# Scaling of Animal Communities: From Local and Landscape to Global Processes

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## Summary

Animal communities are influenced by processes changing from the local to global scale. Local processes include resource and habitat availability, while landscape processes are often driven by habitat availability and heterogeneity that shapes the species pool and population size. At the global scale, area and environmental heterogeneity are major processes influencing animal communities.

I determined the influence of local and landscape scale processes on plant-pollinator communities at different levels of urbanisation (farmland, villages and cities). The influence of landscape was separated from that of the sampling unit by conducting pollinator observations on phytometer plants experimentally placed in the different landscapes (grassy field margins in farmland and gardens in villages and cities). Pollinator diversity and abundance was highest in farmland and villages, but species group identity changed with a number of wild bee species only present in gardens in villages and cities. Plant-pollinator interaction networks in farmland sites were more robust with higher interaction strength compared with networks in villages and cities.

Bumblebee movement patterns were analysed using the same landscapes as the plant-pollinator experiment, but with farmhouse gardens added. I examined how local resources and landscape type affect bumblebee foraging behaviour and colony performance. I placed 32 *Bombus terrestris* colonies along the farmland to urban gradient and analysed local and long-range movement patterns of bumblebees to assess where pollinators forage in urban areas. Additionally, I measured if *B. terrestris* colony growth depends on resource availability in the direct surroundings of the colony or on landscape type. *B. terrestris* workers visited plants providing floral resources in the direct surroundings of the colonies. Furthermore, the workers foraged in greater distances to their colonies, if the mass flowering crop oilseed rape was flowering.

I investigated the influence of urban area size by studying arthropod communities along an urbanisation gradient from small villages to cities. I sampled arthropods in gardens and public green spaces at the edge and centre of urban areas to determine the relative importance of local and landscape influence on community composition. Arthropods sampled were from different taxa: Coleoptera, Araneae and Hymenoptera. Araneae and Hymenoptera were influenced only by the local surroundings (green space type and position in an urban area), whereas Coleoptera

communities were influenced by both local and landscape effects (urban area size).

I also investigated whether environmental heterogeneity (niche processes) or space (neutral processes) are better predictors of mammal species richness patterns at the global scale. The relative influence of these two processes has not been tested at the global level. I used a burning algorithm to increase both area and environmental heterogeneity simultaneously. Niche processes explain global species richness relationships better than neutral processes. The environmental factors that explain most variation in species richness were either the range in elevation or in precipitation.

In conclusion, local and landscape scale processes influenced arthropod community structure in urban areas. Abundance and diversity respond to local resources and habitat type, while community composition was influenced by the heterogeneity of the surrounding landscape in a taxon-specific way. The importance of environmental heterogeneity scales up to the entire globe as I found it is also an important predictor of mammal species richness. By determining at which scale species richness and animal communities are influenced, this study increases our understanding of how the ecological world is structured.

# Chapter 1

# General Introduction

*Misumena vatia* (Clerck) on *Leucanthemum vulagare* (Vaill.), *Bos taurus*, *Bombus lapidarius* (L.) on *Geranium pratense* (L.), *Episyrphus balteatus* (de Geer) on *Hieracium aurantiacum* (L.). ©Kristy Udy.

**Global scale**

Animals are influenced by processes across spatial scales from local (e.g. plant species richness) and landscape (habitat type heterogeneity) to the global scale (climate and topography). Understanding patterns of biodiversity is a core interest in ecology. The most studied global patterns of species richness are the latitudinal gradient and the elevational gradient (Field et al. 2009). The latitudinal gradient in species richness peaks around the equator where species richness is highest (Fig. 1) and the elevational gradient is generally a hump-shaped relationship in species richness when measured from the bottom to the top of mountains (Buckley et al. 2010, McCain and Grytnes 2010). The gradients of species richness with latitude and elevation are just patterns and do not explain the processes causing these relationships (Davies et al. 2007, Field et al. 2009).

A classical explanation for patterns of species richness is niche theory. Niche theory states that the structure of ecological communities is mainly influenced by habitat heterogeneity and niche partitioning of species (MacArthur and Wilson 1967, Kadmon and Allouche 2007). Highly heterogeneous environments offer more niches, allowing for more species to coexist (Potts et al. 2004, Kadmon and Allouche 2007). Indeed, environmental heterogeneity is a strong driver of species richness of various taxonomic groups and across global scales (Stein et al. 2014). Consequently, if niches/ niche differences structure ecological communities, environmental heterogeneity should be the main explanatory variable for species richness at any spatial scale.

Recently, however, ecological thought has given more room to neutral (stochastic) processes in explaining species richness. Hubbell synthesised this idea into the unified neutral theory of biodiversity and biogeography (Hubbell 2001), hereafter 'neutral theory'. This theory assumes that individuals within a particular trophic level have fitness equivalence. Moreover, it assumes that ecological communities are assemblages of species whose presence and absence is governed by ecological drift, paired with random speciation and dispersal. Neutral processes are able to reproduce biodiversity patterns, such as local species abundance distributions and species-area curves, from small to global spatial scales (Rosindell and Cornell 2009, Rosindell et al. 2011). Since environmental niches are assumed to be absent in neutral theory, the main determinant of the species richness of a region is its area, assuming that dispersal and speciation rates are constant.

The species-area relationship is a classic pattern of species richness predicted by

neutral theory (Arrhenius 1921, MacArthur and Wilson 1967). Species richness increases with area because larger areas provide opportunities for species to be present by chance (neutral theory), which inherently includes an increasing range of environmental heterogeneity (niche theory), thus promoting coexistence of more species (Tamme et al. 2010, Stein et al. 2014). Area is also inherent in niche theory, as environmental heterogeneity tends to increase as area increases (Rosenzweig 1995). Generally, it must be noted that biodiversity patterns, local species abundance patterns and species-area curves, can be produced by both neutral and niche processes (Pyšek et al. 2002, Tews et al. 2004, Báldi 2008).

It is not *per se* obvious how to measure the influence of environmental heterogeneity on global species richness, as many potential environmental variables could be considered (Stein and Kreft 2015). Other studies have focused on environmental heterogeneity variables such as climate and elevational heterogeneity (Hawkins et al. 2003, Rodríguez et al. 2005, Tuanmu and Jetz 2015). But, studies do not compare the relative strength of multiple variables on species richness patterns, they only focus on one type of environmental heterogeneity (Pyšek et al. 2002, Báldi 2008). Moreover, there is an inherent problem when analysing environmental variables in isolation, as both niche and neutral processes can act at the same time, and area correlates differently with different environmental variables. Therefore, the influence of area and environmental variables on global species richness relationships should be simultaneously investigated to partition changes in species richness into those components explained by predictors of environmental heterogeneity, and those explained by area (Legendre et al. 2005, Keil et al. 2012, Keil and Jetz 2014).

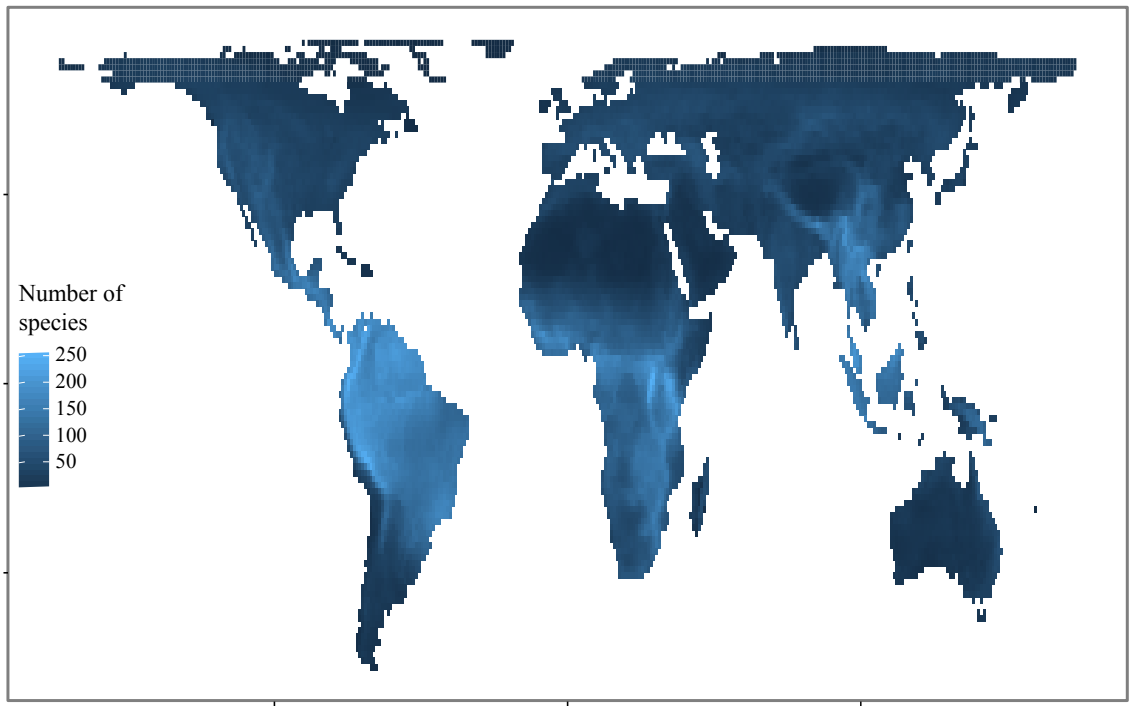


Fig. 1: Terrestrial mammal species richness across the globe,based on Olson et al. (2001), areas with bats and no native terrestrial mammals are excluded.

**Landscape scale**

Landuse change may cause loss of biodiversity. Urbanisation of the landscape is one of the major causes of biodiversity loss and urban areas are increasing worldwide in size and numbers (Foley et al. 2005, Jones and Leather 2012). But they still support some arthropod diversity (McKinney 2008), as gardens, public green spaces and semi-natural habitats within urban areas provide resources for arthropods (Pereira-Peixoto et al. 2016; Fig. 2). The amount of arthropod diversity supported could be related to size of the urban area, as it has a positive influence on plant species richness (Pyšek 1998). This trend in plant species richness is due to increasing numbers and dominance of non-native ornamental species, which are also more prevalent in the city edge than centre (McKinney 2006).

So far, urbanisation gradients tested are always in a single city (Egerer et al. 2017) and are defined by the amount of built-up area or density of people at different locations from the edge to the centre (McDonnell and Hahs 2008). Green areas in the centre of cities are more isolated due to the presence of physical barriers such as roads and buildings (Peralta et al. 2011) and their distance from the urban edge. These barriers also restrict movement of insect foragers, such as bumblebees, throughout urban areas (Bhattacharya et al. 2002). Studies that examine rural-urban gradients find lower diversity of insects in the

middle of an urban area (McKinney 2006, Bates et al. 2011). The same results are found for host-parasitoid communities, but they are related to local habitat quality and to isolation of the study site, since green areas on the edge of an urban area may be colonised from the adjacent habitat and can support higher species richness than green areas in the centre of an urban area (Pereira-Peixoto et al. 2014). The influences of urbanisation on arthropods depends on which taxa they are, as pollinators can be positively affected (Baldock et al. 2015, Sirohi et al. 2015), whereas forest-dependent ground beetles are negatively affected (McKinney 2008, Vergnes et al. 2014). This diversity of responses indicates the existence of individualistic or trait-dependent species responses (Gleason 1926, McDonnell and Hahs 2008). A similar relationship to what is found with increasing urbanisation from the edge to the centre of a city could be expected with increasing urban area size.

Fig. 2: Edinburgh, Scotland, with the main green area types used: gardens, parks and pastures. © Hannah Reininghaus.

**Local scale**

Complex vegetation structure and high plant diversity have positive effects on arthropod richness (Haddad et al. 2001). The structure of urban habitat should also have a strong effect, as, for example, gardens have a diverse structure with lawns, flowers, shrubs and trees within a small area, whereas parks are dominated by short grass with few wild herbs and trees with an occasional flower bed (Mata et al. 2017). The vegetation type is also important for arthropod species, as spiders may thrive in habitats with larger extents of woody areas (Vergnes et al. 2014), which are more extensive in parks. Differences in habitat type could also be characterised by the local plant species richness, as gardens have a

higher number of plant species present and also higher flower cover, which could positively influence flower-visiting insects such as bumblebees (Pyšek 1998, Baldock et al. 2015).

Pollinators need floral resources and nesting sites to survive (Westrich 1996, Ebeling et al. 2008; Fig 3), these are available in green spaces in urban areas, where plant diversity and floral resources are high. Private gardens and parks offer many floral resources with high plant richness and high temporal stability (Fetridge et al. 2008). This resource stability is not the case in farmland, where mass flowering crops can support some pollinator species, but only for a limited time period per year (Westphal et al. 2003). Some pollinators, such as bumblebees, are highly mobile and forage both in the direct surroundings of their colony and throughout the landscape; high local plant richness can support bumblebee populations, but barriers to movement in the landscape may negatively affect access to these resources (Westphal et al. 2006). Solitary bees require semi-natural habitat as nesting resource, whereas syrphid flies are not linked to semi-natural habitat availability in the landscape (Jauker et al. 2009). Syrphid flies are present at much higher diversity and abundance in farmland landscapes with no semi-natural habitats than solitary bees (Verboven et al. 2014, Baldock et al. 2015) and may also be effective pollinators (Orford et al. 2015). Hence, pollinator communities can be expected to show different responses to urbanisation depending on the pollinator group considered.

Plant-pollinator networks are based on the local plant community (Memmott 1999), but are still influenced by the surrounding landscape. It is therefore difficult to disentangle the influences of local from landscape features on plant-pollinator networks. This can be achieved using an experimental approach where the same plant community is replicated in different urban landscapes (Geslin et al. 2013).

Species richness patterns and community composition are influenced by different processes at scales from local and landscape to the entire globe. These processes range from resource provisioning and habitat heterogeneity to the influence of area and environmental heterogeneity. Determining which processes at which scale influence species richness and communities strengthens our understanding and increases our knowledge of how the ecological world is structured.

Fig. 3: Common pollinators found in urban areas. *Bombus lapidarius* (L.) on *Geranium pratense* (L.), *Bombus hortorum* (L.) on *Geranium magnificum*, *Protichneumon pisorius* on *Euphorbia griffithii* (Hook), *Apis mellifera* (L.) on *Kniphofia* spec. (L.), *Syrphus ribesii* (L.) on *Veronica teucrium* (L.), *Episyrphus balteatus* (de Geer) on *Hieracium aurantiacum* (L.). © Kristy Udy.

## Chapter Outline

In this thesis I investigated how animal communities are influenced by urbanisation at the local and landscape scale and how species richness patterns are structured at the global scale.

In **Chapter 2** my aim was to test how pollinator communities change across an urbanisation gradient comparing farmland with villages and cities and how plant-pollinator network structure is altered in these different landscapes. I controlled for the potential influence of the local composition of floral resources by conducting pollinator observations on experimental plant patches where the same plant species were grown under the same conditions along my urbanisation gradient. Species richness of pollinators and community stability decreased with increasing urbanisation, although local plant richness simultaneously increased. Pollinator groups showed differing responses to urbanisation as solitary bees were more often present in city gardens and syrphid flies were more often present in farmland, with both present in village gardens. Enriching the interface between these two landscape types (village gardens) is of particular importance as it supports a complementary pollinator community.

In **Chapter 3** I assessed whether bumblebees in urban areas forage only locally in gardens or search for major floral resources throughout the landscape. This was done by marking and tracking bumblebees to assess their short-range movement, their long-distance movement was studied using pollen collected from the bumblebee colonies. Bumblebee colonies were setup along a contrasting gradient of farmland to urban in settlements of increasing size. This gradient included farmland, farmhouse gardens, village gardens and city gardens. Bumblebee colony performance was measured by calculating weight gain. Bumblebee workers visited plants in the local surroundings and foraged at greater distances to their colonies if oilseed rape was flowering. My results show that resources at both the local and landscape scale should be taken into account for maintenance and conservation of pollinators. It indicates that urban green spaces can serve as reservoirs for bumblebees and it is crucial in this time of high biodiversity loss to raise the attention of urban planners of the importance of flower rich areas for pollinators in urban areas.

In **Chapter 4** I investigated how local vs. landscape scale variables structure plant and arthropod communities in urban areas. The influence of the urban landscape on arthropod communities was tested for the first time along an urbanisation gradient from small villages to a mid-size city, while also analysing the role of the position

in an urban area (edge or centre). The arthropods sampled were functional groups of Coleoptera, Araneae and Hymenoptera. Both local and landscape factors influenced Coleoptera and Araneae species richness but Hymenoptera were only influenced by local factors. Urban area size positively influenced Araneae richness but had a mostly negative impact on Coleoptera richness. My study exhibits contrasting responses of arthropod communities to urbanisation, with different influences at local and landscape scales, which may explain the heterogeneous patterns found in the literature. Also, it deepens our understanding of how arthropod communities respond to urbanisation, as it is the first to investigate the influence of both urban area size and position in an urban area.

In **Chapter 5** I determined the relative importance of niche and neutral processes on species richness patterns for the globe. I also explored how these species richness patterns changed in the different biogeographic regions of the globe. I found that environmental heterogeneity explains species richness relationships better than area does, indicating that niche processes are more prevalent than neutral processes. I conclude that understanding species richness relationships and predicting how they might change under future conditions, requires explicitly considering the role of environmental heterogeneity and its loss.

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# Chapter 2

# Plant-Pollinator Interactions along an Urbanisation Gradient from Cities and Villages to Farmland Landscapes

*Heriades truncorum* (L.) on *Veronica spicata* (L.). © Hannah Reininghaus

Authors: Kristy Leah Udy, Hannah Reininghaus, Christoph Scherber, Teja Tscharntke

## Abstract

Urbanisation affects pollinator diversity and plant-pollinator networks by changing resource availability locally and in the surrounding landscape. To determine how plant-pollinator communities change with increasing urbanisation, we experimentally established N = 12 standardised plant communities in farmland, villages and cities to identify the relative role of local and landscape effects along this urbanisation gradient. We found that species richness of pollinators and plant-pollinator network metrics such as robustness, interaction evenness and interaction diversity decreased with increasing urbanisation, although local plant richness increased in urban areas. Number of flower visits by solitary bees, but not bumblebees, syrphid flies and other flies, were highest in cities and lowest in farmland, with villages being intermediate. The high plant species richness in urban gardens appeared to support solitary bees more than other pollinator groups. In conclusion, urban and farmland landscapes support different pollinator communities. Enriching the interface between these two landscape types is of particular importance for a complementary pollinator community.

Keywords: plant-pollinator network; urbanisation; city size; plant richness; solitary bees; syrphid flies.

## Introduction

Worldwide, the predominant landscape type is farmland interspersed with urban areas, with rural areas generally supporting lower insect diversity than urban areas (Bates et al. 2011). This depends on local habitat quality, as natural areas do support highest insect diversity, but they are often small in size and patchily distributed throughout the landscape. Yet, plant richness in urban areas is often higher due to the presence of many non-native plants in gardens (Pyšek 1998), positively affecting flower-visiting taxa (Baldock et al. 2015, Sirohi et al. 2015). Urban gardens and other green areas play a particularly important role for pollinators as they provide pollen and nectar resources for pollinators (Ahrne et al. 2009).

