strongly associated with which site type or group of site types.

Group 1: Ground sites

Family	Genus and Species	p-value	Notes
Carabidae	*Nebria brevicollis (F.)*	0.009	Invasive ground beetle
Curculionidae	*Sphenophorus parvulus Gyll.*	0.054	Herbivorous pest, introduced
Staphylinidae	*Philonthus cognatus Steph.*	0.056	Generalist predator, introduced
Nitidulidae	*Carpophilus lugubris Murray*	0.061	Small native detritivore
Curculionidae	*Sitona cylindricollis (Fahrs.)*	0.096	Herbivorous pest, introduced
Staphylinidae	*Atheta fungi (Grav.)*	0.091	Generalist small pest predator, introduced

Group 2: Habitat Roofs

Family	Genus and Species	p-value	Notes
Carabidae	*Stenolophus conjunctus (Say)*	0.008	Generalist predator, native
Byrrhidae	*Cytilus sericeus (Forst.)*	0.095	Herbivorous specialist (moss), introduced
Coccinellidae	*Hippodamia convergens Guerin*	0.095	Pest predator, native
Curculionidae	*Dryophthorus americanus Bedel*	0.095	Native weevil, associated with dead wood

Group 3: Stormwater Roofs

Family	Genus and Species	p-value	Notes
Carabidae	*Elaphropus parvulus (Dej.)*	0.007	Small predator, habitat specialist, introduced

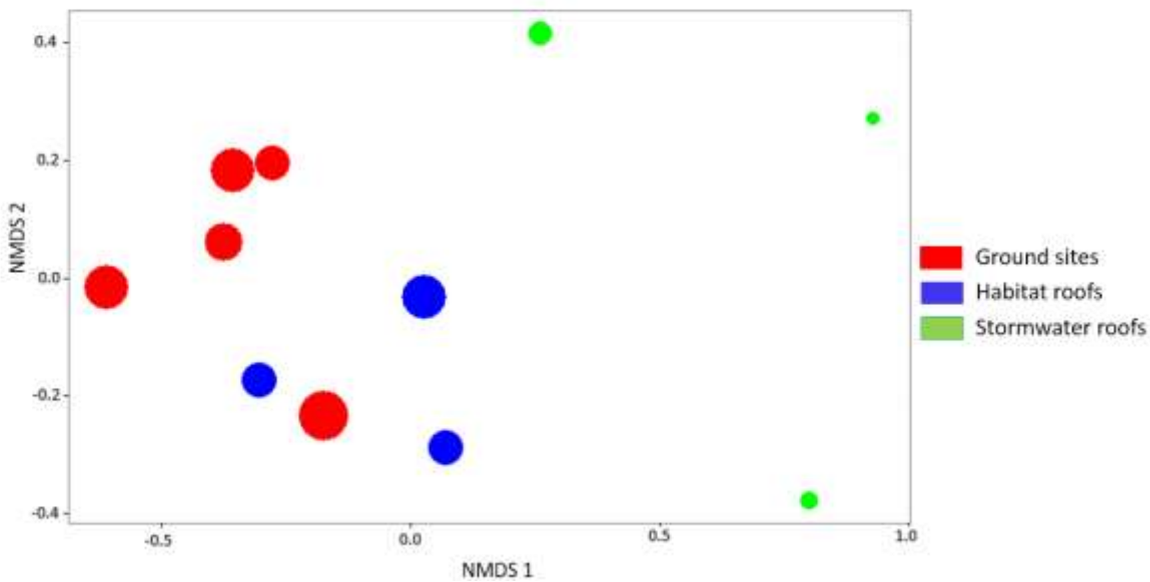

Figure 4: Results of NMDS clustering for urban roof and ground sites showing that in terms of trophic group representation, a measure of functional diversity, the beetle community found on habitat roofs is more similar to ground sites than to stormwater roofs. The size of the bubbles is proportional to the number of trophic groups present.

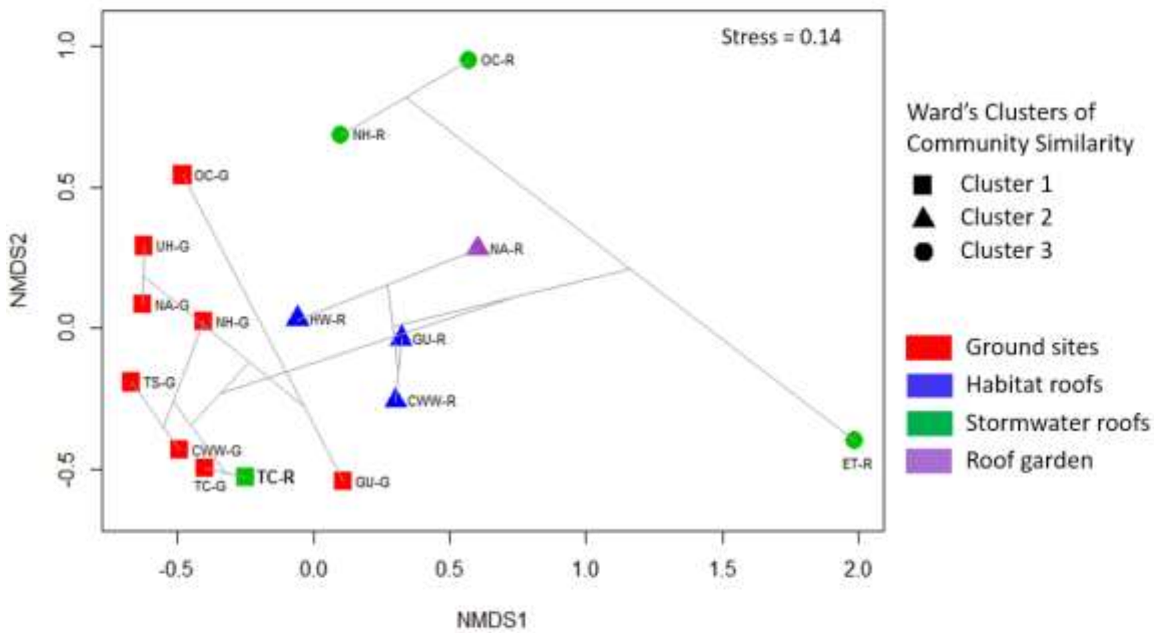

Figure 5: NMDS ordination and Ward hierarchical clustering showing that habitat roofs (blue triangles) and the intensive roof (roof garden, purple triangle) are similar to each other in beetle community. Ground sites (red squares) also cluster distinctively. A suburban stormwater roof (TC-R, green square), the suburban one, was misclassified with the ground sites. Though the urban stormwater roofs (green circles) do not appear to group closely, the Ward cluster lines show that they are more similar to each other than to the other site types.

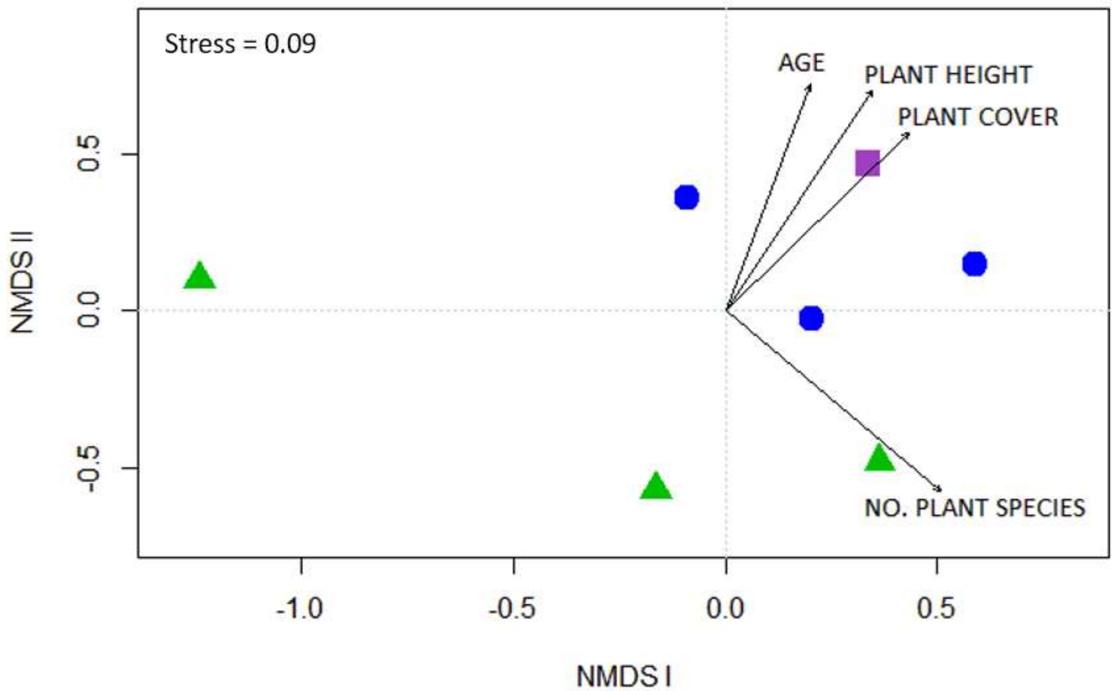

Figure 6: NMDS ordination of community abundance data with significantly correlated environmental variables for the three stormwater roofs (green triangles), three habitat roofs (blue circles), and one intensive roof (purple square) located in Portland's urban core. Environmental variables are roof age (AGE), mean vegetation height (VEG.H), mean vegetation cover (VEG.C), and plant species richness (PSR).

