

INVERTEBRATES ON GREEN ROOFS IN SYDNEY

Running title: Inverts on rooftops in Sydney



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WORD COUNT: 13,069 (excluding abstract and references)

Submitted on the 9th of October 2015

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DECLARATION

I wish to acknowledge the following assistance in the research detailed in this report:

Thanks to the “Green Team” i.e. my supervisors: David Nipperess for his tireless help with statistical analysis and fieldwork, Peter Davies for his logistical assistance and networking skills, and Matthew Bulbert for his advice and methodological guidance in invertebrate identification; and my helpful field assistants: Michelle Valencia and James Bickerstaff.

Thanks to Lesley Nearn-Cavanagh, Nicole Vella and Nadia Suarez-Bosche from the Microscopy Unit, Faculty of Science and Engineering, Macquarie University, for their assistance photographing specimen.

A number of people were crucial in the planning phase of this project for sample site identification and access. Heartfelt thanks goes to the multitude of council workers, building managers, security guards and private land holders who gave their time to give inductions or site access to me.

Specifically, I would like to thank:

Lucy Sharman, formerly City of Sydney Council; Sophie Golding, City of Sydney Council; Niki Carey, North Sydney Council; David Banbury and his team at the Coal Loader Sustainability Centre; Alexandra Vandine and Greg Taylor from Rockdale City Council; Claire Hanley and Jean Brennan at Marrickville Council; Nathan Wills and Jock Gammon from Junglefy; Emma McMahon, Amanda Steele, Ken Forsstrom, Pierre Lawrence and Allan Riches from CBRE; Peter Went, from DEXUS Property Group; the helpful desk staff at Meriton Apartments in Zetland; Tom Skotadis and security staff at Allianz Head Office in Sydney; John Blair and his connections at the UNSW International House; the friendly staff at the Crows Nest Community Centre; Grant Duff and Chris Cairns at Colliers International; Chris and Dieter Knierim from designer constructions; and the private landholders, Maggie and Niki Maloney. Special thanks to Leigh Staas, head of the National Green Infrastructure Network, Macquarie University.

Part of this work has been put forward to present as a conference paper to the State of Australian Cities Conference, Dec 9-11th, 2015.

All other research described in this report is my own original work.

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09/10/2015

ABSTRACT

Rapid urbanisation is a leading cause of habitat loss, worldwide. Green roofs are thought to provide habitat benefits for a range of species, and support biodiversity conservation objectives in cities. Yet, this study is the first to properly quantify the added habitat value of green roofs over conventional bare rooftops. Drawing on classical ecological theory, this study assesses the factors which influence invertebrate diversity and composition on bare and green roofs in urban Sydney. Green roofs with at least 30% green cover are capable of supporting resident populations with up to twice the abundance and three times the variety of invertebrates compared to bare roofs. Bare roofs may provide a peculiar kind of habitat which favours predators or scavengers, but contain mainly transient individuals. The habitat value of green roofs is limited by immigration and resource provision, with large ($>490\text{ m}^2$), structurally diverse, and well-connected green roofs hosting the greatest abundance and richness of invertebrates. Low-mobility taxa may be unable to colonise green roofs without human-mediated translocation. The findings of this study suggest that green roof implementation should consider: 1. landscape context, 2. roof size, 3. vegetation characteristics, 4. maintenance (including translocation of species of conservation concern or ecological value).

1. INTRODUCTION

Urban areas provide both opportunities and challenges for biodiversity conservation in the 21st century. More than half the world's population reside in cities, and this is expected to grow by almost 2% per year (World Health Organisation 2015). In the case of Australia, the proportion of urban residents exceeds 80% (Secretariat of the Convention on Biological Diversity 2012). Increasing urban populations create a high demand for housing and services, which results in increased density and spread of urban land use (Williams, Rayner & Raynor 2010). As city planners are tasked with the challenge of accommodating more people into existing cities, there is a need to identify, develop and implement policies that can offset the environmental impacts of increased urbanisation (United Nations Conference on the Environment and Development 1993).

A key impact of urban population growth is the reduction of vegetated open space and wildlife habitat (collectively referred to as 'green spaces') (Kowarik 2011). This reduction occurs both in areas adjacent to growing suburbs (greenfield development), and within the city itself (infill development). Remaining green spaces are increasingly fragmented, and vulnerable to edge effects and loss of canopy cover (McKinney 2002).

Vegetated rooftops ('green roofs') are a commonly used mechanism to increase green space in cities and have many human benefits. There is evidence that green roofs increase air quality, thermal resilience of buildings and surrounds, water regulation, provide recreational opportunities and improve aesthetics (reviewed in Oberndorfer *et al.* 2007; Berardi, GhaffarianHoseini & GhaffarianHoseini 2014). To date, there has been a large emphasis on understanding how the design of vegetated roofs can enhance thermal and water regulation benefits (e.g. Czemieli Berndtsson 2010). This focus responds to prescriptive targets, such as those set in the NSW State Environmental Planning Policy (Building Sustainability Index: BASIX) 2004 (Department of Planning and Environment 2004) and have been the major drivers of green roof implementation (City of Sydney Council 2014a).

Green roofs are often cited as providing additional environmental benefits, such as maintaining and conserving biodiversity through increasing provision and connectivity of wildlife habitat (Oberndorfer *et al.* 2007; Francis & Lorimer 2011; Cook-Patton & Bauerle 2012). Despite a deficiency in empirical support (Williams, Lundholm & Scott MacIvor 2014), urban planning policies, such as the Urban

Ecology Strategic Plan for Sydney (City of Sydney Council 2014b), offer green roofs as a potential avenue to address biodiversity loss in cities (e.g. Myers 2012). There has subsequently been a rise in green roof designs that claim biodiversity benefits (termed “biodiverse roofs”, Kadas 2006), and which have been incorporated into policy with limited and often retrospective assessment of their effectiveness. Thus, there is a need to understand the degree to which green roofs contribute habitat benefits to the urban environment.

1.1. Types of green roofs

Green roofs can be defined as roofs that are either partially or fully covered in vegetation (Berardi, GhaffarianHoseini & GhaffarianHoseini 2014). Often, terms such as 'living' or 'vegetated roofs' are used to distinguish from green building initiatives that improve sustainability but may not include vegetated surfaces (Francis & Lorimer 2011; Cook-Patton & Bauerle 2012). This broad definition is dependent on what constitutes a roof. A 'green roof' can encompass everything from potted rooftop gardens to parks that cover underground infrastructure but are at ground level. Some green roof design guidelines have precluded ground level surfaces by specifying that the 'roof' structure must be above ground level (e.g. City of Toronto Bylaw, 2009). Other technical manuals (Peck & Kuhn 2003) exclude rooftop gardens (i.e. pot plants on roofs) in their definitions of a 'green roof'. Instead, technical manuals may require that a green roof contains layers of waterproof membranes, drainage and filtering materials, substrate, and plants be present such that at least the substrate covers most if not all of the available roof surface (Peck & Kuhn 2003; Ngan 2004; Oberndorfer *et al.* 2007).

1.1.1. Intensive vs extensive roofs

Green roofs are classified as either extensive or intensive designs according to their structure and purpose (Peck & Kuhn 2003; Oberndorfer *et al.* 2007; Francis & Lorimer 2011; Magill *et al.* 2011; Cook-Patton & Bauerle 2012). *Extensive* green roofs have shallow soil, typically less than 15cm depth (Peck & Kuhn 2003; Cook-Patton & Bauerle 2012), and are planted with shallow-rooted, drought-tolerant plant communities (Francis & Lorimer 2011). Typically, they are installed for a specific function, and hence have greater economic rather than aesthetic value (Francis & Lorimer 2011). Extensive green roofs have been further classified into three main groups (complete, modular and pre-cultivated blanket designs) based on their level of integration with the building structure (Peck & Kuhn 2003;

Oberndorfer *et al.* 2007), but these have not been treated as separate in the literature on functional investigations. In contrast, *Intensive* green roofs have deeper substrate systems, and can range from 20 cm to as deep as 2 m (Oberndorfer *et al.* 2007). This allows for a more complex vegetation composition, which can yield additional habitat benefits and thermal insulation properties (Oberndorfer *et al.* 2007; Madre *et al.* 2013), but comes with higher installation costs (Peck & Kuhn 2003; Oberndorfer *et al.* 2007; Francis & Lorimer 2011). The oldest recognised green roofs are intensive, and were designed for aesthetic and recreational purposes (Oberndorfer *et al.* 2007; Francis & Lorimer 2011).

Although soil depth impacts green roof ecological functions (Brenneisen 2006), the use of an extensive-intensive dichotomy is overly simplistic, and does not in itself provide policy makers with criteria for maximising ecological benefits. Comparative evaluations of extensive and intensive roofs are difficult. Intensive green roofs are inherently more variable and complex in vegetation structure and management (Oberndorfer *et al.* 2007; Cook-Patton & Bauerle 2012), factors known to affect green roof performance (Lundholm *et al.* 2010).

Alternatively, definitions of green roofs based on vegetative cover are often useful in policy applications. For example, Toronto has mandated green roofs but the percent of vegetative cover that is required varies depending on the size of the roof (City of Toronto Bylaw, 2009). However, limited (and often anecdotal) information exists with respect to how the ecosystem services provided by green roofs change with vegetative cover.

The predominance of extensive-intensive green roofs classifications has distracted from a central, but untested, tenant of green roof performance: that green roofs, by virtue of their vegetative cover, provide increased ecosystem services over conventional non-vegetated roofs. Even if this assumption is correct it is difficult to assess the extent that green roofs influence biodiversity without appropriate baselines.

1.1.2. The Australian context

The earliest green roofs in Australia date from the 1960's (Williams, Rayner & Raynor 2010). Most existing green roofs are classified as intensive (deeper soil profile) with stormwater management and climate regulation the major motivations driving their installation (Williams, Rayner & Raynor 2010; City of Sydney Council

2014a). Yet, adoption of green roof industry is in its infancy. Green Roofs Australasia was founded in 2007, marking the first attempt to co-ordinate and grow expertise in green roof technology within Australia (Inkin 2015). Following international examples, the City of Sydney adopted Australia's first (and only) a green roofs and walls policy in 2014. This policy defines green roofs as those with vegetation cover on >30% of the useable roof area (City of Sydney Council 2014a).

There are complications of appropriating European technology and design for green roofs in Australia. Australia's hot, dry climate offers challenges to the creation of sustainable green roof systems, and irrigation is often necessary to sustain vegetation across all seasons (Taylor 2008). Lack of local research is preventing widespread adoption of green roof technology (Williams, Rayner & Raynor 2010; City of Sydney Council 2014a). Recent research efforts from the University of Melbourne has led to the production of the first national technical guidelines for roof construction (Francis *et al.* 2014); and research is ongoing to find suitable native plants for use on Australian green roof sites (*Ozbreed, pers comm*). In spite of these advancements, there are still large gaps in our understanding of how green roofs function under and Australian climate. In particular, there is a looming gap in our knowledge of the biodiversity benefits of green roofs for Australian fauna.

1.2. Faunal utilisation of green roofs

Green roofs are utilised by a range of taxa including birds (reviewed in Fernandez-Canero & Gonzalez-Redondo 2010), bats (Pearce & Walters 2012), and several kinds of invertebrates (Jones 2002; Brenneisen 2006; Kadas 2006; Clark & MacArthur 2007; Oberndorfer *et al.* 2007; Schindler, Griffith & Jones 2011; Madre *et al.* 2013; Rumble & Gange 2013; Braaker *et al.* 2014). While conservation of endangered bird species commonly drives green roof installation (Baumann & Kasten 2010), invertebrates are often the target of studies investigating green roof as habitat for three reasons. Firstly, they provide tractable systems for short term studies enabling quick assessment of habitat quality (e.g. Chessman 1995). Secondly, invertebrates are responsible for a variety of regulating services such as pollination and nutrient cycling (Ksiazek, Fant & Skogen 2012; MacIvor & Ksiazek 2015), and form the basis of many food webs.

Table 1 Factors known to affect biodiversity on green roofs.

Factor	Relation*	Div†	Taxa‡	References
Substrate				
Thickness variation	Positive	Beta	Collembola	(Jones 2002; Brenneisen 2006)
Locally derived	Positive	Alpha	Collembola	(Brenneisen 2006)
Older soils	Positive	Alpha	Collembola	(Schrader & Böning 2006)
Microbial activity	Positive	Alpha	Collembola	(Schrader & Böning 2006)
Vegetation				
Plant species richness	Positive	Beta	Weevils	(Braaker <i>et al.</i> 2014)
	Positive	Alpha	Bats	(Pearce & Walters 2012)
Structural diversity	Positive	Both	Spiders, beetles, bees, wasps, true bugs	(Madre <i>et al.</i> 2013)
Plant cover	Positive	Alpha	True bugs, carabid, spider, weevil	(Madre <i>et al.</i> 2013; Braaker <i>et al.</i> 2014)
Green roof type	Extensive < Intensive	Alpha	Spiders, beetles, bees, wasps, true bugs, birds	(Coffman 2007; Madre <i>et al.</i> 2013)
Specific plant species	Positive	Alpha	Bees, birds	(Coffman 2007)
Local Characteristics				
High temperatures	Filter	Alpha	Spiders, beetles, bees, wasps, true bugs	(Madre <i>et al.</i> 2013)
Water bodies	Filter	Alpha	Birds	(Fernandez-Canero & Gonzalez-Redondo 2010)
Building height	Negative	Both	Spiders, beetles, bees, wasps, bats	(Pearce & Walters 2012; Madre <i>et al.</i> 2013; MacIvor 2015)
Building area	Positive	Alpha	Spiders, beetles, true bugs, bees, wasps	(Jones 2002; Madre <i>et al.</i> 2013)
Age	Positive	Beta	Spiders	(Jones 2002; Braaker <i>et al.</i> 2014)
	None	Both	Insects	(MacIvor & Lundholm 2011)
Maintenance	Not stated	Alpha	Insects, spiders, birds	(Coffman 2007)
Landscape Characteristics				
Connectivity	Positive	Beta	Bees, weevils	(Braaker <i>et al.</i> 2014)
Composition	Varied	Beta	Bees, weevils	(Braaker <i>et al.</i> 2014)
	Not stated	Alpha	Bats	(Pearce & Walters 2012)
Faunal Characteristics				
Dispersal capacity	Filter	Both	Spiders, bees, carabids, weevils	(Madre <i>et al.</i> 2013; Braaker <i>et al.</i> 2014)
Body size	Negative	Beta	Bees	(Ksiazek, Fant & Skogen 2012)
Nest site requirements	Not stated	Alpha	Bees	(Ksiazek, Tonietto & Ascher 2014)

*Where regression analysis was used, or a linear correlation stated, the direction of the relationship is given. In some cases the relationship is 'Varied' depending on the taxa. Other factors may have been implicated as 'Filters' that limit species diversity.

† Diversity components analysed: Alpha = species richness, Beta = species composition.

‡ Taxa included are those for which there was an impact found. Other species may have been studied in the paper but their diversity was not affected by the given factor.

Finally, variation in dispersal ability within and between invertebrate families enables assessment of accessibility and movement of invertebrates between green roof spaces (e.g. Braaker *et al.* 2014). Therefore, invertebrates make excellent indicators of the overall ecological value of green roofs (McGeoch 1998), and are the focus of this study.

The effectiveness of green roofs as habitat for invertebrates is limited by the inherent constraints on green roof design and location (Gedge & Kadas 2005; Dunnett 2006). These constraints include increased exposure to wind, rain and radiation due to high elevation, and relatively shallow soils due to weight limitations (Oberndorfer *et al.* 2007). These are harsh conditions for plant growth, and limit the species available for use in green roof design (Dunnett 2006). The vegetation chosen presumably influences the invertebrate species that are able to colonise green roofs (Lundholm 2006; Hunter & Hunter 2008; Faeth, Bang & Saari 2011; Nipperess *et al.* 2012). For example, host-specific invertebrates will only colonise a roof if their host plant, (or host prey) species is present (Southwood 1988). The assemblage of species on a roof may, therefore, be as unique as every green roof design (Madre *et al.* 2013).

The few pioneering studies in Europe and, recently, America have found several design factors to be important in influencing invertebrate diversity on green roofs (**Table 1**). Species richness (alpha diversity) of invertebrates is higher on roofs with a deep soil layer (Brenneisen 2006; Schrader & Böning 2006), high plant diversity (Cook-Patton & Bauerle 2012), high plant biomass (Cook-Patton & Bauerle 2012; Madre *et al.* 2013), greater structural complexity (Lundholm *et al.* 2010; Madre *et al.* 2013), or large roof area (Madre *et al.* 2013). Invertebrate species composition (beta diversity) is influenced by several roof factors, including substrate variation (Jones 2002), plant species richness (Braaker *et al.* 2014) and building height (Madre *et al.* 2013; Braaker *et al.* 2014; MacIvor 2015). The characteristics of the surrounding landscape (Braaker *et al.* 2014) and the invertebrates themselves (Ksiazek, Fant & Skogen 2012; Braaker *et al.* 2014; Ksiazek, Tonietto & Ascher 2014; Muller *et al.* 2014) also have an impact on which species appear on green roofs. Invertebrate richness and composition is negatively correlated with increased building height (MacIvor 2015) and isolation from surrounding habitat patches (Madre *et al.* 2013; Braaker *et al.* 2014). Importantly, Madre *et al.* (2013) and Braaker *et al.* (2014) show the impact of

height and isolation is dependent on the mobility of the species. However, little is known about the processes underlying invertebrate colonisation and influences of these processes on species diversity.

1.3. Applying classical ecological theory for decision making

There is a need for simple, generalised and quantifiable indicators which predict the biodiversity value of green roofs in the planning phase of construction. Considering the large variation in green roof design possibilities, policies promoting green roofs for biodiversity conservation require appropriate design guidelines to inform implementation. Here, I suggest that such indicators may be generated from applications of classical ecological theory.

Classical ecological theory relies on simple principles to explain the appearance of species within nature. Application of these principles has a long history within conservation biology. Principles of classical ecology are particularly useful when difficult management decisions need to be made despite incomplete knowledge of the study system (Triantis & Bhagwat 2011), which is often the case in highly altered urban areas (Davis & Glick 1978). In the specific context of green roofs, there is a great deal of variation between roofs with respect to architectural and vegetative characteristics such that no two roofs are exactly alike. Thus, in any observational study there are a complex set of uncontrolled factors which are difficult to tease apart. For this reason, understanding of the drivers of faunal biodiversity on green roofs is in its infancy, particularly in Australia (Williams, Lundholm & Scott MacIvor 2014). Hence, classical ecological theory may be applied to assess biodiversity value of green roofs in the absence of data from primary studies.

Understanding the added habitat value of green roofs is the first step in successfully improving biodiversity outcomes. Bare roofs provide a baseline for roof invertebrate diversity in urban areas. Comparison of green roofs to this baseline enables distinction between species that may be already present on rooftops, and species that are actively attracted to green roofs. In both cases, green roofs are contributing to conservation aims through provision of *additional* habitat resources. Most previous studies into the biodiversity on green roofs have neglected to include a proper assessment of invertebrate utilisation of bare roof environments - that is, the pre-intervention state. Only two studies include a comparison of bare and green rooftops (Davies, Simcock & Toft 2010; MacIvor

2015). These studies either focus on a single functional group (cavity nesters, MacIvor 2015), or do not report findings from bare roof traps (Davies, Simcock & Toft 2010). This latter study lacked replication and used methods that appear incompatible with bare roof sampling (such as pitfall traps). Therefore, these studies are insufficient to provide a useful baseline comparison and elucidate the added habitat value of green roofs.

Most studies into green roofs have focused on comparisons exclusively between different types of green roofs. Such studies only highlight potential design factors that make one roof more diverse over others (Coffman 2007). This gives us limited insight into the processes, such as species colonisation and establishment, which make green roofs of greater habitat value than bare roofs. Understanding the processes underlying recruitment and establishment of resident populations is important for effective green roof design. Poor green roof designs can result in ecological traps, where individuals are attracted to the roof but unable to gain sufficient resources from its utilisation (Coffman 2007). For example, some ground-nesting bird species are unable to successfully reproduce on green roofs that were designed to provide nesting resources (Baumann 2006). Similarly, recent studies have shown that solitary bees are unable to successfully breed in nest boxes provided on taller green rooftops (MacIvor 2015). If such a roof is being used by the bees instead of more suitable nest sites (such as on lower green roofs), the population will decline over time.

In addition to vegetation cover, the size and context of a roof are expected to affect invertebrate diversity (MacIvor & Ksiazek 2015). Using the tenets of island biogeography theory, it is expected that size and context influence immigration and extinction rates; that is how fast the pool of species is filled and the rate at which species are removed (**Fig. 1**). The balance of these processes, ultimately, determines the invertebrate community composition on green roofs.

Immigration of invertebrates is dependent on accessibility of the roof. The more isolated the roof from ground source populations, the less likely it is that new individuals will arrive (MacArthur & Wilson 1963; Davis & Glick 1978; Rosenzweig 1995). Unlike traditional applications of island biogeography theory, rooftops are unique in that they can be considered isolated in three dimensions. Immigration of invertebrates is limited by the distance to source populations at the ground level, as well as building height (Madre et al. 2013; Braaker et al. 2014; MacIvor 2015).

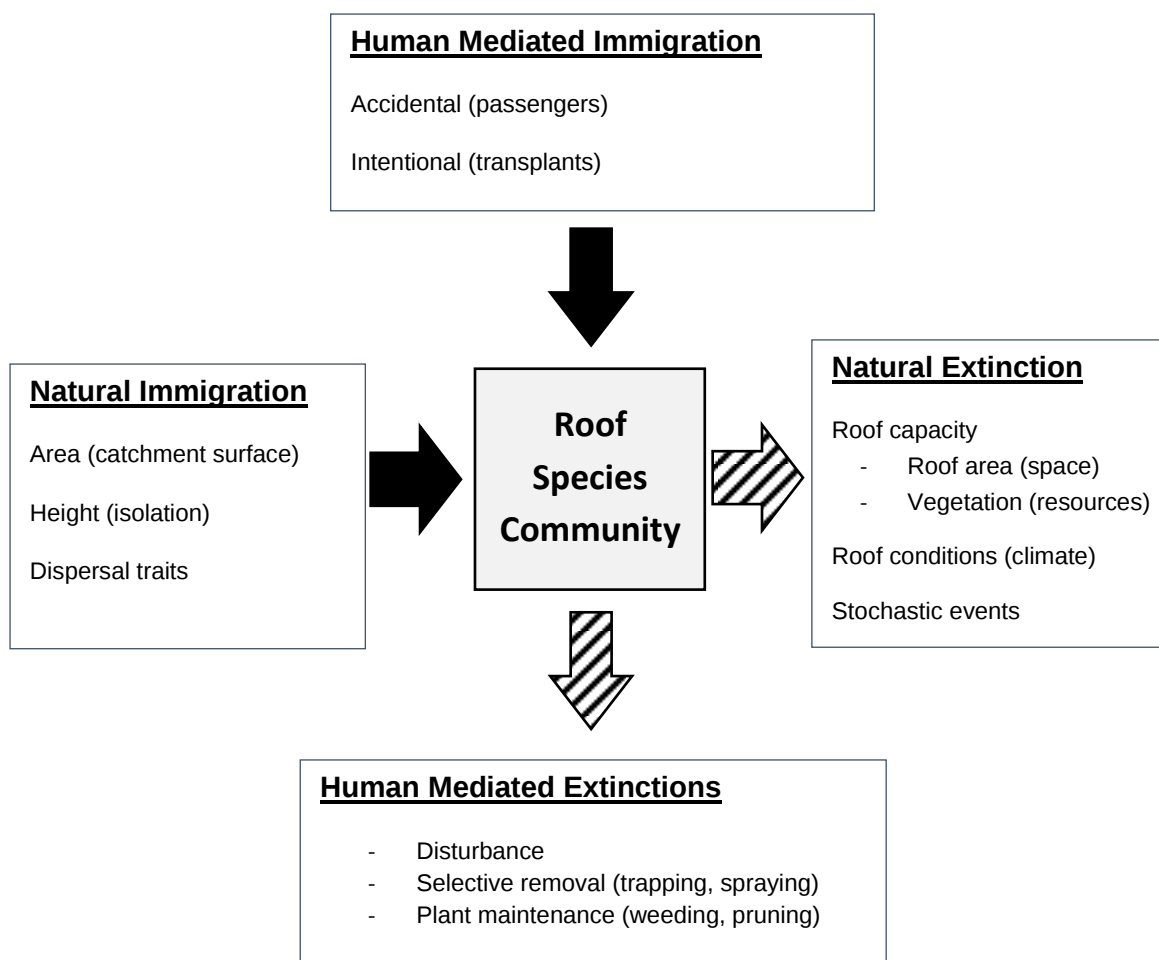


Fig. 1. Island biogeography theory as it applies to green roof environments.