The majority of studies comparing farmland with urban areas find that wild bees are more diverse and abundant in urban areas(Hall et al. 2016). However, Bates et al. (2011) found the opposite, and Ahrne et al. (2009) found that bumblebee richness shows a negative relationship with increasing urbanisation. These contrasting results illustrate that urbanisation effects on pollinators may be diverse. Additionally, urban ecology studies have so far mostly been conducted in a single city and did not compare a range of urban area size on pollinator community composition (Egerer et al. 2017). Here, we employ a novel approach using standardised plant communities along an urban-rural gradient to study a broad range of pollinator groups. This approach allows strong inference (due to its experimental nature) and generalisations extending beyond previous studies (Geslin et al. 2013, Theodorou et al. 2017). Our design also covers a broad gradient in city size, from small villages to mid-size cities.

The structure of plant-pollinator networks may change with community composition and richness of pollinators (higher richness correlates with higher network stability (McCann 2000, Dunne et al. 2002)). These networks are based on the local plant community (Memmott 1999), but are still influenced by the surrounding landscape. It is therefore difficult to disentangle the influences of local from landscape features on plant-pollinator networks. This can be achieved using an experimental approach where the same plant community is replicated in different urban landscapes (Geslin et al. 2013, Theodorou et al. 2017).

Pollinators need floral resources and nesting sites to survive (Westrich 1996, Ebeling et al. 2008), provided by green spaces in urban areas, where plant diversity and floral resources are abundant. Private gardens and parks provide many floral resources with high plant richness and high temporal stability (Fetridge et al. 2008). This resource stability is

not the case in farmland, where mass flowering crops can support some pollinator species, but only for a limited time period per year (Westphal et al. 2003). Wild bee pollinators require semi-natural habitat as nesting resource, whereas syrphid flies are not linked to semi-natural habitat availability in the landscape (Jauker et al. 2009). Syrphid flies are present at much higher diversity and abundance in farmland landscapes with no semi-natural habitats than wild bees (Verboven et al. 2014, Baldock et al. 2015) and may also be effective pollinators (Orford et al. 2015). Hence, pollinator communities can be expected to show different responses to urbanisation depending on the pollinator group considered.

We test how pollinator communities change across an urbanisation gradient comparing farmland with villages and cities and how plant-pollinator network structure is altered in these different landscapes. We controlled for the potential influence of the local composition of floral resources by conducting pollinator observations on experimental plant patches where the same plant species were grown under the same conditions along our urbanisation gradient.

## Methods

### Study sites

The study was conducted in North-Central Germany, in the Southern part of the federal state of Lower Saxony, within a 30 km radius of Göttingen (51°32’28.61”N, 9°54’56.89”E). We sampled along an urbanisation gradient from farmland and villages to cities, including grassy field margins in pure farmland, and gardens in villages and cities. Farmland sites were at least 500 m from the nearest house. Village sites were close to the village edge and were surrounded by a 500 m buffer comprising approximately 50% urban and 50% farmland. City sites were at least 500 m from the city edge and were completely surrounded by a buffer of 100% urban area (Fig. 1). Our urbanisation gradient was constructed in this way to test the influence of amount of farmland in the landscape and the urban area size. N=12 sites were used: four farmland sites (maximum distance 30 km from Göttingen), two villages (two gardens each: Dransfeld (51°50’06.01”N, 9°76’23.95”E) and Diemarden (51°48’72.82”N, 9°98’05.67”E) and two cities (two gardens each: Göttingen and Einbeck (51°49’13.29”N, 9°52’6.14”E), separated by a minimum of 500 m inside the city border).

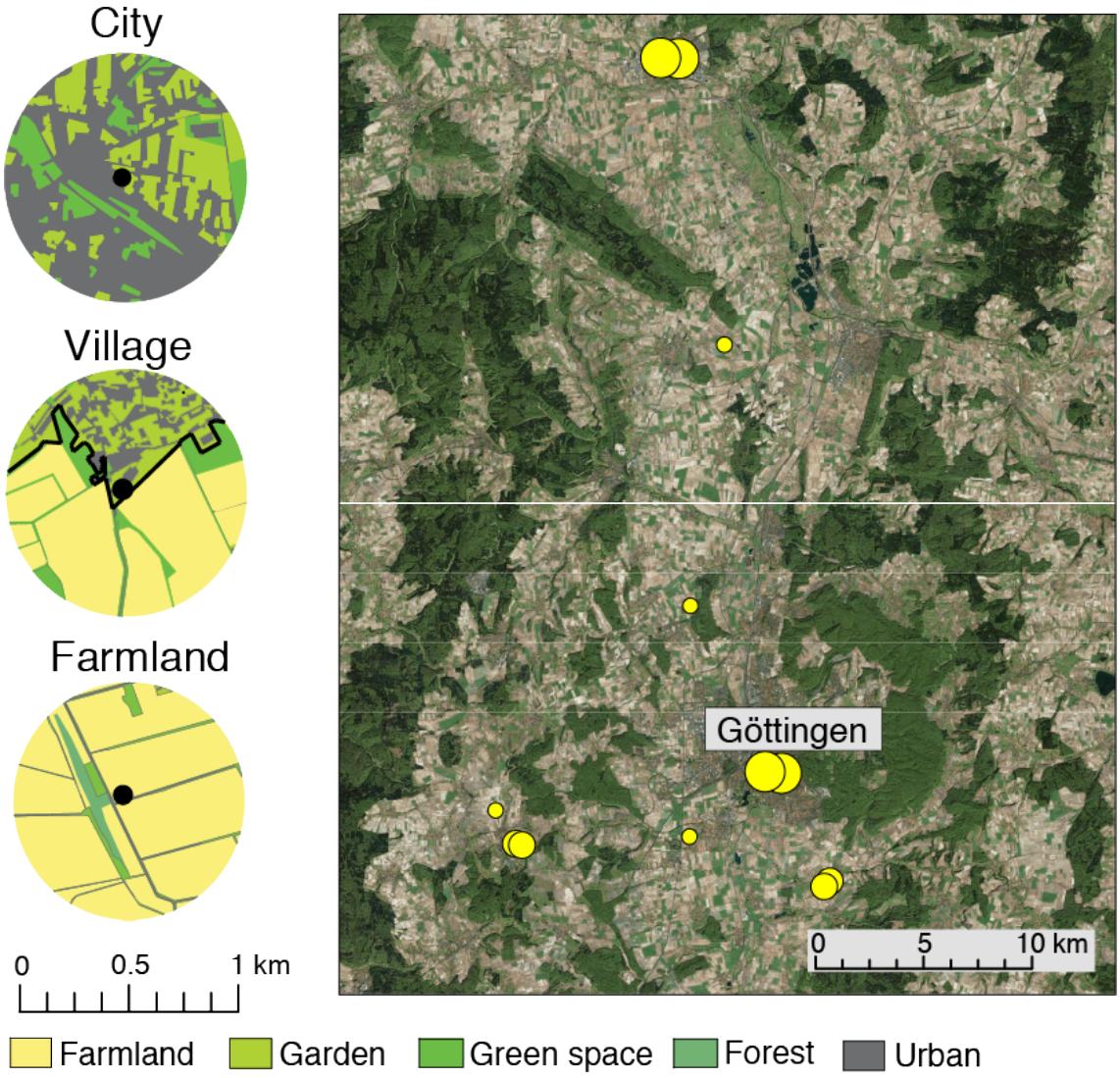


Fig. 1: GIS maps (ArcGIS, v. 10.4.1, ESRI) of the three different landscape types used. Yellow points indicate the sites used and point size denotes urban area type, small = farmland, medium = village and large = city. Buffer is 500 m in radius with colours denoting land-use types in each landscape. The black point on each map denotes our site and the black line in the village landscape indicates the border of the urban area. © Hannah Reininghaus. Basemap source: Esri basemap (Bing).

**Experimental plant plots**

Experimental plant patches were established in April 2015 (size 80 x 80cm) in the 12 sites (Fig. 2). We standardised soil conditions by using a soil mix at all sites (mix from volcanic clay, peat, lime carbonate and NPK fertiliser; 180 mg/L N, 180 mg/L P; 260 mg/L K; 130 mg/L Mg and 100 mg/L of S with a pH of 5.9). Approximately 30 mL of NPK fertiliser was added when the seeds were planted, which contained equal parts N (8%) and P (8%). The numbers of plant seeds used were standardised to approximately 20 seeds per plant species and were evenly scattered over the soil. The plant species

used were: *Phacelia tanacetifolia* (Benth.) and *Sinapis arvensis* (L.). These annual plant species were chosen as they flower in the first year and have a variety of flower shape and colour so they would be attractive to a wide range of pollinators and functional groups. Plant patches were watered once a week with 10 L of water and fertilised once more after one month. The perennial plants *Veronica spicata* (L.) and *Astilbe chinensis* (Maxim.) were added to the plant plots in June. This mixture of four plant species included plants with high quality pollen and nectar that are attractive to pollinators and a mixture of flower types with open and tubular both represented and also a mixture of colours: yellow, white and purple (Pritsch 2007). All our plant species flowered simultaneously at the start of July for 2 weeks.

Fig. 2: Experimental plant plot. Plant species are from top to bottom: *Sinapis arvensis, Phacelia tanacetifolia, Astilbe chinensis* and *Veronica spicata.* © Kristy Udy.

**Pollinator Observations**

Insect observations were run in early July (Leong et al. 2016) 2015 for 15-minute intervals at two different times of the day (total observation hours = 6): morning (10-11:30) and midday (12:45-14:30), these times were centred on midday (13:15), calculated

as the midpoint between sunrise and sunset. Six plant plots were visited each day, three per time period, and the order they were visited was randomised. Observations were conducted on a corner of each plant plot (50 x 50 cm). We observed all insect pollinators that visited a flower, identified them to genus or species level and counted the number of visits (landing on a single flower equals one visit) for each insect until it left the plant plot. We also recorded which plant species each insect pollinator was on. Insect pollinators included: solitary bees (i.e. non-bumblebees), bumblebees, butterflies, syrphid flies, non-syrphid flies and wasps. Honeybees (total = 79 specimens) were observed but later excluded from analysis as their presence in the landscape depends on whether there are hives set up nearby. All flowering plants within a distance of 20 m were identified to species level and total flower cover was estimated.

**Statistics**

We found no differences in pollinator richness and their abundance between morning and mid-day observations; thus, abundances were summed for every observation day, resulting in a total of 363 data points. All analyses were performed using R (version 3.3.0; R core Team 2016). All response variables were tested against the landscape gradient and plant species richness (all plant species within 20 m of plant plot). These variables were always tested in separate models, as plant species richness was influenced by landscape type (Fig. 3). To test these influences on the pollinator richness and their number of visits, we used mixed-effects models (Bates et al. 2015) with site included as a random effect. We tested which distribution fitted each response variable using the fitdistrplus package (Delignette-Muller and Dutang 2015). Poisson models were used to test pollinator richness against the explanatory variables and negative binomial models (Bates et al. 2015) were used to test number of visits as the counts indicated overdispersion (Crawley 2013). Pollinator group was tested using multinomial models (Venables and Ripley 2002) against our explanatory variables. Wasps and butterflies were excluded from all analyses, as they were present in only two of the 12 sites. Bipartite networks (Fig. 7) were created from the plant-pollinator interactions for each site and their structure analysed with network level metrics using the bipartite package (Dormann et al. 2008). The network level metrics used were: robustness, interaction evenness and Shannon diversity of interactions (based on: Blüthgen et al. 2006). All models were simplified using a list of candidate models with all possible combinations of

experimental variables and interactions; models were ranked based on AICc and the model with the lowest AICc value was used (Information Theoretic approach (Mazerolle 2016)).

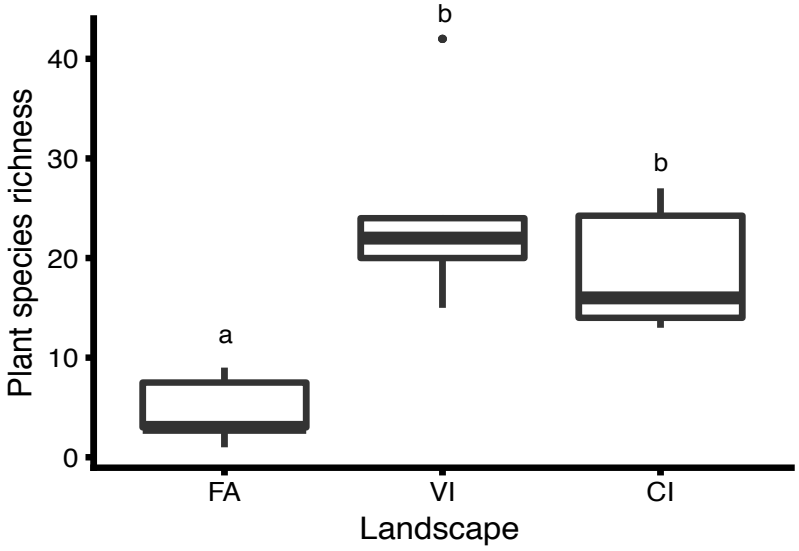


Fig. 3: Flowering plant species richness within 20 m of experimental plant patches in different landscapes along an urbanisation gradient. $N_{FA} = 4$, $N_{VI} = 4$, $N_{CI} = 4$; FA = Farmland, VI = Village, CI = City. Bars that do not share the same letter show significant differences ($p < 0.05$).

## Results

We observed 18 pollinator morphospecies in farmland, and 15 morphospecies in both villages and cities. Of these, there were a total of 117 individuals in farmland, 115 in villages and 79 in cities and total number of flower visits by these individuals was 525 in farmland, 536 in villages and 293 in cities. Flower visitor taxonomic groups were classified into: solitary bees, bumblebees, syrphid flies and non-syrphid flies.

The pollinator group identity (Chi-square = 53.13, d.f. = 3, $p < 0.001$) and an interaction between pollinator group identity and landscape type (Chi-square = 50.46, d.f. = 5, $p < 0.001$) influenced the number of visits by pollinating insects with solitary bees and syrphid flies visiting flowers most often, but in different landscape types (Fig. 4; Table 1). The visits by syrphid flies were higher in farmland and villages than in cities (Chi-square = 51.05, d.f. = 2, $p < 0.001$) and visits by solitary bees were higher in urban areas than in farmland (Chi-square = 6.93, d.f. = 2, $p = 0.031$). The other main pollinator groups, except for solitary bees, also showed a negative trend with increasing urbanisation (Fig. 4). The probability of occurrence of pollinator groups was significantly influenced by landscape type (LR Chi-square = 721.81, d.f. = 2, $p < 0.001$; Supplementary material Fig. S1) and

was also influenced by plant richness in the direct surroundings (LR Chi-square = 185.59, d.f. = 1, $p < 0.001$). With high plant richness, fewer pollinators per group were present. This pattern is most likely due to plant species richness being positively correlated with presence of urban area as plant richness was higher in villages and cities compared to farmland (urban area = impermeable sealed ground; Pearson correlation = 41%; Fig. 3).

Pollinator richness was highest in farmland areas (Chi-square = 8.31, d.f. = 1, $p = 0.016$) where plant richness was lowest (Chi-square = 6.33, d.f. = 1, $p = 0.012$; Fig. 5). Community composition also changed in the different landscapes, with solitary bees dominating in urban areas and syrphid flies dominating in farmland landscapes, but overlapping in the village landscapes (Fig. 4). Plant-pollinator networks (Fig. 7, Supplementary Table S1) were more robust in farmland and in villages compared with cities (F-ratio = 6.962,9, $p = 0.015$; Fig. 6) and had the highest interaction evenness in farmland compared to urban areas (F-ratio = 8.992,9, $p = 0.007$). Shannon diversity of interactions was also highest in farmland and in villages compared with cities (F-ratio = 10.482,9, $p = 0.005$).

Table 1: Chi-square values, degrees of freedom (as subscript) and level of significance for all variables and responses.

| **Pollinators** | | | | |
|---|---|---|---|---|
| | | **No. of visits*[1]** | **No. of visits Syrphid*[1]** | **No. of visits solitary bee*[1]** |
| | **Pollinator type** | $53.13_3$*** | NA | NA |
| | **Landscape type*[5]** | $50.46_5$*** | $51.05_2$*** | $6.93_2$* |
| | **Plant richness** | $0.001_3$ | $0.04_1$ | $0.6_1$ |
| | | **Probability of occurrence*[2,3]** | **Species richness*[4]** | |
| | **Pollinator type** | NA | 0.069 | |
| | **Landscape type** | $721.81_2$*** | $8.31_1$* | |
| | **Plant richness** | $185.59_2$*** | $6.33_1$* | |
| **Network structure (test = linear mixed effects model** | | | | |
| | | **Robustness** | **Interaction evenness** | **Shannon diversity of interactions** |
| | **Landscape type** | $6.96_{2,9}$* | $8.99_{2,9}$** | $10.48_{2,9}$** |

*[1] tested using mixed effects model with negative binomial family

*[2] tested using multinomial with pollinator type as response

*[3] tested with LR Chi-square

*[4] tested using mixed effects model with poisson family

*[5] for 'number of visits' this is an interaction: landscape type*pollinator type

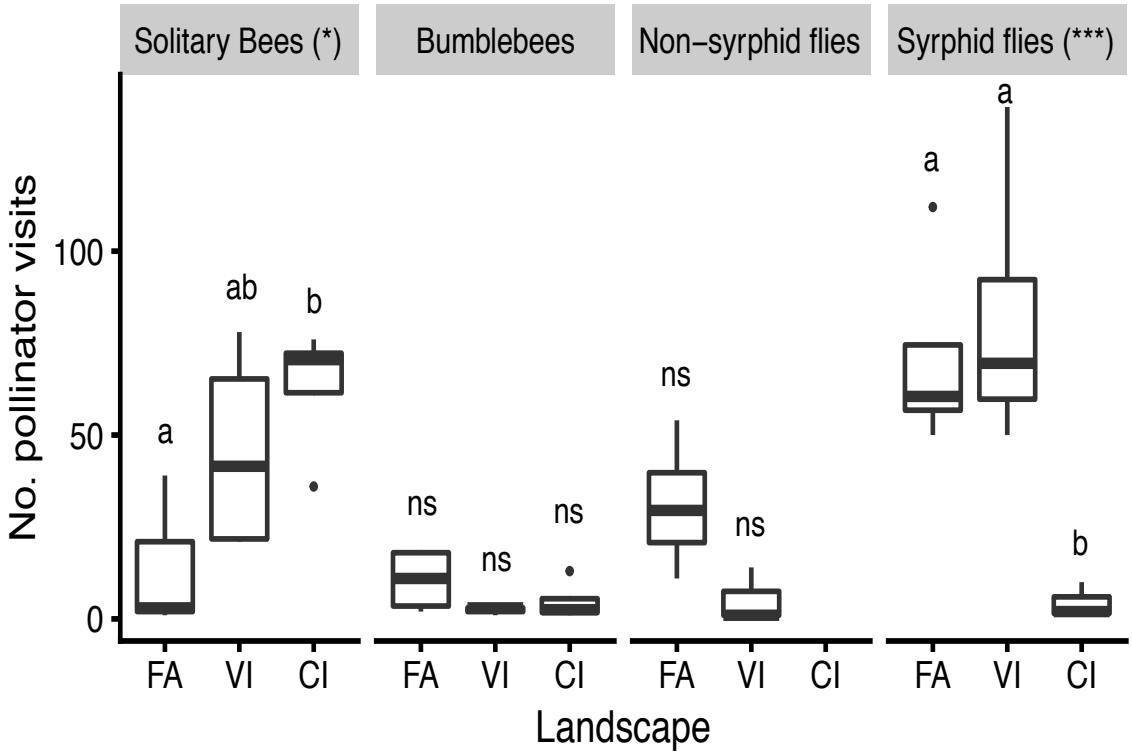


Fig. 4: Number of pollinator visits for each pollinator group. Syrphid flies exhibited more flower visits than the other pollinator groups ($p < 0.001$) and had more visits in farmland and villages than in cities ($p < 0.001$). Solitary bees showed the opposite trend with more visits in urban areas than in farmland ($p = 0.031$). NFA = 4, NVI = 4, NCI = 4; FA = Farmland, VI = Village, CI = City. Bars that do not share the same letter show significant differences ($p < 0.05$). NS = no significant differences ($p > 0.05$).