Discussion

As predicted by the habitat diversity hypothesis, habitat roofs had significantly greater species richness and functional diversity than stormwater roofs. In two other measures, abundance and Shannon-Wiener index, habitat roofs had a higher mean value, continuing the pattern of greater diversity. Habitat roofs were associated with more native species, and were home to ten species not found on the ground. My results support recent findings that arthropod communities on urban green roofs are unique from the ground (MacIvor and Lundholm 2011, Tonietto et al. 2011, Ksiazek et al. 2012) and that total arthropod diversity is higher on roofs designed to have greater vegetation structure (Madre et al. 2013) and add to current knowledge by fully sampling North American green roof beetle community during three seasons and identifying to species level.

Functional diversity

Functional diversity, as measured by presence and abundance of trophic groups, was on average 63% less at stormwater roofs compared to habitat roofs and ground sites, which were statistically similar. Studies of ecosystem stability and resilience indicate that systems with greater functional diversity are better able to adapt to temporal variation in abiotic conditions such as temperature and water availability that are often exacerbated on green roofs (Lefcheck et al. 2015). Mixing plants of multiple functional types increased roof performance in roof experiments where drought tolerant grasses shaded and cooled substrate and so facilitated the survival of herbaceous plants and allowed them to maximize water retention and evapotranspirative cooling, while *Sedum* species best maintained cover during dry periods (Dunnet et al. 2008, Lundholm et al. 2010). The different burrowing, herbivory, and predation of diverse functional groups of beetles may similarly increase tolerance of roof habitats to disturbance. For example, an experiment in a steppe ecotone found that tree seeds and seedlings shaded by shrubs were more susceptible to beetle herbivory (Chaneton et al. 2010). A similar type of interaction could be important on roofs where herbivorous beetles could help reduce establishment of tree seedlings that can lead to waterproof membrane puncture and roof failure; yet, no granviores and a much lower percentage of herbivores in general were found on stormwater roofs. Another study found that grazing on an herbaceous plant by a specialist beetle limited the establishment of the plant's fungal pathogen (Hatcher and Paul 2000). If the increased functional diversity demonstrated in this study leads to similar interactions this could result in a desirable reduction in maintenance needs on green roofs. Changes to functional diversity may also indirectly change biomass and dominant species thereby influencing a system's ability to respond to disturbance by altering cycling of energy and matter (Burke and Laurenroth 2000). Further studies should explore both species interactions and changes to cycles associated with increased functional diversity on green roofs.

Native species

Athough not an explicit research question in this study, another important factor in evaluating the performance of biodiverse roof design is whether it attracts and supports native and rare species since their populations are often reduced in the urban area (Grimm et al. 2008). About 22% of species found at habitat roofs and ground sites in this study were native, but about 3% of those were considered pests or otherwise undesirable. Conversely, the stormwater roofs were home only to one native species, the click beetle *Aeolus mellillus* Say, an agricultural pest whose larvae can significantly damage plant roots (Stirret 1936). Associated 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 also 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.

Community composition

Consistent with previous studies of green roofs (MacIvor and Lunholm 2011, Tonietto et al. 2011, Ksiazek et al. 2012), ground and roof beetle community were compositionally different with only 36% of species in common, 52% of species found only on the ground, and 12% found only on the roofs. The ground sites represented several different green space types and were spatially distributed across the Portland metro area yet cluster analysis showed them to be much more similar to each other than to nearby roof sites (Figure 3). In general, ground site communities were dominated by high abundances of large bodied generalist predator species, while the roofs, especially the habitat roofs, had more representation from omnivorous small-bodied species. Although the proportion of small-winged, large-winged, and wing dimorphic species was not investigated in detail, I observed that roofs tended to have more small and medium sized and more mobile species than ground sites, as expected from studies of other isolated green spaces such as roundabouts and street margins (Jones and Leather 2012). One green roof study found that building height was negatively correlated with bee and wasp nest success (MacIvor 2015), so future studies should investigate how roofs might in influence body size and mobility traits in beetles. None of the species found in this study were considered rare or were listed as threatened or endangered. However, the uniqueness of the green roof beetle community, when considered as a proxy for overall urban invertebrate community, supports the argument that green roofs can be a tool for increasing the diversity of cities.

Influences on beetle community

Evaluation of individual local roof habitat and surrounding land cover variables showed that average vegetation height, average vegetation cover, plant species richness, and roof age were the most correlated variables with differences in beetle community among the roofs. Together, vegetation height, vegetation cover, and plant species richness can be thought of as a proxy for habitat diversity, so the positive correlation of these vectors with sites of increasing beetle diversity is an additional confirmation of the habitat diversity hypothesis. Although the two roof types did not statistically differ in age, the habitat roof group did have an older mean age (by an average of 5 years) than the stormwater roofs, which possibly confounds these results. Age may be important because older roofs would have more time for species to colonize. However, all of the roofs were at least three years old and one study looking at multiple roof types found that colonization rates were highest in the first one-to-two years after installation and that the number of species dropped off in subsequent years (Brenneisen 2003). Other factors such as plant functional richness, irrigation, and surrounding landcover were not found to be strongly correlated with beetle community, yet in ground-level green spaces beetle community composition changed with water availability even in the same habitat type (Angold et al. 2006) and plant functional richness was found to be correlated increased invertebrate diversity (Haddad et al. 2001). Previous green roof studies have found mixed results regarding the influence of surrounding landcover on invertebrate community, with some studies finding little effect (Madre et al. 2013), some finding a strong correlation (Tonietto et al. 2011), and others finding it important to some taxa (Braakar et al. 2013). This suggests that further study with increased replication and quantitative measurement of irrigation is needed to further elucidate the role of plant functional richness, surrounding landcover, and irrigation on green roof beetle communities.

The effect of urbanization

The one stormwater roof that was located outside the urban core in a suburban area had 15 unique species. Although it is difficult to draw conclusions from one site, the diversity found there suggests that any effects of habitat diversity may be masked by the very strong effect of urbanization. Many ground level studies have sampled beetles and other invertebrates along a rural to urban gradient, but no green roof studies have to date. Future studies that sample green roofs along a rural-urban gradient would shed light on how green roof communities vary with urbanization level.

Conclusion

My results showed that by two measures, functional diversity and Shannon-Wiener index, habitat roofs were as diverse as ground sites. In the urban core, habitat roofs were more diverse than stormwater roofs in terms of richness, abundance, and functional diversity. Habitat roofs, therefore, are vital for increasing the square footage of utilized beetle habitat in downtown areas and even facilitate species that may not otherwise exist within urban areas and important native pest control species like ladybird beetles, though they should not be viewed as a replacement for conservation of remnant ground level habitat. For the most part though, green roofs are used as an alternative to conventional black roofs, and as such should be strongly promoted for increasing urban invertebrate biodiversity. Stormwater roofs in this study also provided habitat to some beetles, which is valuable in addition to their well-documented thermal and water management benefits. However, when comparing among roofs located in the same high level of urbanization (downtown), the results of this study indicate that, if increasing urban diversity is a primary goal, biodiverse roofs are recommended over stormwater roofs as they are associated with unique and native species, increased beetle diversity, and greater functional diversity.

