

Confirmed at Last: Green Roofs Add Invertebrate Diversity

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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 (>746 m²), 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. isolation, 2. roof size, 3. vegetation characteristics, 4. maintenance (including translocation of species of conservation concern or ecological value).

1. Introduction

More than half the world's population reside in cities (World Health Organisation, 2015). In Australia, the proportion of urban residents exceeds 80% (The World Bank). Increasing urban populations create a high demand for housing and services, which results in increased density and spread of urban land use (Williams et al., 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.

One of the key impacts of urbanisation is a reduction in vegetated open space and wildlife habitat (collectively referred to as 'green spaces'), both in areas adjacent to growing suburbs, and within the city itself (Kowarik, 2011). Vegetated rooftops ('green roofs') are a commonly used mechanism to increase open space in cities and have many human benefits. These benefits include increased air quality, thermal resilience, water regulation and recreational opportunities (reviewed in Oberndorfer et al., 2007). To date, enhanced thermal and water regulation benefits are the focus of design research (e.g. Czemieli Berndtsson, 2010), and have been the major drivers of green roof implementation (City of Sydney Council, 2014).

Green roofs are often cited as maintaining and conserving biodiversity through provision of wildlife habitat (Cook-Patton and Bauerle, 2012, Francis and Lorimer, 2011, Oberndorfer et al., 2007), yet there is little evidence to support this claim (Williams et al., 2014). As a result, urban development policies include green roofs as mechanisms to mitigate biodiversity loss, while increasing land-use efficiency in cities. Recently, green roof designs that claim biodiversity benefits ("biodiverse roofs", Kadas, 2006) 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.

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 and Bhagwat, 2011), which is often the case in highly altered urban areas (Davis and Glick, 1978). Understanding of the drivers of faunal biodiversity on green roofs is in its infancy, particularly in Australia (Williams et al., 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. Comparisons exclusively between different types of green roofs 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. 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 have included a bare roof reference (Davies et al., 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 et al., 2010).

In addition to vegetation cover, the size and context of a roof are expected to affect invertebrate diversity (MacIvor and 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 (**Error! Reference source not found.**). The balance of these processes, ultimately, determines the invertebrate community composition on green roofs.