The species community is an equilibrium between the influx (solid black arrows), and outflow (grey striped arrows) of species. These flows may be a result of human action (vertical pathway) or natural processes (horizontal pathway).

Taller roofs have a lower probability of colonisation for dispersal-limited species as the vertical distance from source populations increases, and this may restrict the kinds of species that can appear on rooftops based on dispersal ability. The interaction of building height and distance may occur additively, or in accordance with Pythagorean theory (**Fig. 2**), or may show a curvilinear relationship. An additive relationship is most likely, as many insects use navigation strategies that cause them to fly parallel to ground surfaces (e.g. optic flow in honeybees, Srinivasan et al. 1996). Similarly, a larger roof area provides a greater catchment surface for immigrating individuals and increases the probability of arrival to a certain rooftop.

Human activity may also influence immigration of individuals onto green roofs. Green roofs are generated by the intentional movement of plants and soil onto roof surfaces. Similarly, animals may be intentionally introduced onto green roofs, for example, the placement of native or honeybee hives on rooftops (Melbourne City Rooftop Honey 2015). Alternatively, invertebrates may be introduced accidentally as passengers within the soil or on plants that are used in construction of a green roof (Brenneisen 2006). Similarly, birds and even dogs may act as transport vectors for phoretic invertebrates (e.g. mites, Krivolutsky & Lebedeva 2004).

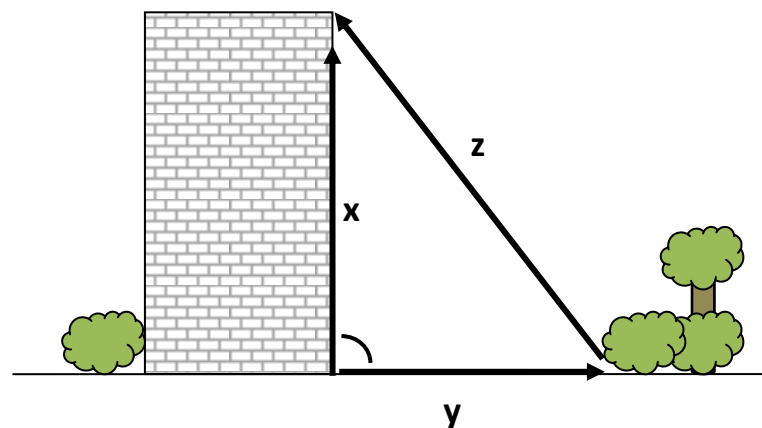


Fig. 2. The impact of isolation on dispersal of invertebrates onto rooftops.

Rooftops are isolated in two ways: the horizontal distance to the nearest neighbours in the landscape (y), and building height (x). These factors may interact to magnify the isolation on green roofs either according to Pythagorean theory (z), or as an additive of nearest neighbour and height distances.

The likelihood of attracting regular visitors or maintaining viable resident populations within a habitat patch is related to the patch size and its quality (**Fig. 1**). Rooftops represent exposed, high temperature environments which limit growth of plants (Lundholm 2006). This environmental filter may impact invertebrates in two ways: it may exclude invertebrates based on climatic tolerance (Madre *et al.* 2013), or the absence of required plant assemblages (the “habitat template” as in Southwood 1988). The strength of the climatic filter may increase with increasing elevation (i.e. roof height), as in natural systems (Lomolino 2001) and restrict colonisation even in species with high dispersal capacity. Hence, rooftop environments may favour certain invertebrate groups as a result of species-specific traits. This could lead to distinct assemblages of species suited to rooftop

conditions. Similar biases in exclusion of species may also result from human-mediated disturbance (**Fig. 1**). Regular human use may deter disturbance-sensitive species or species may be selectively removed as part of maintenance processes.

Habitat quality is also a result of the vegetation type and structure. No two green roofs are exactly alike in vegetation composition, and may, therefore, differ in habitat quality (MacIvor & Ksiazek 2015). This variation has been the basis of previous green roof comparisons (e.g. Madre *et al.* 2013; Braaker *et al.* 2014). Variations in vegetation may offer greater structural complexity and therein a greater number of microhabitats. Larger habitat patches may cover a wider range of vegetation types and, hence, a wider variety of microhabitats. Larger habitat areas can also host larger populations of individuals due to increased biomass and decreased competition for space. Increasing the biomass of vegetative growth (i.e. the vegetative cover on a roof) increases available resources allowing for greater abundances, and hence greater richness (Pearce & Walters 2012). Therefore, larger green roofs are expected to support a greater abundance and diversity of invertebrates. Bare roofs, on the other hand, may represent a more homogenous habitat type, and be more similar in composition across rooftops.

1.4. Objectives

The following project aims to answer two questions:

- Q1. What added habitat value do green roofs provide over bare roofs?
- Q2. Is the presence of vegetation the only factor influencing invertebrate community dynamics on rooftops?

To answer these questions I investigated green and bare roofs as habitat for invertebrates within the context of highly urbanised inner Sydney. The City of Sydney is at the forefront of green roof policy and Australia, and has a recently completed database of 80 green roof sites. It is, therefore, an ideal target area for selecting research sites. Pragmatically, for a comparison of green versus bare rooftops, the present study adopts a definition based on vegetative cover in line with the City of Sydney Green Roofs and Walls Policy (i.e. >30% green cover). Recognisable taxonomic units were used as surrogates for invertebrate species diversity (Section 2.3). All rooftops in Sydney are intensive, removing some confounds of roof type definitions.

Based on the principles of classical ecological theory I made several predictions about the abundance, richness and composition of invertebrates on green roofs. These are numbered below, and followed by a brief justification:

Prediction 1. Green roofs are expected to have a higher abundance, richness and diversity of invertebrates than bare roofs (Q1)

Larger vegetative biomass on green roofs will support a higher abundance of individuals than bare roofs, which will result in higher taxon richness. Increased structural complexity on green roofs is expected to increase microhabitat availability, allowing for a higher abundance, a more diverse assemblage of invertebrates and higher richness.

Prediction 2. Bare roofs are expected to have distinct and more homogenous assemblages than green roofs (Q1)

Green and bare roofs are expected to have different environmental conditions which act as a filter to influence compositional patterns. Invertebrates are expected to have a higher residency on green roofs due to provision of plant resources. Thus, green roof communities are likely to contain more taxa that are dependent on these resources. Variation in green roof design is expected to lead to a larger heterogeneity within and among sites, which could lead to higher variation in the composition of the invertebrate assemblages, compared to bare roofs. In contrast, bare roofs are expected to represent a strong environmental filter which will favour certain taxa and cause more homogenous invertebrate communities.

Prediction 3. Larger roof areas will have a higher abundance and richness of invertebrates (Q2)

Larger roofs have increased immigration (a larger catchment area), and support larger resident populations. Increased resource provision, lower competition for space and higher heterogeneity of microhabitats is expected to lower extinction risk and promote increased invertebrate richness.

Prediction 4. Taller buildings are expected to have less abundance and richness, and a significantly different composition of invertebrates compared to lower roofs (Q2)

Building height represents a larger barrier to dispersal and hence less immigration of individuals. This barrier may also limit the kinds of taxa which can colonise a tall roof.

Prediction 5. Highly isolated roof invertebrate communities are expected to have communities which are dominated by taxa with a high dispersal capacity (Q2)

If the dispersal barrier may limit the kinds of taxa that are able to colonise the roof, this may cause invertebrate communities on tall roofs to be dominated by highly mobile taxa.

Prediction 6. Buildings with close and plentiful ground habitats (i.e. high landscape vegetation cover), will have a higher abundance, richness and diversity of invertebrates (Q2).

Ground habitats represent source populations for roof-dwelling invertebrates. Urban land use is considered inhospitable for a range of species, and hence increased distance to nearby source populations is a significant dispersal barrier.

2. METHOD

2.1. Study sites

This study assessed invertebrate diversity on 11 bare and 13 green rooftops distributed within the Sydney Central Business District and inner metropolitan suburbs (**Fig. 3**). Rooftops were 10 to 8000 m² in area, and ranged from ground level (built over underground car parks) to buildings that were 16 stories (approximately 50 m) tall.

Bare roof surfaces were exposed concrete (**Fig. 4b**), corrugated iron or concrete with a pebble outer layer (**Fig. 4c**). Bare roof sites were obtained through local councils, with the additional aid of the building management company CBRE. Bare roofs had <5% green cover, including overhanging trees. Green roofs had a soil depth greater than 40 cm, and are classed as intensive designs (Section 1.1). Green roofs were selected from a database obtained from the City of Sydney Council and liaison with other councils in the area. In accordance with City of Sydney policy definitions, green roofs had between 30 – 98% of green cover.

Sample sites were largely obtained as a consequence of availability, but there was no autocorrelation in the location of bare and green roof sites (Moran's I: observed = 0.14, expected = -0.04 ± 0.14, p = 0.18). As much as possible, the selection of sites sought to ensure equal representation of building height and areas across both roof types. Similarly, an attempt was made to stratify the sampling across areas and heights. That is, to ensure there were sites with similar area at different heights and similar height with varying areas. Sampling of ground sites was not undertaken due to logistical constraints on acquiring suitable bare ground sites within the CBD, as well as concerns about interference.

2.2. Sampling design

Bare roofs are impermeable hard surfaces that are exposed to high temperatures and strong winds. As a result, most traditional invertebrate sampling methods (such as pitfall traps) are not suitable or difficult to implement for use on bare roof environments. Invertebrates were sampled using a modified yellow pan trap design. Yellow pans are a cost-effective sampling device (typically a plastic picnic bowl), which is placed on flat substrate surfaces (New 1998). This trapping technique is biased towards flying insects (Sutherland 2006), but fauna reaching roofs are likely to be predominantly aerial. Yellow pans will also catch some

highly-active ground dwelling species (New 1998). The use of yellow pans (as opposed to any other colour) maximises the variety of insects caught in the traps (Vrdoljak 2012). This does generate biases in the faunal diversity attracted, but this bias would be consistent across roofs. Given the wind-exposed conditions of the bare roofs, the weight and surface contact of each bowl was increased by attaching a 2kg floor tile, mottled dark grey, 32.5 x 32.5 cm wide and 0.9 cm high. This design increased the weight of each bowl without significantly raising the height of the bowl from the roof surface. A low profile is important to limit deterrence of crawling insects from entering the bowls. Bowls were attached to tiles onsite using a synthetic rubber (“liquid nails”) or silicone adhesive. A set of five yellow pan traps (**Fig. 4**), were placed towards the centre of each roof. Layout of the traps varied due according to the shape of roof and vegetation structure. In most cases a quincunx dice pattern (**Fig. 4a, b**), or checkerboard pattern (**Fig. 4c, d**) was used. The average distance between the bowls was maintained between 50 – 100 cm, and the trap area was not significantly different between sites (ANOVA; $F = 0.746$, d.f. = 1, $p = 0.4$).

Each bowl was filled with 200 – 300ml of a capture solution consisting of 12.5 % propylene glycol (PL010-2.5L-P; ChemSupply Pty Ltd) and tap water. Each site was sampled twice for a period of 7-8 days during January to mid-March 2015. The sample period was determined during a pilot study of the trap design on Macquarie University campus rooftops in October 2014 (unpublished data). To account for weather variation and spatial location, temperature was measured on each roof using ibuttons (Thermochron DS1921G, Thermodata Pty Ltd) housed in PVC tubing and suspended on flyscreen mesh (**Fig. 4e**). This design prevented direct radiation exposure, which is necessary for the detection of ambient temperature (Ashcroft & Gollan 2012). Two ibuttons (and houses) were placed at each site, either attached to a tile or attached to the surrounding substrate. These were set to record the temperature at hourly intervals over the whole study period. The average site temperature was then recorded for each sampling event.

2.3. Invertebrate sample processing

Specimens from each pan were sorted into recognisable taxonomic units using a parataxonomic approach for rapid biodiversity assessment (Oliver and Beattie 1996). Specimens were then pooled from all traps at a given site for a given sampling period. In most cases, specimen were sorted to order or class level

under an objective microscope (Olympus DF Planapo IX). Due to time constraints, only one group was sorted to morphospecies. Hymenoptera was chosen for morphospecies analysis because is a hyperdiverse group, which covers a range of functional groups and dispersal capacity (CSIRO 1991). Many members of this group also form close association of many of these species with plants (Huxley & Cutler 1991) and other fauna (Whitfield 1998). Hymenoptera morphospecies were photographed using a stereo microscope (Olympus SZX16) from the Microscopy Unit, Faculty of Science and Engineering, Macquarie University.

For the purpose of a functional analysis of mobility, nine taxon level groups (Araneae, Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera and Thysanoptera) were split into mobile and less mobile forms (**Table 2**). For Hymenoptera, this information was summarised from the morphospecies data. Highly mobility was defined as specimen which relied on flight or other airborne travel as their primary means for movement. Specimen without or with incompletely formed wings were considered to have low mobility. This included larval or nymph life stages of many otherwise highly mobile taxa. In contrast to the other groups, spiders (order: Araneae) tend to be better dispersers at younger life stages. Spiders were split into groups based on their ability to disperse via ballooning. “Strong ballooners” (or highly mobile spiders) were of the families Linyphiidae and Araneidae, which are commonly known to balloon as juveniles (Greenstone *et al.* 1987, Elizabeth Lowe pers. comm). “Weak ballooners” (i.e. spiders with low mobility) were families of which several species had been observed to balloon, but it was not common (reviewed in Bell *et al.* 2005). All spider families observed on the rooftops were known to have members which could balloon. Mobility class groups were only used in a secondary analysis of compositional changes and were combined for all other measures.

2.4. Data collection

Four measures of invertebrate community response were taken: absolute abundance, site richness (the number of different taxonomic groups present at site), the inverse Simpsons Diversity measure (Jost 2006) and community composition. These were calculated using the average of the two sampling **periods**.

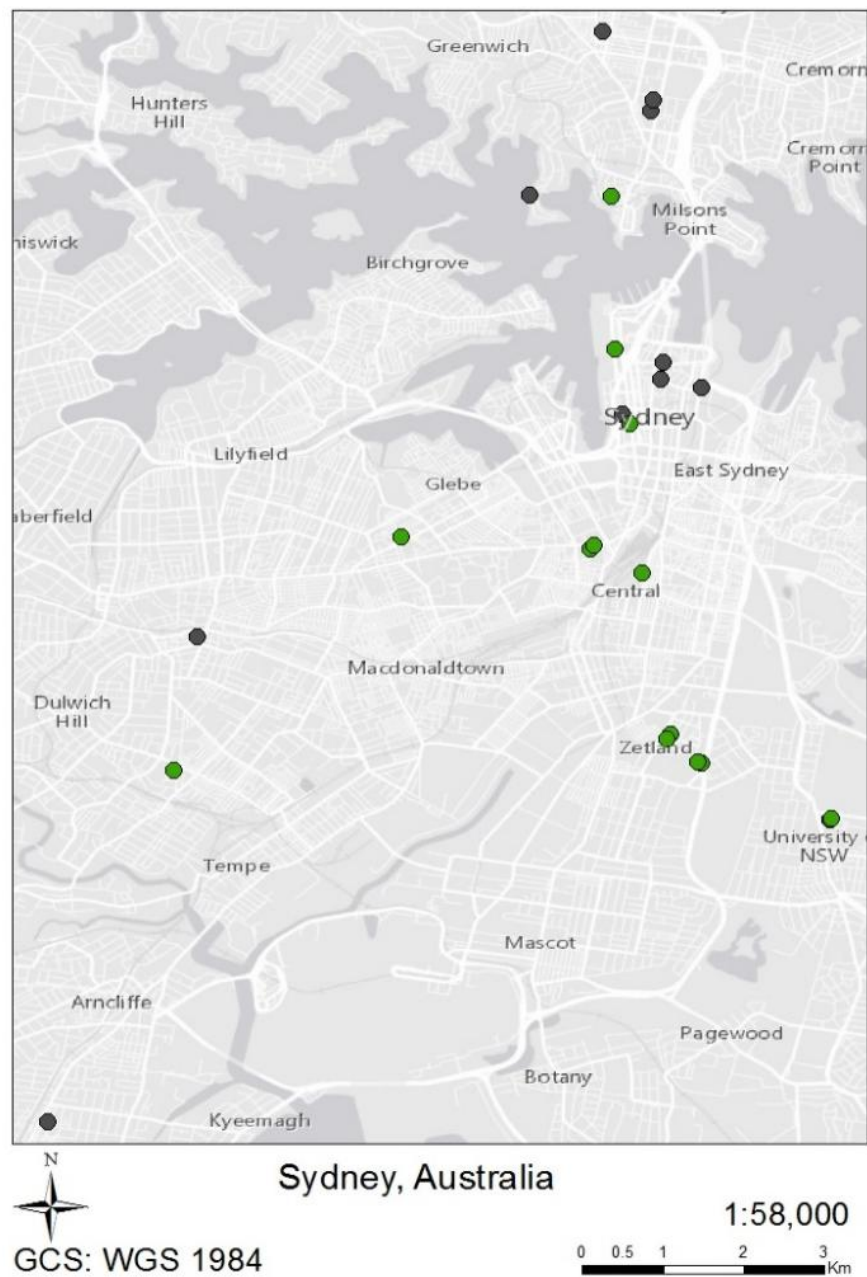


Fig. 3. Map of sample sites.

A total of 13 green (●) and 11 bare (●) roof sites were sampled between January and March 2015. All sites were within 15km of Sydney CBD.

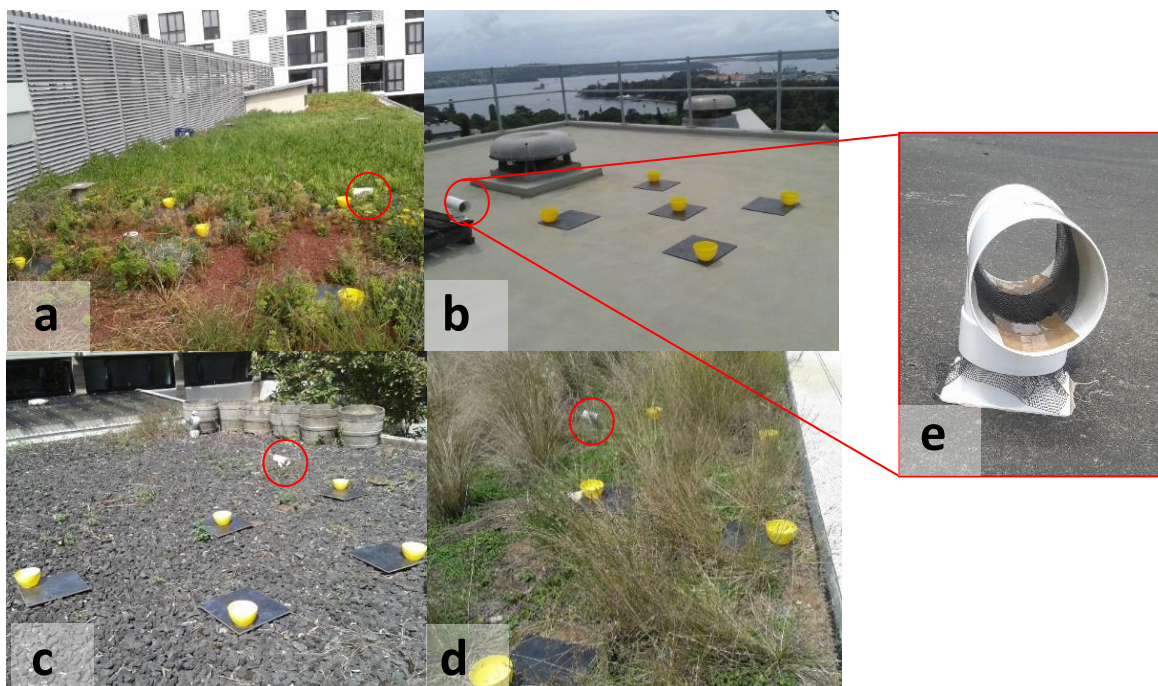


Fig. 4. Trap design and layout.

The traps were arranged as five yellow bowls, usually in a quincunx pattern (a,b), with deviations made to fit to more rectangular rooftops (c,d). Any variations in yellow pan arrangements were mirrored on green (a,d) and bare (b,c) rooftops. Thermochron ibuttons were placed in PVC tubes (e) which were placed next to the trap arrangement (red circles).

Table 2. Functional group classifications.

Higher taxa which encompassed a range of mobility were split into more and less mobile forms. Taxa for which the mobility was relatively uniform were treated as a whole. *Weak* = weak ballooners, *Strong* = strong ballooners. *High* mobility taxa have wings, *low* mobility do not.

Taxa		Mobility	Total abundance		Abundance per site	
			Bare	Green	Bare	Green
Acarina	All	Low	149	1363	6.77	52.42
Amphipoda	All	Low	0	1	0.00	0.04
Annelida	All	Low	0	5	0.00	0.19
Araneae	Araneidae	Strong	3	2	0.14	0.08
	Clubonidae	Weak	1	8	0.05	0.31
	Desidae	Weak	15	19	0.68	0.73
	Linyphiidae	Strong	3	1	0.14	0.04
	Salticidae	Weak	4	6	0.18	0.23
	Therididae	Weak	4	9	0.18	0.35
	Thomisidae	Weak	2	0	0.09	0.00
	Other	Weak	1	7	0.05	0.27
Blattodea	All	Low	0	1	0.00	0.04
Coleoptera	Winged	High	7	76	0.32	2.92
	Larvae	Low	2	14	0.09	0.54
Collembola	All	Low	11	2571	0.50	98.88
Diptera	All	High	43	80	1.95	3.08
Gastropoda	All	Low	0	42	0.00	1.62
Hemiptera	Winged	High	376	334	17.09	12.85
	Non-Winged	Low	237	2229	10.77	85.73
Hymenoptera	Ants	Low	17	552	0.77	21.23
	Wasps/bees	High	233	563	10.59	21.65
Isopoda	All	Low	0	12	0.00	0.46
Lepidoptera	Adult	High	4	22	0.18	0.85
	Larvae	Low	2	30	0.09	1.15
Neuroptera	Adult	High	0	1	0.00	0.04
	Larvae	Low	3	2	0.14	0.08
Orthoptera	All	High	0	8	0.00	0.31
Psocoptera	Adult	High	5	0	0.23	0.00
	Larvae	Low	4	13	0.18	0.50
Thysanoptera	Adult	High	84	472	3.82	18.15
	Nymph	Low	1	53	0.05	2.04

Separate measures were taken for the higher taxonomic level groups (herein “Taxon Level”) and the Hymenoptera morphospecies (herein “Morphospecies Level”). Hymenoptera specimens were counted within the higher level diversity measures as a single taxonomic group.