Chapter 3: Conclusion

In the first part of this study, my literature review looked at the less explored service of habitat provisioning to determine the role green roofs play for invertebrate species in the larger context of the urban ecosystem. The interaction between site type, management intensity, and age was found to be important: for example, whether the site is a new, highly managed roundabout or an unmanaged forest remnant can structure invertebrate community mobility and body size (Jones and Leather 2012, Ksiazek et al. 2012). Connectivity was found to have a strong influence on some taxa but not others (Braaker et al. 2013), indicating that many urban adapted invertebrate species may not be dispersal limited within the built environment (McIntrye et al. 2001, Angold et al. 2006). Finally, local habitat variables such as plant diversity (Madre et al. 2013), including number of flowering plants (Braaker et al. 2013, Tonietto et al. 2011), water availability (Angold et al. 2006), and total cover (Sattler et al. 2010a) were found to influence diversity and community composition, including the proportion of urban generalists. The importance of local habitat variables in urban green spaces and strong support for the habitat complexity hypothesis in a number of other ecosystems has led to proposals that “biodiverse” roofs— those intentionally designed with varied substrate depth, greater plant diversity, or added elements such as logs or stones—would support greater invertebrate diversity, but there is currently only a small body of peer reviewed data to support this. Two studies have found greater invertebrate diversity on biodiverse roofs (Brenneisen 2006, Madre et al. 2013), while one study did not find increased diversity (Kadas 2006).

In the second part of my study I addressed the effect of the habitat complexity hypothesis on green roof invertebrate diversity and community composition by comparing three roofs designed primarily for stormwater management, three biodiverse roofs, and five ground-level green spaces, using beetles as representatives of total species diversity. I found that biodiverse roofs had greater richness, abundance, and diversity of beetle species compared to stormwater roofs, and were as diverse as ground sites in terms of functional diversity and Shannon-Weiner index. Both biodiverse roofs and ground sites had approximately 20% native beetle species while stormwater roofs had only 5%. Functional diversity was higher on biodiverse roofs with an average of 7 trophic groups represented, while stormwater roofs averaged only three. Ground sites, biodiverse roofs, and stormwater roofs each grouped distinctively in terms of beetle community composition and biodiverse roof communities were found to be positively correlated with roof age, percent plant cover, average plant height, and plant species richness. These results support the findings of previous studies on the importance of local variables and habitat complexity in structuring urban invertebrate communities and suggest that biodiverse design can reliably increase greenroof diversity. Habitat roofs are vital for increasing the square footage of utilized beetle habitat in downtown areas and even facilitate species that may otherwise not exist within urban areas, though they should not be viewed as a replacement for conservation of remnant ground level habitat. However, when green roofs are used as a conversion or replacement for conventional black roofs they should be strongly promoted for increasing urban invertebrate biodiversity. Stormwater roofs should not be disregarded since they provide a number of well-documented thermal and water management benefits to urban areas (Mentens et al. 2006, Lundholm et al. 2010) and provide habitat to some beetle species. In some cases, stormwater roofs may be preferred for a number of structural, aesthetic, or performance reasons. However, when comparing among roofs located in the same high level of urbanization, the results of this study indicate that, if increasing urban diversity is a primary goal, biodiverse roofs are recommended over stormwater roofs as they are associated with unique and native species, increased beetle diversity, and greater functional diversity.

Chapter 4: References

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Appendix A: Species accumulation curves

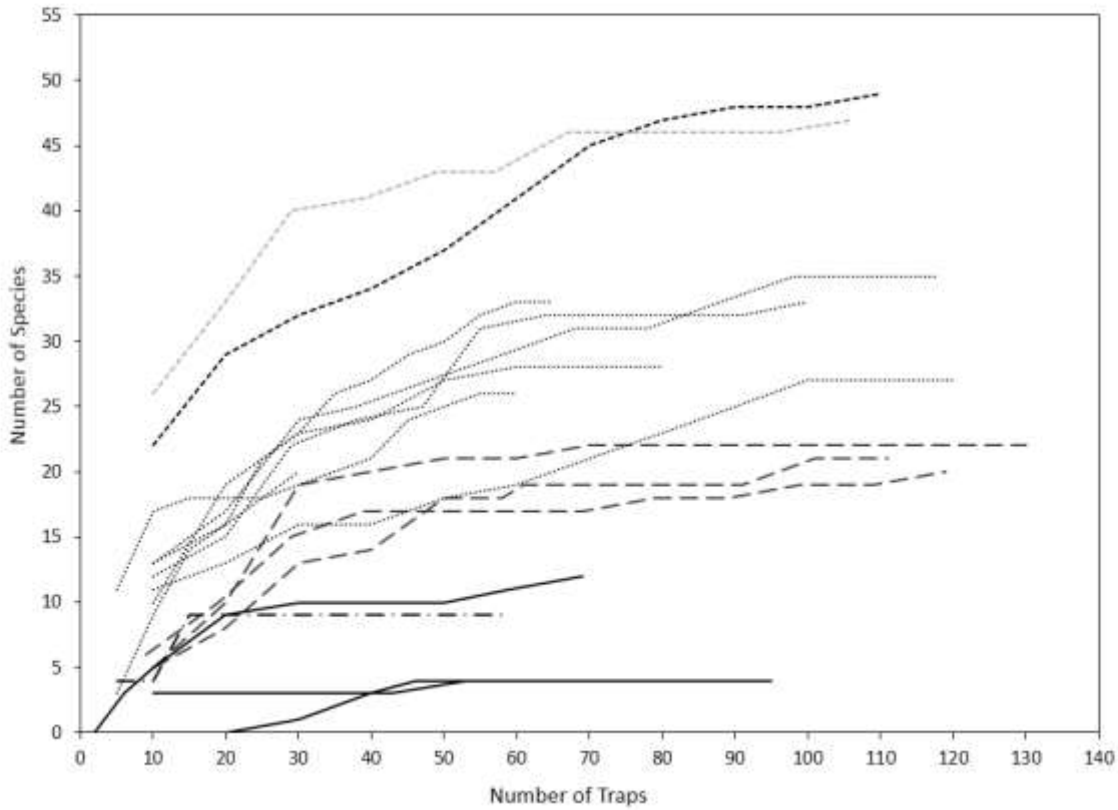

Figure A 1: Species accumulation curves by number of traps showing that urban roof sites were fully sampled by approximately 60 traps. Stormwater roofs are shown in solid black, habitat roofs as large dash, the intensive roof as dot-dash, and ground sites as dotted curves. The roof and ground site located outside Portland city limits are shown as black small dash (roof) and grey small dash (ground).