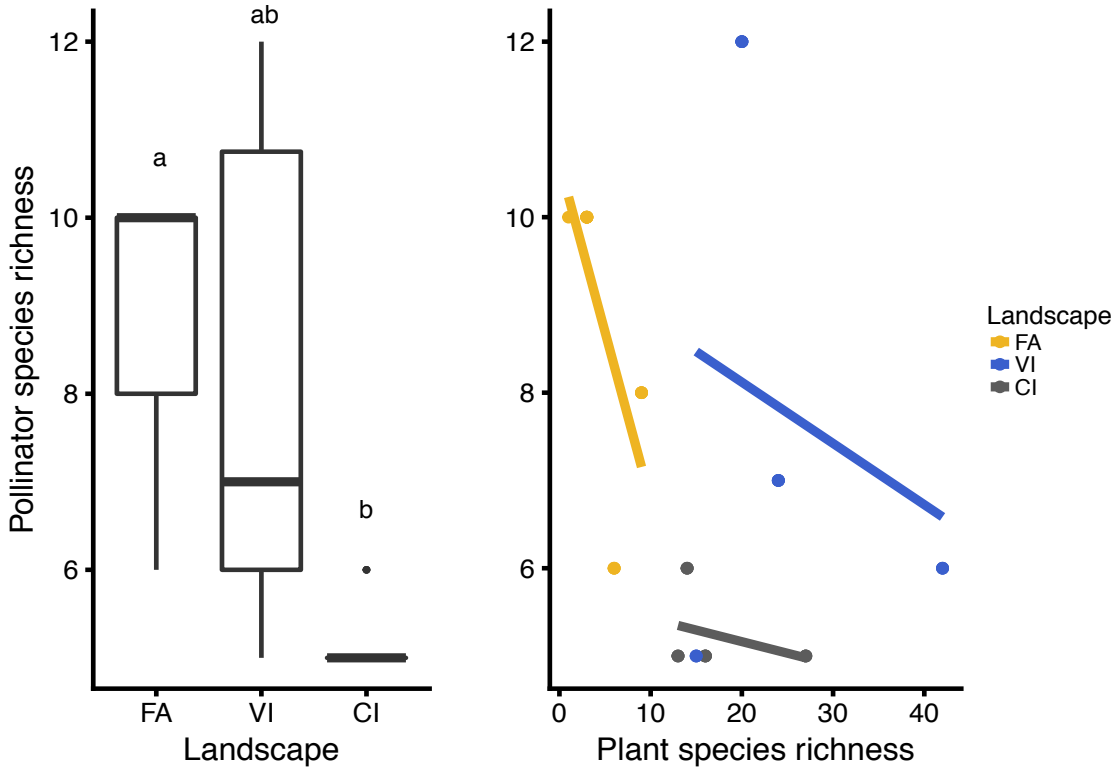


Fig. 5: Pollinator morphospecies richness was influenced by landscape type and plant species richness in the local surroundings. $N_{FA} = 4$, $N_{VI} = 4$, $N_{CI} = 4$; FA = Farmland, VI = Village, CI = City. Bars that do not share the same letter show significant differences ($p < 0.05$).

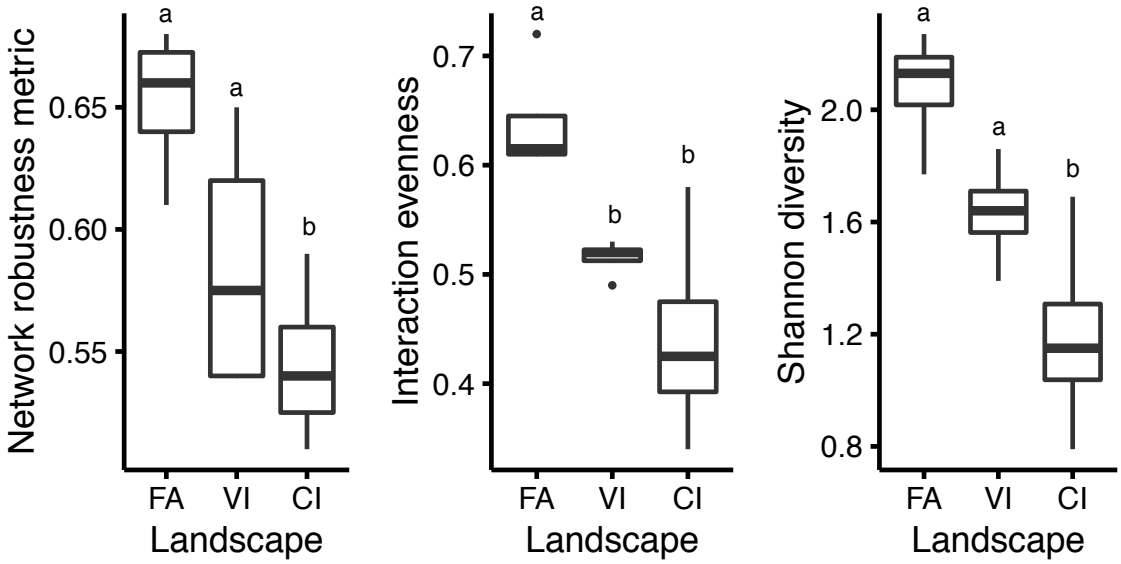


Fig. 6: Network metrics tested against the influence of landscape. Insect communities had significantly higher robustness ($p = 0.014$), interaction evenness ($p = 0.007$) and Shannon diversity ($p = 0.005$) in farmland landscapes. $N_{FA} = 4$, $N_{VI} = 4$, $N_{CI} = 4$; FA = Farmland, VI = Village, CI = City. Bars that do not share the same letter show significant differences ($p < 0.05$).

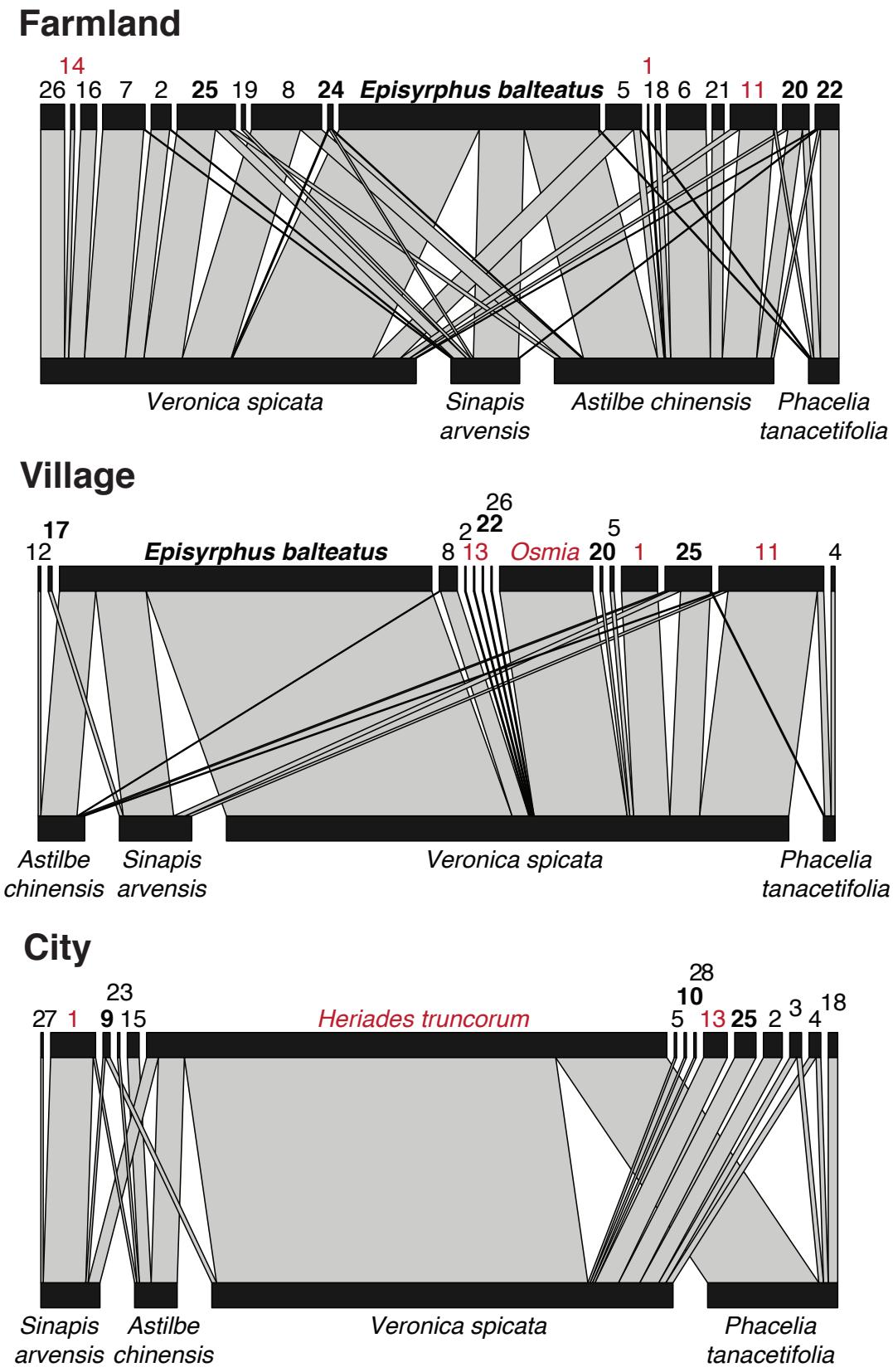


Fig. 7: Plant-pollinator networks in the different landscape types. Numbers correspond to morphospecies (Supplementary Table S1). $N_{Farmland} = 4$, $N_{Village} = 4$, $N_{City} = 4$; Lower section = plant species, upper section = pollinator morphospecies. Names coloured grey are solitary bees and bolded names are syrphid flies.

## Discussion

In the present study, we investigated the influence of city size on plant-pollinator community structure, using observations on experimental study plots along a farmland and village to urban landscape gradient. Our results clearly show that plant species richness was higher in urban areas, but that pollinator richness decreased in urban areas. The pollinators we observed were generalists, as they visited all plant species, regardless of which landscape they were in. The pollinator groups did show some preferences as solitary bees and bumblebees preferentially visited the blue flowering species (*Phacelia tanacetifolia* and *Veronica spicata*) and non-syrphid flies that preferentially visited *Astilbe chinensis*. The pollinator group identity influenced the number of pollinator visits, as solitary bees were mainly present in cities and syrphid flies were mainly present in farmland, while both were present in villages. These changes in pollinator richness and community composition contributed to the network structure, where robustness, interaction evenness and Shannon diversity were all highest in farmland and lowest in cities, with villages being intermediate. Solitary bees were more attracted by high flower diversity and flower cover of urban sites than syrphid flies.

We observed pollinators on experimentally standardised plant plots, which allowed us to directly correlate the pollinator insects with the surrounding landscape type. Theodorou et al. (2017) also used experimental plant communities to separate the influence of local from landscape influences and found that bee richness was positively influenced by high flowering richness in urban areas. We did not observe many pollinator morphospecies at our experimental plant plots, possibly because the four plant species were flowering for only a short time period. But, we observed little change in the pollinator morphospecies present from our first to second round of observations, thus the differences between treatments appear to be fairly robust for this time of the year. However, patterns may change with season and year.

Solitary bees were present in the farmland sites in low numbers, presumably because plant plots in these sites were surrounded only by farmland with few floral resources and little semi-natural areas within the 500 m radius considered. Solitary bees disperse several hundred meters throughout the landscape (Gathmann and Tscharntke 2002). Even though there are suitable nesting sites in farmland areas and some floral resources, these are not necessarily close enough to provide suitable resources for solitary bees to survive (Westrich

1996). Gardens in urban areas provided good habitat for solitary bees, while they had higher solitary bee abundances in cities than in villages. *Heriades truncorum* (no. 11 in Fig. 7), for example, was dominant in cities but its numbers decreased along the urban gradient, with lower abundance in villages and farmland. This supports findings from Banaszak-Cibicka and Zmihorski (2012) and Fortel et al. (2014), in that plant species richness was highest in villages and cities, and solitary bee richness increased in areas with high plant richness.

Syrphid flies showed the opposite relationship, as they were present mostly in farmland and villages, with very low abundance in cities (Jauker et al. 2009, Bates et al. 2011). This was especially apparent for *Episyrphus balteatus* (no. 9 in Fig. 7) as it dominated networks in farmland and village sites, but was rarely observed in city sites. This agrees with findings from Jauker et al. (2009). Syrphid larvae are ubiquitous in crop fields (Tenhumberg and Poehling 1995). The adults feed on pollen and nectar (Haslett 1989) so require floral resources, but as they do not require specific nesting habitat and are very mobile, the fragmentation of floral resources throughout farmland landscapes is not such a problem. These differing resource requirements may have been the reason why we did not observe syrphid flies in the pure urban habitat.

The structure of plant-pollinator networks was more robust and stable in farmland and villages, where also more pollinators were present than in cities. The higher diversity and higher interaction evenness indicate few dominating morphospecies. This absence of dominating (strong) links in a network contributes to network stability and robustness, explaining why these networks are more robust in the farmland sites (May 1973, Tylianakis et al. 2010). Our results of higher interaction evenness in farmland sites contradict those by Geslin et al. (2013) who found that interaction evenness was highest in an urban area compared with farmland, but they found higher numbers of interactions in farmland. The pollinator group present determined the patterns found: there was low interaction evenness in cities with fewer pollinators, which were dominated by solitary bees. In villages and farmland there was higher pollinator richness with no dominant morphospecies, resulting in higher evenness of interactions.

Urban areas do support pollinator insect communities, but they are not optimal habitat, as resources are patchy and often isolated with many barriers to pollinator dispersal in the form of roads and buildings. The size of the built-up area had a strong influence on the pollinator community, as we found that the pollinator community in villages was a mixture of that found in urban areas and in farmland. This agrees with

findings from Bates et al. (2011) who found more syrphid flies in farmland than in urban areas and with Sirohi et al. (2015) who found that native bee richness in urban areas is higher than in nearby farmland. Due to this crossover of farmland and urban insect communities in villages we suggest that habitat enrichment efforts should focus conservation in these areas to promote the largest pollinator richness possible.

In conclusion, conservation of green areas in urbanised landscapes promotes solitary bee communities, while a diverse pollinator community can be found in villages as this is where there is a crossover of the pollinator communities of farmland and urban areas.

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## Supplementary Material

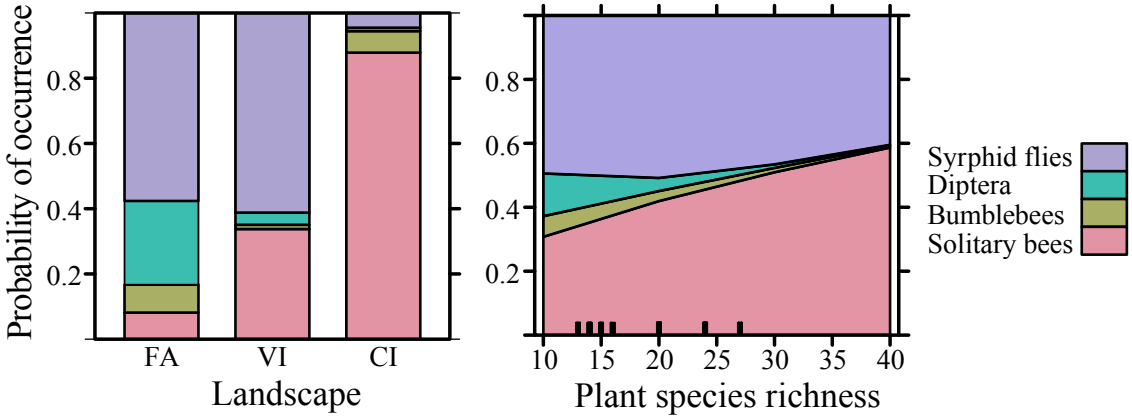


Fig. S1. Predicted probability of pollinator group occurrence in the different landscapes from the multinomial model. Probabilities were calculated using the 'allEffects' function in the effects package in R, back-transforming probabilities from a logit scale with reference to the baseline category (Fox 2003; Fox & Hong 2009). Syrphid flies were present significantly more often in farmland and village landscapes, while solitary bees were present significantly more often in city landscapes. $N_{total}$ = 12, $N_{FA}$ = 4, $N_{VI}$ = 4, $N_{CI}$ = 4; FA = Farmland, VI = Village, CI = City.

Table S1: Pollinators corresponding to numbers in bipartite network diagrams (Fig. 4).

| Number | Pollinators |
|---|---|
| 1 | *Andrena* spec.[1] |
| 2 | *Bombus hortorum* (L.) |
| 3 | *Bombus hypnorum* (L.) |
| 4 | *Bombus pascuorum* (Scopoli) |
| 5 | *Bombus terrestris* (L.) |
| 6 | *Cynomyia* spec. |
| 7 | *Empididae* |
| 8 | *Empis* spec. |
| 9 | *Episyrphus balteatus*[2] (De Geer) |
| 10 | *Eristalis* spec.[2] |
| 11 | *Heriades truncorum*[1] (L.) |
| 12 | *Hydrotaea* spec. |
| 13 | *Hylaeus confuses*[1] (Nylander) |
| 14 | *Hylaeus styriacus*[1] (Förster) |
| 15 | Ichneumonidae gen. spec. |
| 16 | *Maniola jurtina* (L.) |
| 17 | *Meliscaeva cinctella*[2] (Zetterstedt) |
| 18 | *Osmia* spec. |
| 19 | *Pieris brassicae* (L.) |
| 20 | *Platycheirus* spec.[2] |

| | |
|---|---|
| 21 | *Sarcophaga carnaria* (L.) |
| 22 | *Sphaerophoria scripta*[2] (L.) |
| 23 | *Symmorphus* spec. |
| 24 | Syrphidae[2] gen. spec. |
| 25 | *Syrphus ribesii*[2] (L.) |
| 26 | *Thymelicus lineola* (Ochsenheimer) |
| 27 | *Vespula* spec. |
| 28 | *Vespula vulgaris* (L.) |

[1]Solitary bees

[2]Syrphid flies

# Chapter 3

# Reversed Importance of Local vs. Landscape Flower Resources for Bumblebee Foraging and Colony Performance along Farmland-Urban Gradients

*Bombus terrestris* (L.). © Kristy Udy

Authors: Hannah Reininghaus, Kristy Leah Udy, Erin Treanore, Teja Tscharntke and Christoph Scherber

## Abstract

Increasing urbanization may lead to declines in pollinator biodiversity and associated pollination services. Here, we study how floral resources at local and landscape scales affect bumblebee foraging and colony performance along a farmland-urban gradient. Bumblebee colonies were setup along a contrasting farmland to urban gradient in settlements of increasing size. We conducted a marking tracking experiment with fluorescent dye to determine how bumblebees forage in the local surroundings of their colonies and took pollen samples to investigate bumblebee long-range foraging behaviour. From farmland to farmhouses, village gardens and city gardens, distance to mass-flowering crops (i.e. oilseed rape) increased and oilseed rape pollen sampled by bumblebees decreased, from 19% to just 2%. Instead, bumblebees in village and city gardens sampled more pollen, exploiting the high local plant diversity. This counterbalancing resource use may explain why weight of bumblebee colonies did not differ from farmland to cities. In conclusion, the relative importance of garden resources and landscape resources for bumblebee performance reversed along the farmland-urban gradient, which needs to be taken into account for pollinator management. It is crucial in the time of biodiversity loss to raise the attention for the importance of flower rich areas for pollinators in urban and farmland areas.