For each roof site, variables thought to be important in influencing invertebrate communities on rooftops were recorded under five major categories:

1. roof type (bare or green)
2. roof area (m²)
3. building height (stories)
4. landscape composition (NDVI)
5. landscape connectivity (nearest neighbour distance, m²)

Roof type was taken as a binary variable which encompasses several roof characteristics including percent of vegetative cover, structural complexity and temperature. The percentage cover of green (including overhanging trees) was calculated using aerial photography. Since the roofs were selected such that there was a large zero-skew in percent cover values, the impact of percent cover on invertebrates was only able to be analysed for the green roofs (so the data conformed to statistical assumptions). The presence of vegetation on a roof is expected to increase the structural complexity and thus availability of microhabitats. As a baseline, bare roofs may be expected to contain some structural features that generate small hiding places or build-up of windblown debris. Structural complexity was measured for each roof using the habitat feature diversity index developed by Tomoff (1974). This index has been previously been successfully applied to quantify diversity of vegetative and man-made structures in the urban environment (Lancaster & Rees 1979). Using this method a series of habitat features were described and their relative proportions measured using aerial photography. Here, the proportion was taken by measuring the area of each habitat feature and dividing by the total area of all features (**Table S1**). Measures of structural complexity were assumed to provide an indication of habitat quality, and for timely analysis, measures such as plant species diversity, age and soil depth were not included in analyses. This is a significant limitation of the research, but the true power of applying ecological theory is to overcome site-specific complexities and find simple principles that drive species appearance on rooftops. In addition, there is now a well-established literature on the thermal performance

of green roofs (reviewed in Oberndorfer *et al.* 2007), which indicates that bare roofs would have higher and more variable temperature regimes than green roofs. Variables such as structural diversity and site temperature (°C) were taken as secondary explanations for the green roof dichotomy.

Measurements of the total roof area were taken from high resolution aerial photography (NearMap Pty Ltd, 2015). Nearmap imagery was loaded as a basemap into Google Earth and each of the buildings were traced to create a polygon KML (Keyhole Markup Language) file. This was then converted into an ESRI shapefile using online conversion software (<http://converter.mygeodata.eu/>) for later analyses.

Number of stories was taken as a surrogate for building height. The study area does not have a large degree of variation in height above sea level, and it is assumed that one story is equivalent for all buildings. Generally, one story is between 3 to 4 m, in accordance with building codes.

Landscape composition was assessed using the Normalised Difference Vegetation Index (NDVI, Rouse *et al.* 1974) as a measure of the percentage of green cover in the landscape surrounding the roof sites. NDVI values were calculated from Landsat 8 satellite imagery (NASA Landsat Program 2015). Following Braaker *et al.* (2014), the average NDVI score was calculated within a buffer area of 100, 200, 300 and 400 m.

Major vegetation patches within the study area were identified by applying a threshold of NDVI 0.3, and cross checking with ESRI World Imagery basemaps in ArcMap™ (Version 10.2). At a resolution of 30m², small pocket parks and gardens were included in this threshold. This was then converted to a smoothed ESRI polygon shapefile to calculate the distance from each roof to the nearest habitat patch using the Neighbour Distance tool in the Analysis Toolbox.

2.5. Statistical analyses

The influence of the five categories of explanatory variables on invertebrate abundance, richness and diversity was analysed using multiple regression modelling. Each variable category was considered to explain a different habitat filter or dimension of isolation and thus be independent for the purposes of analysis. For the landscape composition measurements, iterative testing of different explanatory models found NDVI at 200 m buffer distance to have the

most explanatory power (lowest AIC of models including NDVI measures), and this was the only landscape composition variable included in the models. Response and explanatory variables were transformed as necessary to conform to the assumption of linearity (**Table 3**). In most cases, explanatory variables were rank transformed, and response variables were log transformed. An exception was the compositional data, which was standardised for abundance across and within samples using the Wisconsin transformation (Bray & Curtis 1957). Following transformation, one of the roof sites was a notable outlier for morphospecies data, containing only one individual of a unique species. This site was removed from analysis for the morphospecies models but was retained at the taxon level analysis.

Table 3. Transformations used for each explanatory and response variable.

Transformations were performed to normalise the data or conform to assumptions of linearity. Variables not listed were not transformed before analysis. T = Taxon level, M = Morphospecies level.

	Log10	Square Root	Rank	Wisconsin	None
Abundance	T, M				
Richness	M				T
Diversity		M			T
Composition				T, M	
Mobility Composition				X	
Roof Area	X				
Structural Diversity	X				
Percentage Green Cover		X (Arcsine)			
Level (Height)			X		
Nearest Neighbour Distance			X		
Temperature			X		

A series of multiple regression models were built using a stepwise process from a priori assumptions based on the hypotheses. Roof type and area were assumed to be important factors determining invertebrate diversity, and were always included in the initial models. The connectivity measures were assumed to be independent as they were measuring different aspects of isolation. All connectivity measures were included in the initial models. Stepwise elimination of variables lead to the

selection of one or two connectivity dimensions per model. Elimination of area and roof type dimensions were also trialled in that order. The top three models for each invertebrate community response measure were then selected using the Akaike Information Criterion (AIC) (Akaike 1973). These regression models were then used to create a series of regression trees. Regression trees are useful in determining important thresholds for explanatory variables, by splitting the data into groups that minimise the error within each group. These thresholds can be used to inform best practices for green roof design. Regression trees were limited to a maximum of three splits, with at least two rooftops per node. This was done for ease of interpretation and to prevent overfitting. All regression trees were run with 999 permutations. Marginal tests suggested that bare and green roofs would have different thresholds. Consequently, separate regression trees were made for bare and green roofs. Similarly, the impact of structural diversity, percentage of green cover and temperature were analysed for each roof type separately using linear regression models.

Compositional differences were assessed using a multivariate perMANOVA method in PRIMER using the PERMANOVA+ extension (PERMANOVA+ version 1.0.2, Anderson 2001). Three separate compositional models were created: for taxon level, morphospecies level and for mobility groups. Models were run for 999 permutations. To understand the taxon groups that were driving differences in composition, a SIMPER analysis was performed in PRIMER (Clarke 1993). For this analysis, continuous variables had to be simplified into categories. A height threshold of 7.5 stories was taken to distinguish high from low rooftops after exploration with single factor regression trees. All other analyses were performed using R for Windows 8 (ver. 3.2.0, R Core Team 2013), and associated packages: *vegan* 2.0-10 (Oksanen *et al.* 2013), *rpart* 4.1-0 (Therneau, Atkinson & Ripley 2012), *MASS* (Venables & Ripley 2002), and *plotrix* 3.5-5 (Lemon 2006). To test for differences in the variability of composition between green and bare roofs, the multivariate analogue of Levene's test for homogeneity of variances (Anderson 2006) was used, and run with 999 permutations.

3. RESULTS

3.1. Green versus bare comparisons

Over the study period, a total of 9736 individuals were captured. 8470 (87%) were found on the 13 green roof (GR) sites and 1266 (13%) were found on the 11 bare roof (BR) sites. Almost all specimens (9711 or 99%) were able to be identified into 17 distinct taxon level groups (**Fig. 5**). Six taxa (Amphipoda, Annelida, Blattodea, Gastropoda, Isopoda, Orthoptera) were only found on green roofs. Bare roofs contained a subset of the taxon groups found on green roofs, but at a significantly lower abundance (ANOVA: $F=17.7$, $d.f.=1$, $n=24$, $p=0.0003$, **Fig. 6a**). The majority of taxon groups on both green and bare roofs were flighted insects (**Fig. 5a**). Non-insect groups represented included arachnids, gastropods and annelids (**Fig. 5**). Hemiptera, followed by Collembola were the most abundant taxa found in the traps, making up 33 and 26% of all specimen, respectively (**Fig. 5**).

Almost all orders present on both rooftops were more abundant on green roofs (**Fig. 5a**). The exceptions were the rarer orders of Psocoptera and Neuroptera which were present either more on bare roofs or equally on both roof types. Six spider families were collected: Desidae, Linyphiidae, Clubionidae, Thomisidae, Araneidae, Theridiidae (**Table 2**). Of these, Thomisidae and Linyphiidae were only found on bare rooftops. All other families had representatives on both roof types (**Table 2**).

Although significantly less abundant overall (ANOVA: $F=8.51$, $d.f.=1$, $n=23$, $p=0.008$, **Fig. 6d**), Hymenoptera were proportionally more abundant on bare roofs (**Fig. 5b**). A total of 129 morphospecies were identified from 1349 (99% of the total) Hymenoptera specimen. The majority of Hymenoptera morphospecies were represented by only one or two individuals. Green roofs contained more rare (34 GR singletons, 29 BR singletons) and unique (72 compared to 23) morphospecies than bare roofs.

Invertebrate richness was up to two times higher on green roofs at both the taxon (ANOVA: $F=17.87$, $d.f.=1$, $n=24$, $p=0.0004$, **Fig. 6b**) and morphospecies level (ANOVA: $F=2.86$, $d.f.=1$, $d.f.=1$, $n=24$, $p=0.1$, **Fig. 6e**). Similarly, invertebrate diversity tended to be higher on green roofs at the taxon level (ANOVA: $F=1.85$, $d.f.=1$, $n=24$, $p=0.2$, **Fig. 6c**). Morphospecies diversity was the same on both roof types (ANOVA: $F=0.27$, $d.f.=1$, $n=23$, $p=0.6$).

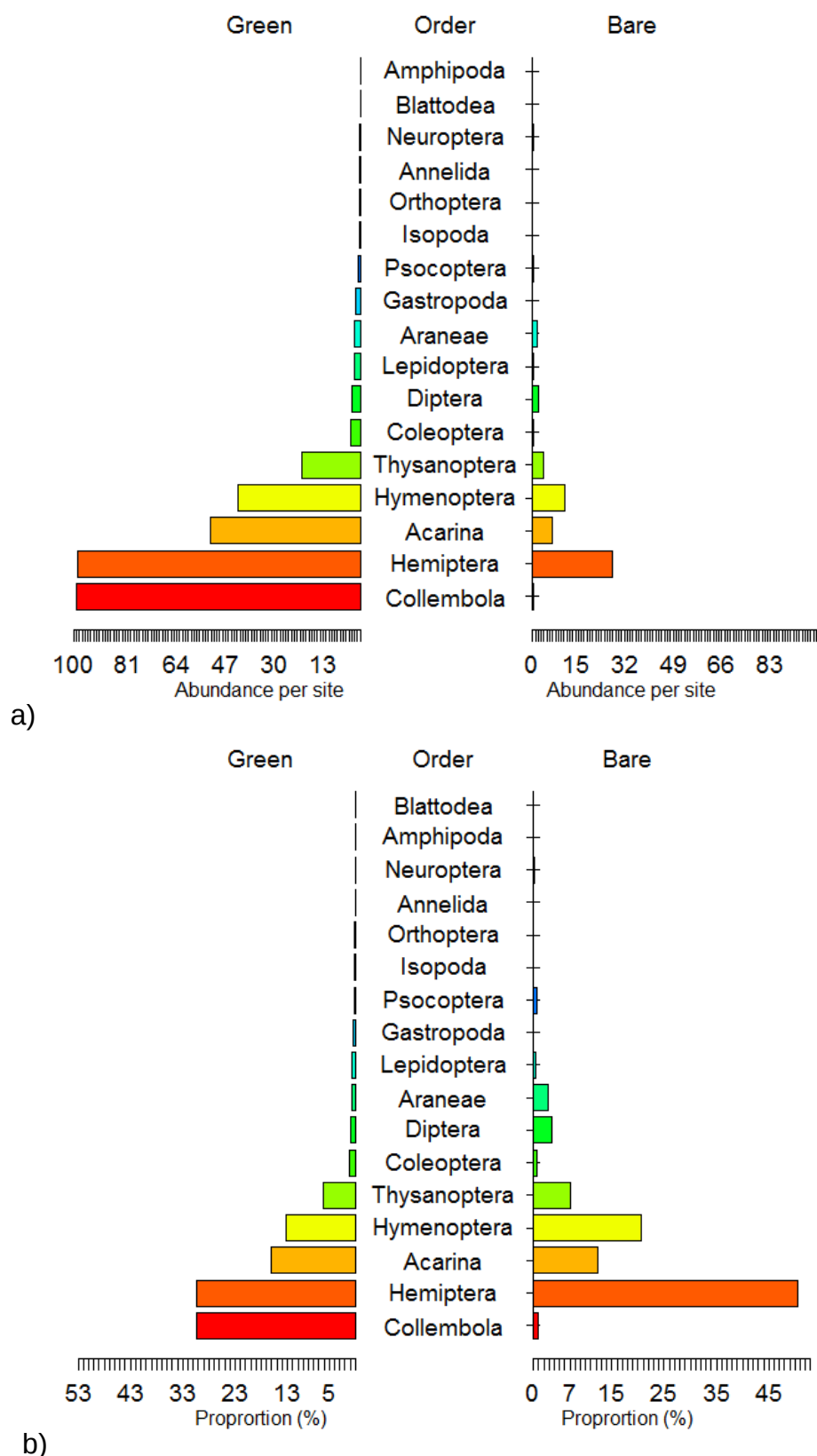


Fig. 5. Summary of taxa on green and bare roofs.

A total of 17 higher taxon groups were caught which differed in their a) total abundance per site and b) the proportional dominance per site, on green and bare roofs. Blattodea and Amphipoda were only represented by a single individual on a single green roof site, and the abundance is too low to be shown accurately here. Psocoptera were also present on green roofs, but in very low numbers.

Green roofs have significantly different invertebrate community composition compared to bare roofs at both the taxon (Pseudo-F=2.23, d.f. =1, n=24, p=0.04, **Fig. 7a**) and morphospecies level (Pseudo-F=1.63, d.f.=1, n=23, p=0.001, **Fig. 7b**). Bare roofs have more homogenous assemblages (have a smaller between-site variation in composition) at the morphospecies level (Pseudo-F=6.8, p=0.016, d.f.=1, n=23, **Fig. 7b**), but not at higher taxon levels (Pseudo-F=0.006, d.f. =1, n=24, p=0.9, **Fig. 7a**). Roof type differences at the taxon level were driven by higher abundances of Psocoptera, Diptera and Araneae on bare roofs (**Table 4**), rather than the appearance of unique taxon groups on green roofs.

Taxa unique to green roofs tended to be obligate soil-dwelling biota such as worms (Annelida), or plant-feeders such as grasshoppers (Orthoptera). Similarly, the soil dwelling Collembola were (rarely) found on bare roofs, but were dominant on green roofs (**Fig. 5a**). Not all plant or soil dwelling taxa were restricted to green roofs, with Hemipteran specimen dominant on both green and bare rooftops (**Fig. 5b**). With the exception of the arachnids, non-insect groups were only found on green roofs. Acarina (mites) were more abundant on green roofs (**Fig. 5a**), but made up a similar proportion of the invertebrate community on both roof types (**Fig. 5b**). Spiders (order: Araneae) and flies (order: Diptera) were proportionally more abundant on bare roofs (**Fig. 5b**), but had a higher total abundance on green roofs (**Fig. 5a**). Insect orders with the highest pollinator representatives (Lepidoptera, Hymenoptera, Thysanoptera, Diptera and Coleoptera) were more abundant on the green roofs although Diptera were unexpectedly low (**Fig. 5a**).

Considering the mobility of the taxa sampled from both roof types revealed a stark dichotomy between invertebrates on green and bare roofs (Pseudo-F=3.32, d.f.=1, n= 24, p=0.03, **Fig. 7c**). Mobility analysis showed differences in composition were driven by a higher prevalence and diversity of low mobility individuals on green roofs, including larger abundances of larval forms (**Table 4**). Conversely, bare roofs tended to contain a higher abundance of high mobility individuals. This trend was present both when comparing between and within taxon groups. For example, Diptera (for which only flighted individuals were captured) were more prevalent on bare roofs, while low mobility groups such as Acarina were more prevalent on green roofs (**Table 4**). Similarly, differences in roof type composition were driven by the presence of wingless Psocoptera on green roofs, while winged Psocoptera

were more abundant on bare roofs (**Table 4**). Weak ballooning, and webless spiders (Family: Salticidae) were also more abundant on green roofs (**Table 2**).

Increasing the percent of green cover on green roofs did not significantly change abundance ($p>0.8$), diversity ($p>0.4$) or richness ($p>0.3$) of invertebrates at either the taxon or morphospecies level (**Fig. 8**). However, green roofs were found to be significantly more structurally diverse ($F=38.9$, $d.f.=1$, $p<0.00001$, **Fig. 6g**) than bare roofs. Structural diversity had a measurable impact on the invertebrate community within each roof type, but the strength and direction of this relationship depended on the community measure. Structural diversity significantly increased Hymenoptera abundance ($\text{adj.}R^2=0.24$, $p=0.09$, **Fig. 9d**), and richness ($\text{adj.}R^2=0.16$, $p=0.14$, **Fig. 9e**) on bare roofs, but not green roofs ($p>0.7$, **Fig. 9**). The relationship between taxon level abundance and structural diversity was entirely driven by roof type differences with no significant impact of structural diversity within bare or green roofs alone ($p>0.35$, **Fig. 9a**). Bare roof taxon abundance tended to decrease with increasing structural diversity ($\text{adj.}R^2=-0.11$, $p=0.35$, **Fig. 9a**). Similarly, taxon richness was negatively associated with structural diversity on bare roofs ($\text{adj.}R^2=0.12$, $p=0.16$), but positively associated with structural diversity on green roofs ($\text{adj.}R^2=0.09$, $p=0.16$, **Fig. 9b**). Neither taxon ($\text{adj.}R^2=-0.02$, $p=0.5$, **Fig. 9c**), nor Hymenoptera diversity ($\text{adj.}R^2=-0.04$, $p=0.8$, **Fig 9f**) were influenced by with structural diversity within either roof type.

There was also no significant difference in the average temperature on bare and green rooftops ($F=1.01$, $p=0.35$, **Fig. 6h**). However, green roofs appeared to have lower variance in average temperature across sites (**Fig. 6h**), and maintained lower temperatures on taller buildings (**Fig. 14g**). Similarly, there was no significant correlations between average temperature and invertebrate abundance or richness at the taxon ($p>0.3$) or morphospecies level ($p>0.4$), though there was a slight trend for taxon diversity to increase at warmer average temperatures ($p=0.2$, **Fig. 10**). Hotter average temperatures on bare roofs tended to negatively affect Hymenoptera abundance, richness and diversity (**Fig. 10g**).

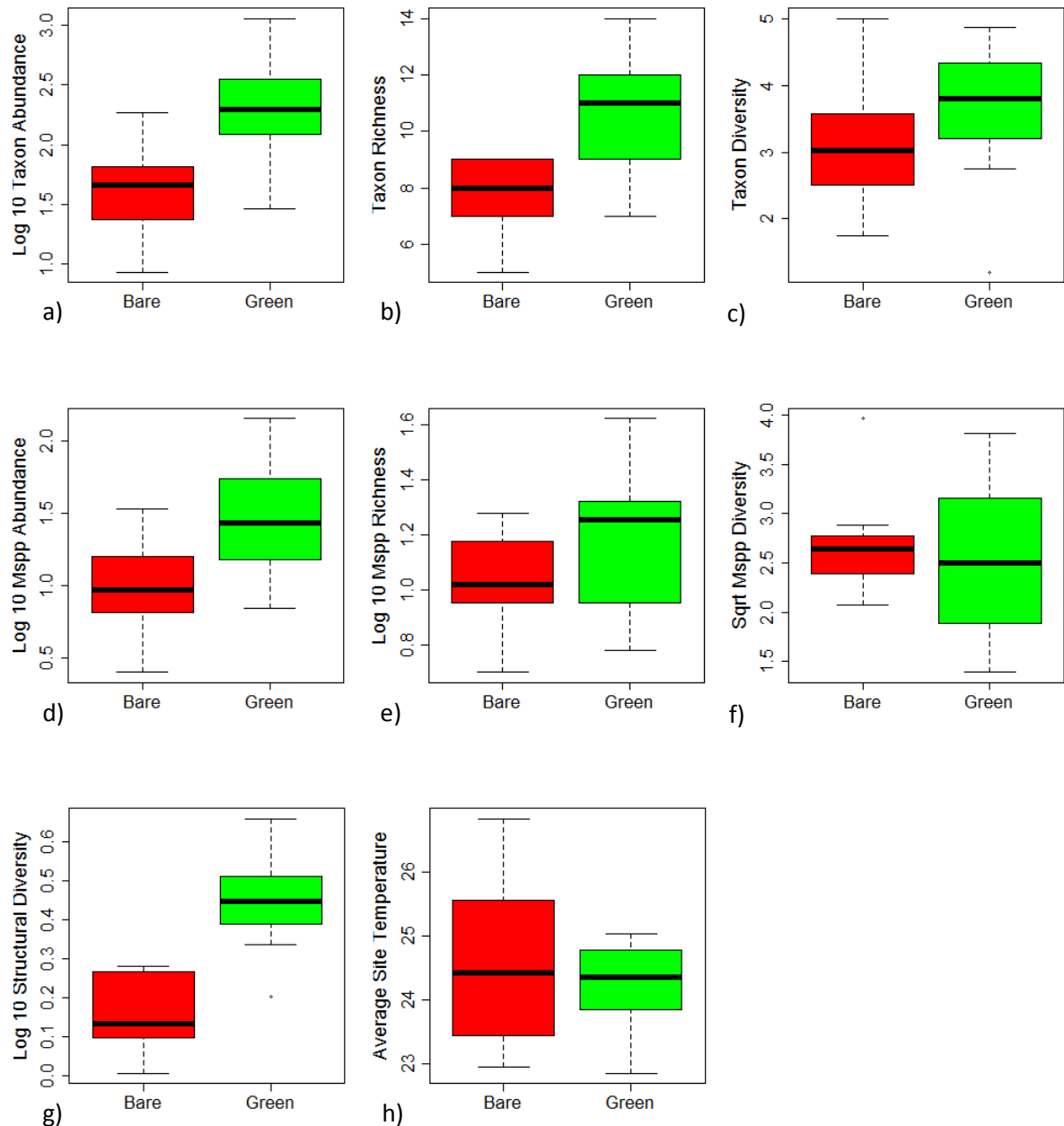
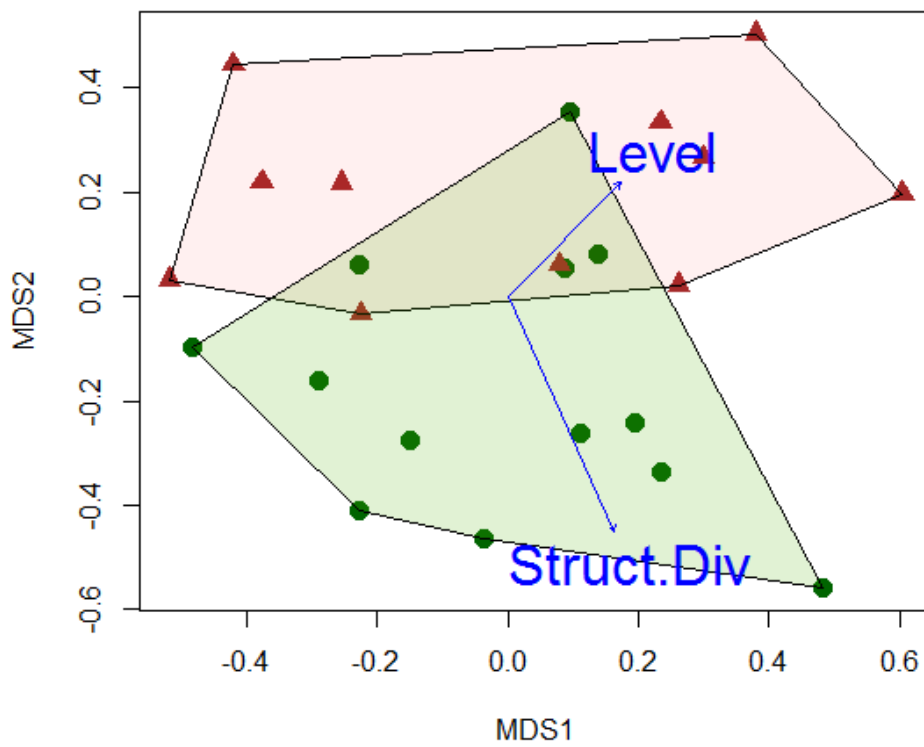