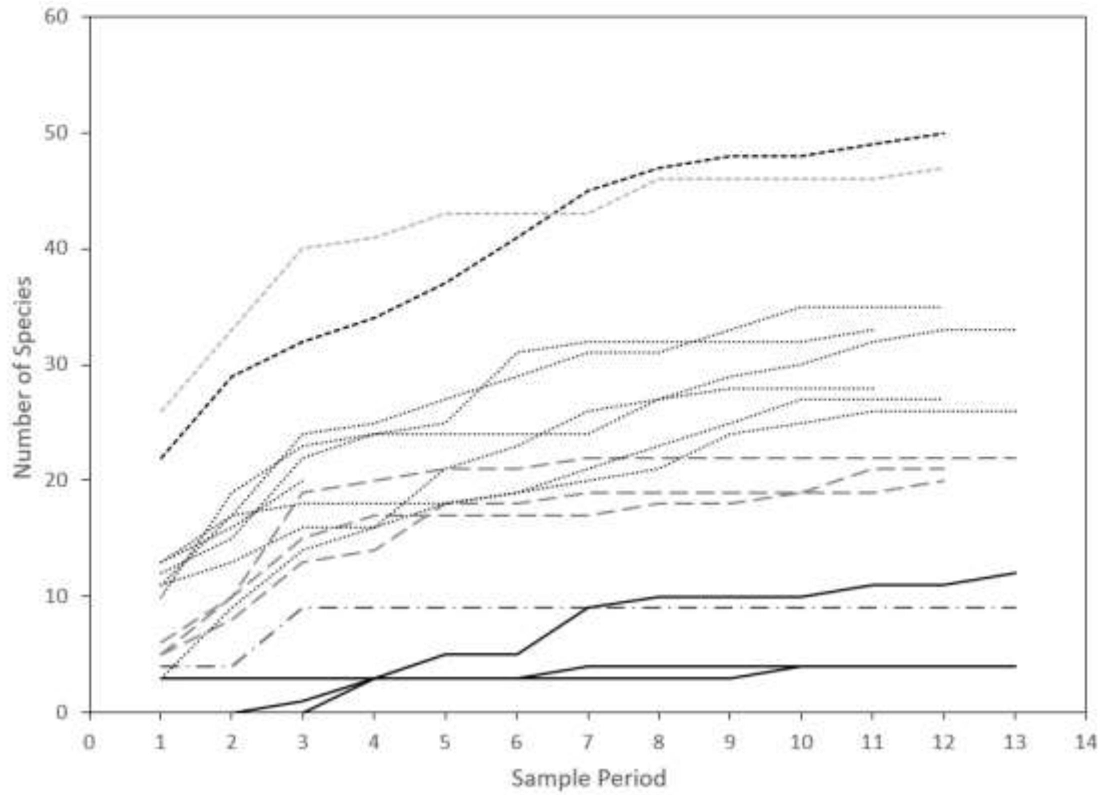

Figure A 2: Species accumulation curves by number of sample periods showing that the urban roof sites were fully sampled by approximately 7 biweekly sample periods. Stormwater roofs are shown as solid black lines, habitat roofs as large grey dashed line, the intensive roof as grey dot-dashed lines, and ground sites as grey dotted lines. The roof and ground site located in a suburban area outside Portland city limits are shown as black small dashed (roof) and grey small dashed (ground) lines.

Appendix B: Beetle species information

Table B 1: Beetle species found at roof sites with total numbers (Num.) caught throughout sample period.

Southest Commercial (CWW-R)

Family	Species	Num.
Byrrhidae	Cytilus sericeus (Forst.)	2
Byrrhidae	Simplocaria semistriata F.	10
Byrrhidae Total		12
Carabidae	Amara aenea (DeG.)	10
Carabidae	Anisodactylus binotatus (F.)	3
Carabidae	Calathus ruficollis Dejean	3
Carabidae	Harpalus affinis (Schrk.)	1
Carabidae	Harpalus herbivagus Say	3
Carabidae	Stenolophus conjunctus (Say)	4
Carabidae	Trechus obtusus Er.	2
Carabidae Total		26
Chrysomelidae	Longitarsus sp 1	1
Chrysomelidae Total		1
Coccinellidae	Coccinella septempunctata L.	7
Coccinellidae	Hippodamia convergens Guerin	2
Coccinellidae Total		9
Curculionidae	Dryophthorus americanus Bedel	1
Curculionidae	Hypera zoilus (Scop.)	2
Curculionidae	Tychius picirostris (F.)	1
Curculionidae Total		4
Staphylinidae	Gabrius appendiculatus Sharp	26
Staphylinidae	Oxypoda praecox Er.	6
Staphylinidae	Philonthus carbonarius (Grav.)	3
Staphylinidae	Tachyporus dispar (Payk.)	1
Staphylinidae	Tachyporus nitidulus (F.)	2
Staphylinidae	Xantholinus linearis (Ol.)	34
Staphylinidae Total		72
Grand Total		124

Pearl District (ET-R)		
Family	Species	Num.
Byrrhidae	Simplocaria semistriata F.	1
Byrrhidae Total		1
Carabidae	Elaphropus parvulus (Dej.)	17
Carabidae Total		17
Curculionidae	Otiorhynchus sulcatus (F.)	1
Curculionidae Total		1
Staphylinidae	Gabrius appendiculatus Sharp	10
Staphylinidae Total		10
Grand Total		29

Northwest Industrial (GU-R)		
Family	Species	Num.
Bruchidae	Bruchidius fasciatus (Ol.)	1
Bruchidae Total		1
Byrrhidae	Cytilus sericeus (Forst.)	1
Byrrhidae	Simplocaria semistriata F.	1
Byrrhidae Total		2
Carabidae	Amara aenea (DeG.)	4
Carabidae	Harpalus affinis (Schrk.)	1
Carabidae	Stenolophus conjunctus (Say)	4
Carabidae	Trechus obtusus Er.	2
Carabidae Total		11
Coccinellidae	Coccinella californica Mannh.	1
Coccinellidae	Coccinella septempunctata L.	7
Coccinellidae	Hippodamia convergens Guerin	6
Coccinellidae Total		14
Curculionidae	Dryophthorus americanus Bedel	1
Curculionidae	Hypera zoilus (Scop.)	12
Curculionidae Total		13
Elateridae	Limonius lanei Van Dyke	1

Elateridae Total		1
Nitidulidae	Carpophilus lugubris Murray	4
Nitidulidae Total		4
Scolytidae	Hylurgops rugipennis (Mannh.)	1
Scolytidae Total		1
Silvanidae	Silvanus bidentatus (F.)	1
Silvanidae Total		1
Staphylinidae	Atheta (Microdota) sp.	1
Staphylinidae	Oxypoda praecox Er.	2
Staphylinidae	Philonthus carbonarius (Grav.)	2
Staphylinidae	Tachyporus dispar (Payk.)	1
Staphylinidae	Tachyporus nitidulus (F.)	4
Staphylinidae	Xantholinus linearis (Ol.)	5
Staphylinidae Total		15
Grand Total		63

Downtown 1 (HW-R)

Family	Species	Num.
Carabidae	Anisodactylus binotatus (F.)	7
Carabidae	Calathus fuscipes (Goeze)	4
Carabidae	Calathus ruficollis Dejean	8
Carabidae	Harpalus affinis (Schrk.)	105
Carabidae	Microlestes minutulus (Goeze)	1
Carabidae	Nebria brevicollis (F.)	1
Carabidae	Stenolophus conjunctus (Say)	7
Carabidae	Trechus obtusus Er.	12
Carabidae Total		145
Curculionidae	Otiorhynchus ovatus (L.)	3
Curculionidae	Otiorhynchus rugosostriatus (Goeze)	1
Curculionidae	Otiorhynchus sulcatus (F.)	9
Curculionidae	Tychius picirostris (F.)	6
Curculionidae Total		19
Staphylinidae	Ocypus aeneocephalus (DeG.)	2
Staphylinidae	Oxypoda praecox Er.	1
Staphylinidae	Philonthus carbonarius (Grav.)	7

Staphylinidae	Tachyporus dispar (Payk.)	10
Staphylinidae	Tachyporus nitidulus (F.)	5
Staphylinidae	Tasgius winkleri (Bernh.)	4
Staphylinidae	Xantholinus linearis (Ol.)	23
Staphylinidae Total		52
Grand Total		216

Downtown 2 (NAC-R)

Family	Species	Num.
Carabidae	Agonum muelleri (Hbst.)	1
Carabidae	Anisodactylus binotatus (F.)	3
Carabidae	Nebria brevicollis (F.)	1
Carabidae	Stenolophus conjunctus (Say)	2
Carabidae	Trechus obtusus Er.	19
Carabidae Total		26
Curculionidae	Otiorhynchus sulcatus (F.)	3
Curculionidae Total		3
Staphylinidae	Tachyporus dispar (Payk.)	1
Staphylinidae	Tachyporus nitidulus (F.)	1
Staphylinidae	Xantholinus linearis (Ol.)	3
Staphylinidae Total		5
Grand Total		34

Old Town 2 (NH-R)

Family	Species	Num.
Carabidae	Amara aenea (DeG.)	1
Carabidae	Elaphropus parvulus (Dej.)	1
Carabidae	Harpalus affinis (Schrk.)	6
Carabidae	Microlestes minutulus (Goeze)	1
Carabidae	Nebria brevicollis (F.)	2
Carabidae Total		11
Coccinellidae	Coccinella septempunctata L.	1
Coccinellidae Total		1
Elateridae	Aeolus mellillus (Say)	1
Elateridae Total		1

Staphylinidae	Atheta fungi (Grav.)	1
Staphylinidae	Atheta sp. 1	1
Staphylinidae	Ocypus aeneocephalus (DeG.)	8
Staphylinidae	Philonthus carbonarius (Grav.)	2
Staphylinidae	Tachyporus nitidulus (F.)	1
Staphylinidae	Xantholinus linearis (Ol.)	2
Staphylinidae Total		15
Grand Total		28