Key words: Apidae, *Bombus terrestris*; urbanisation; city size; resources; bee decline; pollinator; gradient; fluorescent dye; movement

## Introduction

Urbanisation is a major threat to natural habitats and associated biodiversity in anthropogenic landscapes (Goulson et al. 2005, Biesmeijer et al. 2006, Potts et al. 2010) The increase of urban areas results in landscape modification through the conversion of crop lands, pastures and natural habitats into built-up areas and urban and suburban environments (Grimm et al. 2008) However, urban areas may serve as refuges for pollinator communities, when agricultural landscapes are dominated by farmland, as long as sufficient green areas are available that can support high pollinator species richness (Goddard et al. 2010, Williams et al. 2015, Hall et al. 2016).

Most urban ecology studies sample along a farmland to urban gradient in a single city where they focus on natural habitats within the farmland landscape or on biodiversity conservation (Egerer et al. 2017). To increase our understanding of how urbanisation affects biodiversity services, broad-scale, highly replicated studies of resource use in different settlements with increasing amount of urbanisation will be beneficial. As little is known about resource use of pollinators in response to contrasting amounts of farmland and urban area, we focus here on bumblebees and how they are influenced by landscape-wide mass flowering crop or local garden flower resources. Although the flowering period of mass-flowering crops is limited, they may positively affect bumblebee colony growth as they provide additional foraging habitat and resources (Westphal et al. 2003, 2009).

Bumblebees (*Bombus* spp.) are important pollinators of wild plants and provide pollination services to crop plants (Velthuis and van Doorn 2006). Yet, both their nesting sites and food resources currently decline at alarming rates in response to anthropogenic pressures, such as habitat conversion to farmland or urbanisation. Such loss of habitat and flowering plant resources may contribute to overall pollinator declines across Europe (Potts et al. 2010, Winfree 2010), with potentially negative impacts on pollination services (Allen-Wardell and Others 1998, Biesmeijer et al. 2006, Klein et al. 2007)

Bumblebees are highly mobile pollinators and forage both in the direct surroundings of their colony and at the landscape scale (Chapman et al. 2003, Westphal et al. 2006a, 2006b). The foraging distance of *Bombus terrestris* workers is highly variable and ranges from a few meters around the colony to 2.8 km (Walther-Hellwig and Frankl 2000, Redhead et al. 2016), but fragmented green spaces and barriers in cities can restrict bumblebee movement through the landscape (Bhattacharya et al. 2002). Collecting pollen loads is an established

method to test bumblebee flight distance and resource preference (Beil et al. 2008, Kleijn and Raemakers 2008). Another way to study bumblebee flight distance and short-distance forage behaviour is by marking individuals with fluorescent dye (Osborne et al. 2008).

In this study, we assessed whether bumblebees in urban areas forage only locally in gardens or search for major floral resources throughout the landscape. Additionally, we test whether this foraging behaviour depends on distance to farmland areas. Bumblebee colonies were setup along a contrasting gradient of farmland to urban in settlements of increasing size. This gradient included farmland, farmhouse gardens, village gardens and city gardens. To test whether bumblebees forage in their local surroundings, we experimentally marked bumblebees with fluorescent dye. Long-range movement was studied by analysing the proportion of oilseed rape (OSR) pollen in pollen samples and this was tested against the distance to local mass-flowering crop fields. Bumblebee colony performance was measured by calculating weight gain (Westphal et al. 2009).

## Material and Methods

### Study sites

The study was conducted in May 2015 in 32 sites within a radius of approximately 30 km from the city of Göttingen (central Germany). The study area consisted mainly of crop fields, permanent pastures and interspersed by forest patches and urban areas. The study sites were selected based on the amount of urban area and farmland area within a radius of 500 m. We used ArcGIS 10.4.1 (ESRI) to calculate the size of each settlement in the surroundings of Göttingen (within 30km). We selected randomly four small villages (around 0.7 $km^2$ size, Diemarden, Dransfeld, Moringen and Ebergötzen) and four cites (up to 16 $km^2$, Duderstadt, Einbeck, Göttingen and Northeim; Table S2). The farmhouse gardens and farmland sites were selected by not more than 10% urban area in a radius of 500 m (Fig. 1). Within the cities and villages we selected gardens with a size of at least 1000 $m^2$. In cities, gardens had just urban area within a radius of 500 m, whereas village gardens contained 50% urban area and 50% farmland in a radius of 500 m. The selected sites were separated by at least 500 m. In total we selected eight city gardens, eight village gardens, eight farmhouse gardens and eight farmland sites.

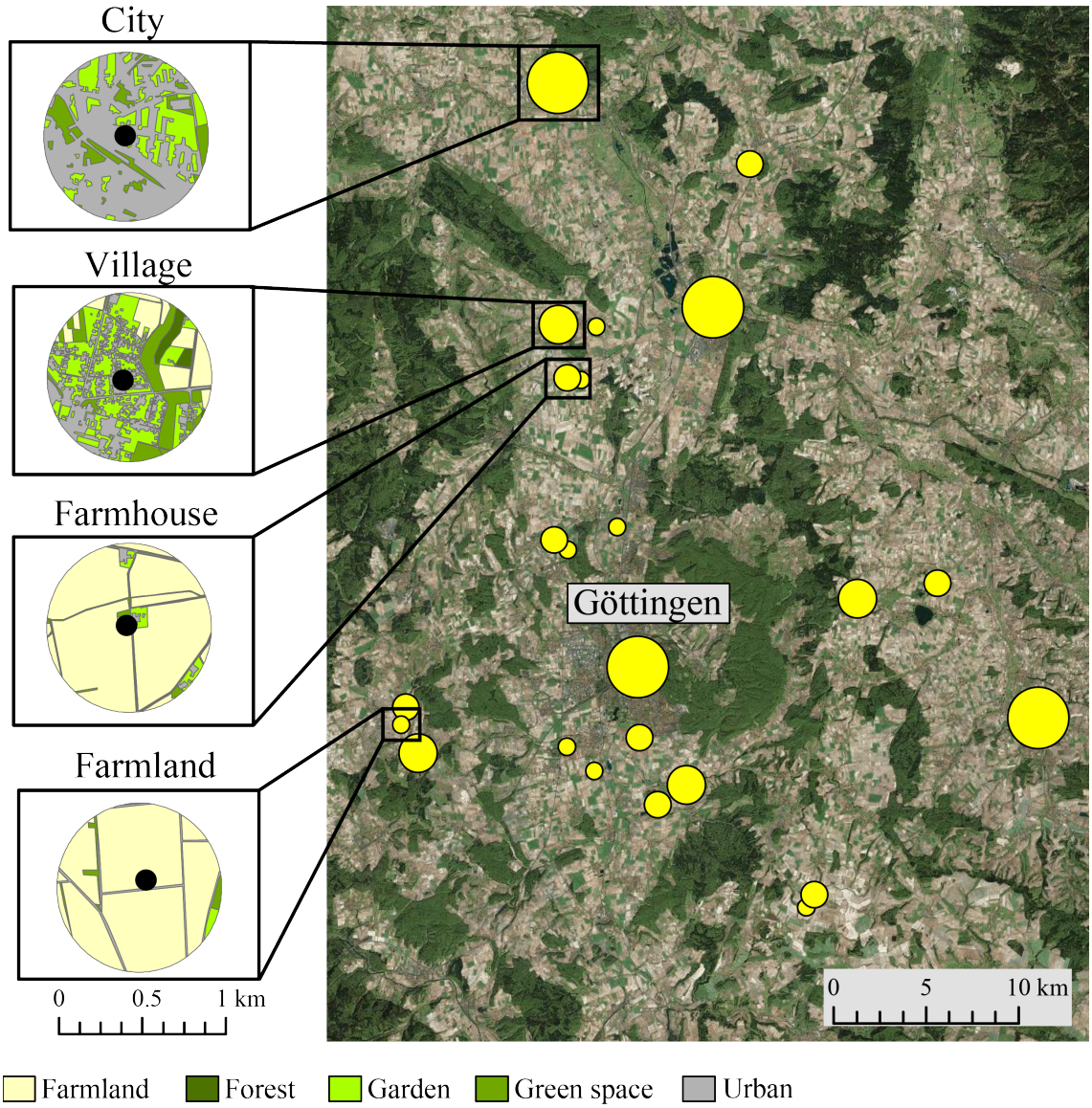


Fig. 1: Map of 32 different sized urban areas, size of circle indicates the different landscape type from farmland to farmhouse and village to city. Insets show examples of amount of urban area and farmland in a 500 m radius.

**Bumblebee colonies**

*Bombus terrestris* colonies were purchased from Biobest (Westerlo, Belgium). Bumblebee colonies were placed at field sites for three weeks from May 6th to May 28th, 2015. The colonies were setup in semi shady areas and were sheltered from the sun and rain by a wooden roof and secured to the ground with nails. One colony from the farmland

landscape was vandalised, therefore it was excluded from analysis. Before colonies were collected, we closed the exit for 24 h to prevent bumblebees from exiting the hive but left the entrance open so that forging bumblebees could enter the hive. When we collected the colonies, we closed them completely and froze them in a cool chamber. We weighed the bumblebee colonies before and after they had been setup at the field sites to calculate weight gain as a measure of bumblebee colony performance. We setup eight bumblebee colonies in farmland sites, farmhouse gardens, villages and cities.

**Movement Experiment**

To measure bumblebees´ short-range movement, we marked individuals using fluorescent dye. We put a teaspoon of fluorescent dye powder (Dane Colour UK Ltd: Swada brand) in the exit of each colony in the early morning between 6 and 7 am. Bumblebees exiting the colony were thereby coated with dye. We visited sites again the same night to remove the dye from the colonies and to check for fluorescent dye on flowers within a radius of approximately 20 m from the colonies. We searched for fluorescent dye using UV-torches (Solarforce L2P HighEnd) and mapped every plant that was visited and covered with dye powder. The experiment was conducted once per colony.

All flowering plant species per site were mapped within a radius of 20 m around each colony and we estimated the flower cover per site and calculated the species richness of flowering plants.

We used ArcGIS (v10.4.1, ESRI) to calculate the amount of urban area (streets, buildings), green area (pastures, grassland, parks and hedges), gardens, forest, water bodies and farmland within a 500 m radius around the bumblebee colonies. We also measured the distance from each colony to the next OSR field and calculated the amount of OSR fields in the bumblebee colonies surroundings.

To measure long-range movement of the bumblebees, we collected pollen samples from the colony. We used the Acetolysis method to prepare pollen samples from wax and honey (Table S3) and counted 100 pollen grains per colony and calculated the proportion of oilseed rape pollen per colony.

**Statistics**

All analyses and data visualization was performed in R 3.3.0 (R Core Team 2016). To test which local and landscape variables affected bumblebee colony growth and long and short-range foraging, we used mixed effects models with location of the bumblebee colonies

(if possible) as a random effect to control for spatial non-independence. All proportion and percentage variables (percentage flower cover, percentage urban area, proportion of OSR, proportion of OSR pollen) were transformed using the logit transformation (Fox and Weisberg 2011) and then tested against influence of increasing urbanisation using linear mixed-effects models fit by penalized quasi-likelihood (Pinheiro et al. 2016).The influence of increasing urbanisation on plant richness and the number of visited plants (fluorescent dye experiment) was investigated using generalized linear mixed-effects models with negative binomial errors (Bates et al. 2015, Venables and Ripley 2002) and distance to the next OSR field was investigated using a linear mixed effects model. Generalized linear mixed-effects models with Gamma errors were used to analyse colony weight gain in response to different landscape types and local and landscape variables. All models were simplified using AICc.

## Results

There were significant differences in the proportion of urban area between the experimental sites in the surroundings (500 m) of the colonies (Chi-square = 370.91, d.f. = 3, $p < 0.001$). Farmland contained the lowest proportion of urban area (n = 8, mean ± SD, 3.85 ± 2.14%; Figure S1), farmhouse and village gardens comprised intermediate amounts of urban area (villages: n = 8, mean ± SD, 29.27 ± 12.81%, farmhouses: n = 8, mean ± SD, 4.64 ± 2.38%) and cities had the highest amount of urban area (S1, n = 8, mean ± SD, 59.50 ± 0.86%). The amount of crops in the surroundings showed the opposite gradient (high amount of arable in farmland sites compared to city sites with very little crop land in the surroundings; within a 500 m radius).

The distance to the next OSR field increased from farmland sites to city sites (Chi-square = 18.078, d.f. = 3, $p < 0.001$). The largest distance was more than 2 km from a city garden to the next OSR field. Additionally, the amount of OSR fields in the surrounding landscape decreased significantly from farmland sites to city sites (Chi-square = 15.334, d.f. = 3, $p = 0.002$, Fig. 2 C, D).

Local plant richness was higher in urban sites compared to farmland sites and flowering plant cover increased with amount of urban area (Chi-square = 2.757, d.f. = 3, $p = 0.431$, Fig. 2 A and B).

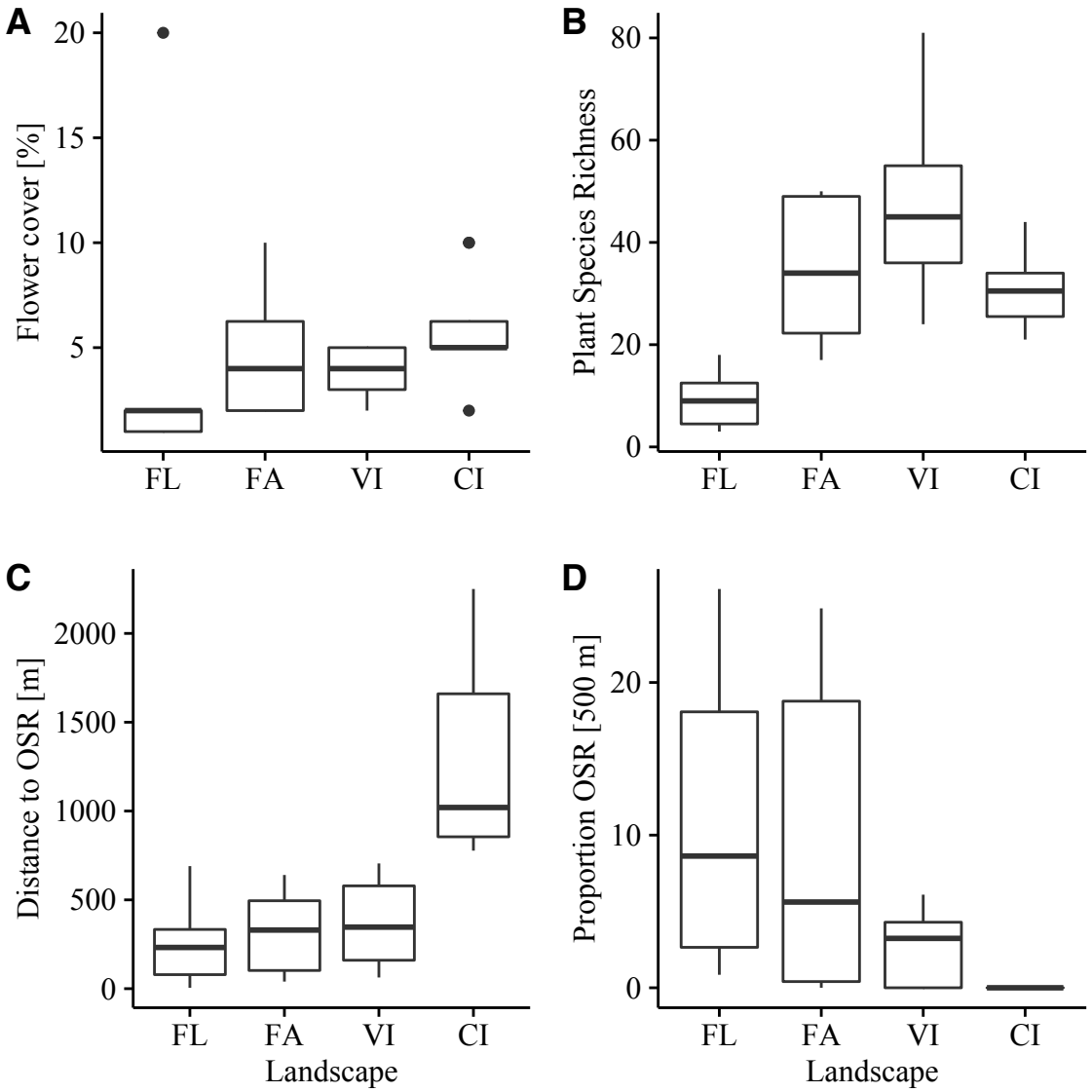


Fig. 2: Landscape type in relation to floral resources. A and B: local plant communities, C: distance to the next OSR field, D: amount of OSR in the landscape (within a radius of 500 m). FL = Farmland, n = 7; FA = Farmhouse, n = 8; VI = Village n = 8; CI = City, n = 8.

During our short-range movement experiment we found fluorescent dye on a total of 65 flowering plant species. The number of plant species visited in the different sites increased with the number of flowering plant species in the local surroundings (Chi-square = 10.335, d.f. = 1, p = 0.001, Fig. 3). In farmland sites the richness of flowering plants was much lower compared to the other study systems (Chi-square = 63.744, d.f. = 3, $p<0.001$).

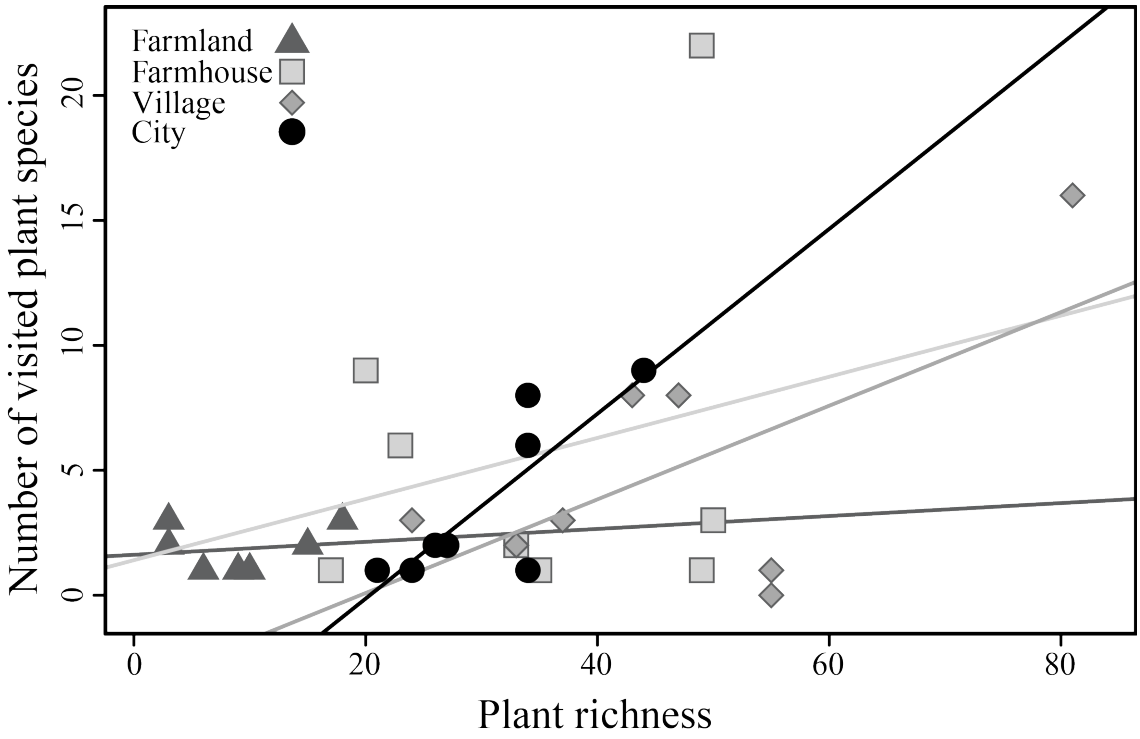


Fig. 3: Fluorescent dye experiment and number of visited plant species per site against plant richness per site.