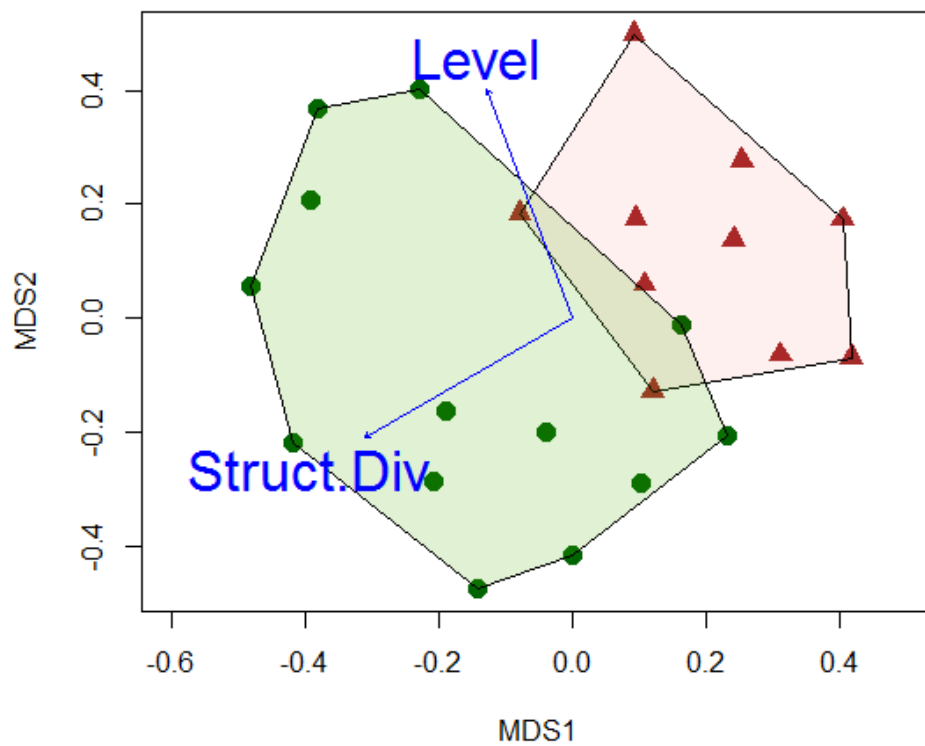
Fig. 6. Marginal effects of roof type.

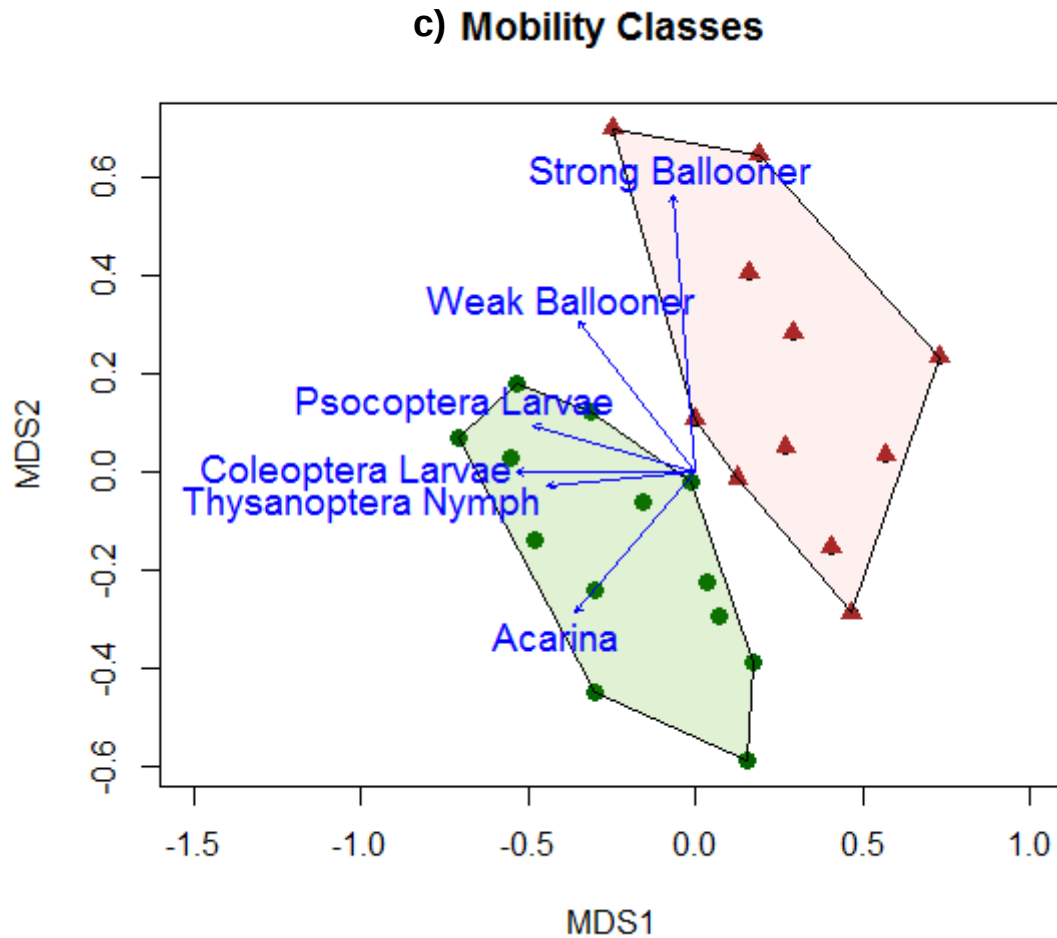
Roof type significantly impacted invertebrate richness, abundance and diversity at both the taxon (a-c) and morphospecies level (d-f). Structural diversity was higher on green roofs compared to bare roofs (g), but there was no difference in average site temperature (h). Sqrt = square root transformation, Mspp = Hymenoptera morphospecies, Taxon = taxon level (class or order) analysis.

a) Taxon Composition



b) Morphospecies Composition





c)

Fig. 7. Invertebrate composition MDA plots.

Composition of invertebrates on bare and green roofs at the a) taxon and b) morphospecies level, as well as for c) mobility classes. The first two axes of the MDS plot are shown. Points which are closer together are more similar in invertebrate composition. Polygons delineate the boundary containing all green roof (●) or bare roof (▲) sites. Biplots show the major variables contributing to differences in composition.

Table 4 . SIMPER analysis results.

The top five groups contributing to differences in invertebrate community composition on a) bare versus green roofs, b) low vs high green roofs, and c) low vs high bare roofs. A threshold of 7.5 stories was taken to distinguish low and high roof heights. The relative contribution to that difference (%) and the factor level associated with the highest abundance are also given. Factor levels: BR = bare roof, GR = green roof, HG = green roofs above 7.5 stories, LG= green roofs shorter than 7.5 stories, HB = bare roofs above 7.5 stories, LB= bare roofs shorter than 7.5 stories

a) Bare vs Green

	Taxon Group	% Contribution	Higher Abundance:	Mobility Class	% Contribution	Higher Abundance:
1	Psocoptera	21	BR	Psocoptera Larvae	13.6	GR
2	Diptera	18	BR	Diptera	11.3	BR
3	Araneae	12.7	BR	Winged Hemiptera	10.6	BR
4	Acarina	6.3	GR	Strong Ballooner	8.44	BR
5	Neuroptera	6.2	GR	Weak Ballooner	6.68	BR

b) Height – Green Roofs

	Mobility Class	% Contribution	Higher Abundance:	Mobility Class	% Contribution	Higher Abundance:
1	Psocoptera Larvae	21.06	HG	Strong Ballooner	21.45	HB
2	Diptera	9.98	LG	Weak Ballooner	12.48	HB
3	Winged Hemiptera	6.54	HG	Diptera	11.82	LB
4	Winged Hymenoptera	6.32	HG	Psocoptera Larvae	11.05	LB
5	Coleoptera Larvae	5.25	HG	Winged Hemiptera	9.36	LB

c) Height – Bare Roofs

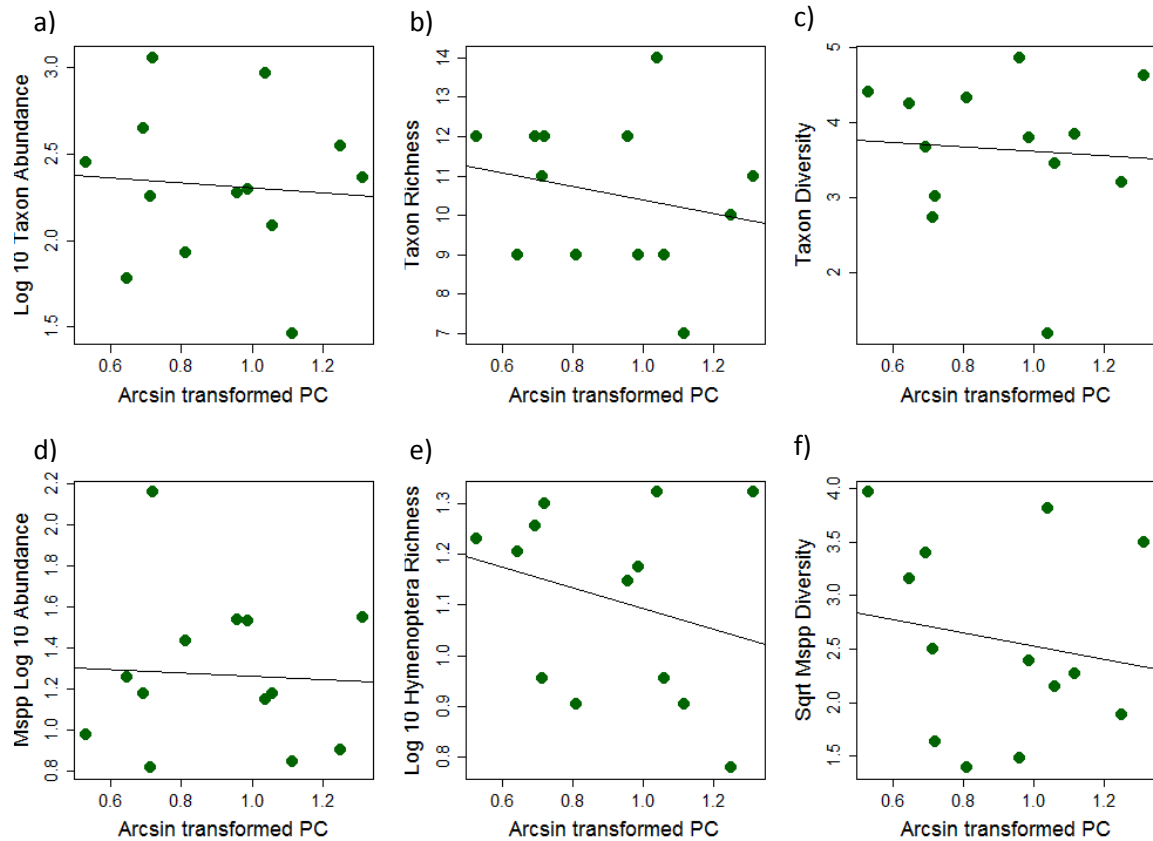


Fig. 8. The impact of percent cover on green roofs.

The change in abundance (a,d), richness (b,e), and diversity (c,f) of invertebrates in response to changes in vegetation cover on green roofs (measured as percentages). Each point is a separate green roof site. Trends are indicated by the line of best fit (black line), but none are significant. Sqrt = square root transformation, Msp = Hymenoptera morphospecies, Taxon = taxon level (class or order) analysis.

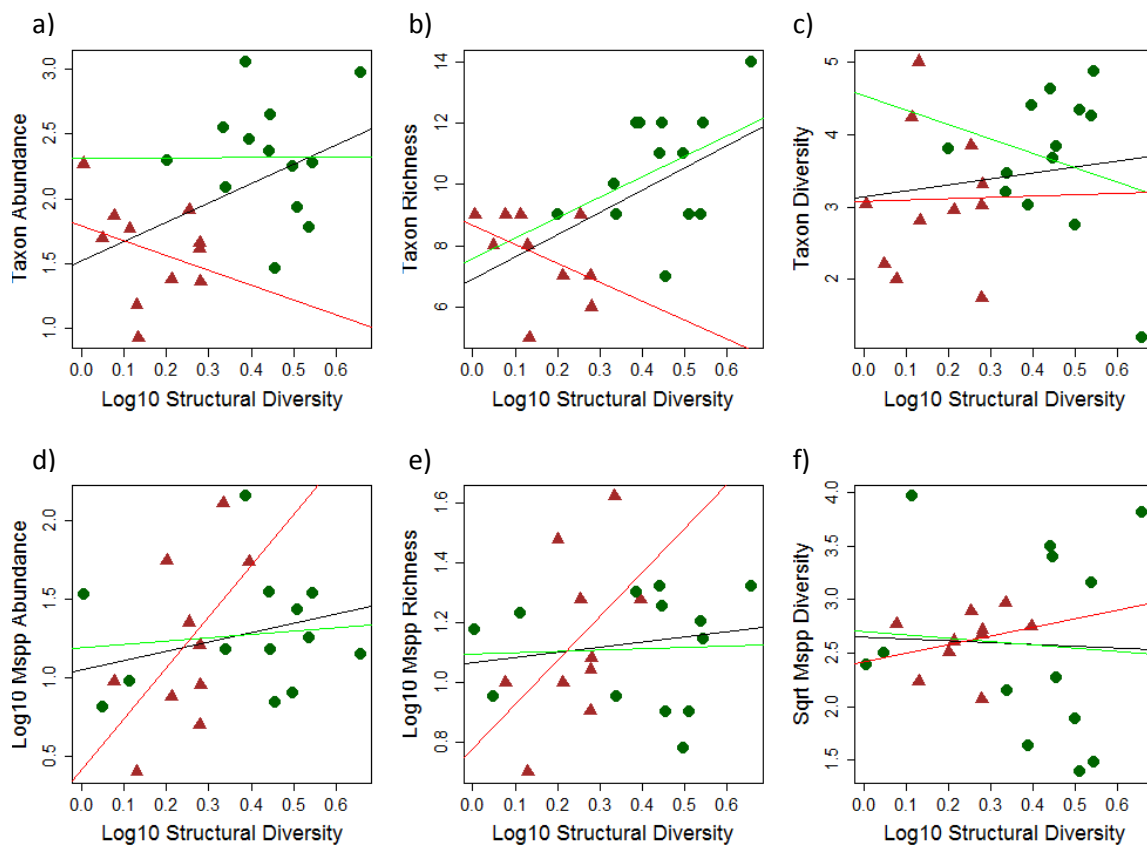


Fig. 9. Relationship between structural diversity and invertebrate responses

The change in abundance (a,d), richness (b,e), and diversity (c,f) of invertebrates in response to structural complexity on rooftops. Structural complexity on green roofs (●) was comprised of both changes in vegetation type, and inclusion of man-made structural components. Structure on bare roofs (▲) was primarily from machinery, or other man-made structures. Overall (black line), structural diversity positively impacted the invertebrate community. The magnitude and direction of invertebrate responses to structural complexity differed on bare (red line), and green roofs (green line). Sqrt = square root transformation, Mspp = Hymenoptera morphospecies, Taxon = taxon level (class or order) analysis.

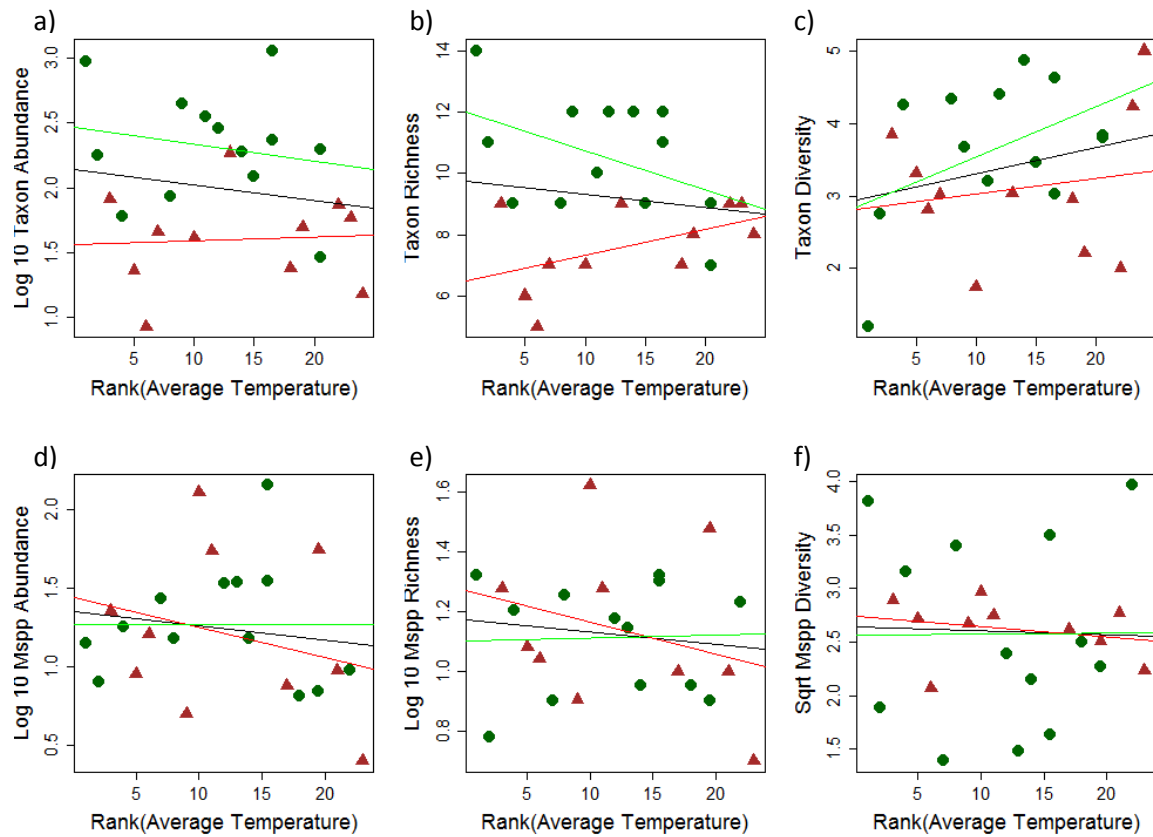


Fig. 10. Impacts of temperature changes on invertebrate abundance, richness and diversity

The change in abundance (a,d), richness (b,e), and diversity (c,f) of invertebrates in response to average site temperature on green (●) and bare (▲) roof sites. Average site temperature was taken as the average of hourly temperatures over both sampling events. Overall (black line), temperature had no significant impact on the invertebrate community. The magnitude and direction of invertebrate responses to temperature differed on bare (red line), and green roofs (green line). Sqrt = square root transformation, Mspp = Hymenoptera morphospecies, Taxon = taxon level (class or order) analysis.

3.2. Roof size and landscape context

Apart from roof type, regression models showed a significant influence of total roof area and some measure of connectivity on taxon richness, abundance and diversity (**Table 5**). The relevant measure(s) of connectivity differed for each invertebrate community response. A similar trend was present in the morphospecies data, with the exception of morphospecies diversity. Morphospecies diversity was unable to be reliably related to any of the explanatory variables ($p > 0.4$, **Table 5**). Invertebrate composition was largely a factor of roof type and connectivity, and was not impacted by roof area (**Table 5, Fig. 7**). The optimal model (as measured by AIC) for Hymenoptera richness and abundance were simpler than those for the taxon level (**Table 5**). In general, taxon richness and abundance was more strongly influenced by roof type than area or connectivity. A similar trend was found for Hymenoptera richness and taxon diversity, but connectivity was relatively more important than area. Contrastingly, Hymenoptera richness was more strongly influenced by roof area and connectivity rather than roof type.

Larger rooftops had a significantly higher taxon richness (adj.R²=0.19, d.f. =1,22, n=24, $p=0.02$, **Fig. 11b**), and tended to have a greater abundance (adj.R²=0.09, d.f. =1,22, n=24, $p=0.08$, **Fig. 11a**) and lower diversity (adj.R²=0.04, d.f.=1,22, n=24, $p<0.2$, **Fig. 11c**) of taxa, regardless of roof type. Similar trends were present for Hymenoptera morphospecies, but this appeared to be largely driven by changes on bare roofs (**Fig. 11**). Richness and abundance of higher taxa is maximised on green roofs that are larger than 490 m² (**Fig. S1b,f**). A similar threshold (482 m²) is present for taxon diversity on bare roofs, but smaller roofs are more diverse (**Fig. S1i**). A maximum taxon diversity is actually achieved at a moderate roof area (between 250 – 482 m²).

The roof area threshold for maximising Hymenoptera richness on bare roofs was dependant on the connectivity of the landscape. Roofs that have closer ground habitats require substantially larger roof area thresholds. Similarly, having a roof larger than 447 m² significantly increased taxon abundance, but only for isolated bare roofs (nearest neighbour >47 m, **Fig. S1e**).