Old Town 1 (OC-R)		
Family	Species	Num.
Carabidae	Amara aenea (DeG.)	2
Carabidae	Elaphropus parvulus (Dej.)	1
Carabidae Total		3
Staphylinidae	Tachyporus nitidulus (F.)	1
Staphylinidae	Xantholinus linearis (Ol.)	8
Staphylinidae Total		9
Grand Total		12

Suburban (TC-R)		
Family	Species	Num.
Anthicidae	Anthicus cervinus LeFerte	17
Anthicidae Total		17
Byrrhidae	Cytilus sericeus (Forst.)	13
Byrrhidae	Simplocaria semistriata F.	4
Byrrhidae Total		17
Carabidae	Agonum canadense Goulet	7
Carabidae	Agonum muelleri (Hbst.)	20
Carabidae	Amara aenea (DeG.)	8
Carabidae	Amara ovata (F.)	4
Carabidae	Anisodactylus binotatus (F.)	75
Carabidae	Bembidion lampros (Hbst.)	20
Carabidae	Elaphropus parvulus (Dej.)	2
Carabidae	Harpalus affinis (Schrk.)	2
Carabidae	Loricera foveata (LeConte)	1
Carabidae	Microlestes minutulus (Goeze)	10
Carabidae	Nebria brevicollis (F.)	14

Carabidae	Pterostichus melanarius (Ill.)	2
Carabidae	Trechus obtusus Er.	155
Carabidae Total		320
Chrysomelidae	Altica sp. 1	1
Chrysomelidae	Diabrotica undecimpunctata Mannh.	1
Chrysomelidae Total		2
Coccinellidae	Coccinella septempunctata L.	39
Coccinellidae	Coccinellidae sp 1	1
Coccinellidae	Hippodamia variegata (Goeze)	1
Coccinellidae Total		41
Curculionidae	Otiorhynchus sulcatus (F.)	6
Curculionidae	Sitona hispidulus F.	6
Curculionidae	Sphenophorus parvulus Gyll.	1
Curculionidae	Tychius picirostris (F.)	7
Curculionidae Total		20
Dermestidae	Trogoderma sp.1	1
Dermestidae Total		1
Lathridiidae	Melanophthalma sp 1	1
Lathridiidae Total		1
Monotomidae	Monotoma longicollis (Gyll.)	3
Monotomidae Total		3
Mycetophagidae	Mycetophagus quadriguttatus Mull.	1
Mycetophagidae Total		1
Nitidulidae	Carpophilus lugubris Murray	1
Nitidulidae Total		1
Pselaphidae	Bibloplectus sp.	2
Pselaphidae	Brachygluta sp 1	1
Pselaphidae Total		3
Scarabaeidae	Aphodius badipes Melsh.	2
Scarabaeidae	Aphodius sp2	1
Scarabaeidae Total		3
Staphylinidae	Acrotona parens (Muls.Rey)	1

Staphylinidae	Aleochara lanuginosa Grav.	10
Staphylinidae	Aloconota gregaria (Er.)	2
Staphylinidae	Atheta coriaria (Kr.)	1
Staphylinidae	Gabrius appendiculatus Sharp	76
Staphylinidae	Lobrathium sp.1	1
Staphylinidae	Oxypoda opaca (Grav.)	1
Staphylinidae	Oxypoda praecox Er.	4
Staphylinidae	Philonthus carbonarius (Grav.)	24
Staphylinidae	Philonthus cognatus Steph.	3
Staphylinidae	Quedius curtipennis Bernh.	1
Staphylinidae	Rugilus orbiculatus (Payk.)	2
Staphylinidae	Tachyporus dispar (Payk.)	7
Staphylinidae	Tachyporus nitidulus (F.)	4
Staphylinidae	Xantholinus linearis (Ol.)	341
Staphylinidae Total		478
Tenebrionidae	Blapstinus moestus Melsh.	4
Tenebrionidae Total		4
Grand Total		912

Table B 2: Beetle species found at ground sites with total number (Num.) caught throughout the sample period.

Southeast Commercial (CWW-G)		
Family	Species	Num.
Carabidae	Agonum canadense Goulet	13
Carabidae	Amara aenea (DeG.)	285
Carabidae	Amara familiaris (Duft.)	1
Carabidae	Anisodactylus binotatus (F.)	1
Carabidae	Calathus fuscipes (Goeze)	4
Carabidae	Calathus ruficollis Dejean	15
Carabidae	Harpalus affinis (Schrk.)	2
Carabidae	Microlestes minutulus (Goeze)	1
Carabidae	Nebria brevicollis (F.)	80
Carabidae	Trechus obtusus Er.	11
Carabidae Total		413
Coccinellidae	Coccinella septempunctata L.	3
Coccinellidae Total		3
Cryptophagidae	Atomaria fuscata (Schoenh.)	1
Cryptophagidae Total		1

Curculionidae	Hypera nigrirostris (F.)	5
Curculionidae	Hypera zoilus (Scop.)	7
Curculionidae	Otiorhynchus ovatus (L.)	2
Curculionidae	Sitona cylindricollis (Fahrs.)	3
Curculionidae	Sitona hispidulus F.	46
Curculionidae	Sitona lepidus Gyll.	8
Curculionidae	Sphenophorus parvulus Gyll.	1
Curculionidae	Tychius picirostris (F.)	7
Curculionidae Total		79
Dryopidae	Dryops sp 1	1
Dryopidae Total		1
Elateridae	Aeolus mellillus (Say)	4
Elateridae Total		4
Nitidulidae	Carpophilus lugubris Murray	1
Nitidulidae Total		1
Scarabaeidae	Aphodius badipes Melsh.	6
Scarabaeidae Total		6
Staphylinidae	Amischa sp.	3
Staphylinidae	Atheta fungi (Grav.)	2
Staphylinidae	Gabrius appendiculatus Sharp	1
Staphylinidae	Ocypus aeneocephalus (DeG.)	8
Staphylinidae	Oxypoda praecox Er.	1
Staphylinidae	Philonthus carbonarius (Grav.)	188
Staphylinidae	Philonthus cognatus Steph.	827
Staphylinidae	Rugilus orbiculatus (Payk.)	1
Staphylinidae	Tachyporus dispar (Payk.)	11
Staphylinidae	Tachyporus nitidulus (F.)	23
Staphylinidae	Xantholinus linearis (Ol.)	51
Staphylinidae Total		1116
Tenebrionidae	Blapstinus moestus Melsh.	389
Tenebrionidae Total		389
Grand Total		2013

Northwest Industrial (GU-G)

Family	Species	Num.
Byrrhidae	Simplocaria semistriata F.	1
Byrrhidae Total		1
Carabidae	Amara aenea (DeG.)	14
Carabidae	Amara municipalis (Duft.)	2

Carabidae	Amara ovata (F.)	2
Carabidae	Amara sp.1	1
Carabidae	Anisodactylus binotatus (F.)	1
Carabidae	Calathus ruficollis Dejean	3
Carabidae	Carabus nemoralis Müll.	1
Carabidae	Harpalus affinis (Schrk.)	2
Carabidae	Microlestes sp. 2	2
Carabidae	Nebria brevicollis (F.)	3
Carabidae	Stenolophus conjunctus (Say)	1
Carabidae	Syntomus americanus (Dejean)	14
Carabidae	Trechus obtusus Er.	1
Carabidae Total		47
Coccinellidae	Coccinella septempunctata L.	7
Coccinellidae	Hippodamia variegata (Goeze)	1
Coccinellidae Total		8
Curculionidae	Hypera postica (Gyll.)	1
Curculionidae	Mecinus sp 1	2
Curculionidae	Sitona cylindricollis (Fahrs.)	1
Curculionidae	Sitona lepidus Gyll.	2
Curculionidae	Sphenophorus parvulus Gyll.	1
Curculionidae	Tychius picirostris (F.)	1
Curculionidae Total		8
Languriidae	Cryptophilus integer (Heer)	1
Languriidae Total		1
Nitidulidae	Carpophilus lugubris Murray	23
Nitidulidae	Epuraea biguttata Thunb.	1
Nitidulidae Total		24
Staphylinidae	Amischa sp.	1
Staphylinidae	Atheta fungi (Grav.)	3
Staphylinidae	Dinaraea angustula (Gyll.)	3
Staphylinidae	Gabrius appendiculatus Sharp	3
Staphylinidae	Oxypoda praecox Er.	28
Staphylinidae	Xantholinus linearis (Ol.)	10
Staphylinidae Total		48
Tenebrionidae	Blapstinus moestus Melsh.	11
Tenebrionidae Total		11
Grand Total		148