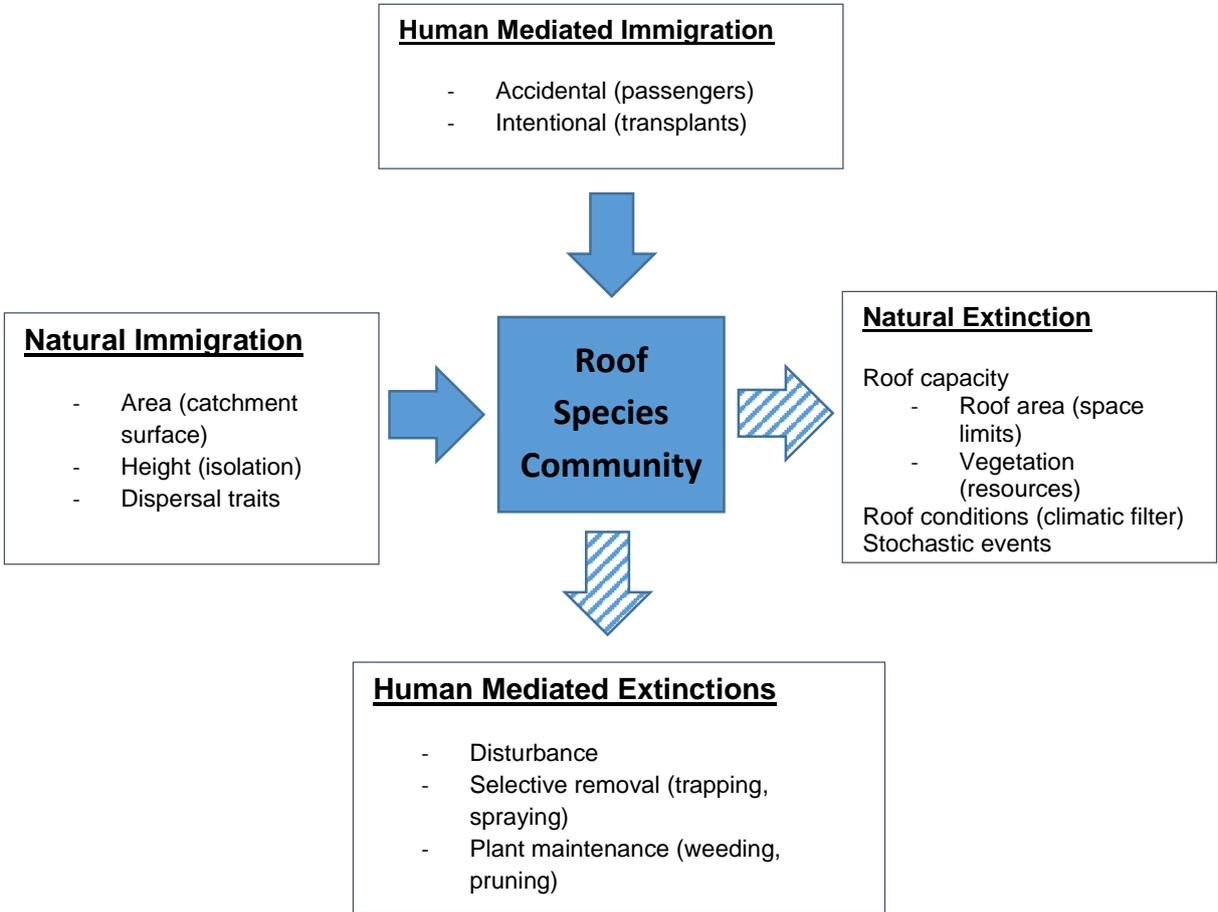


Figure 1. Island biogeography theory as it applies to green roof environments. The species community is an equilibrium between the influx (solid black arrows), and outflow (grey striped arrows) of species. See text for detailed descriptions of each element.

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 (Davis and Glick, 1978, MacArthur and Wilson, 1963, 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 (Braaker et al., 2014, Madre et al., 2013, MacIvor, 2015) (**Error! Reference source not found.**). 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. Similarly, a larger roof area provides a greater catchment surface for immigrating individuals and increases the possibility of arrival to a certain rooftop. Immigration of individuals onto green roofs may also be a consequence of human activity. For example, the intentional placement of native or honeybee hives on rooftops (Melbourne City Rooftop Honey, 2015). Alternatively, invertebrates may be introduced accidentally as passengers, in the soil or on plants, during construction of a green roof (Brenneisen, 2006).

The likelihood of attracting regular visitors or maintaining viable resident populations within a habitat patch is related to the patch size (i.e. roof area) and its quality (**Error! Reference source not found.**). 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 (**Error! Reference source not found.**). Regular human use may deter disturbance-sensitive species or species may be selectively removed as part of maintenance processes.

The following project investigated green and bare roofs as habitat for invertebrates within the context of highly urbanised inner Sydney. Pragmatically, green roofs are considered roofs with greater than 30% green cover in line with the City of Sydney Green Roofs and Walls Policy (City of Sydney Council, 2014). Based on the principles of classical ecological theory we make several clear predictions about the invertebrates on green roofs:

1. Green roofs are expected to have a higher abundance and richness than bare roofs. Larger vegetative biomass on green roofs and greater habitat heterogeneity should support a greater abundance and diversity of taxa than bare roofs.
2. Green and bare roofs are expected to host distinct compositions as they offer different habitat conditions in terms of climate and resource availability. 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.
3. Larger roof areas will have a higher abundance and richness of invertebrates through increased immigration (a larger catchment area), lower competition for space and heterogeneity of microhabitats.
4. Taller buildings are expected to have less abundance and richness than lower roofs. Taller buildings represent a larger barrier to dispersal and hence less immigration of individuals.
5. High roofs would be expected to contain a larger number of highly dispersing invertebrates, and may host significantly different assemblages compared to lower roofs.