The amount of 'green' in the landscape (measured by NDVI) was the most important connectivity measure overall (**Table 5**), but the impact of connectivity

varied depending on roof type (**Fig. S1**) and there was a significant correlation between the NDVI and nearest neighbour distance ($\text{adj.R}^2=0.37$, d.f. =1,22, n=24, $p<0.001$). Taxon richness ($\text{adj.R}^2=0.03$, d.f. =1,22, n=24, $p=0.2$, **Fig. 13b**), and abundance ($\text{adj.R}^2=0.16$, d.f. =1,22, n=24, $p=0.03$, **Fig. 13a**), as well as morphospecies richness ($\text{adj.R}^2=0.25$, d.f. =1,22, n=24, $p=0.008$, **Fig. 13e**) and abundance ($\text{adj.R}^2=0.18$, d.f. =1,22, n=24, $p=0.03$, **Fig. 13f**) increased with increasing NDVI in the 200m surrounding the roof. These trends were strongly driven by changes in bare roofs. There was no significant impact of NDVI on taxon diversity ($F=6.5$, d.f.=1,22, n=24, $p=0.8$, **Fig. 13c**). Taxon diversity appeared to increase on more isolated green rooftops i.e. those with distant neighbours ($\text{adj.R}^2=0.05$, d.f.=1,11, n=13, $p=0.16$, **Fig. 12c**). Bare roofs showed a similar increase in taxon diversity with increasing neighbour distance ($\text{adj.R}^2=0.12$, d.f.=1,8, n=11, $p=0.16$, **Fig. 12c**), and building height ($\text{adj.R}^2=0.36$, d.f.=1,8, n=11, $p=0.03$, **Fig. 14c**). The distance to the nearest neighbour was negatively correlated with taxon level abundance ($\text{adj.R}^2=0.2$, d.f.=1,22, n=24, $p=0.02$, **Fig. 12a**) and richness ($\text{adj.R}^2=0.13$, d.f.=1,22, n=24, $p=0.05$, **Fig. 12b**) for both bare and green roofs. A similar negative correlation was found for morphospecies abundance ($\text{adj.R}^2=0.05$, d.f.=1,21, n=23, $p=0.15$, **Fig. 12d**) and richness ($\text{adj.R}^2=0.13$, d.f. =1,21, n=23, $p=0.05$, **Fig. 12e**), but this was only true for bare rooftops. Taxon abundance was negatively correlated with building height ($\text{adj.R}^2=0.08$, d.f. =1,22, n=24, $p=0.09$, **Fig. 14a**), but this was not true for morphospecies ($\text{adj.R}^2=-0.01$, d.f. =1,21, n=23, $p>0.4$, **Fig. 14d**). There was a trend for decreased morphospecies richness on taller buildings ($\text{adj.R}^2=0.02$, d.f. =1,21, n=23, $p=0.2$, **Fig. 14e**), but not at the taxon level ($\text{adj.R}^2=0.02$, d.f. =1,22, n=24, $p=0.3$, **Fig. 14b**). Both abundance and richness trends with building height appear to be driven by changes on bare roofs (**Fig. 14**). Similarly, there was a trend for increased average temperatures on taller bare roofs ($\text{adj.R}^2=0.08$, d.f. =1,8, n=11, $p=0.2$, **Fig. 14g**), but not green roofs ($\text{adj.R}^2= -0.05$, d.f. =1,11, n=13, $p=0.5$, **Fig. 14g**).

The important thresholds for each of the connectivity measures were dependant on the invertebrate response, interactions with other connectivity measures, roof type, and in some cases the roof area (**Fig. S1**). For example, a higher landscape NDVI increased Hymenoptera abundance for bare roofs that have nearby ground habitats, but decreased Hymenoptera abundance on more isolated bare roofs. In

either case, Hymenoptera abundance is maximised on bare roofs which have ground habitat patches within a distance of 147 m. Bare roofs that were isolated (NDVI is low), show an increase in Hymenoptera diversity when the building height is low (<2.5 stories). A similar trend was seen on isolated green roofs (distant neighbours) for taxon diversity, but the building height threshold is lower (1.5 stories, **Fig. S1**). Oppositely, taxon richness on isolated bare roofs (nearest neighbour >47 m) is higher when the building is tall (>11.5 m). Only two sites were taller than this, and one of these (Central Park) contained numerous green walls leading to the green roof. Hymenoptera diversity and abundance is higher on green roofs with closer neighbours (<127 m). Similarly, taxon richness and abundance is higher on bare roofs which have ground habitat patches within 47 m, and Hymenoptera richness is greater on bare roofs with ground habitat patches within 106 m. Tall green roofs (>5.5 stories) with close ground habitats (<127 m) have a higher Hymenoptera diversity than lower roofs. For green roofs with larger roof areas, a lower threshold of NDVI is necessary to obtain the maximum predicted taxon abundance (**Fig. S1**).

Building height was the most important connectivity measure that influenced invertebrate composition. There was a significant difference in composition of both higher taxa (PERMANOVA: Pseudo-F=2.2, d.f.=1,22, n=24, $p<0.05$, **Fig. 7a**) and morphospecies (PERMANOVA: Pseudo-F=1.3, d.f.=1,22, n=24, $p<0.01$, **Fig. 7b**). This was the case for both bare and green roof communities. Given a height threshold of 7.5 stories, bare roof composition differences were driven by the relatively higher prevalence of spiders (order: Araneidae), and the relatively lower prevalence of Diptera or Psocoptera individuals on tall roofs compared to shorter roofs. Contrastingly, green roof composition differences were driven by a higher prevalence of Diptera and Psocoptera individuals on tall roofs. Poor mobility taxa, such as worms (Class: Oligochaeta), were completely absent or in low abundance on taller rooftops (**Table 4**). There was also a higher abundance of larvae on lower rooftops. High mobility taxa, such as ballooning spiders, were more prevalent on taller bare roofs than shorter roofs (**Table 4**). This effect was stronger for bare roofs compared to green roofs. Unlike the taxon level composition, morphospecies composition was influenced by landscape connectivity (**Table 5**), with some morphospecies only occurring on very isolated rooftops.

Table 5. Multiple regression models.

Only the top three alternative models (as measured by AIC) are reported for each invertebrate community response at a) the taxon level, and b) the morphospecies level. For a full breakdown of model selection see **Table S2 and S3**.

a) Taxon level analyses

	Taxon Richness ~	R ²	p	AIC
1	5.6±1.3 + 2.6±0.6 Green Roof + 1.2±0.4 log ₁₀ (Area) - 0.07±0.04 Neighbour	62 %	0.00005	18.5
2	3.2±1.4 + 2.5±0.6 Green Roof + 1.5±0.4 log ₁₀ (Area) + 7.6±5.5 NDVI_200	60 %	0.00008	19.6
3	5.6±1.4 + 2.6±0.6 Green Roof + 1.2±0.4 log ₁₀ (Area) + 0.04±0.06 rank(Height) - 0.1±0.06 rank(Neighbour)	61 %	0.0002	20.0
	Log ₁₀ (Total Abundance) ~			
1	0.48±0.34 + 0.57±0.15 Green Roof + 0.3±0.11 log ₁₀ (Area) + 3.6±1.3 NDVI_200	61 %	0.00006	-48.2
2	0.82±0.55 + 0.57±0.15 Green Roof + 0.3±0.12 log ₁₀ (Area) + 2.6±1.8 NDVI_200 - 0.01±0.1 rank(Neighbour)	60 %	0.00019	-46.9
3	1.45±0.35 + 0.62±0.15 Green Roof + 0.2±0.11 log ₁₀ (Area) - 0.02±0.01 rank(Neighbour)	58 %	0.00012	-46.5
	Taxon Diversity~			
1	3.39±0.8 + 0.75±0.4 Green Roof + 0.06±0.03 rank(Height) - 0.4±0.3 log ₁₀ (Area)	23 %	0.04	-3.1
2	1.23±0.8 + 0.60±0.4 Green Roof + 0.09±0.03 rank(Height) + 6.3±4.2 NDVI_200	22 %	0.05	-2.6
3	2.37±1.2 + 0.67±0.4 Green Roof + 0.08±0.03 rank(Height) + 4.8±4.3 NDVI_200 - 0.35±0.27 log ₁₀ (Area)	24 %	0.06	-2.6
	Taxon Composition~			
1	Roof Type + Level	17 %	0.19	179.2
2	Level	9 %	0.049	179.4
3	Roof Type	9 %	0.044	179.4

b) Hymenoptera level analyses

	Log10(Hymenoptera Richness) ~	R ²	p	AIC
1	0.56±0.19 + 0.09±0.06 log10(Area) + 2.62±0.7 NDVI_200	35 %	0.006	-76.2
2	0.55±0.19 + 0.09±0.06 log10(Area) + 2.42±0.72 NDVI_200 + 0.09±0.08 Green Roof	37 %	0.008	-75.6
3	0.34±0.27 + 0.11±0.06 log10(Area) + 3.01±0.89 NDVI_200 + 0.09±0.08 Green Roof + 0.13±0.12 rank(Height)	36 %	0.015	-74.6
	Log10(Hymenoptera Abundance) ~			
1	0.67±0.19 + 0.39±0.15 Green Roof + 2.8±1.39 NDVI_200	35 %	0.0005	-45.0
2	0.37±0.38 + 0.38±0.15 Green Roof + 3.1±1.4 NDVI_200 + 0.10±0.11 log10(Area)	35 %	0.011	-44.0
3	0.05±0.52 + 0.38±0.15 Green Roof + 4.1±1.8 NDVI_200 + 0.12±0.12 log10(Area) + 0.013±0.01 rank(Height)	35 %	0.018	-43.4
	Hymenoptera Diversity~			
1	2.35±0.36 + 1.96±2.6 NDVI_200	-2 %	0.47	-15.1
2	2.68±0.22 - 0.15±0.29 Green Roof	-3 %	0.61	-14.8
3	1.84±0.74 + 2.45±2.73 NDVI_200 + 0.17±0.22 log10(Area)	-4 %	0.57	-13.8
	Hymenoptera Composition~			
1	Roof Type	7 %	0.001	194.0
2	Roof Type + Neighbour	13 %	0.001	194.3
3	Roof Type + Level	13 %	0.007	193.3

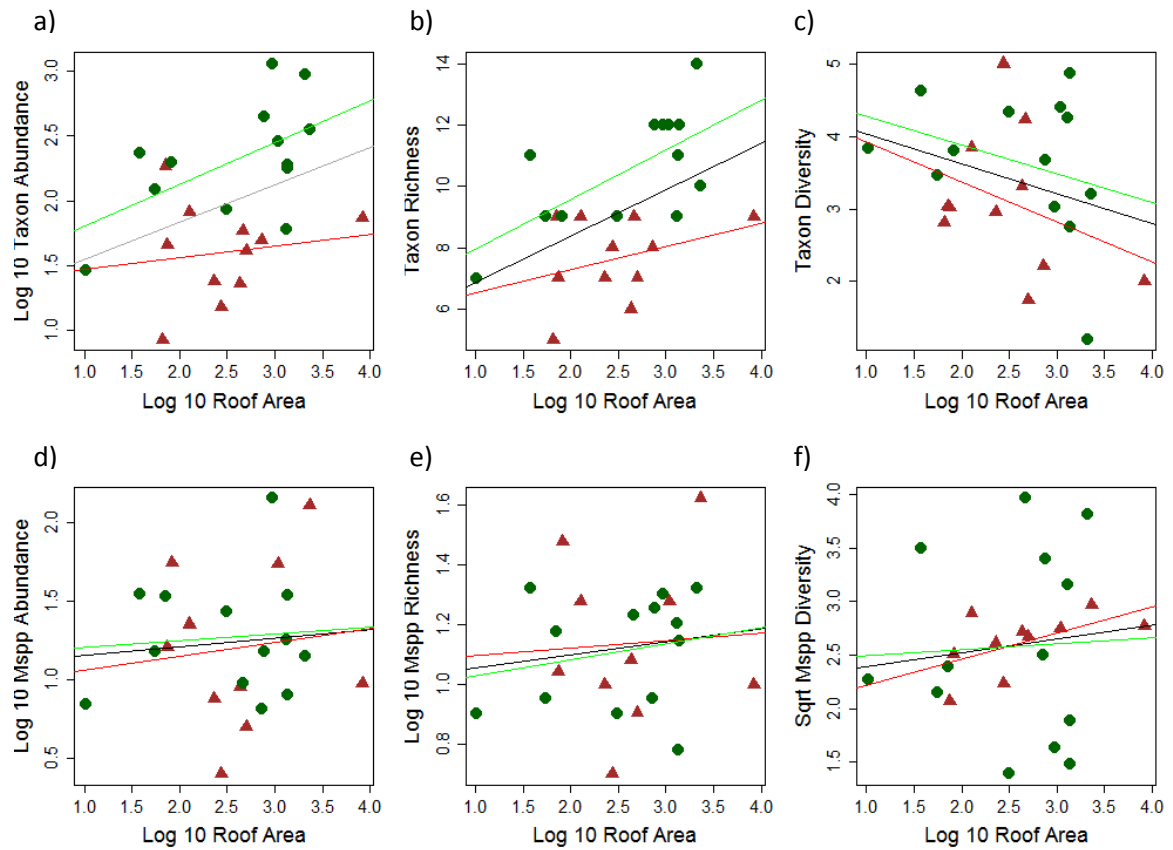


Fig. 11. Main effects of area on each of the invertebrate community response variables.

The change in abundance (a,d), richness (b,e), and diversity (c,f) of invertebrates in response to roof area. Overall (black line), increasing roof area positively impacted the invertebrate community. The magnitude of invertebrate responses to roof area differed on bare (red line), and green roofs (green line). Roof area had a larger effect on green roofs (●), compared to bare roofs (▲). Sqrt = square root transformation, Mspp = Hymenoptera morphospecies, Taxon = taxon level (class or order) analysis.

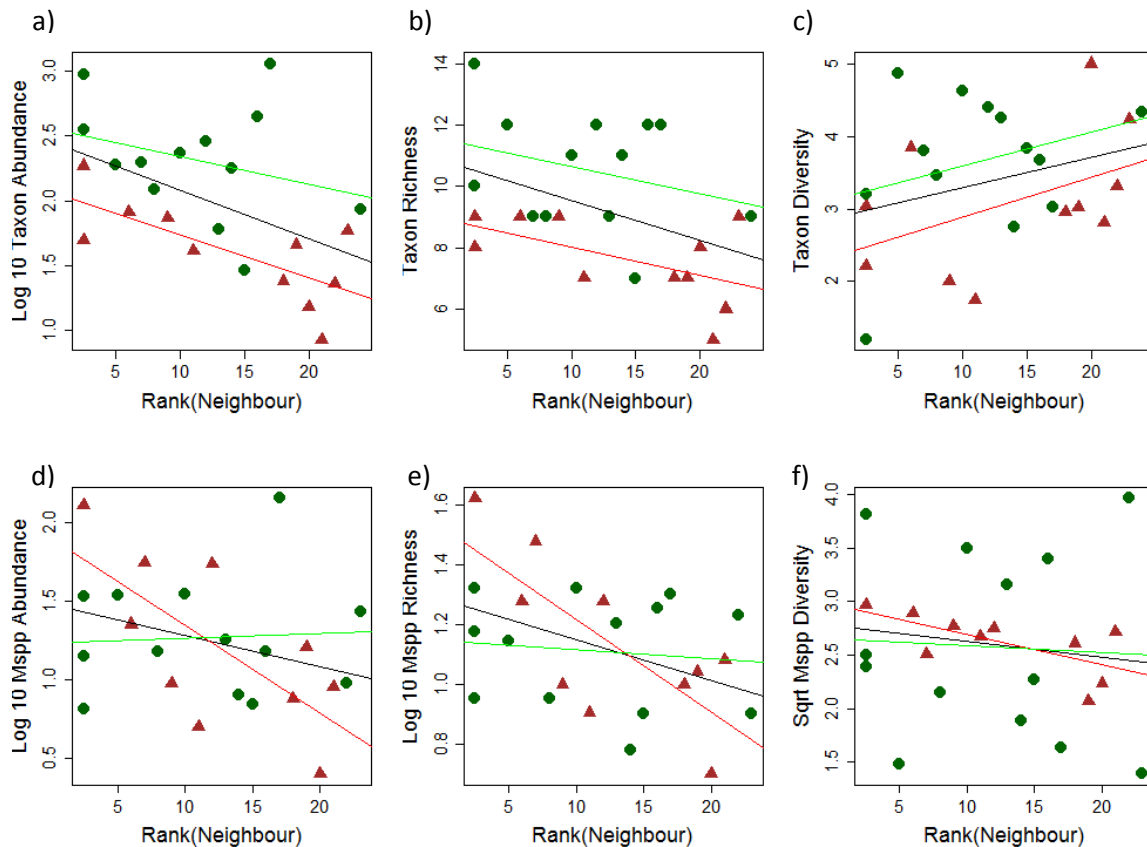


Fig. 12. Impact of landscape connectivity (nearest neighbour distance).

Changes in invertebrate community abundance (a,d), richness (b,e) and diversity (c,f) in response to landscape connectivity. Connectivity is measured as the distance to nearest neighbouring habitat patch (i.e. nearest neighbour), using GIS software. Large habitat patches were identified using a threshold cut off of 0.3 NDVI at 30 m resolution. Overall (black line) increasing landscape connectivity had a positive impact on invertebrate communities. The magnitude of invertebrate responses to landscape connectivity differed on bare (red line), and green roofs (green line). Nearest neighbour distance had a larger effect on bare roof (▲) invertebrate communities compared to green roofs (●).

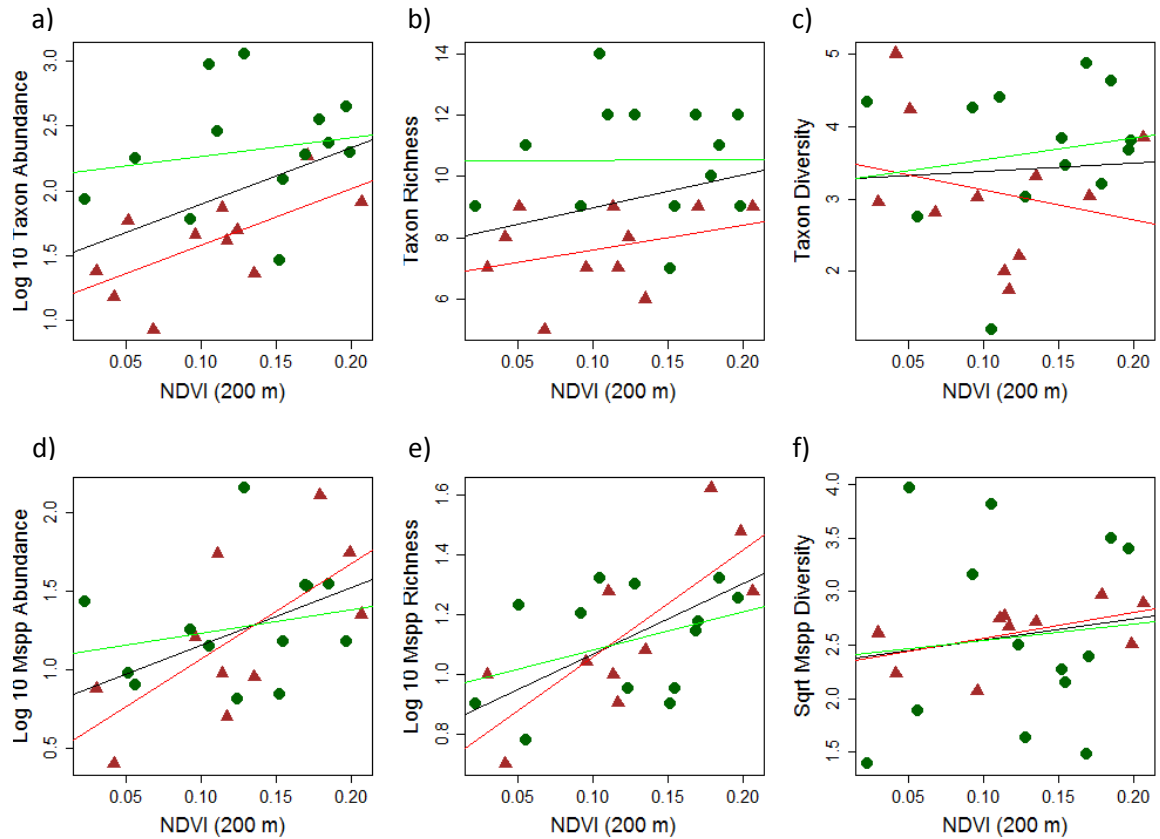


Fig. 13. Impact of the average NDVI in the surrounding 200 m

The change in abundance (a,d), richness (b,e), and diversity (c,f) of invertebrates in response to landscape composition. The percent of green cover in the landscape was approximated using the average NDVI within 200 m of the roof. Overall (black line), increasing NDVI has a positive impact on the invertebrate community. The magnitude and direction of invertebrate responses to temperature differed on bare (red line), and green roofs (green line). The invertebrate community on bare roofs (▲) was more strongly impacted by NDVI than green roof (●) communities. Sqrt = square root transformation, Mspp = Hymenoptera morphospecies, Taxon = taxon level (class or order) analysis.

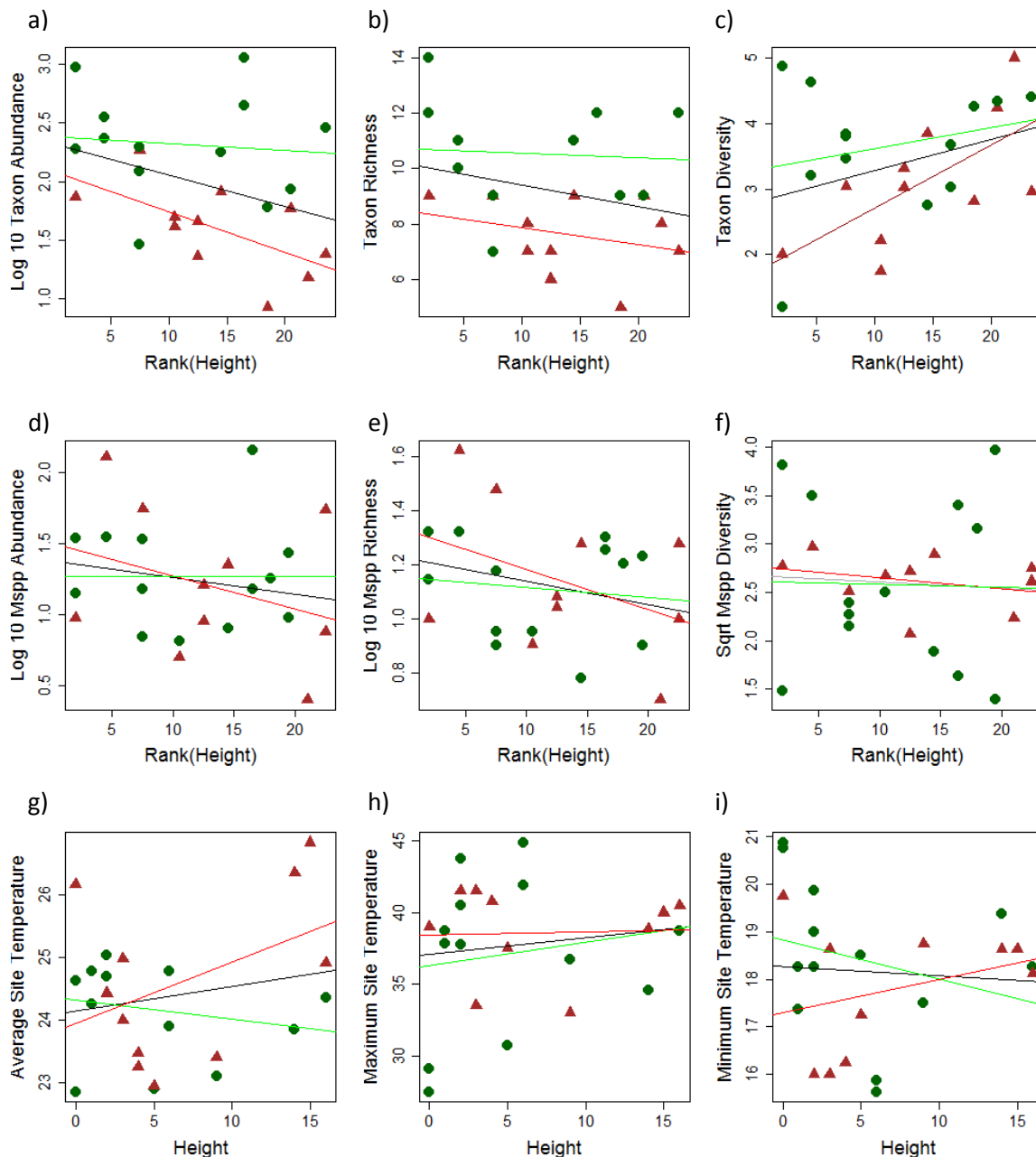


Fig. 14. Impact of height on explanatory and response variables

Changes in invertebrate abundance (a,d), richness (b,e) diversity (c,f) and temperature (g-i) with increasing height (measured as number of stories). Both temperature and height were rank transformed for analysis, but are plotted untransformed here for ease of interpretation. Overall (black line), increasing height had a negative impact on the invertebrate community. There was no significant change in average temperature on taller roofs. The magnitude and direction of invertebrate responses to height differed on bare (red line), and green roofs (green line). Green roofs (●) tended to maintain lower temperatures on taller buildings, whereas average temperature tended to increase with height for bare roofs (▲).