Bumblebee colonies collected less OSR pollen with increasing distance to the next OSR field (Chi-square = 11.846, d.f. = 1, $p < 0.001$) and decreasing amount of OSR fields (Chi-square = 4.779, d.f. = 1, $p = 0.029$). Bumblebee colonies from farmland sites collected around 19% ± 8 SE of OSR pollen, whereas urban colonies collected only 2% ± 0.4 SE (Table S1, Fig. 4). Distance to the next OSR field increased with increasing urbanisation. Additionally, the proportion of OSR fields decreased in the surroundings (500 m) with increasing urbanisation and the proportion of OSR pollen collected decreased, too. In village gardens, distance to the next OSR field is the same as in farmland (Fig. 2 C), but the colonies in village gardens collected less OSR pollen than the colonies in farmland (Farmland = 19% ± 8 SE, Village = 5% ± 2 SE, Fig. 4). Colonies in farmhouse gardens collected 12% ± 3 SE of OSR pollen.

The starting weight of all 31 bumblebee colonies was 781.13 ± 21.66 g (mean ± SD). All colonies gained weight during the experiment (weight gain: mean ± SD 585.19 ± 171.69 g), but there were no differences in weight gain in the different landscape types along the urbanisation gradient (Chi-square = 0.778, d.f. = 3, $p = 0.855$).

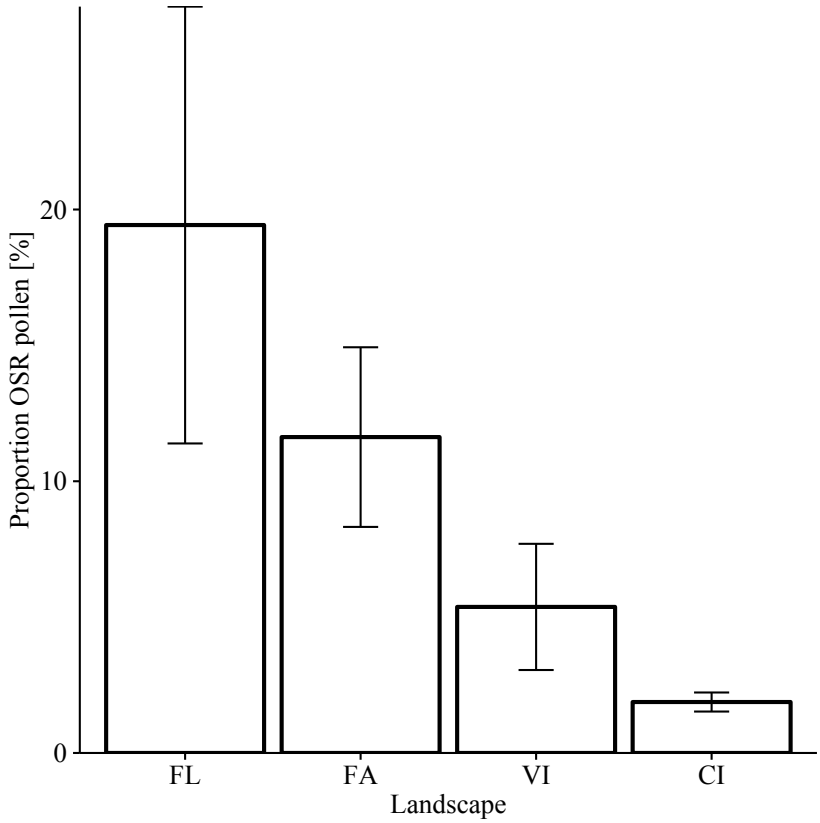


Fig. 4: Proportion of OSR pollen collected in different landscapes. Mean ± SE. FL = Farmland, n = 7; FA = Farmhouse, n = 8; VI = Village, n = 8; CI = City, n = 8.;

Bumblebee colony weight slightly increased with increasing proportion of OSR fields in the surroundings (Chi-square = 1.243, d.f. = 1, p = 0.265; Fig. 5) and decreased slightly with increasing distance to the next OSR field (Chi-square = 0.596, d.f. = 1, p = 0.440). The amount of plant species (Chi-square = 2.274, d.f. = 1, p = 0.132) and the cover of flowering plants (Chi-square = 0.122, d.f. = 1, p = 0.726) had no impact on the weight gain of bumblebee colonies along the gradient.

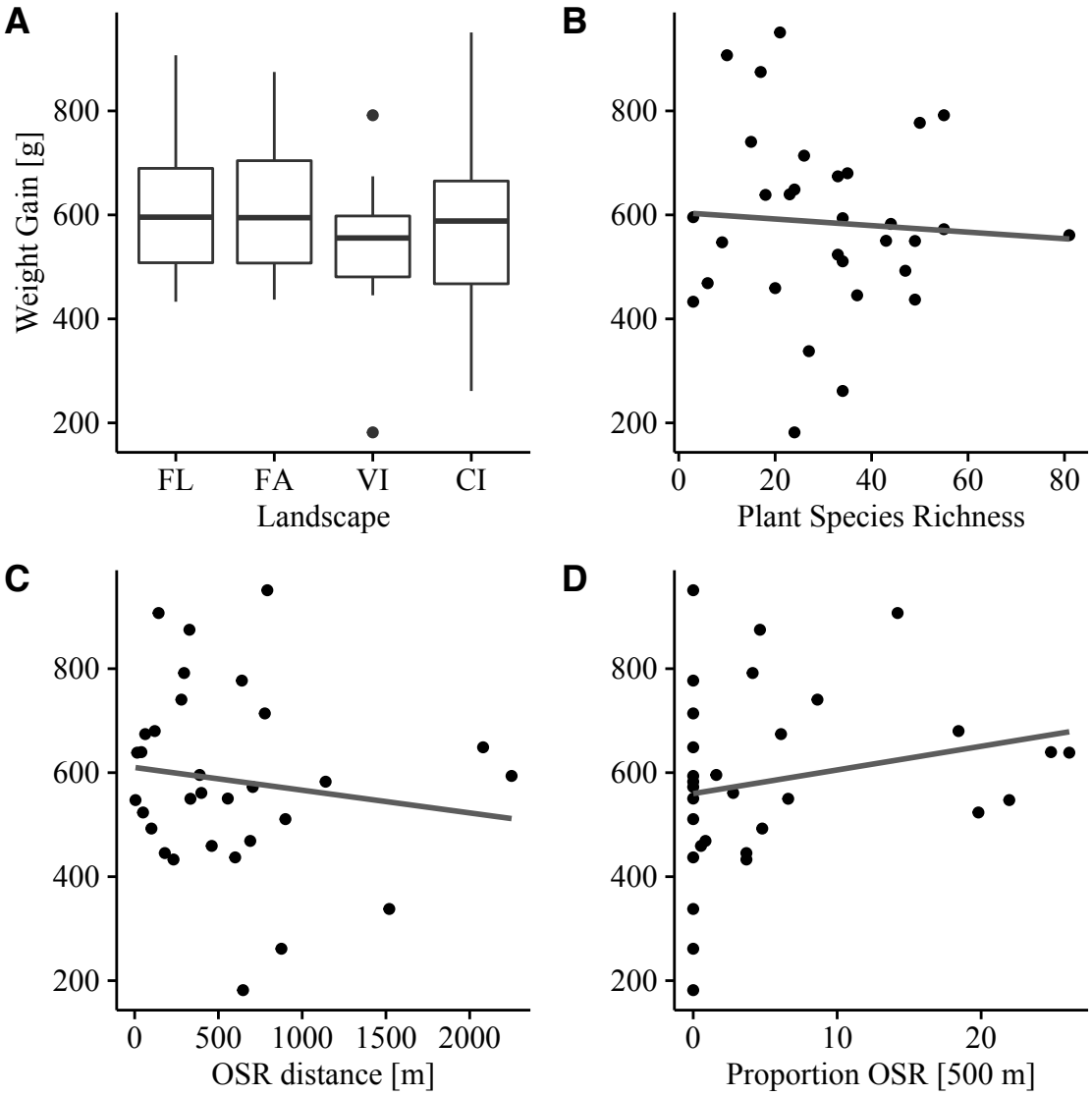


Fig. 5: Bumblebee colony weight gain in the four landscapes and influenced through local and landscape factors. FL = Farmland, FA = Farmhouse, VI = Village, CI = City.

## Discussion

Our results show that bumblebee foraging changed along a farmland-urban gradient with settlements of different sizes. We found that bumblebee workers in urban areas remained within the urban boundaries when the colony was setup at least 500 m from the city edge. This could be due to buildings, roads and railroads, which act as barriers for bumblebee foraging (Bhattacharya et al. 2002). However, urban areas consist not just of built-up area but also of home gardens and parks that may provide nectar and pollen resources. Bumblebee colonies can benefit from these urban green areas in the local surroundings (Baldock et al. 2015, Crone and Williams 2016). In our study the bumblebee colonies in urban areas and in farmland sites increased in weight. This could be due to the amount of flower resources in

city gardens, as Goulson et al. (2002) show that gardens provide enough local resources for bumblebee colony growth. High flower cover and plant richness in urban areas mitigates the fact that resources in the surroundings are often missing (Gunnarsson and Federsel 2014).

In farmland sites, the amount of OSR fields in the surrounding landscape was highest and the distance to the next OSR field was lowest. The bumblebee colonies from the farmland sites collected the highest amount of OSR pollen suggesting that OSR is an important resource for bumblebees in farmland. Other studies show that bumblebee colonies profit highly from mass flowering crops and develop better close to OSR fields (Westphal et al. 2009), which reinforces our findings.

Hence, bumblebee colonies in urban areas benefited from the nectar and pollen resources provided by plants in the gardens, whereas colonies in farmland benefited from the short distance to and high amount of oilseed rape fields. This could explain why all bumblebee colonies gained the same amount of weight, regardless of the surrounding landscape type.

We showed in this replicated study that bumblebees in farmland foraged throughout the landscape and collected OSR pollen, while bumblebees from urban gardens benefited from flowering plants in the gardens. This finding supports the idea that the landscape scale, as well as local resource availability in gardens, influences bumblebee colony health depending on where colonies are along the farmland-urban gradient. Due to these switches in resource use, bumblebee colony growth remained the same regardless of city size and landscape type. In conclusion, the relative importance of local garden resources and OSR resources for bumblebee performance reversed along the farmland-city gradient, which needs to be taken into account for pollinator management.

## Acknowledgements

We thank Siria Biagioni from the Department of Palynology and Climate Dynamics of the University of Goettingen for help with pollen preparation and identification. We are grateful to all student helpers and gardens owners. We thank the RTG 1644 “Scaling Problems in Statistics” and the German Research Foundation (DFG) for funding.

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## Supplementary Material

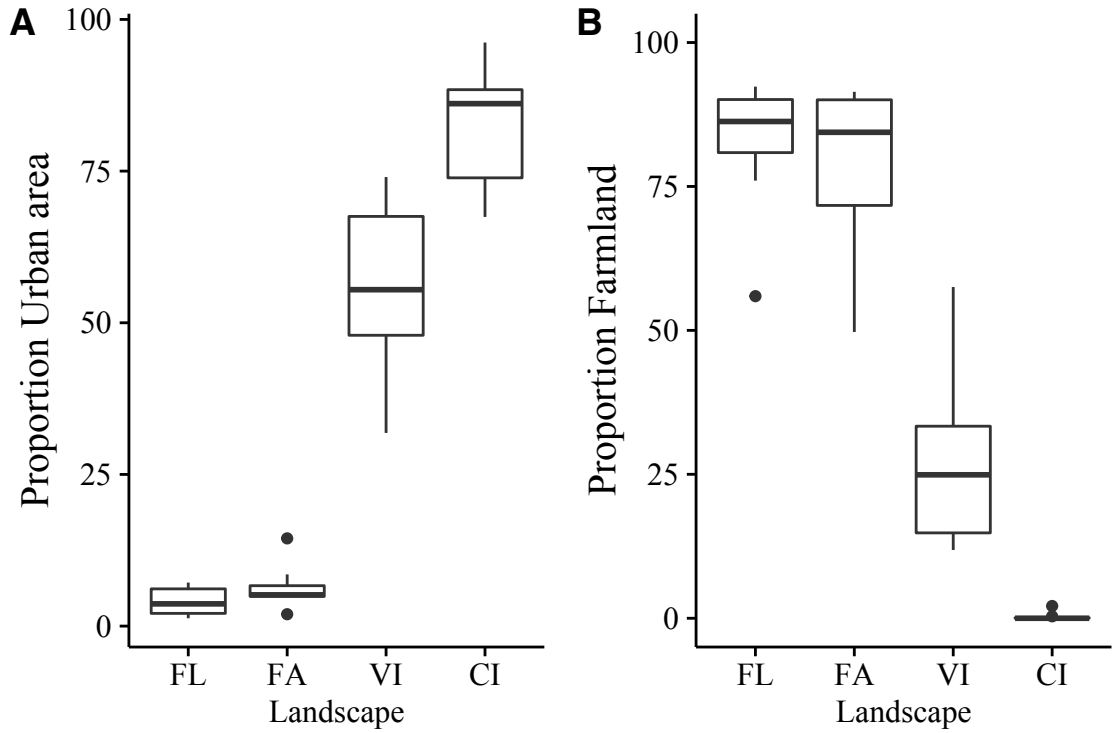


Fig. S1: Proportion urban area and farmland in 500 m around the sites. FL = Farmland, n = 7; FA = Farmhouse, n = 8; VI = Village n = 8; CI = CccCCity, n = 8.

Table S1: Proportion of OSR in pollen samples collected from the bumblebee colonies with standard deviation (sd), standard error (se) and confidence interval (ci).

| Landscape | No. | OSR pollen | sd | se | ci |
|---|---|---|---|---|---|
| FL | 7 | 19.42857 | 21.26701 | 8.0381742 | 19.6687038 |
| FA | 8 | 11.625 | 9.3493697 | 3.3055014 | 7.8162687 |
| VI | 8 | 5.375 | 6.5669628 | 2.321772 | 5.4901183 |
| CI | 8 | 1.875 | 0.9910312 | 0.3503824 | 0.8285228 |

Table S2: Coordinates of 32 different sites

| Site | Land-scape | Lat. | Long. | Site | Land-scape | Lat. | Long. |
|---|---|---|---|---|---|---|---|
| Bremke | FL | 51.424 | 10.073 | Diemarden | VI | 51.483 | 9.978 |
| Dransfeld | FL | 51.512 | 9.753 | Diemarden | VI | 51.489 | 9.981 |
| Göttingen | FL | 51.501 | 9.884 | Dransfeld | VI | 51.498 | 9.766 |
| Göttingen | FL | 51.490 | 9.905 | Dransfeld | VI | 51.501 | 9.757 |
| Lenglern | FL | 51.596 | 9.884 | Ebergötzen | VI | 51.572 | 10.12 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Moringen | FL | 51.677 | 9.895 | Ebergötzen | VI | 51.570 | 10.11 |
| Moringen | FL | 51.703 | 9.907 | Moringen | VI | 51.704 | 9.876 |
| Nörten-Hardenberg | FL | 51.607 | 9.923 | Moringen | VI | 51.692 | 9.880 |
| Bremke | FA | 51.430 | 10.079 | Duderstadt | CI | 51.515 | 10.26 |
| Dransfeld | FA | 51.520 | 9.756 | Duderstadt | CI | 51.510 | 10.27 |
| Friedland | FA | 51.473 | 9.955 | Einbeck | CI | 51.820 | 9.876 |
| Göttingen | FA | 51.506 | 9.941 | Einbeck | CI | 51.816 | 9.885 |
| Kalefeld | FA | 51.781 | 10.028 | Göttingen | CI | 51.527 | 9.946 |
| Lenglern | FA | 51.601 | 9.873 | Göttingen | CI | 51.540 | 9.939 |
| Moringen | FA | 51.678 | 9.883 | Northeim | CI | 51.712 | 9.999 |
| Wollbrands-hausen | FA | 51.580 | 10.176 | Northeim | CI | 51.701 | 9.998 |

Table S3: Preparation of pollen samples from honey and wax

| |
|---|
| University of Jambi, Department of Palynology and Climate Dynamics |
| Suggested number of samples per time: 10 |
| Always wear gloves and lab coat when working in the lab. |
| 1) Switch on the water bath; check if there is enough water in it (it takes more than 30 minutes to heat up to 90°C). |
| 2) Transfer the honey and or wax in a conical test tube. Make sure to wash all the tools to avoid contamination between samples. |
| 3) Only for the honey (for the wax move to step 5): add 4 ml of concentrated acetic acid (CH3COOH) to the sample (for dehydration) and mix the content. |
| 4) Centrifuge the tubes for 5 min at 3500 RPM and pour of the supernatant in a beaker and then in the acetic acid waste container). |
| 5) Acetolysis: make sure all the tools are dry including the gloves! Use the measuring cylinder to prepare a mixture of 9 parts acetic anhydride ((CH3CO)2O) and 1 part concentrated sulphuric acid (H2SO4). Fill in first the acetic anhydride then the sulphuric acid. Add the one part of sulphuric acid into the measuring cylinder using a plastic pipette very slowly (exothermic reaction, might get warm). Be careful H2SO4 reacts with water! |
| e.g. of calculation – 4 ml per sample: |
| For 1 sample à 3.6 ml (CH3CO)2O + 0,4 ml H2SO4 |
| For 10 samples à 36 ml (CH3CO)2O + 4 ml H2SO4 |
| It is recommended to prepare a bit more, e.g. per 10 samples ca. 39.6 ml (CH3CO)2O + 4.4 ml H2SO4 |
| 6) Add ca. 4 ml of the Acetolysis mixture to each sample (first 2 ml and then the other 2 ml) using the plastic pipette. Mix, if necessary, thoroughly with a plastic stick, one for each sample (be careful not to use wet tools). Remove the plastic sticks. |
| 7) Put the tubes into the water bath for 10 minutes at 90°C. Leave the water bath open! You will see the colour turning dark yellow. Centrifuge the tubes for 5 min. at 3500 RPM and pour off the supernatant in a beaker. |

8) Wash the samples with distilled water one or more times (until the water is clear): fill them up equally with water mix with clean plastic sticks if necessary, centrifuge for 5 min. at 3500 RPM, pour off the supernatant in the beaker. If the sample is solid add acetic acid to the top and centrifuge.
At the end empty the beaker into the Acetolysis waste container.
9) If necessary sieve the sample with a 150 µm filter and then back sieve in the original tubes
10) Transfer the residues into labelled Eppendorf-tubes.
11) Centrifuge the Eppendorf tubes for 3 minutes at 12000 RPM and pour off the water supernatant.
12) Create pollen slides using glycerine gel as fixer.

# Chapter 4

# Contrasting responses of arthropod diversity to urbanisation along a gradient of city size

*Misumena vatia* (Clerck) on *Leucanthemum vulagare* (Vaill.). © Kristy Udy

Authors:

Kristy Leah Udy*, Hannah Reininghaus*, Christoph Scherber, Teja Tscharntke

* These authors contributed equally to this work (shared first author).