2. Method

Study Sites

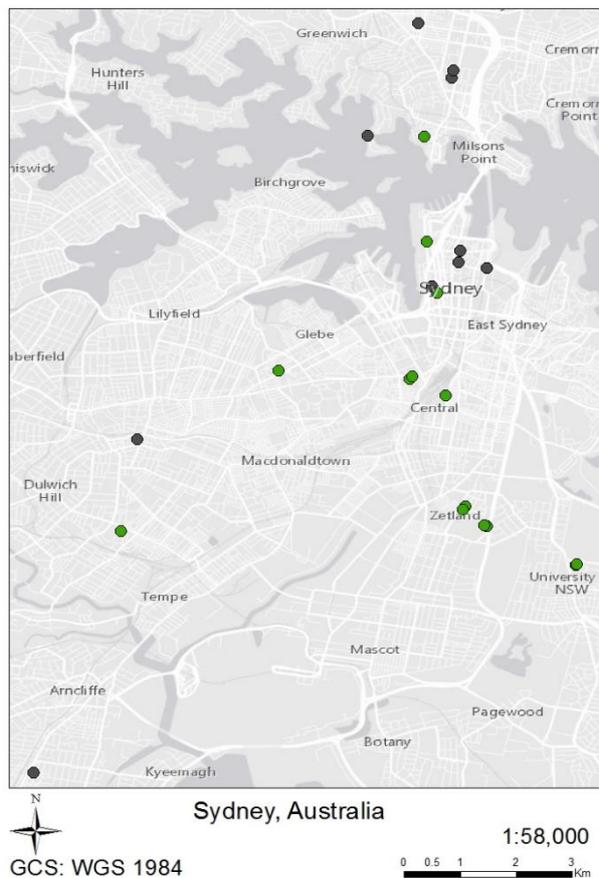


Figure 2. Map of green (green points) and bare (grey points) rooftop sites included within this study. All sites are within 15km of Sydney CBD.

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 (to limit deterrence of crawling insects 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 (Figure 2), were placed towards the centre of each roof. Layout of the traps varied due to variation in the shape of roof and vegetation structure, but 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 (12.5 %, propylene glycol : tap water). Each site was sampled twice for a period of 7-8 days during January to mid-March 2015. To account for weather variation, temperature was measured on each roof using ibuttons (Thermochron DS1921G, Thermodata Pty Ltd) housed in PCV tubing and suspended on flyscreen mesh (Figure 2e) to prevent direct radiation exposure (which is necessary for the detection of ambient temperature (Ashcroft and Gollan, 2012)).

Sample processing and analysis

Specimens from each pan were sorted into distinct taxonomic units (order, class or phyla) 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. Absolute abundance, site richness (the number of different taxonomic groups present at site) and community composition were then calculated using the average of the two sampling periods. Abundances were log-transformed (base 10) before analysis to normalize the data and conform to the assumptions of the statistical tests.

This study assesses invertebrate diversity on 13 vegetated and 11 bare rooftops distributed in and around the Sydney Central Business District (Figure 1). Roofs were 10 to 8000 m² in area, and ranged from ground sites to buildings that were 16 stories tall. All green roofs had a soil depth greater than 40cm, and are classed as *intensive* designs. Bare roof surfaces were exposed concrete (Figure 2b), corrugated iron or concrete with a pebble outer layer (Figure 2c). Green roofs were selected from a database obtained from the City of Sydney Council and liaison with other councils in the area. Green roofs had between 30 – 98% of green cover. Bare roofs were similarly obtained through local councils and the building management company CBRE. Bare roofs had <5% green cover, including overhanging trees.

Sampling design

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 individuals (New, 1998). Given the wind-exposed conditions of the bare roofs, we increased the weight and surface contact of each bowl by attaching a 2kg floor tile, mottled

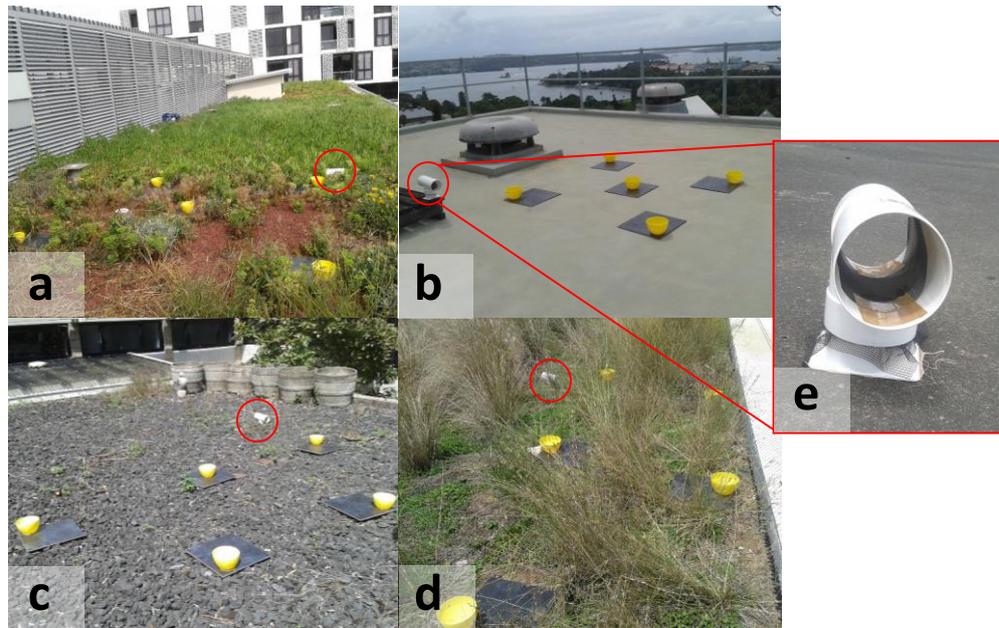


Figure 3. Trap design and layout. The predominant arrangement was five yellow bowls in a quincunx pattern (a,b), with deviations made to fit to more rectangular rooftops (c,d). Any variations in yellow pan arrangements were mirrored on green (a,d) and bare (b,c) rooftops. Thermochron ibuttons were placed in PVC tubes (e) which were placed next to the trap arrangement (red circles).