Downtown 2 (NAC-G)

Family	Species	Num.
Carabidae	Agonum muelleri (Hbst.)	4

Carabidae	Amara aenea (DeG.)	14
Carabidae	Amara anthobia Villa	1
Carabidae	Amara ovata (F.)	3
Carabidae	Anisodactylus binotatus (F.)	7
Carabidae	Bembidion lampros (Hbst.)	2
Carabidae	Bradycellus sp 1	2
Carabidae	Carabus nemoralis Müll.	83
Carabidae	Harpalus affinis (Schrk.)	1
Carabidae	Nebria brevicollis (F.)	109
Carabidae	Pterostichus melanarius (Ill.)	4
Carabidae	Trechus obtusus Er.	1
Carabidae Total		231
Curculionidae	Barypeithes pellucidus (Boh.)	9
Curculionidae	Cryptolepidus sp.	1
Curculionidae	Otiorhynchus rugosostriatus (Goeze)	2
Curculionidae	Sciaphilus asperatus (Bonsd.)	1
Curculionidae Total		13
Hydrophilidae	Cercyon sp1	1
Hydrophilidae Total		1
Staphylinidae	Dinaraea angustula (Gyll.)	1
Staphylinidae	Ocypus olens (Muell.)	15
Staphylinidae	Philonthus carbonarius (Grav.)	11
Staphylinidae	Philonthus cognatus Steph.	10
Staphylinidae	Quedius curtipennis Bernh.	15
Staphylinidae	Rugilus orbiculatus (Payk.)	1
Staphylinidae	Tachyporus dispar (Payk.)	3
Staphylinidae	Tachyporus nitidulus (F.)	3
Staphylinidae	Xantholinus linearis (Ol.)	9
Staphylinidae Total		68
Throscidae	Trixagus sp 1	1
Throscidae Total		1
Grand Total		314

Old Town 2 (NH-G)

Family	Species	Num.
Carabidae	Amara aenea (DeG.)	2
Carabidae	Anisodactylus binotatus (F.)	14
Carabidae	Harpalus affinis (Schrk.)	8
Carabidae	Nebria brevicollis (F.)	88
Carabidae	Notiophilus sylvaticus Eschsch.	3
Carabidae	Pterostichus melanarius (Ill.)	1
Carabidae	Trechus obtusus Er.	1

Carabidae Total		117
Chrysomelidae	Longitarsus sp 1	5
Chrysomelidae Total		5
Coccinellidae	Coccinella septempunctata L.	2
Coccinellidae Total		2
Curculionidae	Barypeithes pellucidus (Boh.)	3
Curculionidae	Hypera nigrirostris (F.)	1
Curculionidae	Hypera zoilus (Scop.)	1
Curculionidae	Mecinus pyraster (Hbst.)	2
Curculionidae	Otiorhynchus ovatus (L.)	1
Curculionidae	Sitona hispidulus F.	1
Curculionidae	Sphenophorus parvulus Gyll.	15
Curculionidae Total		24
Dermestidae	Anthrenus verbasci (L.)	1
Dermestidae Total		1
Nitidulidae	Carpophilus lugubris Murray	8
Nitidulidae	Epuraea marseuli Reitter	1
Nitidulidae Total		9
Scarabaeidae	Onthophagus nuchicornis (L.)	1
Scarabaeidae Total		1
Staphylinidae	Ocypus aeneocephalus (DeG.)	8
Staphylinidae	Oxypoda praecox Er.	2
Staphylinidae	Philonthus carbonarius (Grav.)	13
Staphylinidae	Philonthus cognatus Steph.	62
Staphylinidae	Tachyporus dispar (Payk.)	1
Staphylinidae	Tachyporus nitidulus (F.)	1
Staphylinidae	Tasgius winkleri (Bernh.)	1
Staphylinidae	Xantholinus linearis (Ol.)	13
Staphylinidae Total		101
Grand Total		260

Old Town 1 (OC-G)

Family	Species	Num.
Carabidae	Amara aenea (DeG.)	2
Carabidae	Clivina fossor (L.)	1
Carabidae	Harpalus affinis (Schrk.)	4
Carabidae	Nebria brevicollis (F.)	17
Carabidae	Notiophilus sylvaticus Eschsch.	22
Carabidae	Trechus obtusus Er.	1

Carabidae Total		47
Coccinellidae	Exochomus quadripustulatus (L.)	1
Coccinellidae Total		1
Curculionidae	Barypeithes pellucidus (Boh.)	14
Curculionidae	Sitona cylindricollis (Fahrs.)	1
Curculionidae Total		15
Nitidulidae	Carpophilus lugubris Murray	3
Nitidulidae	Glischrochilus quadrisignatus (Say)	4
Nitidulidae	Pocadius fulvipennis Er.	1
Nitidulidae Total		8
Scarabaeidae	Aphodius badipes Melsh.	1
Scarabaeidae Total		1
Staphylinidae	Atheta fungi (Grav.)	1
Staphylinidae	Dinaraea angustula (Gyll.)	1
Staphylinidae	Gabrius appendiculatus Sharp	1
Staphylinidae	Omalium rivulare (Payk.)	2
Staphylinidae	Philonthus cognatus Steph.	1
Staphylinidae	Quedius curtipennis Bernh.	1
Staphylinidae	Xantholinus linearis (Ol.)	10
Staphylinidae Total		17
Grand Total		89

Suburban (TC-G)

Family	Species	Num.
Anthicidae	Anthicus cervinus LeFerte	11
Anthicidae Total		11
Byrrhidae	Simplocaria semistriata F.	13
Byrrhidae Total		13
Carabidae	Agonum canadense Goulet	9
Carabidae	Agonum cupreum Dejean	1
Carabidae	Agonum muelleri (Hbst.)	9
Carabidae	Amara aenea (DeG.)	26
Carabidae	Amara ovata (F.)	1
Carabidae	Amphasia sericea (Harris)	2
Carabidae	Bembidion lampros (Hbst.)	5
Carabidae	Calathus fuscipes (Goeze)	6
Carabidae	Cicindela purpurea Ol.	2
Carabidae	Harpalus affinis (Schrk.)	17
Carabidae	Loricera foveata (LeConte)	10

Carabidae	Microlestes minutulus (Goeze)	105
Carabidae	Microlestes sp.	1
Carabidae	Nebria brevicollis (F.)	187
Carabidae	Notiophilus biguttatus (F.)	2
Carabidae	Notiophilus sylvaticus Eschsch.	13
Carabidae	Stenolophus conjunctus (Say)	2
Carabidae	Syntomus americanus (Dejean)	1
Carabidae	Trechus obtusus Er.	42
Carabidae Total		441
Chrysomelidae	Diabrotica undecimpunctata Mannh.	1
Chrysomelidae Total		1
Coccinellidae	Coccinella septempunctata L.	13
Coccinellidae	Hippodamia variegata (Goeze)	7
Coccinellidae	Scymnus rubromaculatus (Goeze)	1
Coccinellidae Total		21
Curculionidae	Barypeithes pellucidus (Boh.)	1
Curculionidae	Hypera nigrirostris (F.)	2
Curculionidae	Hypera postica (Gyll.)	10
Curculionidae	Hypera zoilus (Scop.)	1
Curculionidae	Rhinoncus castor (F.)	1
Curculionidae	Sitona cylindricollis (Fahrs.)	1
Curculionidae	Sitona hispidulus F.	33
Curculionidae	Sphenophorus parvulus Gyll.	3
Curculionidae	Tychius picirostris (F.)	10
Curculionidae Total		62
Elateridae	Aeolus mellillus (Say)	17
Elateridae Total		17
Lathridiidae	Melanophthalma distinguenda (Com.)	1
Lathridiidae Total		1
Melyridae	Malachius sp 1	1
Melyridae Total		1
Nitidulidae	Carpophilus lugubris Murray	9
Nitidulidae Total		9
Staphylinidae	Gabrius appendiculatus Sharp	1
Staphylinidae	Gauropterus fulgidus (F.)	1
Staphylinidae	Oxypoda praecox Er.	58
Staphylinidae	Philonthus carbonarius (Grav.)	3
Staphylinidae	Philonthus cognatus Steph.	6
Staphylinidae	Tachyporus dispar (Payk.)	8