## Abstract

Urban areas may support a diverse arthropod community but increasing levels of urbanisation affect taxa differently. Further, arthropod taxa may differ in their response to local or landscape scale factors. We tested the influence of increasing urbanisation along different sizes of urban areas and in different positions in the urban areas, comparing edge vs. centre, on functional groups of Coleoptera, Araneae and Hymenoptera. We also tested the influence of green area type (garden vs. grassland) and plant richness on these arthropod communities. Local (i.e. plant species richness) and landscape factors (i.e. increasing urbanisation) influenced Coleoptera and Araneae, while Hymenoptera were influenced by only local factors. Species richness of Hymenoptera was higher in gardens than grassland, whereas species richness of Coleoptera, in particular that of herbivores, carnivores and omnivores, was higher in grasslands and responded negatively to plant richness. Size of urban area was positively related to species richness of Araneae, but mostly negatively to that of Coleoptera. Our study exhibits contrasting responses of arthropod communities to urbanisation, with different influences at local and landscape scales, which may explain the heterogeneous patterns found in the literature. It deepens our understanding of how arthropod communities respond to urbanisation, as it is the first to investigate the influence of both urban area size and position in an urban area.

Keywords: urban area size; arthropod richness; Coleoptera; Araneae; Hymenoptera.

## Introduction

Land use change causes widespread loss of biodiversity in anthropogenic landscapes. Urban areas are a dominant part of landscapes worldwide and do support some arthropod diversity (McKinney, 2008; Egerer et al., 2017). The amount of arthropod diversity supported could be related to size of the urban area, which has a positive influence on plant species richness (Pyšek, 1998). This trend in plant species richness is due to increasing numbers and dominance of non-native species, which are also more prevalent at the city centre than edge (McKinney, 2006).

So far, urbanisation gradients were always tested in a single city and are generally defined by the amount of built-up area or density of people at different locations from the edge to the centre (McDonnell & Hahs, 2008; Egerer et al., 2017). Green areas in the centre of cities are more isolated due to the presence of physical barriers such as roads and buildings (Peralta et al., 2011) and their distance from the urban edge. Studies that examine rural-urban gradients find lower diversity of insects in the middle of an urban area (McKinney, 2006; Bates et al., 2011). The same results are found for host-parasitoid communities, but they are related to local habitat quality and to isolation of the study site, since green areas on the edge of an urban area may be colonised from the adjacent habitat and can support higher species richness than green areas in the centre of an urban area (Pereira-Peixoto et al., 2014). The influences of urbanisation on arthropods depends on which taxa they are, as pollinators are positively affected (Baldock et al., 2015; Sirohi et al., 2015), whereas forest-dependent ground beetles are negatively affected (Niemela et al., 2002; Vergnes et al., 2014). This diversity of responses indicates the existence of multi-causality and individualistic or trait-dependent species responses (Gleason, 1926; McDonnell & Hahs, 2008). A similar relationship to what is found with increasing urbanisation from the edge to the centre of a city could be expected with increasing urban area size.

The type of urban habitat should also have a strong effect, as, for example, gardens have a diverse structure with lawns, flowers, shrubs and trees within a small area, whereas parks are dominated by short grass with few wild herbs and trees and an occasional flower bed (Mata et al., 2017). Both these green area types are highly managed, as dead branches and often leaf litter are removed from under trees, grassland is frequently mown and flower beds are regularly weeded to remove any unwanted plants (Pyšek, 1998; Mata et al., 2017).

Differences in habitat type could also be characterised by the local plant species

richness, as gardens have a higher number of plant species present and also higher flower cover than parks, which could positively influence flower-visiting insects (Pyšek, 1998; Baldock et al., 2015). Other aspects than plant species richness, such as vegetation type, are also important for arthropod species, as spiders may thrive in habitats with larger extents of woody areas (Sattler et al., 2010; Vergnes et al., 2014), which are more extensive in parks.

We investigated how local vs. landscape scale variables structure plant and arthropod communities in urban areas. The influence of the urban landscape on arthropod communities in gardens and grassland was tested for the first time along an urbanisation gradient from small villages to a mid-size city, while also analysing the role of the position in an urban area (edge or centre). The arthropods sampled were functional groups of Coleoptera, Araneae and Hymenoptera.

## Material and Methods

Arthropods were sampled from 15 urban areas (Fig. 1, Table S1) that covered a size gradient from villages (150 residents, 0.1 km2) to cities (118,000 residents, 16.6 km2). Urban areas were selected using ArcGIS (v. 10.4.1, ESRI), where the size in km2 of all settlements within a 30 km radius of Göttingen was calculated by overlaying a polygon over each settlement. Urban area boundary was defined as the urban edge where buildings and gardens border agriculture or forest (Fig. 1 inset). Three similar sized small villages and three similar sized mid-size cities were used to sample both ends of the size gradient more completely. Urban areas were categorised by size from 1-11 (1 = small village, 11 = mid-size city, both replicated three times; categories 2-10 were replicated once) and we randomly selected an urban area within each category. All urban areas had a similar proportion of green area within their urban boundaries (Fig. S1).

To test the effect of the surrounding landscape, we sampled in green areas at different positions in the urban areas, both the centre and the edge of all urban areas. Green areas were home gardens and grasslands, either parks or pastures, as they are ubiquitous in all urban areas and have a similar structure (grassland and trees/shrubs). Both parks (grassland with shrubs and trees) and pastures were used as grasslands. All green areas (gardens and grasslands) had a size of 1,000 m2 – 3,000 m2. Within each urban area two gardens and two grasslands were selected, one garden and one grassland (within 100 m of each other) at both the centre and edge of an urban area (60 sites

in total; Fig. 1 inset). The urban centre was defined as the geographical centre, with approximately equal distance from all edges, while the urban edge was defined as where houses and gardens bordered on the surrounding landscape (always farmland). We created GIS maps for each site and measured the amount of urban area (buildings and roads), home gardens, grasslands, forest and agriculture within a 500 m radius.

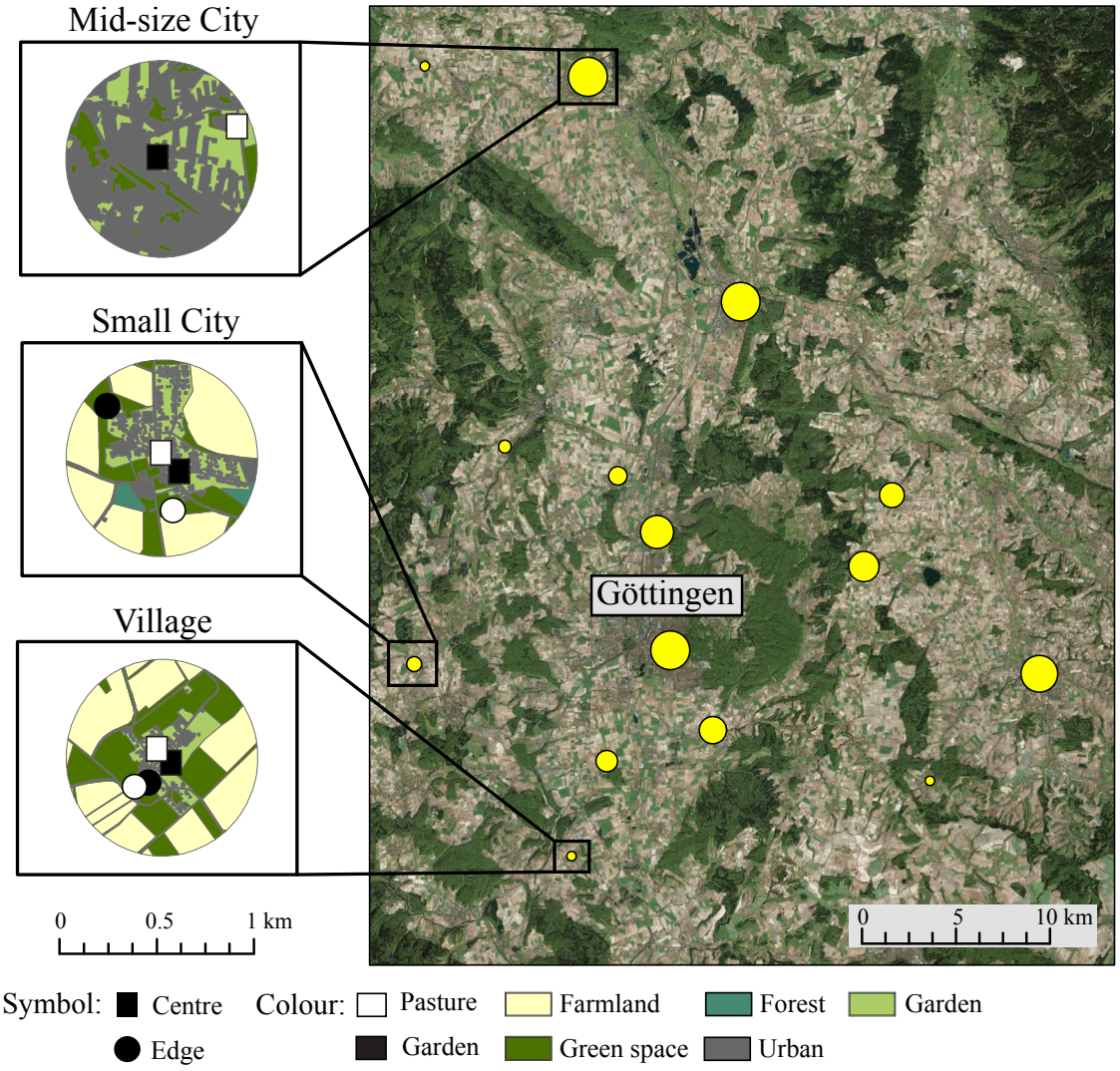


Fig. 1: Map of all urban areas, size of circles corresponds to urban area size. Insets show examples of plot positions in the urban areas and their structure within a 500 m radius. The symbols and colours relate to the inset maps.

Arthropod sampling was repeated three times from spring (late April) until late summer (end of August) in 2014. Each sampling round took four weeks with four urban areas sampled per week. Arthropods were sampled using: pan traps, pitfall traps and sweep nets. Two pan traps and pitfall traps were placed in each garden and grassland and

were separated by a minimum of five metres. Pan traps were bowls (11 cm diameter, 7 cm depth) painted yellow with an additional UV top-coat, these were placed in the lawn edge/pasture edge and staked to the ground. Pitfall traps were constructed using a bottle and funnel placed inside a tube (11 cm diameter) that was buried in the ground so that the funnel edge was flush with the soil surface. A cover was placed above the funnel at a height of 15 cm so that detritus could not fall in and block the pitfall trap. Pan traps and pitfall traps were filled with water mixed with liquid soap and were set for three days. Sweep netting was done along four 15 m long transects; we swept the lawn and the flowerbeds in gardens and the grass and any flowerbeds in grasslands. Sweep netting was done when it was not raining during the period the pan traps and pitfall traps were set. Arthropod samples were preserved in ethanol and were sorted in the lab to order level and identified to species level by taxonomists. The orders we had identified were: Coleoptera, Araneae and Hymenoptera. These arthropods were separated into functional groups using information from insect identification keys (Royal Entomological Society: Hymenoptera) and from the database compiled by Gossner et al. (2015). Functional groups for Coleoptera were: carnivore, omnivore, fungivore, detritivore and herbivore. Araneae were split into hunting mode: hunter or web-builder and Hymenoptera were split by functional groups of: wasp, wild bee and parasitoid. Red list status was obtained from the IUCN (2013).

All plants within each garden and grassland were identified to species level and we recorded which species were flowering during each sampling round. Flower cover within each garden and grassland was also estimated per sampling round.

**Statistics**

The arthropod samples were combined from all different trapping methods for statistical analysis. Species richness was calculated using the exponential of the Shannon Diversity Index (hereafter SR) as this method is numbers equivalent (assumes equal abundance for each species; (Jost, 2007) and allows comparison across multiple taxa.

All analyses were performed using R (version 3.3.0; R core Team, 2016). We used Principle Components Analysis to derive linearly independent variables as indicators of amount of urbanisation and plant species richness (Oksanen et al., 2017); we used urban area size and total plant Shannon richness, which were not correlated (Pearson correlation = -0.02; Fig. S2; Crawley, 2013). Community dissimilarity between edge and centre of

urban areas along our urbanisation gradient was calculated with the 'vegdist' function using the Bray-Curtis index and significance was tested with a permutation test that utilises pseudo F-ratios (Permutational Multivariate Analysis of Variance Using Distance Matrices; (Oksanen et al., 2017). The community dissimilarity was then visualised using nonmetric multidimensional scaling (metaMDS; Crawley, 2013; Oksanen et al., 2017). Our experimental design was nested, thus we always used mixed effects models with a random error term composed of position in urban area (centre or edge) nested in urban area (random effect: urban area name/position in urban area; (Bates et al., 2015). SR was calculated per site and per functional group for all taxa and was tested against the experimental variables of urban area size, urban area section and green area type (e.g. glmer(SR~urban_area, urban_position, green_area+(1|city/urban_position); (Bates et al., 2015). The arthropod response variables were tested against plant SR in a separate model, not including the experimental design variables, as plant SR was itself influenced by our urban gradient and by the green area type (Fig. 2). Response variables tested were always rounded SR (to the nearest integer), to convert them to true count data; therefore, models used were always Poisson or Negative Binomial (depending on which provided best model fit based on AICc; (Bates et al., 2015). All models with experimental variables were simplified using a list of candidate models with all possible combinations of experimental variables and interactions; models were ranked based on AICc and the model with the lowest AICc value was used (Information Theoretic approach; (Mazerolle, 2016).

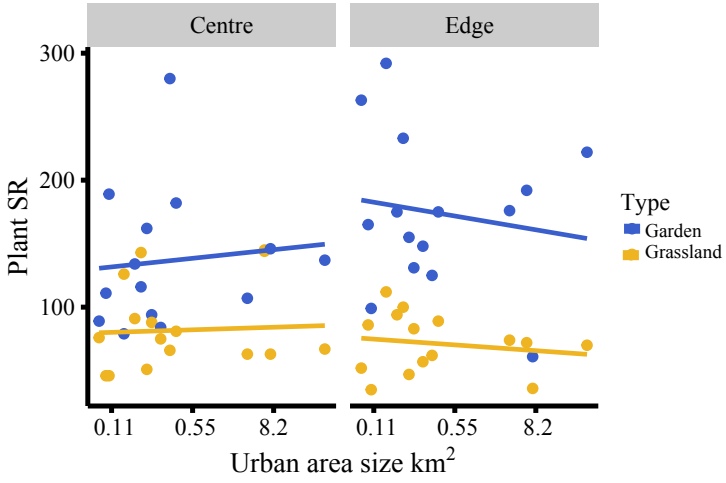


Fig 2: Plant Shannon richness (SR) influenced by experimental variables. Green area type had a significant influence (Chi-square = 72.3, d.f. =1, $p < 0.001$). Urban area size is measured in square kilometres ($km^2$).

## Results

We caught a total of 17,229 Coleoptera from 634 different species, 36 of which have a red list status of threatened. 15,475 Araneae were caught from 202 species, 5 of which are threatened and 33,881 from 177 species of Hymenoptera were captured. Plant SR was higher in gardens than grasslands (Chi-square = 72.333, d.f. = 1, $p < 0.001$; Fig. 2) and was higher in gardens at the edge than gardens in the centre of urban areas (Chi-square = 4.242, d.f. = 1, p = 0.039).

Urban area size had no direct influence on Coleoptera SR but did interact with urban area section (Chi-square = 8.447, d.f. = 1, p = 0.004; Fig. 3) and with green area type (Chi-square = 5.66, d.f. = 1, p = 0.017), as Coleoptera SR decreased with increasing urban area size except in edge grasslands. Coleoptera SR was higher at the edge than the centre of urban areas (Chi-square = 8.44, d.f. = 1, p = 0.004; Fig. 3). Coleoptera community similarity in our largest size urban areas was significantly different between urban area edge and centre (Pseudo F-ratio = 2.241,10, p = 0.008; Fig. S3). Urban area size directly positively influenced Araneae SR (Chi-square = 7.8, d.f. = 1, p = 0.005; Fig. 3).

Of the different functional groups from the different taxa, fungivorous Coleoptera SR was higher in the centre of urban areas (Chi-square = 6.867, d.f. = 1, p = 0.009; Fig. 4) and hunting Araneae richness was higher at the edge of urban areas (Chi-square = 10.27, d.f. = 1, p = 0.001). The other functional groups were not influenced by urban area size or green area type.

Coleoptera SR was higher in grasslands than in gardens (Chi-square = 7.258, d.f. =1, p = 0.007; Fig. 3) and highest when plant SR was low (Chi-square = 4.985, d.f. = 1, p = 0.026). This is because plant SR was lowest in grasslands where Coleoptera SR was highest (Fig. 2). Of these two variables, green area type had a stronger influence as the R-squared was higher (green area type model = 14.5, plants model = 9.3) and model fit was better (green area type model AICc = 482.04, plants model AICc = 484.773). Coleoptera SR for the feeding groups of carnivores (Chi-square = 8.318, d.f. = 1, p = 0.004; Fig. 4), omnivores (Chi-square = 3.962, d.f. = 1, p = 0.047) and herbivores (Chi-square = 8.169, d.f. =1, p = 0.004) was higher in grasslands than in gardens. Carnivorous Coleoptera SR was also negatively influenced by plant SR (Chi-square = 22.91, d.f. = 1, $p < 0.001$; Fig. 4), which had a stronger influence than green area type as the R-squared was higher (plant model = 54.3, green area type model = 50) and model fit was better (plant model AICc = 95.273, green area type model AICc = 117.15).

Plant SR positively influenced Hymenoptera SR (Chi-square = 23.817, d.f. = 1, $p < 0.001$; Fig. 3). Wild bee and wasp SR were positively influenced by plant SR (wild bees: Chi-square = 16. 13.467, d.f. = 1, $p < 0.001$; wasps: Chi-square = 9.728, d.f. = 1, $p = 0.002$; Fig. 4) and wasp SR was higher in gardens than in grasslands (Chi-square = 8.49, d.f. = 1, $p = 0.004$). Plant SR had a slightly stronger influence on wasp SR (plant model R-squared = 17.6, green area type model = 15.3) with a slightly better model fit (plant model AICc = 255.942, green area type model = 257.165).