Variables thought to be important in determining diversity on rooftops fall into four broad categories:

1. roof area,
2. building height (number of stories),
3. climate and
4. vegetation characteristics.

Measurements of the total roof area were taken from aerial photography using NearMap (NearMap Pty Ltd, 2015), and number of stories was taken as a proxy for building height. Roof area was log-transformed (base 10) before analysis to normalise the data. The vegetation characteristics of the roof were measured in two ways: a binary green/bare categorical variable was used to assess presence/absence of vegetation; and percentage green cover to investigate whether amount of vegetation influenced invertebrate diversity. Finally, temperature (°C) during the sampling was included as a measure of climatic effects. All variables were tested for independence (i.e. a lack of correlation with other variables) using a series of linear regression models.

The influence of the four variables on the total abundance and ordinal richness of the invertebrate community were then examined using a combination of methods. First, the marginal effects of each variable were tested using a series of linear regressions. The impact of green cover on diversity was only analysed for the green roof sites. Then, the best multivariate explanatory model for predicting invertebrate diversity on rooftops was found using stepwise multiple regression with the Akaike Information Criterion (AIC) for model selection. Since the percentage of green cover and roof type were correlated, and the design of this study precluded collection of a full range of percent cover values, only roof type was included in the multiple regression models. The resulting 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.

Compositional differences were assessed using a univariate perMANOVA method. 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. All statistical 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 et al., 2012), and plotrix 3.5-5 (Lemon, 2006).

3. Results

A total of 9718 individuals were captured, of which 9692 (99%) were identified into 19 distinct taxonomic groups. Hemiptera (plant-feeders) and Collembola (soil-dwellers) were the most abundant across all sites (Figure 4a). There were no significant correlations between any of the explanatory variables ($p > 0.4$) except green cover and roof-type ($\text{adj.}R^2 = 0.68$, $p = 3.9 \times 10^{-7}$).

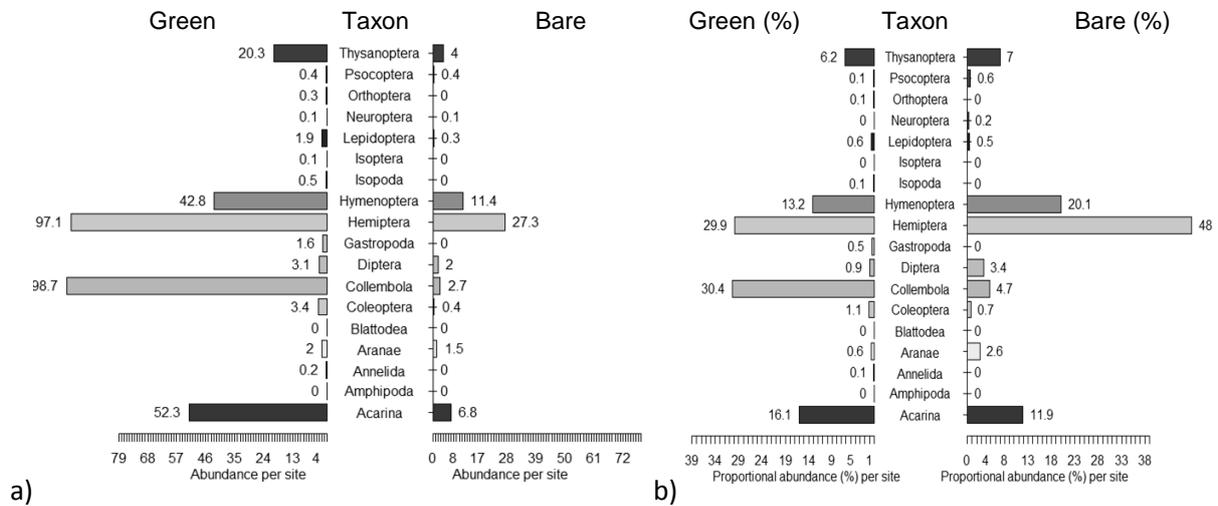


Figure 4. a) The total abundance of invertebrates collected within each taxonomic group per site and b) the proportional dominance of each taxon group per site.