4. DISCUSSION

4.1. Green is better than bare

This study is the first to show quantitatively that green rooftops have added habitat value over conventional bare rooftops. Green roofs host up to three times the number of invertebrates and twice as many invertebrate taxa than bare roofs. Green roofs also contained a number of taxa not found on bare roofs. No taxa were found on bare roofs that were not present on green roofs. The composition differences between green and bare roofs were driven by relative abundances, with bare roofs appearing to have an upper limit of richness which they can support. Differences between bare and green roofs were apparent even at a coarse taxonomic resolution (that of order or class level). This contrasts with Norton *et al.* (2014) who found coarse taxonomic resolution was insufficient to differentiate between bare and vegetated ground. The presence of differences in higher taxa highlights the strength of the impact of vegetation on rooftop invertebrate communities.

Contrastingly, there was no significant increase in the diversity of invertebrates on green roofs. At the taxon level, this may be because of restrictions in the types of taxa able to be caught, and thus maximum diversity. In particular, the yellow colour used in the sampling method creates a bias towards some species of Hymenoptera, to the notable exclusion of others (such as native honeybees which are attracted by blue bowls), and thus constitutes a significant limitation in assessing diversity of invertebrates on rooftops. Alternatively, considering there were strong correlations between roof type and invertebrate richness, a lack of association with diversity may be a result of the high unevenness of roof communities. Indeed, a large number of Hymenoptera morphospecies were singletons, with more singletons appearing on green roofs. This is not uncommon for Hymenoptera collections (Lassau & Hochuli 2005), and makes trends in Hymenoptera diversity difficult to interpret at a community ecology scale (Lassau & Hochuli 2007). Hymenoptera assemblages are more similar across bare roofs, whereas green roofs maintain high between-site variation. As a result, bare roof communities likely have a higher evenness, which may superficially increase the diversity index despite limitations in richness (Jost 2006). More homogenous communities indicate a strong environmental filter preventing colonisation on bare

roofs. As such, bare roofs may provide a peculiar kind of habitat that favours certain taxa. Invertebrate groups that appear to benefit from bare roof spaces are predatory (e.g. spiders) or scavengers (e.g. flies), and may benefit from the influx of transient individuals, or a build-up of wind-blown debris.

The presence, extent, and type of vegetation coverage within natural (Cook-Patton & Bauerle 2012; Nipperess *et al.* 2012) and urban (Norton *et al.* 2014) ground habitats are known to have positive impacts on invertebrate diversity and abundance. For example, Norton *et al.* (2014) found that ground vegetated areas in urban environments hosted more individuals and greater diversity than bare ground covers that were found to be more similar to non-vegetated habitat types such as leaf litter. Similarly, the presence and types of plant species has been shown to alter the richness (Coffman 2007), and composition (Braaker *et al.* 2014) of invertebrates on green roofs and other urban infrastructure (Davies, Simcock & Toft 2010; Norton *et al.* 2014; MacIvor 2015; Madre *et al.* 2015). For example, Madre *et al.* (2015) found more abundant and species rich assemblages of spiders and beetles on vegetated rather than non-vegetated walls. Accordingly, this study shows that the mere provision of vegetation results in an increase in invertebrate abundances in comparison with non-vegetated roofs. Similarly, Davies *et al.* (2010), report a lower abundance of invertebrates on a bare roof reference, but did not quantify this difference, nor further analyse bare roof communities. Contrastingly, MacIvor (2015) showed no impact of vegetation type (including bare roof references) on the richness and abundance of bee species on rooftops. The reason for this contrast may be active attraction of Hymenoptera in response to perceived resource provision, for nesting (MacIvor 2015), or foraging (yellow pans, New 1998).

The influence of vegetation on green roofs is two-fold in that it is likely providing a viable food resource as well as providing suitable microhabitat for shelter and breeding (reviewed in Cook-Patton & Bauerle 2012). In response to the provision of plant resources, most obligate plant-feeding taxa were only found on green roofs. Similarly, the substrate on green roofs was obviously responsible for soil-dwelling biota such as worms (Annelida) and Collembola occurring almost exclusively on green roofs. Unexpectedly, the plant dwelling Hemiptera were dominant on both green and bare roofs. Closer examination revealed Hemiptera on bare roofs were primarily winged adults i.e. the wingless nymphs were

noticeably absent from bare roofs but had strong representation on green roofs. The lack of wingless individuals on bare roofs suggests bare roofs do not support resident populations, and that the traps caught individuals in transit. The high prevalence of nymphs and other wingless individuals on green roofs suggest they not only attract Hemiptera but also sustain resident populations. Overall, green roof invertebrate communities are composed of higher proportions of larvae and low mobility individuals. For example, the abundance of Psocoptera drives differences in composition between bare and green roofs. When examined closer, this is actually driven by a prevalence of larval individuals on green roofs, and winged individuals on bare roofs. Resident populations of invertebrates on green roofs may have wider ecosystem benefits and promote the presence of vertebrate taxa. This presence of pollinators such as Hymenoptera promote plant diversity on green roofs (Ksiazek, Fant & Skogen 2012), and invertebrates such as Collembola provide nutrient cycling and improve water retention (Schrader & Böning 2006). Invertebrates are also a food source for birds and bats (Fernandez-Canero & Gonzalez-Redondo 2010; Pearce & Walters 2012).

Structural complexity provided by a combination of vegetation and soil structure may generate microhabitats which favour different taxa and thus increase invertebrate richness (Schrader & Böning 2006; Schindler, Griffith & Jones 2011; Madre *et al.* 2013). Invertebrate communities have been known to respond to changes in structural complexity of habitats in natural areas (Tomoff 1974; Lassau & Hochuli 2004; Lassau *et al.* 2005a; Lassau & Hochuli 2005), and on green roofs (Madre *et al.* 2013). Accordingly, this research has shown increased invertebrate richness with structural diversity on green roofs. Similarly, bare roofs which overlapped with green roofs in taxon composition, tended to have higher structural complexity in the form of maintenance structures (such as air conditioning units), or different kinds of roof substrates (such as pebbles or corrugation). This structural complexity may be expected to generate microhabitats which invertebrates may respond to in the same way as they do to changes in vegetative structure. While this appears to be true for Hymenoptera morphospecies, taxon level richness was negatively impacted by bare roof structural complexity. Bare roof trends had a very poor fit to the data and may be explained as artefacts of sampling (i.e. yellow pan biases) and the constraints of measuring structural complexity on bare roofs. Yellow pans are an active trapping technique, which are

a visual substitute for floral resources in the environment, and are, therefore, biased towards catching pollinators in search of yellow flowers. On green roofs, there is likely competition between yellow pan traps and actual floral resources, which could lead to Hymenoptera visitation being less sensitive to other structural components of the roof. Visibility of the yellow pans is likely higher on bare roofs, and may attract invertebrates that would otherwise not visit bare roofs, regardless of structural diversity. In addition, it is not well known what components of a bare roof contribute to structural complexity, and the measure of structural complexity used limits the maximum structural complexity that bare roofs can achieve. Yellow pans may also contribute a large structural component of the roof by providing a water source and structure for web building. The use of vacuum sampling enables collection of invertebrates without these biases, and may compliment yellow pans to enable clarification of the important structural components of bare roofs.

4.1.1. How much green is enough?

Although increasing green cover has been shown to increase plant-feeding Hemipteran species on green roofs (Madre *et al.* 2013), I found no impact of increasing green cover above the 30% threshold set by the City of Sydney Council (2014a). Measurement of the percent cover of green does not take into account the quality or structural complexity of the habitat provided. Investigation into the differences in green roof types have shown that variation in vegetation and soil characteristics on a green roof significantly impact the invertebrate community (Jones 2002; Brenneisen 2006; Coffman 2007; MacIvor & Lundholm 2011; Madre *et al.* 2013; Braaker *et al.* 2014). Similarly, age of the roof has been shown to influence the composition of invertebrates (Jones 2002; Braaker *et al.* 2014), and invertebrates are known to fluctuate in abundance throughout the year (Rumble & Gange 2013). The green roof sites in this study varied in structural complexity and age across all levels of percent cover. A small sample size paired with these confounding factors reduced the power to assess the true impact of green cover. Thus, any conclusions about the impact of green cover remain tentative. What these results suggest is that a percent cover of above 30% provides significant habitat value over none at all.

4.2. Green roofs as “Islands in the Sky”

This study demonstrates that invertebrate diversity on green roofs can largely be explained by limitations in immigration and resource provision. The importance of

these processes was inferred from the influence of roof area and isolation on measured trends in invertebrate diversity. Similar principles of island biogeography have been used to explain urban patterns of diversity in plants (Hobbs 1988), birds (Marzluff 2005), and invertebrates (Rodrigues, Brown Jr & Ruszczyk 1993; Helden & Leather 2004; Fattorini 2014). Application of these principles to green roofs is a logical extension of existing frameworks for managing urbanisation impacts in urban areas (Alberti 2010; Ramalho & Hobbs 2012). Similar frameworks for green roofs focus on the impact of local roof variables on biodiversity (Dunnett 2006).

As expected, larger and more well-connected rooftops had a higher abundance and richness of invertebrates. Isolation, as measured by building height, also significantly altered invertebrate composition. Contrary to expectations, invertebrate diversity decreased on larger roofs, and increased with increasing isolation. This latter result is likely a consequence of an increased number of rare (low abundance) taxa, resulting in more uneven communities (Jost 2006). Invertebrate responses varied depending on whether the roof was bare or green. This indicates differences in the dominant processes of immigration and extinction.

4.2.1. How do they get there?

There are two main pathways for invertebrate immigration onto a green roof: natural dispersal or human transfer (**Fig. 1**). Previous studies have found speculative evidence for the accidental transfer of invertebrates onto a green roofs, either in the soil or on plants that are used during construction (Brenneisen 2006). Deliberate transfer of individuals onto green roofs (e.g. placement of bee hives on rooftops) is possible, but was not a factor for the green roofs included in this study. Evidence has also been found for dispersal of individuals from ground habitats onto green roofs (Braaker *et al.* 2014). Bare rooftops are infrequently accessed by humans (usually for maintenance of building equipment) and human activity is unlikely to transfer invertebrates onto the roof in this way. Thus, the occurrence of invertebrates on bare roofs is primarily a result of natural dispersal processes. By comparing green and bare roof assemblages, we can infer the significance of natural versus human-mediated immigration on green roofs, with some caveats. The migration of individuals is a combination of both deterministic and stochastic processes. For example, invertebrates may be actively attracted to a green roof (a deterministic process) or arrive via accidental travel on air currents in the urban environment (a stochastic process). Similarly, yellow pan trapping

techniques are biased towards flighted (i.e. immigrating) individuals (New 1998), and my ability to infer trends based on mobility of invertebrates is limited. There is also some evidence that the trapping method was biased towards small bodied individuals. For example, bumble bees have been known to escape yellow traps (*Kelly Ksiazek, pers. comm.*), and very few large individuals were caught. These sampling biases were present for both roof types and do not prohibit comparison between them.

The results of this study give several lines of evidence that green roofs are colonised primarily by human-transfer. First, connectivity measures (i.e. building height, distance to ground habitats, and NDVI) had a relatively larger influence on invertebrate communities on bare roofs compared to green roofs. For example, building height has a significant influence on the abundance and richness of invertebrates on bare roofs but not green roofs. Similarly, bare roof, but not green roof, invertebrate abundance and richness increases with increasing landscape connectivity as measured by NDVI. There was also a much stronger negative association between Hymenoptera abundance and richness with increasing nearest neighbour distance for bare roofs. Since bare roofs represent a baseline of dispersal, we can conclude that isolation has a very small effect on the appearance of taxa on green roofs. Secondly, green roofs contain a more consistent if not higher representation of less mobile individuals on taller rooftops. Bare roofs, on the other hand, had a lower representation of low mobility individuals on taller rooftops. There is also a higher presence of taxa such as gastropods and annelids present on green roofs, which would be incapable of immigrating without human aid. The rarity of these in the samples is likely as a result of the biases of the trapping method used (New 1998). In addition, several previous studies have showed that green roof composition is peculiar compared to that of nearby ground habitats (Jones 2002; Colla, Willis & Packer 2009; Coffman & Waite 2010; Tonietto *et al.* 2011; Madre *et al.* 2013), which may indicate the influence of chance migration during construction, especially if the plants were not locally sourced. Contrastingly, several studies have shown no compositional differences between green roofs and ground sites (Schrader & Böning 2006; MacIvor & Lundholm 2011; Braaker *et al.* 2014), which suggests that ground habitats can also form source populations for invertebrates on green roofs.

While comparison to ground sites was not possible in this study, limitations on immigration from ground sites can be implied from the influence of connectivity measures on invertebrate abundance and richness. If invertebrates were emigrating from ground habitats onto rooftops, increasing proximity to the rooftop should enable higher rates of movement and thus higher abundance and richness. As expected, this study showed that proximity to ground habitats significantly increased invertebrate abundance and richness, regardless of roof type. However, this was only true at the taxon level. For Hymenoptera, there was only a significant influence of isolation (for all connectivity measures) on bare roofs. Similarly, closer neighbour distances were necessary to maximise taxon level richness and diversity compared to the morphospecies level. As in previous studies (Madre *et al.* 2013; Braaker *et al.* 2014), this indicates the impact of isolation was dependent on the mobility of the taxa. Hymenoptera are highly mobile organisms, and actively disperse to forage, sometimes over distances of several kilometres (Schmidt 1995). As pollinators, Hymenoptera visitation to green roofs is associated with the prevalence of flowering resources (Benvenuti 2014). It is possible that a lack of distance association with green roofs reflects active dispersal of Hymenoptera to utilise the roof. Active dispersal may also explain why some Hymenoptera species were only found on rooftops with distant ground habitats.

Differences in the response of invertebrates to each connectivity measure may be a consequence of geographic scale. Overall, the total amount of greenspace in the landscape was the most important connectivity measure. In natural habitats, NDVI has been used to predict habitat distributions (Leyequien *et al.* 2007), structural complexity (Lassau *et al.* 2005a), and seasonal changes in habitat quality (Wiegand *et al.* 2008). Thus, NDVI takes into account the quality and amount of greenspace surrounding the green roofs, which is not possible using simple distance measures. This may make it a better measure of potential source populations for roof invertebrates, and explain its prevalence in the regression models. Similarly, NDVI has been shown to have strong positive associations with beetle (Lassau *et al.* 2005b), as well as wasp (Lassau & Hochuli 2005; Lassau & Hochuli 2007) diversity.

Of the distance measures used, building height appeared the least frequently in the selected regression models. This is consistent with previous studies have found limited impact of building height on invertebrate diversity (Madre *et al.* 2013)

or composition (Colla, Willis & Packer 2009; MacIvor & Lundholm 2011; Braaker *et al.* 2014) on green roofs. Alternatively, Madre *et al.* (2015) have recently shown that breeding success of solitary bees, as well as overall abundance and diversity is decreased on buildings greater than 5 stories tall. One possible reason for the inconsistency in these results may be interaction of building height with the horizontal distance to the nearest habitat patch (**Fig. 2**). This may occur either in accordance with Pythagorean Theorem, or as an additive of ground and vertical distances, or as an inverse curvilinear relationship (**Fig. 2**). For invertebrates that are capable of dispersing between ground habitat patches, building height may not represent a significant increase in dispersal limitation when habitat patches are close. When ground habitat patches are far, decreasing building height lowers the relative isolation of the roof. Green roofs showed some exceptions to this, where the existence of the Central Park roof site skewed the data such that taller buildings were more diverse (e.g. Hymenoptera Diversity, **Fig. S1**). Central Park has well established green walls on all sides of the building, which may facilitate connectivity of the roof garden with ground level habitats. No studies have investigated the possibility for synergistic effects between green walls and green roofs, and this is an important area for future study. However, Madre *et al.* (2015) have shown the potential for green walls to host a range of taxa.

4.2.2. Can they survive?

The ability of invertebrates to survive on rooftops will be dependent on their resource needs and climatic tolerances (Southwood 1988). For green roofs, provision of resources is expected to increase with habitat area, as a result of increasing biomass and decreases in competition for microhabitats (Cook-Patton & Bauerle 2012). On the other hand, resource provision on bare roofs is likely to be a result of accumulated debris or transiently passing invertebrates, processes which are largely independent of roof area. Accordingly, habitat area, as measured by the total area of the roof, significantly increased the total abundance and richness of invertebrate taxa on green roofs, but not for bare roofs. Taxon diversity was significantly lower on larger roofs of both roof types, possibly because of increased rare taxa causing more uneven communities on larger roofs. Similarly, Madre *et al.* (2013) found invertebrate abundance to increase on larger roofs, but only for Hymenopteran species. In this study, Hymenoptera were less sensitive to total roof area, possibly because they are responding to specific plant resources

rather than total plant biomass (Benvenuti 2014). Similarly, Schindler *et al.* (2011) showed no impact of total roof area on soil communities, but rather an association between invertebrate abundance and green cover.

There is expected to be a strong environmental filter impacting invertebrate survival on rooftops, as there is for plants (Lundholm 2006). Rooftop environments are characterised by strong winds, high levels of radiation and hot temperatures (Lundholm & Richardson 2010). These harsh conditions are likely to be exaggerated on taller rooftops, as is the case with increasing altitude in natural systems (Lomolino 2001). Green roofs have been shown to alter the climatic conditions on rooftops, providing more stable and lower temperatures compared to conventional rooftops (reviewed in Oberndorfer *et al.* 2007). Similarly, studies of green walls show significantly different microhabitat characteristics between bare and vegetated surfaces (Madre *et al.* 2015). Thus, a climatic filter should be more pronounced on bare roofs. This study found no significant difference in temperature between green and bare roofs (**Fig. 6**), and there was no significant change in temperature with height. However, green roofs appeared to have lower variance in average temperature, and maintained lower temperatures on taller buildings. Similarly, there was no significant impact of temperature on invertebrate communities, but hotter temperatures on bare roofs tended to negatively affect Hymenoptera abundance, richness and diversity (**Fig. 10**). Invertebrates on green roofs have been shown to be largely xerothermic (Madre *et al.* 2013) and respond to microhabitat changes as a result of seasonal temperature fluctuations (Rumble & Gange 2013; Benvenuti 2014). It is possible that strong temperature responses were not detected in this study due to measurement of ambient rather than surface temperature. Studies on the thermal properties of green roofs often use membrane surface (Liu & Baskaran 2003) or soil (Simmons *et al.* 2008) temperatures. In addition, temperature is just a single dimension of climatic changes associated with green roofs. Green roofs modify the patterns of solar radiation, soil humidity, and water availability on rooftops (Liu & Baskaran 2003; Simmons *et al.* 2008; Jaffal, Ouldboukhite & Belarbi 2012; Muller *et al.* 2014). Humidity, in particular, is an important component of microhabitat changes (Ashcroft & Gollan 2012), and is known to impact invertebrate richness and diversity in ground habitats (Shochat *et al.* 2004; Buchholz, Rolfsmeier & Schirmel 2013) and on green roofs (Muller *et al.* 2014).

4.3. Management Implications

Green roofs with at least 30% green cover have significant biodiversity benefits compared to conventional bare rooftops. An increase in percent cover above 30% does not significantly increase biodiversity. These findings provide support for the use of a minimum 30% threshold for green cover in the City of Sydney Green Roof Implementation Plan (City of Sydney Council 2014a).

This does not mean that 30% cover is optimal, nor sufficient for green roof design. The size of the roof, and the landscape context are also important factors in enhancing biodiversity outcomes of green roofs. By applying the principles of island biogeography, this study extends current research on the factors influencing invertebrate diversity on green roofs (reviewed in MacIvor & Ksiazek 2015). These findings can be used to generate a hierarchy of management decisions for implementation of green roof policies. That is, green roof implementation strategies should address four questions, in order: 1. Where to build? 2. How big to build? 3. What to build? 4. How to maintain?

1. Location

In the first instance, the landscape context of the green roof has important implications for invertebrate diversity. My results suggest that biodiversity conservation on green roofs is most effective when it is well-connected to ground habitat patches. This includes connectivity to small pocket parks, which are more common, and make up a larger contribution to the greenspace in higher density cities. This conclusion is consistent with previous studies which show the biodiversity value of private gardens in providing important connections and resources for urban birds (Goddard 2010). Hence, strategic identification and installation of green roofs within potential biodiversity corridors may enhance regional biodiversity connectivity and the biodiversity on individual green roofs.

The connectivity of green roofs to ground habitats may be enhanced by provision of adjacent green walls. Green walls may provide potential avenues for poor mobility invertebrates to migrate onto the roof. Potential evidence of this is the high invertebrate biodiversity on the Central Park roof in Sydney CBD. Synergies between green roof sites are also possible, but the ability of organisms to disperse amongst green roofs remains an open question.

In addition, there are significant biodiversity benefits of green roofs even on very isolated rooftops. These may provide important resources for Hymenoptera and other pollinators in areas with low landscape green. For isolated green roofs, larger roof areas on lower buildings provide greater biodiversity benefits. Similarly, MacIvor (2015) showed that building heights lower than 5 stories were necessary to provide viable nesting habitat for bees.

2. Roof size

Once certain areas are identified for implementation of green roofs, green roof construction must take into account available roof area. Larger green roofs provide greater biodiversity benefits. My results suggest that among the roofs sampled, a minimum roof size of approximately 500 m² with at least 150 m² (30%) of green cover was necessary to achieve maximal biodiversity benefits. This does not suggest that smaller roofs should not be candidates for green roofs, but rather that rooftops above 500 m² without green roofs may be a wasted opportunity. Smaller green roofs still have a large amount of invertebrate diversity, and may be useful as stepping stones to provide added connectivity in biodiversity corridors (Braaker *et al.* 2014). Roof size considerations may also include extent of green cover, such as in the Toronto city guidelines (Currie & Bass 2010).