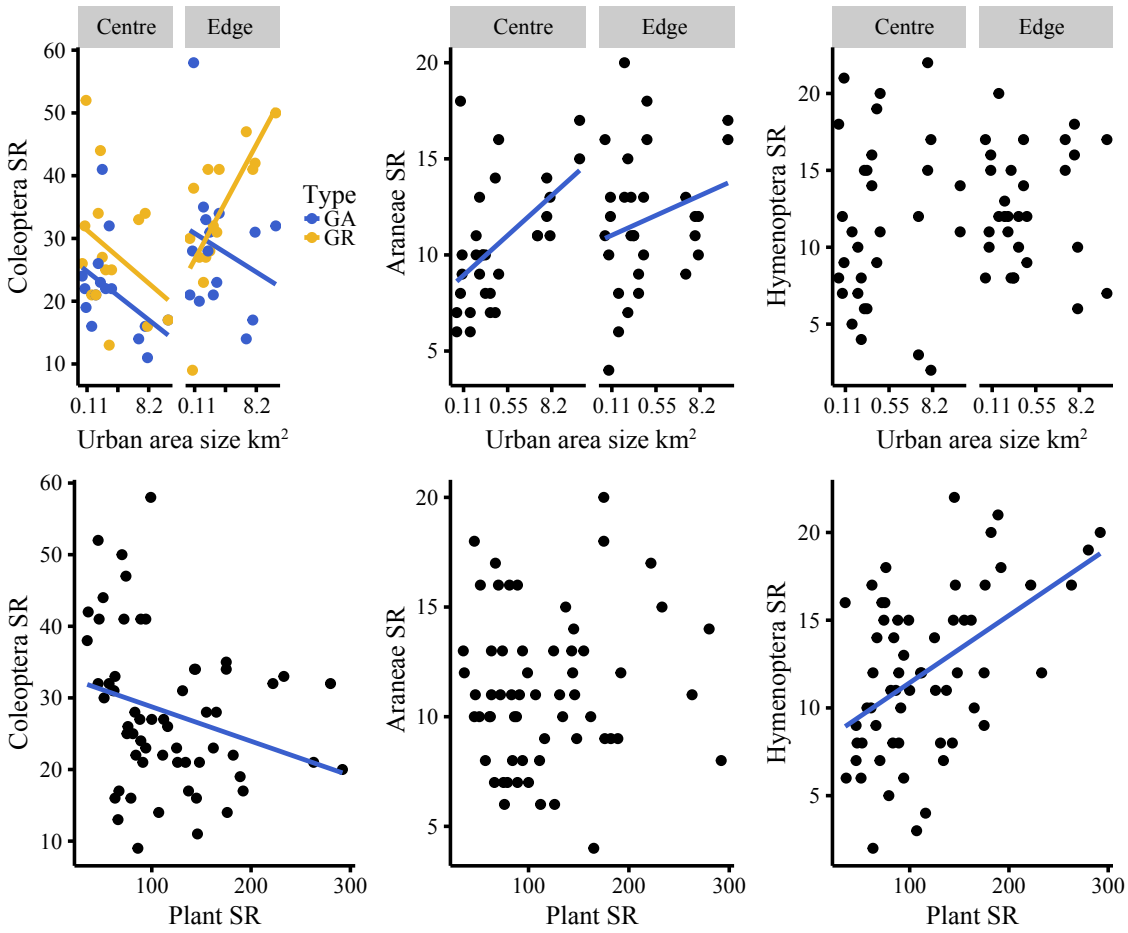


Fig. 3: Shannon richness (SR) relationships for all taxa (Coleoptera, Araneae and Hymenoptera) against experimental variables of urban area size, position in an urban area, green space type and plant Shannon richness (SR). Only significant responses are shown. GA = garden, GR = grassland. Urban area size is measured in square kilometres (km²).

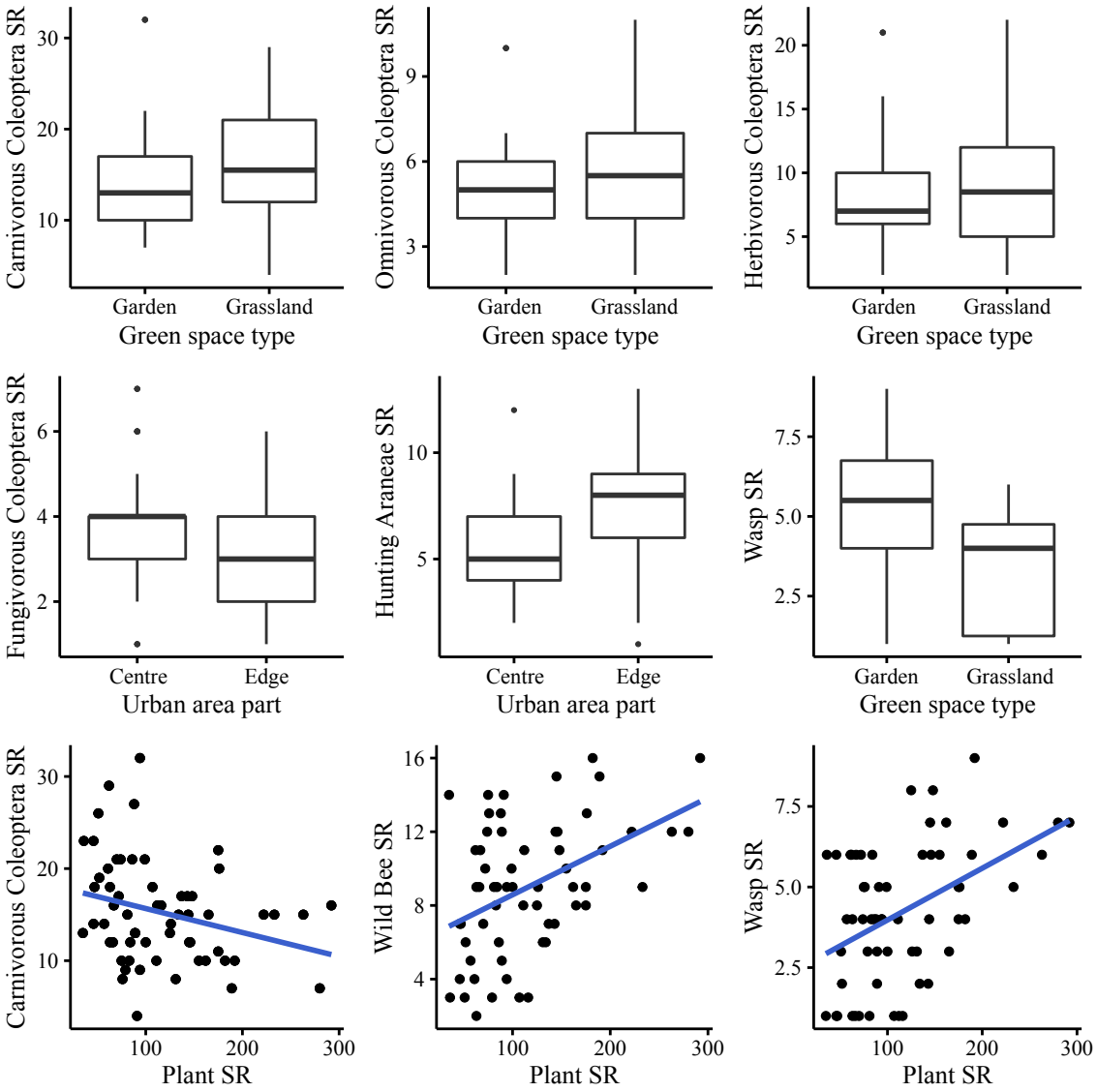


Fig. 4: Functional group Shannon richness (SR) was tested against experimental variables and plant SR. Only functional groups with significant responses are shown.

## Discussion

This is the first study to investigate urban area size influences along a gradient from villages to cities on Coleoptera, Araneae and Hymenoptera, while simultaneously investigating the influence of position in an urban area. We found that landscape scale variables (urban area size and centre vs. edge) influenced species richness of Coleoptera and Araneae, while only local variables (garden vs grassland and plant species richness) influenced that of Hymenoptera.

### Landscape variables

Coleoptera SR was negatively influenced by urban area size, except at the edge in grasslands where Coleoptera SR increased with urban area size. Fungivorous Coleoptera, but not the other functional groups (carnivores, detritivores, herbivores or omnivores), were influenced by the surrounding landscape, with higher species richness found in the centre of urban areas. Some studies have found no difference in Coleoptera richness with increasing urbanisation (Elek & Lovei, 2007; Hartley et al., 2007). But Niemela et al. (2002) found a decrease in carabid species richness with increasing urbanisation, which agrees with our findings. The pattern of higher richness at the edge in grassland could be due to spill over from adjacent agriculture of species that specialise on grassy habitats.

Araneae species richness was positively influenced by urban area size and hunting Araneae species richness was highest at the edge of urban areas. This latter effect is likely due to spill over from the adjacent farmland, which positively enhances species richness in these edge areas. Sattler et al. (2010) find that Araneae are more influenced by local scale variables, which is in direct contrast to our results as we found that Araneae were only influenced by landscape variables. This could be because they sampled across a gradient of increasing management in urban areas and found that Araneae communities are negatively influenced in intensively managed areas. They sampled in gardens and public green areas as well, but their experiment was specifically setup to test management intensity. Kaltsas et al. (2014) also found a negative trend in Araneae richness with increasing urbanisation, but they only worked with Araneae from the Gnaphosidae family. Araneae can disperse up to 10 km (Vergnes et al., 2014) and could therefore be mainly influenced by landscape factors rather than the local surroundings. Additionally, Araneae species richness is positively influenced by increasing urbanisation (distance from urban area edge) and is highest at approximately 50% built-up area, as habitat at intermediate levels of urbanisation is more heterogeneous and therefore allows increased species coexistence (Vergnes et al., 2014). This pattern

in Araneae richness could explain our finding of highest Araneae species richness in larger urban areas where amount of built-up areas was highest (roughly 50%, Fig. S1).

We sampled in urban areas with significant amounts of green area, but patterns in arthropod richness could be different for other urban areas with higher proportions of built-up area. For example, in large cities like Paris, there is a sharp decline in arthropod richness from the suburbs to the heavily built-up central areas (Vergnes et al., 2014). However, our results are generalisable across urban areas with a high proportion of green area. Furthermore, we found that when the distance from urban area edge is greater than approximately 600 m, the Coleoptera community became distinct with different community composition in the urban centre compared with the urban edge (Fig. S3: city, Table S1). Therefore, when sampling in green areas further than 600 m from the urban edge, the species present may change and become distinct to those present in the adjacent landscape.

**Local variables**

Coleoptera were the only taxon influenced by green area type, as they had higher species richness in grassland than in gardens. They were also negatively influenced by increasing plant species richness, but this was correlated with green area type, as plant species richness was lowest in grassland where Coleoptera species richness was highest. Coleoptera functional groups species richness were also influenced by the local scale experimental variable of green area type, as carnivores, omnivores and herbivores all had higher species richness in grasslands than in gardens. These findings agree with other studies that found higher arthropod richness, specifically herbivores and predators, in grassland habitats (golf courses) than in gardens (Colding & Folke, 2009; Mata et al., 2017). These differences in functional groups species richness between gardens and grassland could be due to the local habitat structure and extent, as in parks and pastures there are large expanses of lawn/grass mixed with herbs bordered by shrubs and trees, whereas in gardens these same habitat types are present but in smaller areas (Colding & Folke, 2009; Mata et al., 2017). Therefore it makes sense that herbivorous Coleoptera had higher species richness in grasslands than gardens, as they require larger extents of grassy habitat. This could also be due to presence of a smaller predator community present in urban areas (Hanks & Denno, 1993) and corroborates findings by Denys & Schmidt (1998), who found higher herbivore abundance in urban areas than in rural areas.

Hymenoptera species richness was only influenced by the local variable of

increasing plant species richness (positive effect), as were the functional groups of wasps and wild bees. Wasps exhibited highest species richness in gardens where plant species richness was highest; plant species richness had the strongest affect. The results for wild bees are well corroborated in the literature where plant species richness has a positive influence on wild bee species richness and urban areas support a diverse community (Ahrne et al., 2009; Hall et al., 2016). We found no influence of urban area size or position in an urban area on Hymenoptera species richness. However, Hymenoptera abundance was higher at the edge of urban areas than in the centre (Fig. S4), which agrees with findings from other urban studies (McKinney, 2008; Ahrne et al., 2009). For wasps, there have been no effects found of urbanisation on total wasp richness and abundance (Zanette et al., 2005; Christie & Hochuli, 2009). However, there is a positive influence of flowering plants on wasps (Pereira-Peixoto et al., 2014), which agrees with what we found. This could be because wasps feed on herbivores that are found on flowering plants and they also benefit from nectar resources (Pereira-Peixoto et al., 2014).

The influence of urbanisation depends strongly on the taxonomic group and the scale studied at as we found that Coleoptera and Araneae richness was influenced by increasing urbanisation and that Hymenoptera richness was influenced only by local plant richness. To aid conservation efforts for these taxa it is crucial to investigate in more detail how and why arthropods respond to increasing urbanisation. We provide evidence that differences found by other urban studies may be due to differences in the surrounding landscape and the size of the city. Our study deepens our understanding of how arthropod communities respond to urbanisation, as it is the first to investigate the influence of both urban area size and position in an urban area.

## Acknowledgements

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## Supplementary Material

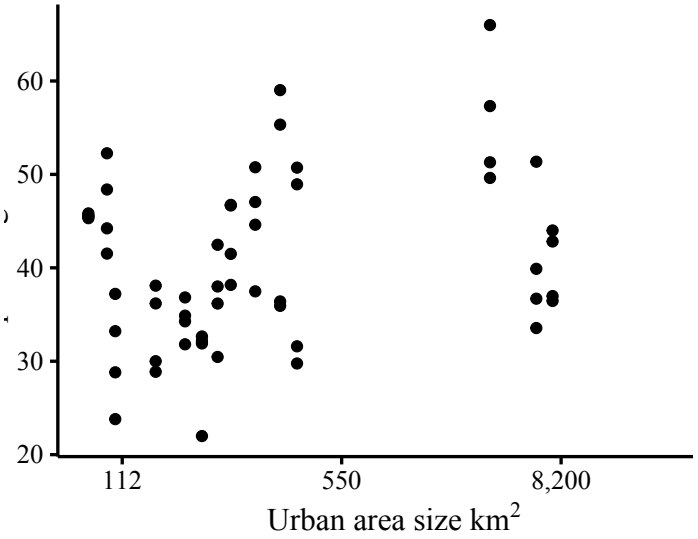



Fig. S1: Proportion of green area measured inside urban area boundaries plotted against urban area size in $km^2$.

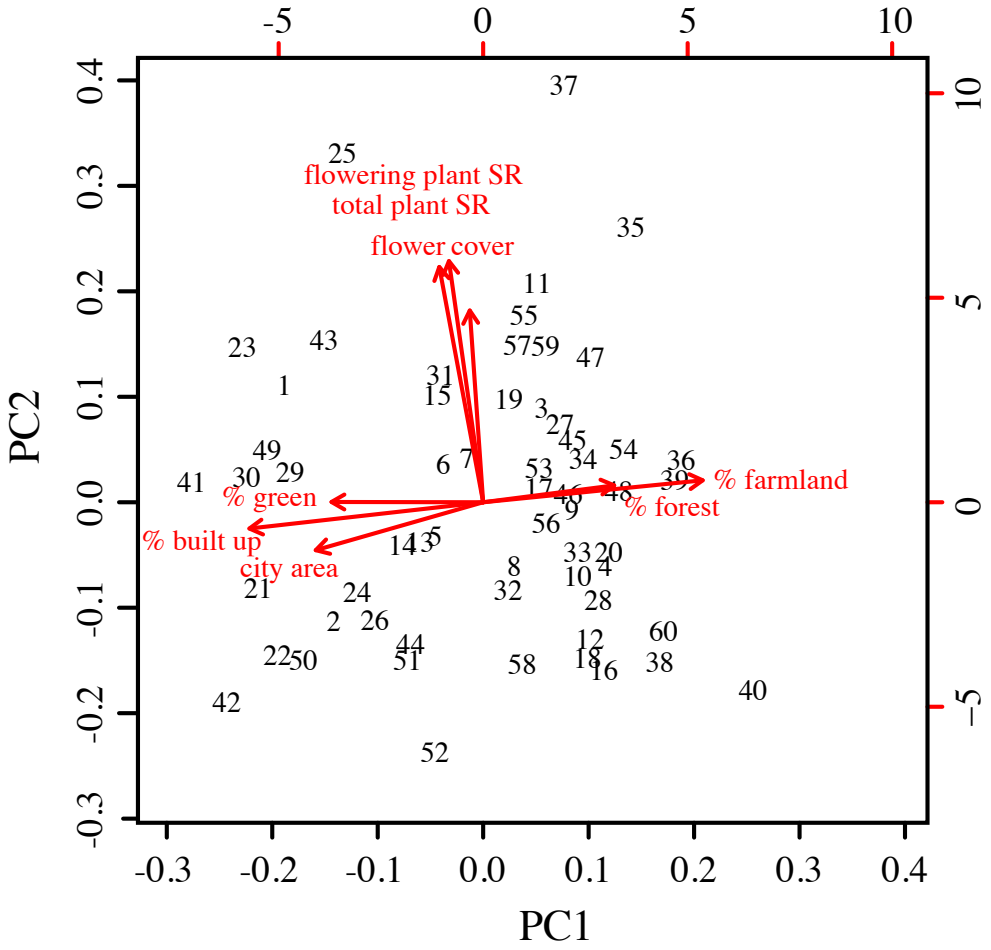



Fig. S2: Principle components analysis of our variables. GIS variables calculated in a 500 m radius for each site: % green = proportion of urban area that is green (urban gardens + parks/pastures), % built up = proportion of urban area that is built up (buildings and roads + gardens; everything within the urban boundary), % farmland = proportion of farmland, % forest = proportion of forest. City area (urban area size) is calculated in km$^2$. Plant variables are calculated per site in the gardens and grassland: flower cover, flowering plant SR = Shannon richness of flowering plants, total plant SR = Shannon richness of all plants (flowering + non-flowering).

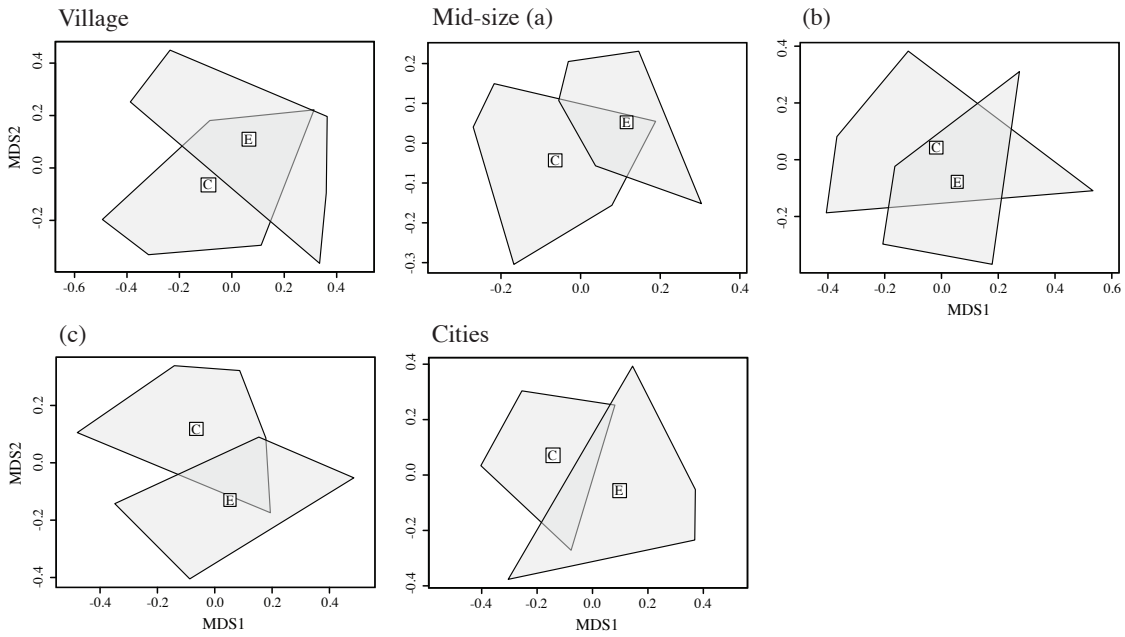



Fig. S3: Ordination plots for Coleoptera in different size categories of urban areas comparing differences between centre (C) and edge (E). Urban areas were grouped by size into categories and NMDS ordinations using the Bray-Curtis method were calculated. The 15 urban areas were grouped by three i.e. three urban areas per plot.