Invertebrate abundance and diversity differed between green roofs and bare roofs. There was an order of magnitude more individuals on green roofs than bare roofs ($\text{adj.}R^2 = 0.20$, $p = 0.016$, Figure 5). Almost all orders present on both rooftops were more abundant on green roofs (Figure 4a). Neuroptera and Psocoptera groups were equally abundant on both roof types. Likewise, green roofs hosted a greater richness of taxa than bare roofs ($\text{adj.}R^2 = 0.35$, $p = 0.001$, Figure 5). Increasing the percent of green cover on green roofs did not significantly change abundance ($\text{adj.}R^2 = 0.107$, $p = 0.065$, Figure 5) or richness ($\text{adj.}R^2 = -0.018$, $p = 0.371$, Figure 5).

Green and bare roofs contained significantly different compositions ($\text{adj.}R^2 = 0.093$, $p = 0.02$, Figure 6). Where green and bare roof compositions overlapped, bare roofs had high structural complexity e.g. in the form of pebbled substrate (Figure 3c). Green roof communities were dominated by Hemiptera and Collembola, whereas bare roof communities were dominated by Hemiptera and Hymenoptera individuals. Some orders, such as Diptera and Aranae, were proportionally more dominant on bare roofs compared to green roofs (Figure 4b). Seven orders were unique to green roof environments (Amphipoda, Annelida, Blattodea, Gastropoda, Isopoda, Isoptera and Orthoptera). There was a similar level of variation (spread) in community composition between green and bare roof sites (Figure 6).

Larger rooftops had a significantly higher richness ($\text{adj.}R^2 = 0.18$, $p = 0.0214$, Figure 5) and abundance ($\text{adj.}R^2 = 0.093$, $p = 0.08$, Figure 5), regardless of roof type. There was a trend of decreasing abundance with height ($\text{adj.}R^2 = 0.05$, $p = 0.16$, Figure 5), but this did not translate into a change in invertebrate richness ($\text{adj.}R^2 = -0.032$, $p = 0.597$, Figure 5). Similarly, there was no significant difference in composition with changes in height ($R^2 = 0.067$, $p = 0.13$). In all cases, temperature had no significant impact on invertebrate abundance ($\text{adj.}R^2 = -0.04$, $p = 0.643$, Figure 5) or richness ($R^2 = -0.038$, $p = 0.691$, Figure 5).

Table 1. Final multiple regression models selected from the stepwise procedure.

Abundance Model	AIC	R ²	p
$\log_{10}(\text{Abundance}) \sim (1.06 \pm 0.30) + (0.23 \pm 0.11) * \log_{10}(\text{Roof Area}) + (0.65 \pm 0.15) * \text{Roof Type}$	-44.6	0.491	0.0003
Richness Model	AIC	R ²	p
$\text{Richness} \sim (4.38 \pm 1.2) + (1.35 \pm 0.47) * \log_{10}(\text{Roof Area}) + (2.50 \pm 0.63) * \text{Roof Type}$	23.7	0.509	0.0002