Staphylinidae	Tachyporus nitidulus (F.)	5
Staphylinidae	Xantholinus linearis (Ol.)	11
Staphylinidae Total		93
Tenebrionidae	Blapstinus moestus Melsh.	13
Tenebrionidae Total		13
Grand Total		683

Pearl District (TS-G)		
Family	Species	Num.
Carabidae	Agonum muelleri (Hbst.)	4
Carabidae	Amara aenea (DeG.)	3
Carabidae	Amara municipalis (Duft.)	1
Carabidae	Amara ovata (F.)	16
Carabidae	Amara plebeja (Gyll.)	8
Carabidae	Anisodactylus binotatus (F.)	46
Carabidae	Calathus fuscipes (Goeze)	18
Carabidae	Loricera foveata (LeConte)	1
Carabidae	Nebria brevicollis (F.)	57
Carabidae	Pterostichus melanarius (Ill.)	79
Carabidae	Trechus obtusus Er.	16
Carabidae Total		249
Coccinellidae	Hippodamia convergens Guerin	1
Coccinellidae Total		1
Corylophidae	Sericoderus lateralis (Gyll.)	7
Corylophidae Total		7
Curculionidae	Otiorhynchus sulcatus (F.)	1
Curculionidae	Sitona cylindricollis (Fahrs.)	1
Curculionidae	Sphenophorus parvulus Gyll.	3
Curculionidae Total		5
Nitidulidae	Carpophilus lugubris Murray	1
Nitidulidae	Glischrochilus quadrisignatus (Say)	1
Nitidulidae Total		2
Scarabaeidae	Aphodius badipes Melsh.	6
Scarabaeidae Total		6
Staphylinidae	Amischa sp.	1
Staphylinidae	Atheta fungi (Grav.)	13
Staphylinidae	Ocypus aeneocephalus (DeG.)	68
Staphylinidae	Oligota sp	1
Staphylinidae	Oxypoda praecox Er.	1
Staphylinidae	Philonthus carbonarius (Grav.)	25

Staphylinidae	Philonthus cognatus Steph.	184
Staphylinidae	Quedius curtipennis Bernh.	39
Staphylinidae	Rugilus orbiculatus (Payk.)	3
Staphylinidae	Stenus fulvicornis Steph.	1
Staphylinidae	Tachyporus dispar (Payk.)	3
Staphylinidae	Tachyporus nitidulus (F.)	7
Staphylinidae	Tachyporus sp 1	1
Staphylinidae	Xantholinus linearis (Ol.)	40
Staphylinidae Total		387
Grand Total		657

Downtown 1 (UH-G)		
Family	Species	Num.
Carabidae	Agonum muelleri (Hbst.)	3
Carabidae	Amara aenea (DeG.)	3
Carabidae	Anisodactylus binotatus (F.)	5
Carabidae	Bembidion doris (Panzer)	1
Carabidae	Bembidion lampros (Hbst.)	1
Carabidae	Harpalus affinis (Schrk.)	1
Carabidae	Nebria brevicollis (F.)	181
Carabidae	Notiophilus biguttatus (F.)	19
Carabidae	Notiophilus sylvaticus Eschsch.	2
Carabidae	Pterostichus melanarius (Ill.)	93
Carabidae Total		309
Curculionidae	Barypeithes pellucidus (Boh.)	30
Curculionidae	Otiorhynchus ovatus (L.)	2
Curculionidae	Otiorhynchus rugosostriatus (Goeze)	4
Curculionidae	Otiorhynchus sulcatus (F.)	1
Curculionidae Total		37
Elateridae	Aeolus mellillus (Say)	1
Elateridae Total		1
Nitidulidae	Carpophilus lugubris Murray	1
Nitidulidae	Colopterus unicolor (Say)	2
Nitidulidae	Glischrochilus quadrisignatus (Say)	1
Nitidulidae Total		4
Staphylinidae	Aleochara diversa (Sahlb.)	1
Staphylinidae	Atheta fungi (Grav.)	2
Staphylinidae	Ocypus olens (Muell.)	2
Staphylinidae	Philonthus cognatus Steph.	1
Staphylinidae	Tachyporus dispar (Payk.)	1

Staphylinidae	Tachyporus nitidulus (F.)	3
Staphylinidae	Xantholinus linearis (Ol.)	16
Staphylinidae Total		26
Throscidae	Trixagus sp 1	2
Throscidae	Trixagus sp 2	1
Throscidae Total		3
Grand Total		380

Table B 3: All beetle species found classified by trophic group, native status, and body size (mm), with numbered refereces (Refs.). Abbreviations for trophic groups are predator (PRED), megapredator (MPRED), omnivore (OMNV), parasitoid (PARAS), generalist herbivore (HERB), granivore (GRAN), root chewer (RCHEW), moss eater (MOSS), fungivore (FUNG), and detritivore (DETR). Abbreviations for origin designations are native (NAT), native pest (NATP), non-native (NON), non-native species of concern (NON-SOC), and unknown (UNK). List of numbered references follows table.

Family	Species	Trophic Group	Origin	Body Length	Refs.
Anthicidae	Anthicus cervinus LeFerte	OMNV	NAT	3	58
Bruchidae	Bruchidius fasciatus (Ol.)	PARAS	NON-SOC	3	66, 20
Byrrhidae	Cytilus sericeus (Forst.)	MOSS	NON	5	66,60
Byrrhidae	Simplocaria semistriata F.	MOSS	NON	4	42
Carabidae	Agonum canadense Goulet	PRED	NAT	7	59,70,9
Carabidae	Agonum cupreum Dejean	PRED	NAT	10	59,70,30
Carabidae	Agonum muelleri (Hbst.)	OMNV	NON	10	59,70,53
Carabidae	Amara aenea (DeG.)	OMNV	NON	8	59,70,95,26
Carabidae	Amara anthobia Villa	OMNV	NON	7	76,26
Carabidae	Amara familiaris (Duft.)	OMNV	NON	6	59,70,95,26
Carabidae	Amara municipalis (Duft.)	OMNV	NON	6	72,26
Carabidae	Amara ovata (F.)	OMNV	NON	8.5	59,52
Carabidae	Amara plebeja (Gyll.)	OMNV	NON	7	88
Carabidae	Amara sp.1	OMNV	UNK	7	26
Carabidae	Amphasia sericea (Harris)	GRAN	NAT	10	3,53
Carabidae	Anisodactylus binotatus (F.)	MPRED	NON	12	85,73
Carabidae	Bembidion doris (Panzer)	PRED	NON	3.5	64,65,71
Carabidae	Bembidion lampros (Hbst.)	PRED	NON	3.5	64,65,71,48
Carabidae	Bradycellus sp 1	PRED	UNK	5	3
Carabidae	Calathus fuscipes (Goeze)	OMNV	NON	13	3,89
Carabidae	Calathus ruficollis Dejean	OMNV	NON	9	77,79
Carabidae	Carabus nemoralis Müll.	MPRED	NON	23	59,3, 27
Carabidae	Cicindela purpurea Ol.	PRED	NAT	14	3,31