3. Roof design

The selection of plants and soil substrate during construction of a green roof will influence the biodiversity outcomes. Invertebrates respond to the quality and structure of vegetation and soil on green roofs. This study shows that invertebrate richness increases with increasing structural diversity on green roofs, including both vegetated and non-vegetated components. This is unable to be mimicked by increasing structural diversity on bare roofs, possibly because man-made structures alone do not provide the food or microhabitat resources to sustain invertebrates. Plant choice has been shown to be important in providing specific habitat requirements for specialist species (Tonietto *et al.* 2011) or species of conservation concern (Brenneisen 2006). This is often achieved by increasing plant species diversity, and ensuring use of native plants (Dunnett 2006; Cook-Patton & Bauerle 2012). To date, green roof research has focused on the plant species combinations that optimise thermal and water regulations on green roofs (Lundholm *et al.* 2010). Recently, work at the University of Melbourne has

produced local plant selection guidelines (Francis *et al.* 2014), but are just the beginning for optimising green roof design in Australia. More work is necessary to understand how vegetation and faunal diversity interact on Australian rooftops, and create design selection guides to attract local fauna. In particular, the contribution of man-made structures to the structural diversity of green roofs needs to be further investigated.

4. Maintenance and translocation of fauna

A final consideration in green roof design should be the ability of faunal species to colonise and utilise new habitats. My results suggest that green roofs do attract biodiversity, giving some kudos to the “build it and they will come” philosophy. However, this is only true for highly dispersing taxa. My research suggests that the majority of invertebrates rely on human-mediated actions in order to colonise. Thus, seeding of the soil or plants with beneficial invertebrates may be necessary to maximise the biodiversity conservation potential of green roofs. Translocation (or assisted colonisation) is an emerging topic in conservation biology, and the few experiments performed on ground level habitats have had varying levels of success (Gallagher *et al.* 2015). There have been successful translocations of pollinators onto green roofs (Melbourne City Rooftop Honey 2015), but these have been restricted to a single species. In addition, the management practices of a green roof have been shown to influence invertebrate diversity (Coffman 2007). Therefore, translocation may form part of a wider set of management practices to maintain faunal diversity once the roof is built.

5. Conclusion

Green roofs provide substantial added habitat value for invertebrates, and sustain taxa which otherwise cannot survive on a rooftop. The vegetation on green roofs provides habitat structure and food resources which together support higher abundances and a wider variety of invertebrates than that which appear on bare roofs. Contrary to popular belief, bare roofs may provide some habitat value, and may actually favour a select number of taxa. A threshold of 30% green cover on a roof allows for a combination of vegetative and man-made components on a green, which may enhance the benefits provided by green roofs (e.g. energy provision from solar panels).

Green roofs may provide important habitat linkages within the urban environment, and form part of biodiversity corridors. Using a framework based on principles of island biogeography, invertebrate biodiversity on green roofs can be maximised by framing implementation in a hierarchy of placement, size, and design. Increasing the size of a roof, and increased connectivity with ground habitats, will increase the biodiversity value of a green roof. Increasing connectivity may be achieved by investigating synergies between green roofs and walls, as well as ground habitats. While there is some evidence that invertebrates can freely colonise green roofs, future research should include translocation experiments of invertebrates of significant ecological and/or conservation value.

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7. APPENDIX

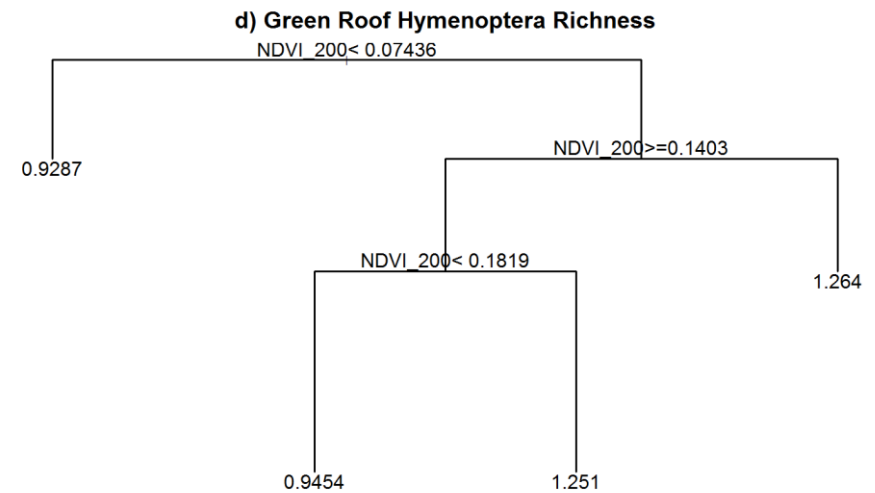
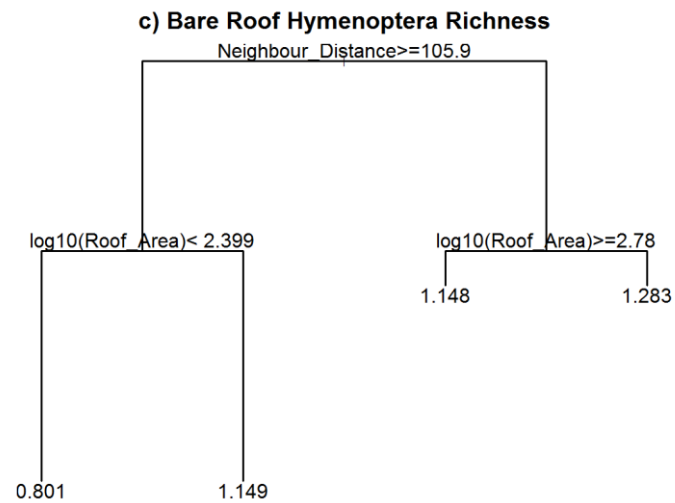
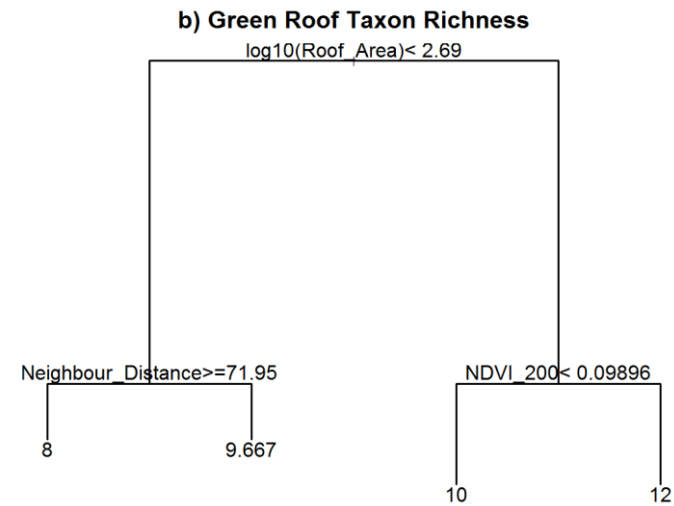
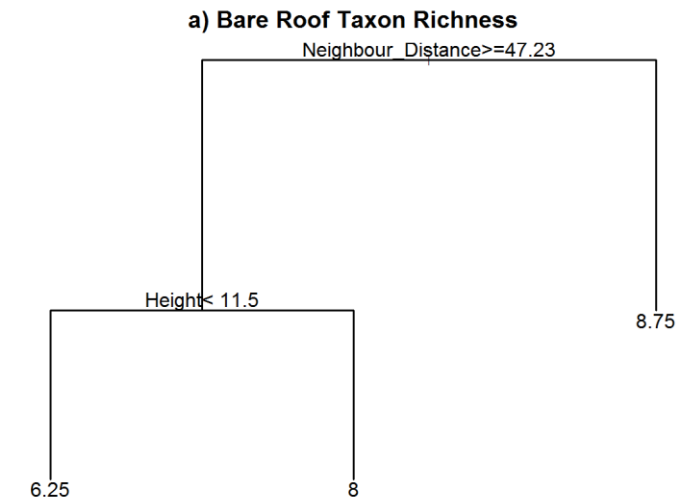
Table S1. Habitat feature diversity (D) as calculated for each site. Area (m²) of each feature was measured using satellite imagery.

SITE	Bare*	Concrete*	Imp†	Permeable†	Short†	Tall†	Trees†	Variegated*	Water*	Total	D
2BMH	24.84	0.00	0.00	521.69	128.72	255.11	0.00	0.00	0.00	930.36	2.44
4BMJ	17.00	0.00	0.00	324.11	301.83	128.81	0.00	0.00	0.00	771.75	2.80
ALL	32.20	0.00	0.00	53.12	0.00	114.30	0.00	125.58	0.00	325.20	3.23
BDG	0.00	227.83	0.00	41.10	0.00	0.00	0.00	0.00	0.00	268.93	1.35
BON	446.57	111.72	0.00	341.78	209.94	86.88	0.00	12.69	0.00	1209.58	3.85
CLP	0.00	8106.18	0.00	449.30	0.00	0.00	0.00	152.17	166.84	8874.49	1.19
CMR	7.51	0.00	0.00	0.91	7.11	18.18	0.00	0.11	1.05	34.87	2.77
CRO	0.00	33.80	0.00	54.09	0.00	0.00	0.00	0.00	0.00	87.89	1.90
E11C	0.00	548.09	0.00	83.77	194.01	113.16	518.1	24.69	0.00	1481.80	3.50
E13C	0.00	559.99	0.00	421.63	417.07	144.17	1106.5	454.01	0.00	3103.39	4.55
FOS	0.76	0.00	0.00	38.18	0.00	21.35	0.00	3.36	1.26	64.91	2.19
HSR	0.00	106.21	0.00	37.78	0.00	0.00	0.00	0.00	0.00	143.99	1.63
JAM	0.00	0.00	0.00	41.21	0.00	0.00	0.00	83.43	0.00	124.64	1.79
MAC	0.00	0.00	0.00	166.65	0.00	0.00	0.00	261.82	0.00	428.47	1.91
MST	0.00	57.43	0.00	10.66	0.00	0.00	0.00	0.00	0.00	68.09	1.36
MMR	0.00	0.00	0.00	12.97	3.66	10.36	0.00	1.93	0.00	28.92	2.86
NSC	0.00	190.00	0.00	305.62	0.00	0.00	0.00	0.00	0.00	495.62	1.90
PAP	0.00	276.31	0.00	150.28	430.59	1545.01	0.00	0.00	0.00	2402.20	2.16
PPL	0.00	610.86	117.73	0.00	62.49	266.45	0.00	0.00	199.84	1257.37	3.15
RCC	0.00	0.00	0.00	42.43	0.00	0.00	0.00	716.19	0.00	758.62	1.12
SSP	0.00	356.47	0.00	351.56	0.00	95.35	0.00	0.00	0.00	803.38	2.48
SUS	0.00	394.40	0.00	60.32	0.00	0.00	0.00	0.00	0.00	454.72	1.30
USC	0.00	0.00	0.00	0.00	0.50	0.00	0.00	85.41	0.00	85.91	1.01
UGR	0.00	0.00	0.00	0.40	0.00	40.95	0.00	12.70	0.00	54.05	1.59

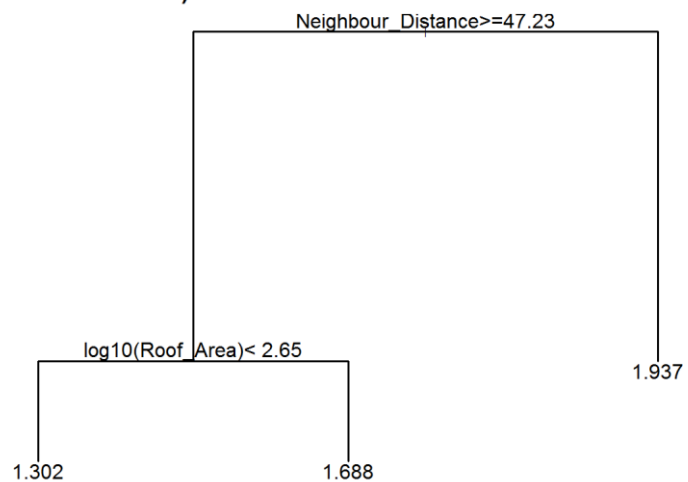
*Ground covers: Bare = bare ground, Concrete = flat concrete, Variegated = variable ground cover e.g. pebbles, water = ponds or other waterbodies.

† Structures: Imp = impermeable concrete, perm = permeable e.g. aircon-vents; Short plants (<30 cm), Tall plants (30 cm – 2 m), Trees (>2m)