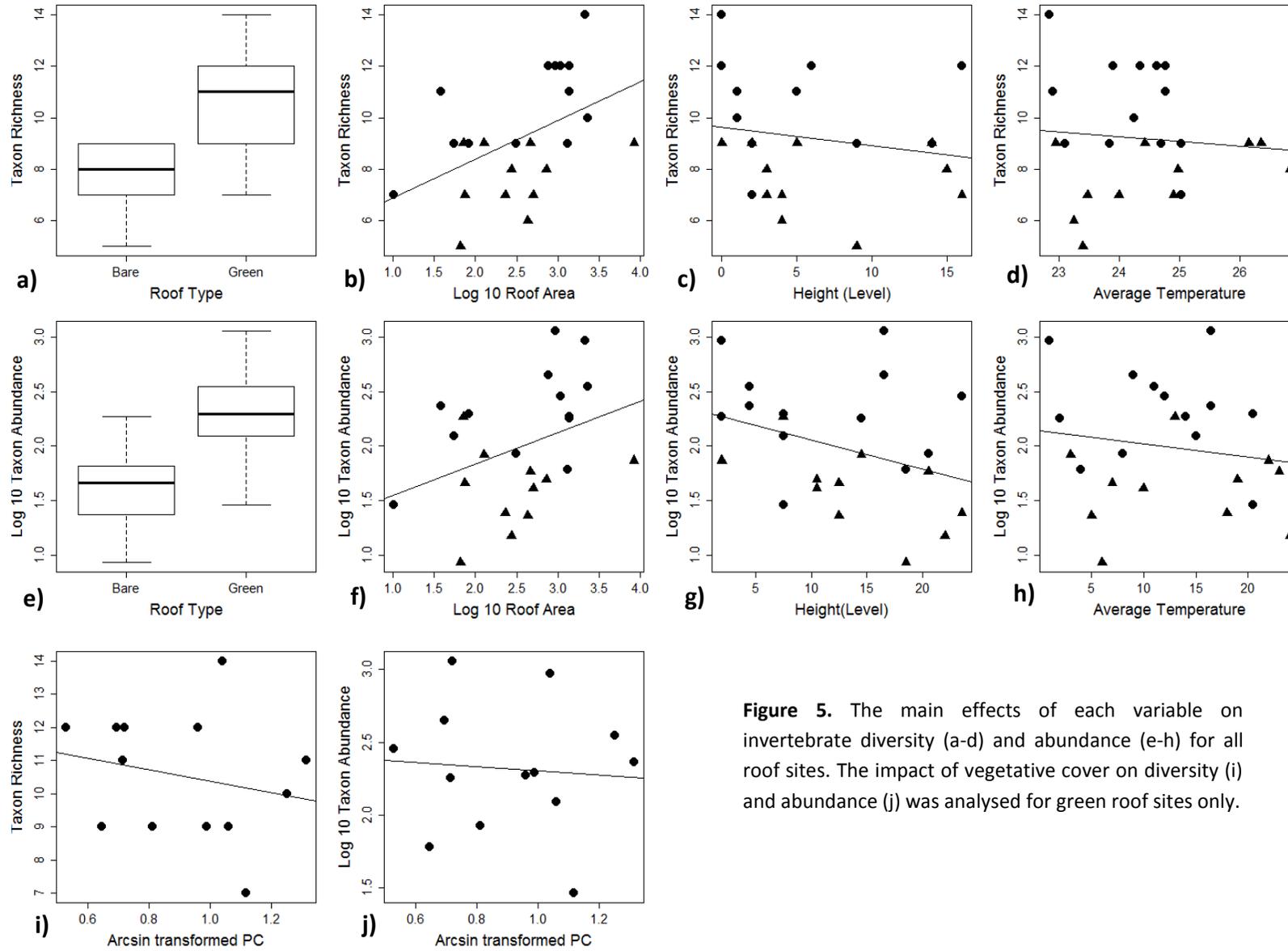


Figure 5. The main effects of each variable on invertebrate diversity (a-d) and abundance (e-h) for all roof sites. The impact of vegetative cover on diversity (i) and abundance (j) was analysed for green roof sites only.

The most important variable for predicting invertebrate abundance and richness was roof type, followed by roof area. Together, these explained almost 50% of the variation in the regression models (Table 1). Invertebrate richness was maximised above a threshold of 746 m² regardless of roof type. To maximise abundance, the threshold value for roof size varied depending on the roof type. A smaller threshold is necessary for green compared to bare roofs. Bare roofs need to be larger than 68 m² in order to maximise abundance, whereas green roofs need to be larger than just 24 m².

4. Discussion

Green roofs have greater habitat value than bare rooftops

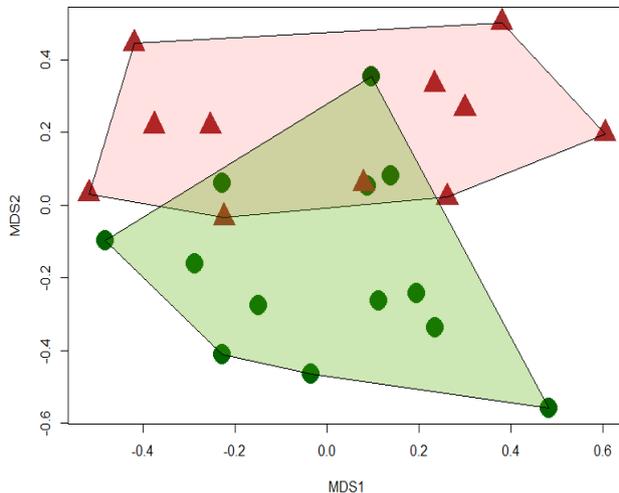


Figure 6. Ordination plot of invertebrate composition on bare (red triangles) and green (green circles) roof sites. Points which are close together have a similar composition. Two distinct but overlapping assemblages are present (coloured polygons) and driven by roof type.