Carabidae	Clivina fossor (L.)	OMNV	NON	6	84,59, 53
Carabidae	Elaphropus parvulus (Dej.)	PRED	NON	2	47
Carabidae	Harpalus affinis (Schrk.)	OMNV	NON	10	87
Carabidae	Harpalus herbivagus Say	OMNV	NAT	8	87
Carabidae	Loricera foveata (LeConte)	PRED	NAT	9	12
Carabidae	Microlestes minutulus (Goeze)	PRED	NON	3	39,8
Carabidae	Microlestes sp. 1	PRED	UNK	3	29
Carabidae	Microlestes sp. 2	PRED	UNK	3	29
Carabidae	Nebria brevicollis (F.)	MPRED	NON-SOC	12	46
Carabidae	Notiophilus biguttatus (F.)	PRED	NON	5.5	59,22,2
Carabidae	Notiophilus sylvaticus Eschsch.	PRED	NAT	5	44,55
Carabidae	Pterostichus melanarius (Ill.)	MPRED	NON	16	46,86
Carabidae	Stenolophus conjunctus (Say)	PRED	NAT	4	70,11
Carabidae	Syntomus americanus (Dejean)	PRED	NAT	3	59,70
Carabidae	Trechus obtusus Er.	PRED	NON	4	66,49
Chrysomelidae	Altica sp. 1	HERB	UNK	4	66,4
Chrysomelidae	Diabrotica undecimpunctata Mannh.	HERB	NATP	7	25,68
Chrysomelidae	Longitarsus sp 1	HERB	UNK	2	66,4
Coccinellidae	Coccinella californica Mannh.	PRED	NAT	7	66,4
Coccinellidae	Coccinella septempunctata L.	PRED	NON-SOC	8	66,90,33
Coccinellidae	Coccinellidae sp 1	PRED	UNK	8	66,33
Coccinellidae	Exochomus quadripustulatus (L.)	PRED	NAT	4.5	66,33
Coccinellidae	Hippodamia convergens Guérin	OMNV	NAT	5.5	66,33,68
Coccinellidae	Hippodamia variegata (Goeze)	PRED	NON	4.5	66,24
Coccinellidae	Scymnus rubromaculatus (Goeze)	PRED	NON	2	66,81
Corylophidae	Sericoderus lateralis (Gyll.)	FUNG	NON	1	4,74

Cryptophagidae	Atomaria fuscata (Schoenh.)	FUNG	NAT	1.5	57
Curculionidae	Barypeithes pellucidus (Boh.)	HERB	NON	4	14
Curculionidae	Cryptolepidus sp.	HERB	NAT	5.5	4
Curculionidae	Dryophthorus americanus Bedel	HERB	NAT	3	4
Curculionidae	Hypera nigrirostris (F.)	HERB	NON-SOC	3.5	1
Curculionidae	Hypera postica (Gyll.)	HERB	NON-SOC	4.5	93
Curculionidae	Hypera zoilus (Scop.)	HERB	NON-SOC	7	59
Curculionidae	Mecinus pyraster (Hbst.)	HERB	NON	4	81,10
Curculionidae	Mecinus sp 1	HERB	UNK	4	81,10
Curculionidae	Otiorhynchus ovatus (L.)	HERB	NON-SOC	5	14,62
Curculionidae	Otiorhynchus rugosostriatus (Goeze)	HERB	NON-SOC	7	14,62
Curculionidae	Otiorhynchus sulcatus (F.)	HERB	NON-SOC	8	14,62
Curculionidae	Rhinoncus castor (F.)	HERB	NON	2.5	14,62
Curculionidae	Sciaphilus asperatus (Bonsd.)	HERB	NON	5	14,62
Curculionidae	Sitona cylindricollis (Fahrs.)	HERB	NON-SOC	4.5	14
Curculionidae	Sitona hispidulus F.	HERB	NON-SOC	3.5	59,14
Curculionidae	Sitona lepidus Gyll.	HERB	NON-SOC	5	91
Curculionidae	Sphenophorus parvulus Gyll.	HERB	NON-SOC	7	59,94
Curculionidae	Tychius picirostris (F.)	HERB	NON	3	59
Dermestidae	Anthrenus verbasci (L.)	DETR	NON	2.5	59,10
Dermestidae	Trogoderma sp.1	DETR	UNK	4	4
Dryopidae	Dryops sp 1	HERB	UNK	4.5	4
Elateridae	Aeolus mellillus (Say)	RCHEW	NATP	6.5	66,13
Elateridae	Limonius lanei Van Dyke	RCHEW	NATP	6	66,21
Hydrophilidae	Cercyon sp1	DETR	UNK	4	66,28

Languriidae	Cryptophilus integer (Heer)	FUNG	UNK	2	78
Lathridiidae	Melanophthalma distinguenda (Com.)	FUNG	NON	1.5	51
Lathridiidae	Melanophthalma sp 1	FUNG	UNK	1.5	4
Melyridae	Malachius sp 1	PRED	UNK	6	4
Monotomidae	Monotoma longicollis (Gyll.)	DETR	NON	1.5	56
Mycetophagidae	Mycetophagus quadriguttatus Mull.	FUNG	NAT	3.5	35
Nitidulidae	Carpophilus lugubris Murray	DETR	NAT	3.5	68
Nitidulidae	Colopterus unicolor (Say)	FUNG	NATP	4	23
Nitidulidae	Epuraea biguttata Thunb.	FUNG	NON	3.5	32
Nitidulidae	Epuraea marseuli Reitter	DETR	NON	3	32
Nitidulidae	Glischrochilus quadrisignatus (Say)	FUNG	NAT	5	75,17
Nitidulidae	Pocadius fulvipennis Er.	FUNG	NAT	4	19
Pselaphidae	Bibloplectus sp.	PRED	UNK	1.5	3
Pselaphidae	Brachygluta sp 1	PRED	UNK	1.5	3,18
Scarabaeidae	Aphodius badipes Melsh.	DETR	NAT	10	34
Scarabaeidae	Aphodius sp2	DETR	NAT	10	34
Scarabaeidae	Onthophagus nuchicornis (L.)	DETR	NON	7	36
Scolytidae	Hylurgops rugipennis (Mannh.)	HERB	NAT	4.5	37,63
Silvanidae	Silvanus bidentatus (F.)	FUNG	NON	3	61,69
Staphylinidae	Acrotona parens (Muls.Rey)	PRED	NON	3	5
Staphylinidae	Aleochara diversa (Sahlb.)	PARAS	NON	5	3
Staphylinidae	Aleochara lanuginosa Grav.	PARAS	NON	4	66,7
Staphylinidae	Aloconota gregaria (Er.)	PRED	NON	3	6,41,5
Staphylinidae	Amischa sp.	PRED	UNK	2.5	5
Staphylinidae	Atheta (Microdota) sp.	PRED	UNK	3	3
Staphylinidae	Atheta coriaria (Kr.)	PRED	NON	3.5	92
Staphylinidae	Atheta fungi (Grav.)	PRED	NON	3	82,45
Staphylinidae	Atheta sp. 1	PRED	UNK	3	3
Staphylinidae	Dinaraea angustula (Gyll.)	PRED	NON	4	7,61

Staphylinidae	Gabrius appendiculatus Sharp	PRED	NON	12	7,55
Staphylinidae	Gauropterus fulgidus (F.)	PRED	NON	12	83
Staphylinidae	Lobrathium sp.1	PRED	UNK	6	3
Staphylinidae	Ocypus aeneocephalus (DeG.)	MPRED	NON	20	3
Staphylinidae	Ocypus olens (Muell.)	MPRED	NON	25	3
Staphylinidae	Oligota sp	PRED	UNK	1	3
Staphylinidae	Omalium rivulare (Payk.)	PRED	NON	4	61,81
Staphylinidae	Oxypoda opaca (Grav.)	PRED	NON	4.5	7,61
Staphylinidae	Oxypoda praecox Er.	PRED	NON	4	3,50
Staphylinidae	Philonthus carbonarius (Grav.)	MPRED	NON	10	66,61,80
Staphylinidae	Philonthus cognatus Steph.	MPRED	NON	12	66,61,43
Staphylinidae	Quedius curtipennis Bernh.	MPRED	NON	13	54,67
Staphylinidae	Rugilus orbiculatus (Payk.)	PRED	NON	4	54,38
Staphylinidae	Stenus fulvicornis Steph.	PRED	NON	4	3,7
Staphylinidae	Tachyporus dispar (Payk.)	PRED	NON	4	66,61
Staphylinidae	Tachyporus nitidulus (F.)	PRED	NON	3	61,16
Staphylinidae	Tachyporus sp 1	PRED	UNK	4	3
Staphylinidae	Tasgius winkleri (Bernh.)	MPRED	NON	18	54, 15
Staphylinidae	Xantholinus linearis (Ol.)	PRED	NON	7	66,61,83
Tenebrionidae	Blapstinus moestus Melsh.	GRAN	NAT	5	13,40
Throscidae	Trixagus sp 1	FUNG	UNK	2.5	66,4, 96
Throscidae	Trixagus sp 2	FUNG	UNK	2.5	66,4, 96

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