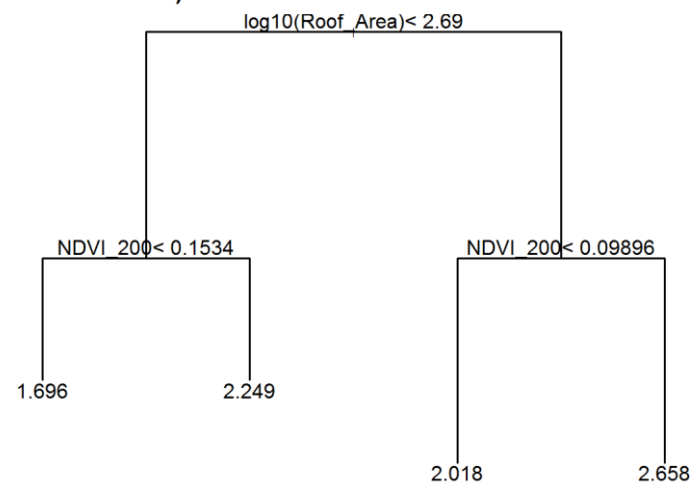
Fig. S1. Regression trees



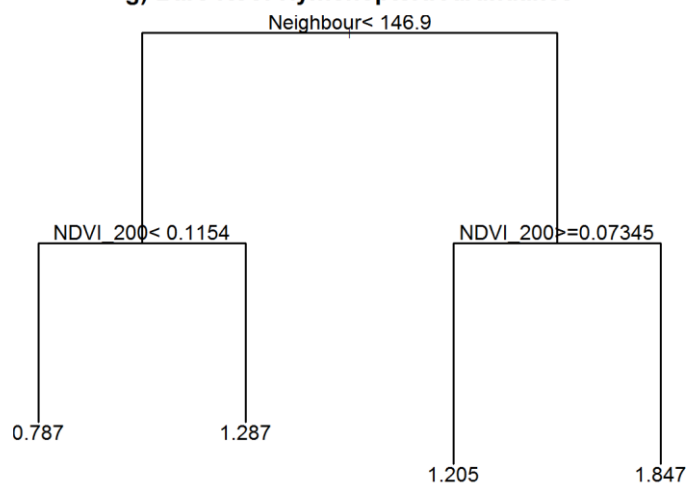
e) Bare Roof Taxon Abundance



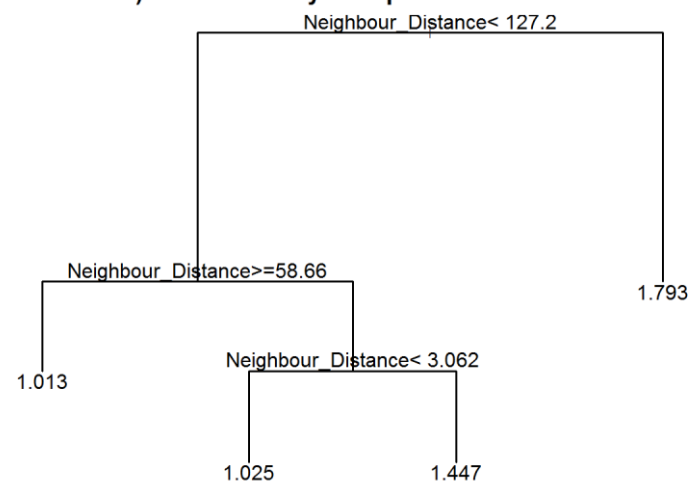
f) Green Roof Taxon Abundance



g) Bare Roof Hymenoptera Abundance



h) Green Roof Hymenoptera Abundance



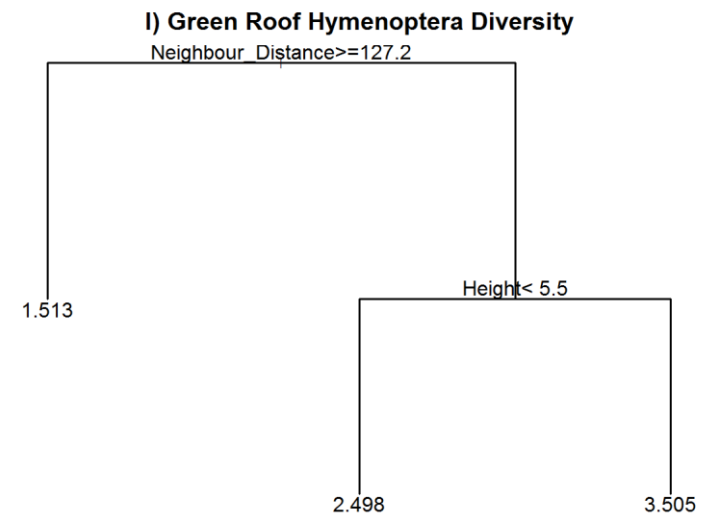
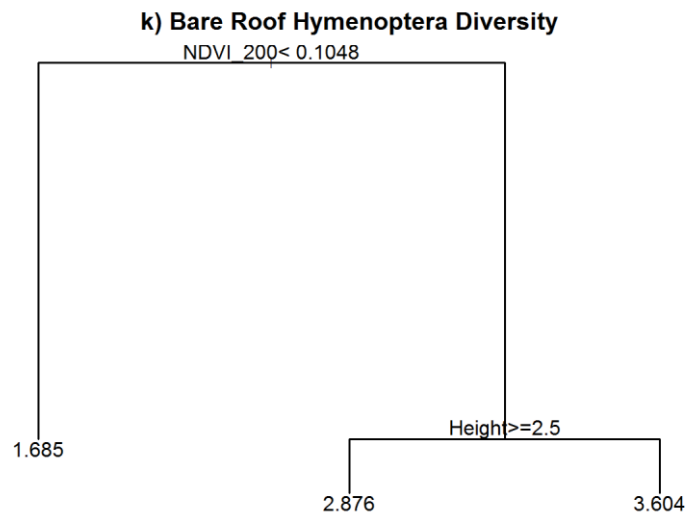
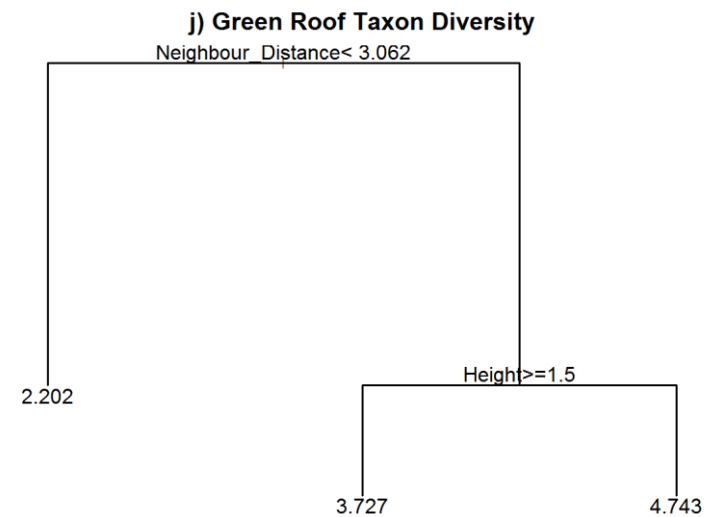
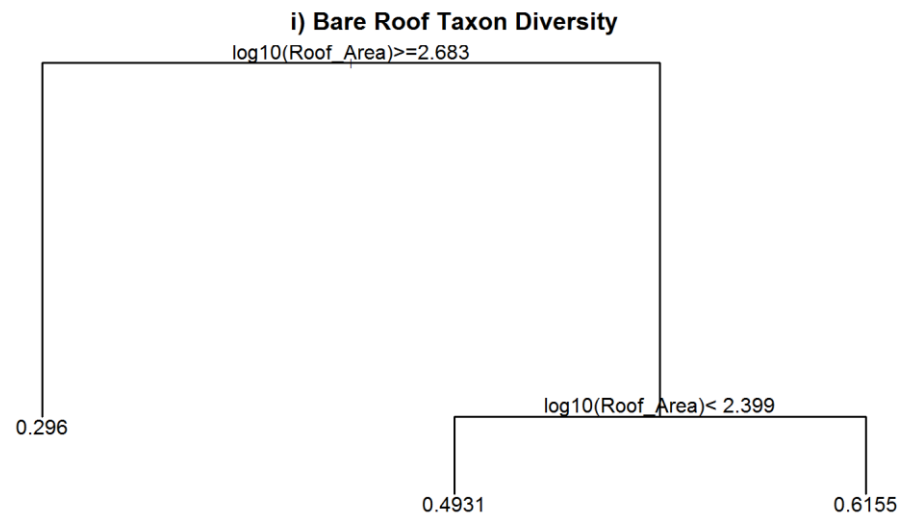
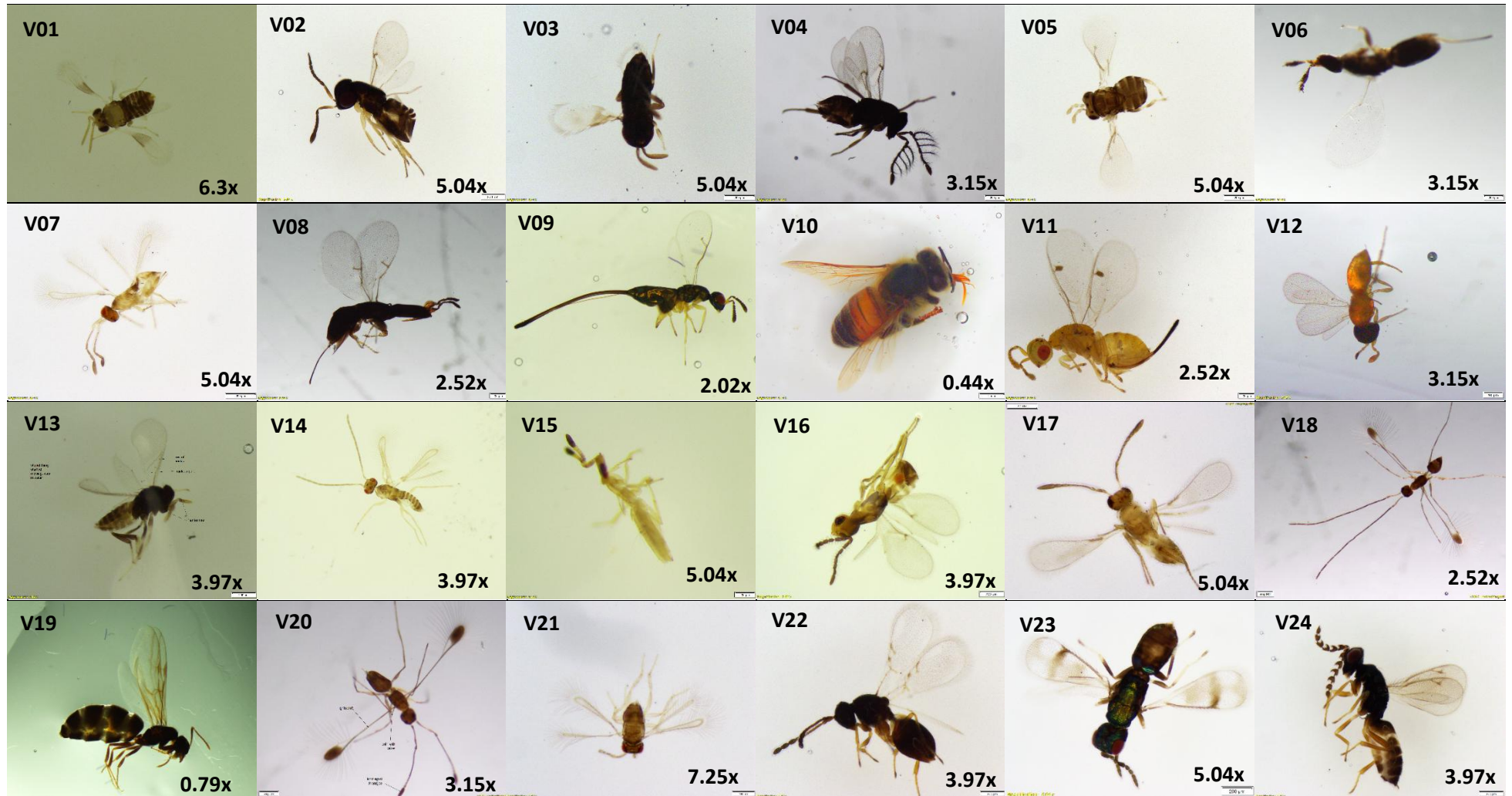
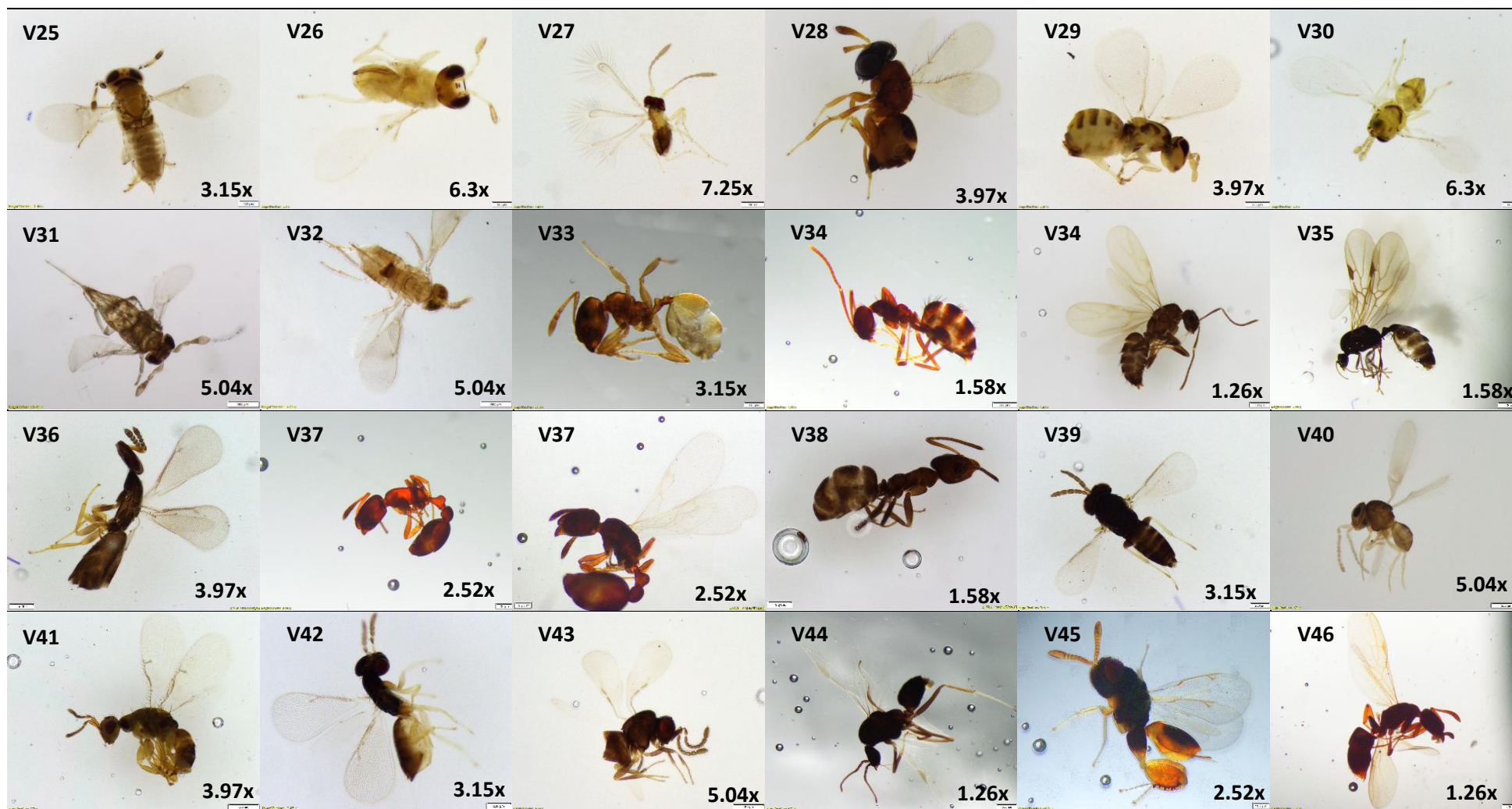
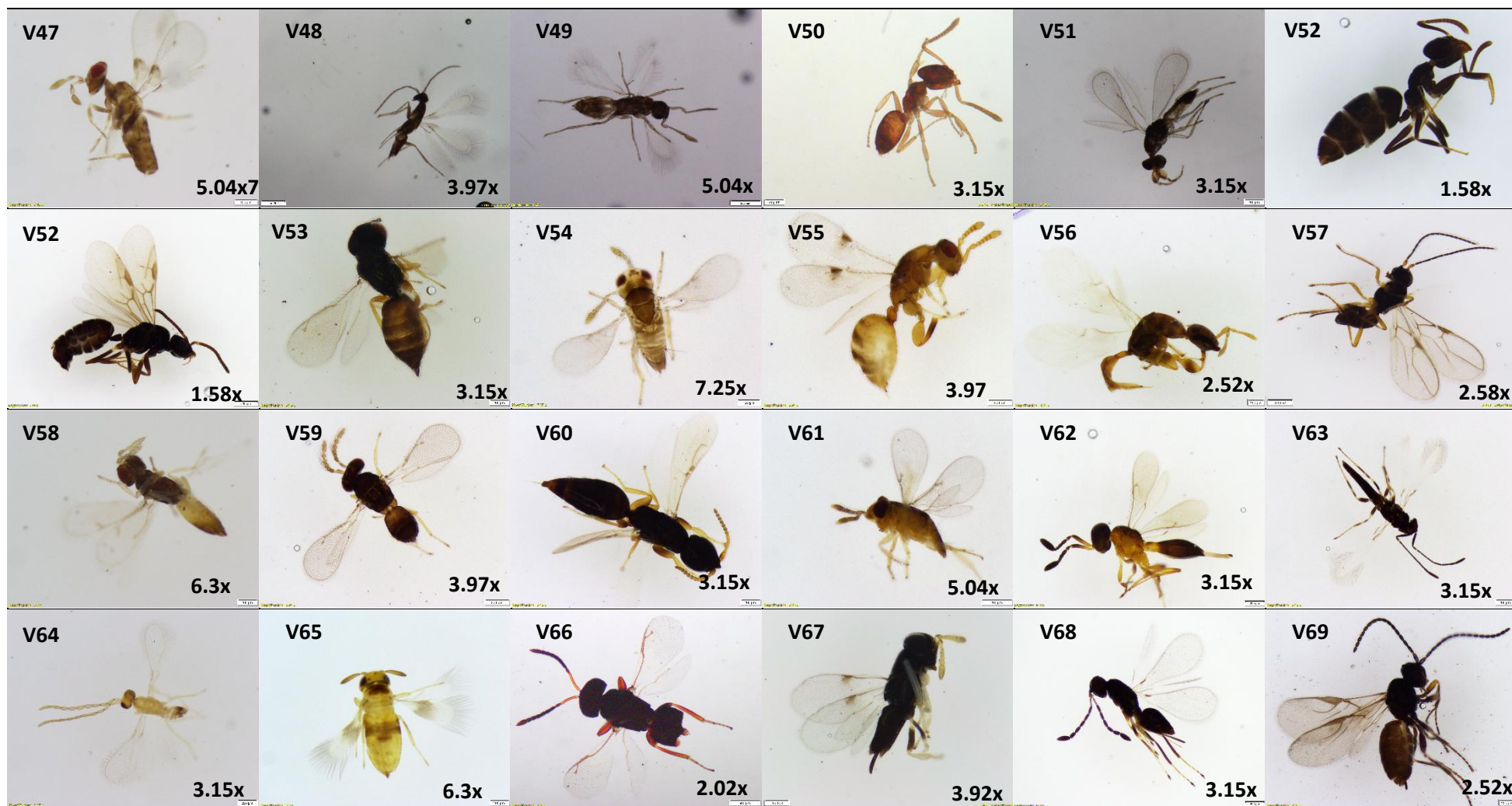


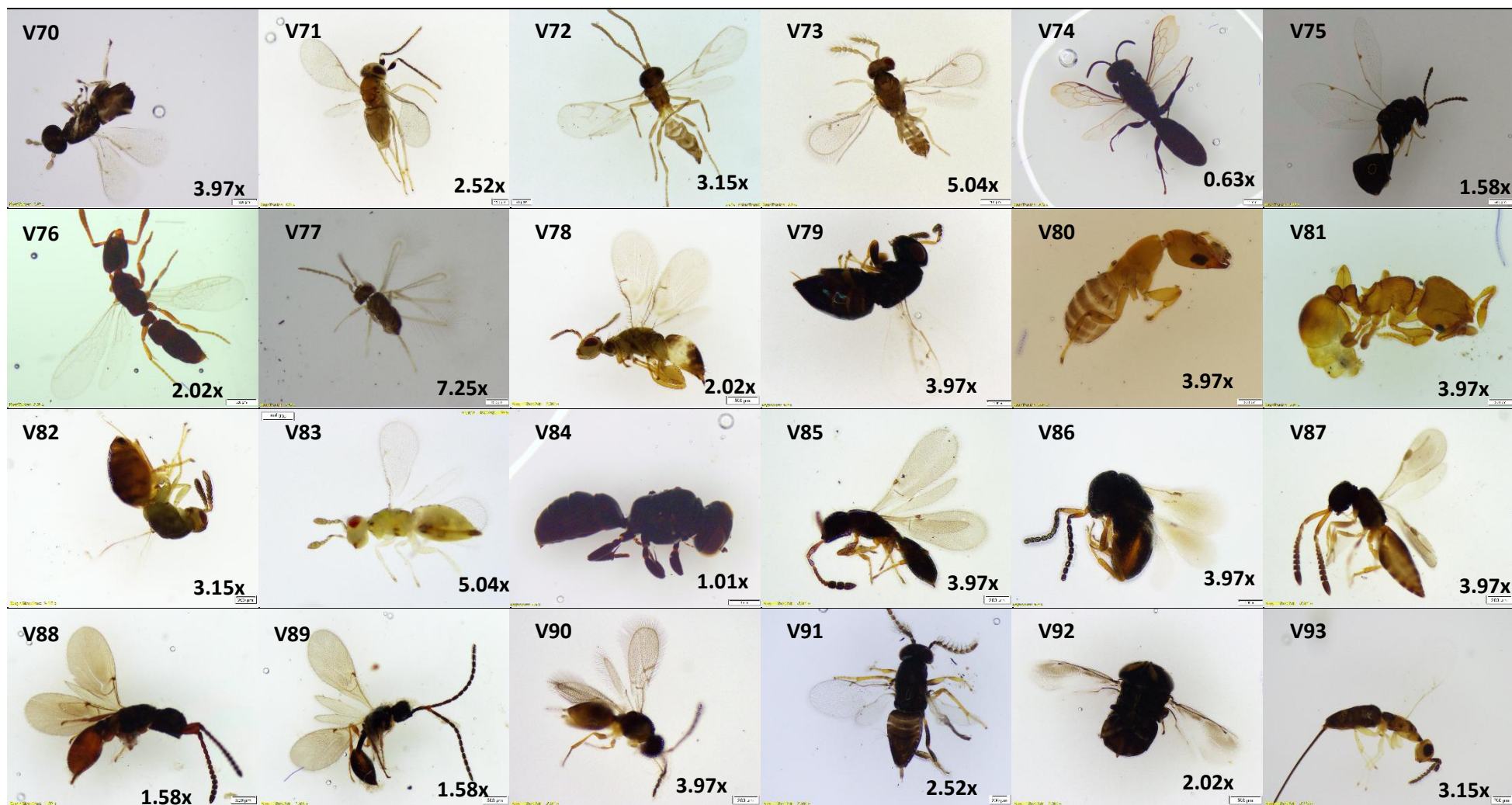
Fig. S2. Morphospecies pictures

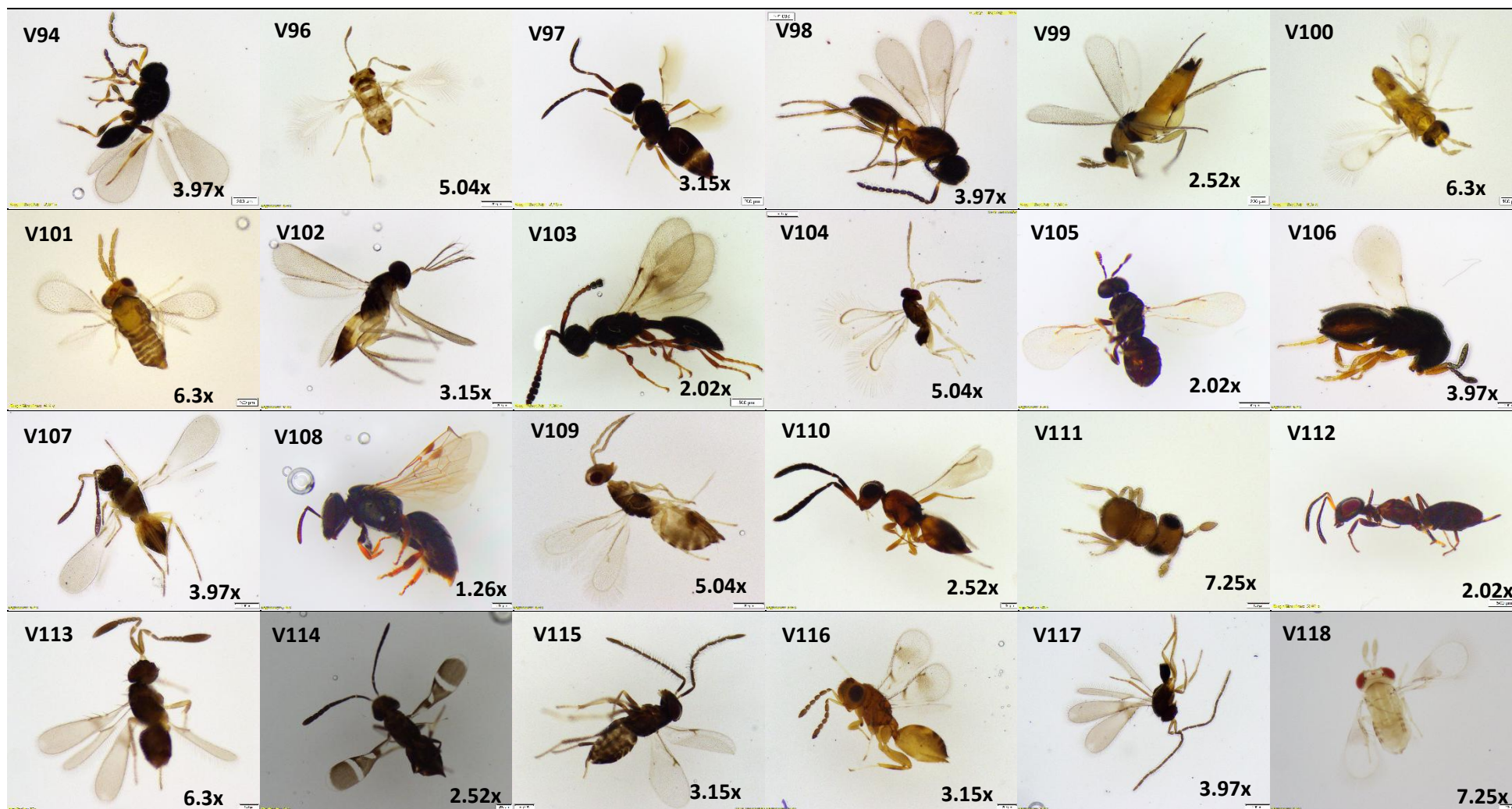
A representative microscope picture is given for each of the 129 morphospecies identified using an Olympus SZX16 stereo microscope.











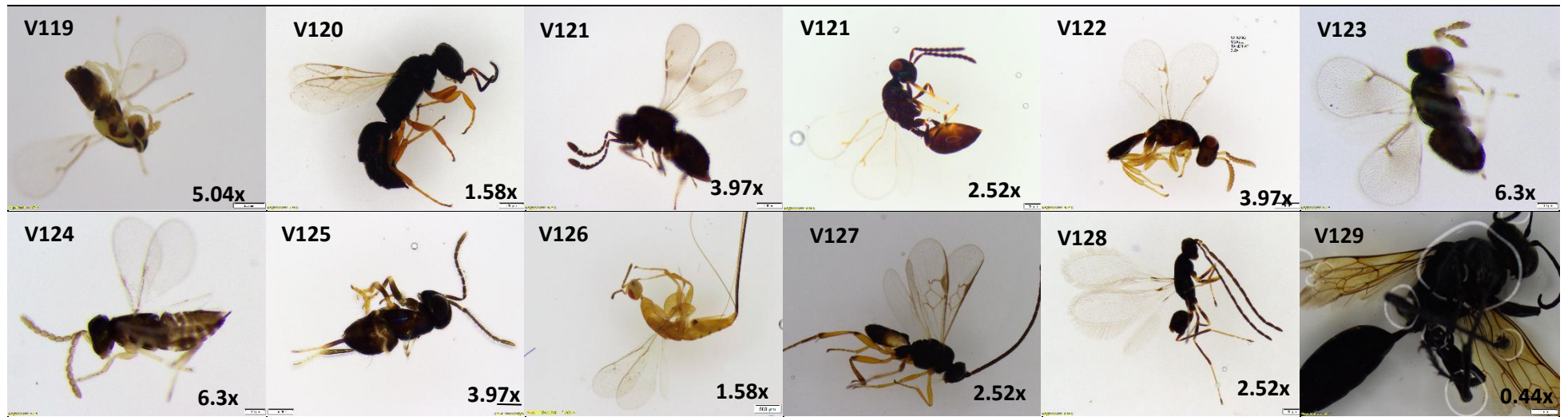


Table S2. Multiple regression models for taxon level invertebrate measures.

Model*	Taxon Richness~	AIC
1	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 100 m	22.1
2	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 200 m	21.7
3	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 300 m	21.7
4	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 400 m	22.0
5	Roof Type + log10(Area) + rank(Height) + rank(Neighbour)	20.0
6	Roof Type + log10(Area) + rank(Height) + NDVI 200 m	21.6
7	Roof Type + log10(Area) + rank(Neighbour) + NDVI 200 m	20.4
8	Roof Type + log10(Area) + rank(Height)	21.2
9	Roof Type + log10(Area) + NDVI 200 m	19.6
10	Roof Type + log10(Area) + rank(Neighbour)	18.5
11	Roof Type + log10(Area)	19.8
12	Roof Type + NDVI 200 m	28.3
13	Roof Type + rank(Neighbour)	24.9
Model	Taxon Abundance~	
1	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 100 m	-43.8
2	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 200 m	-45.2
3	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 300 m	-46.3
4	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 400 m	-43.7
5	Roof Type + log10(Area) + rank(Height) + rank(Neighbour)	-44.5
6	Roof Type + log10(Area) + rank(Height) + NDVI 200 m	-46.2
7	Roof Type + log10(Area) + rank(Neighbour) + NDVI 200 m	-46.9
8	Roof Type + log10(Area) + rank(Height)	-43.2
9	Roof Type + log10(Area) + NDVI 200 m	-48.2
10	Roof Type + log10(Area) + rank(Neighbour)	-46.5
11	Roof Type + log10(Area)	-42.8
12	Roof Type + NDVI 200 m	-41.9
13	Roof Type + rank(Neighbour)	-44.6
Model	Taxon Diversity~	
1	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 100 m	-0.3
2	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 200 m	-1.5
3	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 300 m	0.67
4	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 400 m	0.42
5	Roof Type + log10(Area) + rank(Height) + rank(Neighbour)	-1.2
6	Roof Type + log10(Area) + rank(Height) + NDVI 200 m	-2.6
7	Roof Type + log10(Area) + rank(Height)	-3.1
8	Roof Type + log10(Area) + NDVI 200 m	1.7
9	Roof Type + log10(Area) + rank(Neighbour)	-1.1
10	Roof Type + log10(Area)	-0.1
11	Roof Type + NDVI 200 m	2.5
12	Roof Type + rank(Neighbour)	-1.1

*Note: The models are not necessarily listed in the order of the stepwise trials, but are listed consistently for ease of interpretation.

Table S3. Multiple regression models for Hymenoptera morphospecies

Model*	Mspp Richness~	AIC
1	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 100 m	-72.7
2	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 200 m	-72.8
3	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 300 m	-68.0
4	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 400 m	-66.8
5	Roof Type + log10(Area) + rank(Height) + rank(Neighbour)	-66.7
6	Roof Type + log10(Area) + rank(Height) + NDVI 200 m	-74.7
7	Roof Type + log10(Area) + rank(Height)	-66.1
8	Roof Type + log10(Area) + NDVI 200 m	-75.6
9	Roof Type + log10(Area) + rank(Neighbour)	-68.6
10	Roof Type + log10(Area)	-67.0
11	Roof Type + NDVI 200 m	-75.0
12	Roof Type + rank(Neighbour)	-70.4
13	log10(Area) + NDVI 200 m	-76.2
Model	Log10(Mspp Abundance)~	
1	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 100 m	-39.5
2	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 200 m	-41.2
3	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 300 m	-38.6
4	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 400 m	-38.0
5	Roof Type + log10(Area) + rank(Height) + rank(Neighbour)	-38.9
6	Roof Type + log10(Area) + rank(Height) + NDVI 200 m	-43.0
7	Roof Type + log10(Area) + rank(Neighbour) + NDVI 200 m	-42.0
8	Roof Type + log10(Area) + rank(Height)	-39.1
9	Roof Type + log10(Area) + NDVI 200 m	-44.0
10	Roof Type + log10(Area) + rank(Neighbour)	-40.5
11	Roof Type + log10(Area)	-40.8
12	Roof Type + NDVI 200 m	-45.0
13	Roof Type + rank(Neighbour)	-42.5
14	log10(Area) + NDVI 200 m	-39.7
Model	Mspp Diversity~	
1	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 100 m	-9.3
2	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 200 m	-8.6
3	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 300 m	-7.8
4	Roof Type + log10(Area) + rank(Height) + rank(Neighbour) + NDVI 400 m	-7.7
5	Roof Type + log10(Area) + rank(Height) + rank(Neighbour)	-9.7
6	Roof Type + log10(Area) + rank(Height) + NDVI 200 m	-10.6
7	Roof Type + log10(Area) + rank(Height)	-11.3
8	Roof Type + log10(Area) + NDVI 200 m	-12.5
9	Roof Type + log10(Area) + rank(Neighbour)	-11.7
10	Roof Type + log10(Area)	-13.2
11	Roof Type + NDVI 200 m	-13.6
12	Roof Type + rank(Neighbour)	-13.4
13	Log10(Area) + NDVI 200 m	-13.8
14	NDVI 200	-15.1

*Note: The models are not necessarily listed in the order of the stepwise trials, but are listed consistently for ease of interpretation.

8. AUTHOR GUIDELINES: Journal of Applied Ecology

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