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. Bare and green roofs contain significantly different compositions, with a number of taxa found on green but not found bare roofs. No taxa were found on bare roofs that were not present on green roofs. 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.

Our results concur with the limited number of studies that have examined the relationship between vegetation gradients, invertebrate diversity and urban infrastructure. 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 amount 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 et al., 2010, Madre et al., 2015, Norton et al., 2014, Maclvor, 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. Here, we show the mere presence of at least 30% vegetation cover on a roof increases invertebrate diversity and abundance. 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, Maclvor (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 (Maclvor, 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 and 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.

Interestingly, bare roofs supported a unique assemblage of invertebrates, suggesting they may have some habitat value. However, our results suggest that bare roofs have an upper limit of invertebrate

richness that they can support, and that most roofs are already at or close to this maximum (Figure 5). Invertebrate groups that appear to benefit from bare roof spaces include mostly predatory orders such as spiders (Araneae), which catch passing winged insects. Contrary to our predictions, bare roofs were no less varied in assemblage composition, compared to green roofs. This may be because of variations in structural complexity among bare roofs such as presence of maintenance structures (such as air conditioning units), or different kinds of roof substrates (such as pebbles or corrugation). This structural complexity may generate microhabitats which invertebrates may respond to in the same way as they are to changes in vegetative structure (Madre et al., 2013).

Contrary to expectations, there was no significant difference in invertebrate richness with increasing green cover above the 30% threshold set by the City of Sydney Council (2014). Surprisingly, the trend was towards lower richness at higher green cover levels (Figure 5). This may be because of declining bare roof-like habitat, because the abundance of individuals is relatively the same (Figure 5). Alternatively, changes in richness may occur at a lower taxonomic level (e.g. Madre et al., 2013), and be masked by lumping variation into higher taxonomic classes. This may explain the high variation in richness at high green cover levels (Figure 5), if habitat heterogeneity favoured increased richness of particular taxon groups. In either case, we can see the importance of providing habitat heterogeneity, whether in the form of mixed bare and green habitat types, or in a variety of green roof habitats as demonstrated by previous comparisons of green roofs (Madre et al., 2013, Coffman and Waite, 2010).

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 were inferred from the influence of roof area and isolation on measured trends in invertebrate diversity. 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. Similar principles of island biogeography have been used to explain urban patterns of diversity in plants (Hobbs, 1988), birds (Marzluff, 2005), and invertebrates (Fattorini, 2014, Rodrigues et al., 1993, Helden and Leather, 2004).

Impact of roof area

As in studies of bushland reserves (Rosenzweig, 1995) and urban remnants (Bolger et al., 2000), rooftop invertebrate abundance increases with habitat area, as measured by total roof area. This is true regardless of the presence of vegetation (Figure 5). Madre et al. (2013) also found invertebrate abundance to increase on larger roofs, but only for Hymenopteran species. Contrastingly, Schindler et al. (2011) showed no impact of total roof area on soil communities. Although increasing green cover has been shown to increase plant feeding Hemipteran species (Madre et al., 2013), we found no impact of increasing green cover at higher taxonomic levels (Figure 5). The presence of vegetation changes the roof capacity for maximising abundance, with green roofs able to support more individuals per unit area. Abundance may be higher on green roofs as there is increased provision of resources (Cook-Patton and Bauerle, 2012). Hence, the presence of vegetation on rooftops likely lowers the probability of extinction for a given roof size.

To maximise invertebrate richness, rooftops are required to be substantially larger (i.e. >746 m²) than for maximising abundance, regardless of vegetation type. This suggests that the primary mechanism by which total roof area drives increased richness is through a greater catchment surface for immigration rather than roof capacity (Figure 1). However, the method used in this study is biased towards flying insects (Sutherland, 2006) and may measure immigration more accurately than residency. Previous studies have shown a boom-bust type cycle for soil invertebrates (Rumble and Gange, 2013), indicating that both immigration and extinction events are important in determining diversity on rooftops. The data suggest that roof area has an influence on both of these factors, and the size of a roof is an important design consideration in green roof implementation.

Impact of roof height

As expected, abundance tended to decrease with increasing roof height (Figure 5). This did not translate into a decrease in invertebrate richness and there was no significant difference in composition on higher rooftops. In contrast, invertebrate diversity has been shown to decrease with increasing height (Madre et al., 2013), for buildings that are comparatively lower than in the present study (25 m compared to 48 m). Taller buildings are expected to have lower diversity due to less favourable climatic conditions (exposure to higher winds and solar radiation), and increased isolation from source populations. Yet, we found no evidence that tall roofs have a significantly different climatic conditions

compared to lower roofs and there was no significant difference in temperature between green and bare rooftops. This suggests that there is not a significant climatic filter preventing colonisation success on rooftops, possibly because the range of building heights does not compare to classical cases of climatic gradients which occur over kilometre scales (Lomolino, 2001). In contrast, studies of green walls show significantly different microhabitat characteristics between bare and vegetated surfaces (Madre et al., 2015). 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 changes (Rumble and Gange, 2013, Benvenuti, 2014). Similarly, several studies show temperature regulation benefits of green roofs compared to bare roofs (e.g. Oberndorfer et al., 2007). It is possible that climatic responses were not detected in this study due to measurement of ambient rather than surface temperature. Due to large amounts of rain and wind during the sampling period, ambient temperature may have been more impacted by regional rather than site specific weather conditions.

In the absence of a climatic filter, the major factor determining colonisation success on rooftops is likely to be dispersal capacity. Previous studies comparing ground and roof sites have found dispersal ability to be a factor influencing invertebrate colonisation onto green roofs (Madre et al., 2013, Braaker et al., 2014), as well as a decrease in invertebrate diversity with increasing roof height (Madre et al., 2013). At a coarse taxonomic resolution, it appears that the major dispersal barrier is from ground to roof habitats, as richness is unrelated to roof height (Figure 5). That is, members of higher taxon levels, which have the ability to disperse to lower rooftops, are able to colonise higher rooftops as well; but there is a lower probability of happening upon a higher roof when lower roofs are available. This may mean some taxa are unable to reach taller rooftops without human intervention. Contrastingly, Madre et al. (2013) found that species richness decreased with increasing building height. The coarse taxonomic resolution used in this study prohibited accurate distinction between different dispersal classes, and gives a poor picture of dispersal capacity of roof invertebrates. Viewing trends in richness and abundance at lower taxonomic level would reveal mechanisms of dispersal with greater confidence. It is likely, therefore that there were changes in diversity within the higher level taxa, but that these were not detected.

5. Concluding Remarks

We have shown quantitatively that green roofs host a greater abundance and variety of organisms than conventional bare roofs. Design guidelines should take into account thresholds in roof size that can maximise invertebrate richness and abundance. Specifically, bare roofs are required to be a minimum of 68 m² to maximise invertebrate abundance, whereas green roofs achieve this at a threshold of just 24 m². To maximise overall invertebrate richness, total roof area is required to be greater than 746 m² and contain both vegetated and bare earth areas at a threshold of *at least* 30% green cover. Green and bare roofs each contain a unique assemblage of species that may be catered for by such designs. The data suggest that this diversity is capable of being maintained even on tall rooftops, but this is tentative considering the design limitations of this study.

In addition, our study demonstrates the applicability of island biogeography theory to investigate the diversity of invertebrates on green and bare roof environments. The data suggest that invertebrate diversity can be predicted from information about the roof area and degree of isolation from source populations. However, several gaps remain in our knowledge of the processes influencing invertebrate diversity on green roofs. These gaps continue to restrict informed decision about green roof design. In particular, future studies should use lower taxonomic classification and spatial analysis techniques to increase understanding of the isolating effect of building height, the influence of landscape factors and the implications of increased diversity on green roofs for ecosystem function.

6. Acknowledgements

The authors are grateful to Macquarie University HDR department for provision of a generous stipend, without which this project would not have been possible. 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 the researchers. This includes to Lucy Sharman, former Green Roofs and Walls Officer of the City of Sydney Council; Sophie Golding, the Urban Ecologist of City of Sydney Council; Niki Carey, the Sustainability Officer of North Sydney Council; David Banbury and his team at the Coal Loader Sustainability Centre; Alexandra Vandine, Environmental Strategy Coordinator and Greg Taylor, Facility Manager from Rockdale City Council; Claire Hanley and Jean Brennan at Marrickville Council; Nathan Wills, One Central Park Maintenance Manager for Jungleyf/Frasers Property; Emma McMahon, Sustainability Manager for CBRE, and the CBRE building services managers Amanda Steele, Ken Forsstrom, Pierre Lawrence and Allan Riches; Peter Went, Building Manager for DEXUS Property Group; the helpful desk staff at Meriton Apartments in Zetland; the

building manager and security staff at Allianz Head Office in Sydney; John Blair, Lecturer in Built Environment at UNSW 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; Maggie and Niki Maloney. Special mention goes to Leigh Staas and her connections of the National Green Infrastructure Network.

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