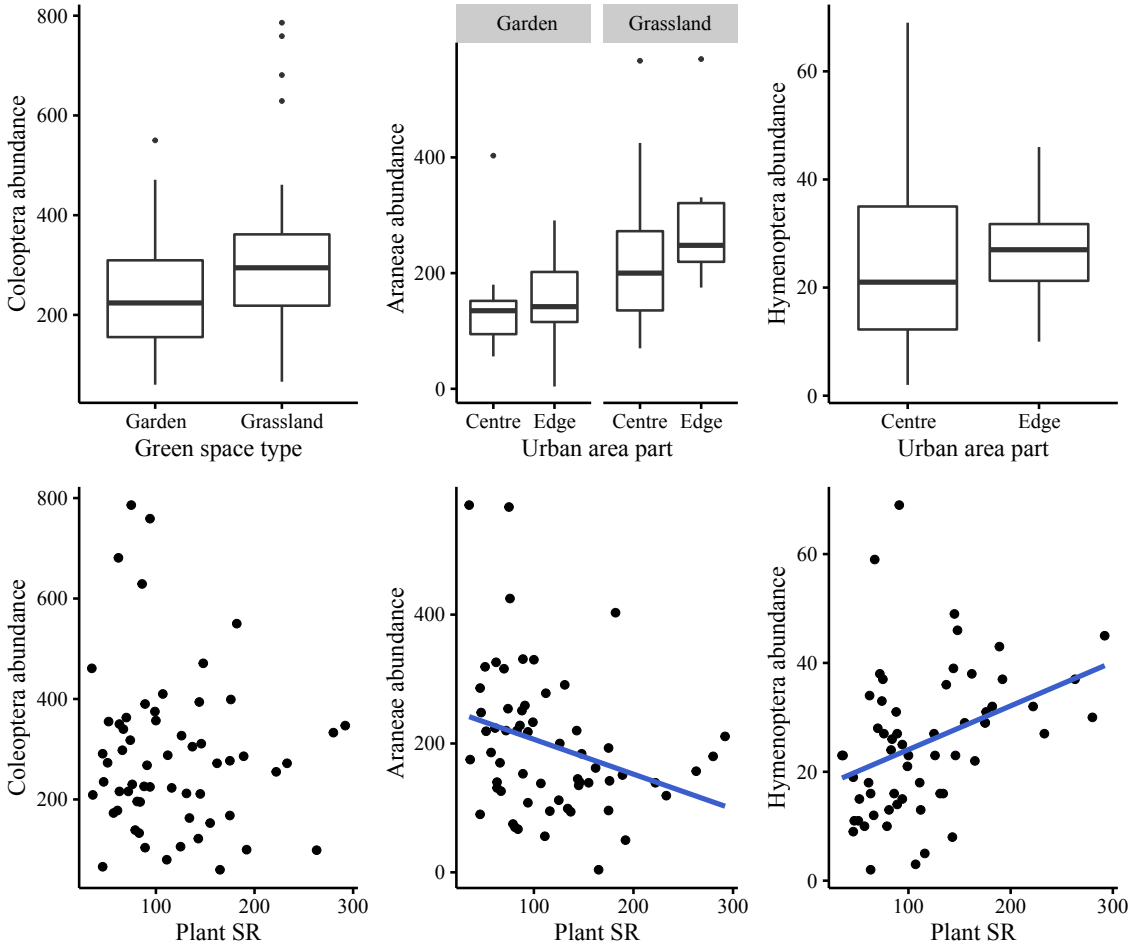


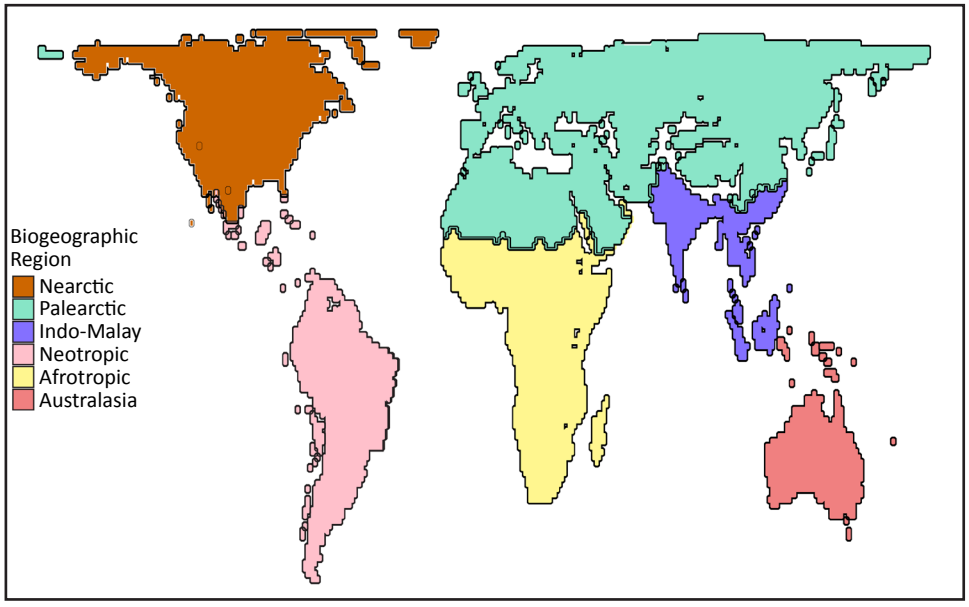

Fig. S4: Abundance relationships for all taxa against experimental variables and plant SR. Only significant releationships are plotted.

Table S1: Urban area size, position in latitude and longitude and distance to centre garden for all urban areas arthropods were sampled in.

| **Urban area** | **Area (km²)** | **Latitude** | **Longitude** | **Distance (m)** |
|---|---|---|---|---|
| Deiderode | 0.1 | 51°25’21.24”N | 9°51’49.25”E | 100 |
| Deitersen | 0.1 | 51°49’28.25”N | 9°44’15.56”E | 60 |
| Etzenborn | 0.1 | 51°27’38.58”N | 10° 9’56.71”E | 90 |
| Ellierode | 0.2 | 51°37’54.16”N | 9°48’27.09”E | 110 |
| Imbsen | 0.3 | 51°31’16.32”N | 9°43’52.60”E | 130 |
| Parensen | 0.3 | 51°36’54.90”N | 9°54’17.39”E | 130 |
| Sieboldshausen | 0.4 | 51°28’13.99”N | 9°53’35.04”E | 220 |
| Bodensee | 0.4 | 51°36’23.07”N | 10° 7’57.66”E | 230 |
| Diemarden | 0.5 | 51°29’13.24”N | 9°58’58.73”E | 210 |
| Ebergotzen | 0.7 | 51°34’14.32”N | 10° 6’27.41”E | 180 |
| Bovenden | 2.7 | 51°35’11.18”N | 9°56’0.81”E | 570 |
| Duderstadt | 4.5 | 51°30’45.79”N | 10°15’34.68”E | 540 |
| Einbeck | 7.1 | 51°49’13.29”N | 9°52’6.14”E | 800 |
| Northeim | 8.5 | 51°42’21.76”N | 9°59’48.62”E | 1,000 |
| Göttingen | 16.6 | 51°32’28.61”N | 9°54’56.89”E | 1,600 |

# Chapter 5

# Environmental Heterogeneity Predicts Global Species Richness Better Than Area




World map with biogeographic regions denoted by colour. © Kristy Udy

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## Abstract

It is widely accepted that both niche and neutral processes determine biodiversity from local to global scales. Their relative importance, however, is still disputed, and empirical tests are particularly scarce at the global scale. Here, we compare the explanatory power of area (proxy for neutral processes) and environmental heterogeneity (proxy for niche processes) for native mammal richness relationships in major global biogeographic regions. The environmental heterogeneity measures tested were elevation and precipitation ranges as these are well known environmental factors that explain variation in species richness. We find that environmental heterogeneity explains species richness relationships better than area does, suggesting that niche processes are more prevalent than neutral processes at large scales. Our results have wide implications for understanding species richness and species-area relationships, but also how they might change with global climate change.

Keywords: species richness; environmental heterogeneity; species-area relationship; area; biogeographic region; biodiversity

## Introduction

Understanding biodiversity patterns is a core interest in ecology. A classical explanation for patterns of species richness is niche theory, which posits that ecological communities are mainly structured by niche partitioning between species (MacArthur & Wilson 1967; Kadmon & Allouche 2007). As heterogeneous environments offer more niches, coexistence and species richness should increase with environmental heterogeneity (Potts et al. 2004). Indeed, it has been shown that environmental heterogeneity is a strong driver of species richness of various taxonomic groups and across spatial scales (Stein et al. 2014). Thus, if niche differences structure ecological communities, environmental heterogeneity should be the main explanatory variable for species richness at any spatial scale.

In recent decades, however, ecological thought has given more room to neutral (stochastic) processes in explaining species richness. Hubbell (2001) synthesized these ideas into the unified neutral theory of biodiversity and biogeography, hereafter 'neutral theory'. Neutral theory assumes that communities assemble, form and drift randomly, also that individuals have equal fitness and are subject to random speciation and dispersal (Hubbell 2001). It has been shown that neutral processes are able to reproduce important biodiversity patterns, such as species richness and abundance distributions, from small to large spatial scales (Chave 2004; Rosindell et al. 2011). If dispersal and speciation rates are assumed to be constant, neutral theory predicts that the main determinant of the species richness of a region is its area.

The ability to predict richness as a function of area means that neutral theory also predicts the classic macroecological pattern, the species-area curve (Arrhenius 1921; MacArthur & Wilson 1967). Species-area curves compare the number of species found in a region against its area (Triantis et al. 2012). They can be constructed nested, meaning that the larger area always contains the smaller area, and non-nested, where the curve is simply constructed from areas of different size (Rosenzweig 1995; Scheiner 2004). For a nested design, species richness must increase with area. However, also for a non-nested design, richness will usually increase with area, as larger areas generally harbor more individuals as well as more environmental heterogeneity, and would thus be expected to contain more species from both neutral and niche-based viewpoints (Tamme et al. 2010; Stein et al. 2014).

As indicated, the ability to explain species-area curves is not unique to neutral theory. The species-area relationship is also a fundamental prediction of niche theory,

as environmental heterogeneity tends to increase as area increases (Rosenzweig 1995). It has been demonstrated that important biodiversity patterns, including local species abundance patterns and species-area curves, can be produced by both neutral and niche processes (Pyšek et al. 2002; Tews et al. 2004; Báldi 2008). The question for contrasting niche and neutral theory is thus not so much about whether species richness correlates with area or environmental heterogeneity (as both theories predict these patterns), but rather which of the two potential predictors better explains richness.

One problem with conducting such a test is that it is not obvious how to measure the influence of environmental heterogeneity on species richness, as many potential environmental variables could be considered (Stein & Kreft 2015). Previous studies have mainly focused on variables such as climate and elevational heterogeneity (Hawkins et al. 2003; Rodríguez et al. 2005; Tuanmu & Jetz 2015). But biogeography studies do not compare the relative strength of multiple variables on species richness patterns, they only focus on one type of environmental heterogeneity (Pyšek et al. 2002; Báldi 2008). Moreover, there is an inherent problem when analyzing environmental variables in isolation, as both niche and neutral processes can act at the same time, and area correlates with different environmental heterogeneity, meaning that either environment or area could act as confounders. To partition the effects of niche and neutral processes the influence of area and environmental heterogeneity on species richness relationships should be simultaneously investigated (Legendre et al. 2005; Keil et al. 2012; Keil & Jetz 2014).

Next to climate and area, a further potential confounder is the region of analysis. Biogeographic regions are ecologically distinct areas of the globe and are based on phylogenetic information that groups species in a biologically meaningful way between the continents (Kreft & Jetz 2010; Carstensen et al. 2013). These regions all have different climate and geomorphological characteristics that influence current species distributions and richness. Therefore, environmental heterogeneity in the different biogeographic regions of the globe could influence species richness relationships differently.

Here, we use the global terrestrial mammal fauna to empirically investigate the (relative) influence of area and environmental heterogeneity on species richness. The dataset comprises several empirical studies on the relationship between spatial environmental heterogeneity and species richness of terrestrial mammals in terrestrial systems (outlined in Stein et al. (2015). We split the dataset into biogeographic regions to test if environmental conditions in the different regions resulted in different species distribution relationships.

We use environmental heterogeneity and area as predictor variables to model regional and global patterns of species richness. Elevation range and precipitation range are commonly used environmental heterogeneity variables (Rodríguez et al. 2005; Tuanmu & Jetz 2015). Elevation range is a broad proxy for climatic gradients, habitat turnover, refugial opportunities and isolation and diversification probabilities (Kallimanis et al. 2010). It incorporates multiple factors promoting mammal species richness, including ecological and evolutionary aspects (Stein et al. 2015). Precipitation range is a proxy for climate, which is important for broad-scale mammal species richness (Hawkins et al. 2003; Field et al. 2009). Simultaneously investigating the influences of area and environmental heterogeneity on species richness relationships gives us an indication of the relative contributions of niche and neutral processes to species richness patterns at global and biogeographical scales.

Our analysis allows us to determine the relative importance of niche and neutral processes on species richness patterns for the globe. We also explore how these species richness patterns change in the different biogeographic regions of the globe.

## Material and Methods

Our global terrestrial mammal data comprised 4954 native species derived from distribution maps provided by IUCN (2013), from which richness per grain at a 111 km grid size was aggregated by Stein et al. (2015). This dataset was split into seven mammalian biogeographic regions (Olson et al. 2001; Kreft & Jetz 2010). We excluded introduced species, vagrant species, bats and species for which no specific localities were known. We removed grid cells with no indigenous terrestrial mammals present (excluding the biogeographic regions Antarctica and Oceania) and grid cells containing only water (oceans and large lakes).

We analyzed two measures of environmental heterogeneity in grid cells of 111 km × 111 km in all biogeographic regions of the globe (except for Antarctica and Oceania): elevation range and precipitation range. These two measures of environmental heterogeneity are known to be strong predictors of terrestrial mammal species richness at broad scales and are uncorrelated at this scale, whereas temperature and elevation are highly correlated (Table S1, Fig. S2; Rahbek 2005; Rodríguez et al. 2005; Tuanmu & Jetz 2015). Elevation and precipitation ranges were aggregated by Stein et al. (2015) from elevation and climate surfaces produced by Hijmans et al. (2005) at a 111 x 111 km grain.

We analyzed species richness as a function of area, elevation range and precipitation range for the globe and the six remaining biogeographic regions (Fig. 3) at scales ranging

from one to 50 grid cells. Grid cells were selected using a "random walk algorithm" that randomly selected neighboring cells from an initially selected grid cell (Appendix S1; run in R 3.3.0 (R Core Team 2016)). In short, starting from an initial ("focal") cell, the second cell was randomly selected within the 8-cell neighborhood. The next cell was chosen from the 8-cell neighborhoods of the previously selected cells, excluding cells already selected. The algorithm stopped when a cell group had no not-yet-selected neighboring cells, or when the maximum of 50 cells was reached. Each cell served 50 times as focal cell (i.e. 50 iterations per focal cell). To account for spatial autocorrelation, we randomly reduced the number of focal cells analyzed to a number based on a specified sample precision in species richness. For each biogeographic region a respective sample size was calculated to achieve a sample precision of +/- 4 species. For further details and dataset biogeographic region sizes see the supplementary material (Appendix S1).

**Statistics**

Multivariate quadratic polynomial models with all three variables (area, elevation range and precipitation range) were run on every dataset (Global, Nearctic, Palearctic, Indo-Malay, Neotropic, Afrotropic and Australasia). Model selection was done using AIC but the model with all predictors always fit the data best (Table S3). Predictions for species richness were calculated from these models. All models were run inside a bootstrapping framework with 500 iterations over each focal cell, replicates were iterations based on each focal cell. Predictions of species richness were limited to a minimum of zero, as it is biologically impossible to have a negative number of species.

To calculate which variable (area, elevation range or precipitation range) had the largest influence on species richness relationships, we partitioned the variance using polynomial models. Variance partitioning was calculated using the varPart function from the modEvA package (Barbosa et al. 2016) that is based on R-squared values.

## Results

Both environmental heterogeneity variables showed saturating relationships with area, where an increase in area corresponded to an increase in range of each variable (Fig. S1). The results from variance partitioning (Fig. 1) indicate for the globe and all assessed biogeographic regions that environmental heterogeneity variables -

elevation range and precipitation range - explain more of species richness than area alone does. The variance values for area alone are always smaller in comparison to the variation accounted for by our environmental heterogeneity variables.

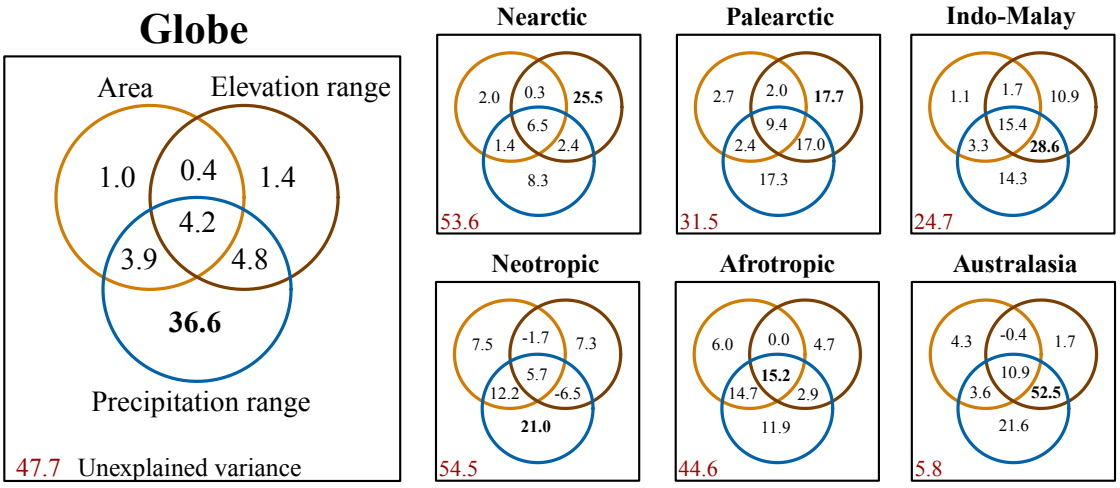


Fig. 1: Variation partitioning diagrams for the globe and each biogeographic region were calculated from multivariate quadratic (second-order) polynomial models. The colors of the circles correspond to each variable, bold values indicate the highest explained variance and red values indicate unexplained variance.

The nature of the relationship between species richness and environmental heterogeneity was, however, not as simple as between species richness and area (Fig. 2). While increasing area always resulted in an increase in species richness, the response to elevation range and precipitation range was more diverse. The pattern with respect to elevation range was complex, with flat, hump-shaped and negatively arched responses. Species richness in response to an increase in precipitation range followed a hump-shaped relationship for the globe and all biogeographic regions, except Australasia, where species richness showed a monotonic increase with precipitation range. These relationships with elevation range indicate the prevalence of high richness centers, where adding specific range values yielded a rapid increase in richness, and low richness centers where increasing the range of elevation yielded little or no increase in species-richness. Since predictions for all variables were calculated from multivariate models, where all variables were present, the strength of the relationships between species richness and each variable is indicated by the slope of the line i.e. when the line is flat that variable had no influence on species richness. This slope corresponds to results from variance partitioning as, for example, species richness for the globe is better explained by precipitation range (explained variation = 30.3) than by elevation range (explained variation = 0.7).

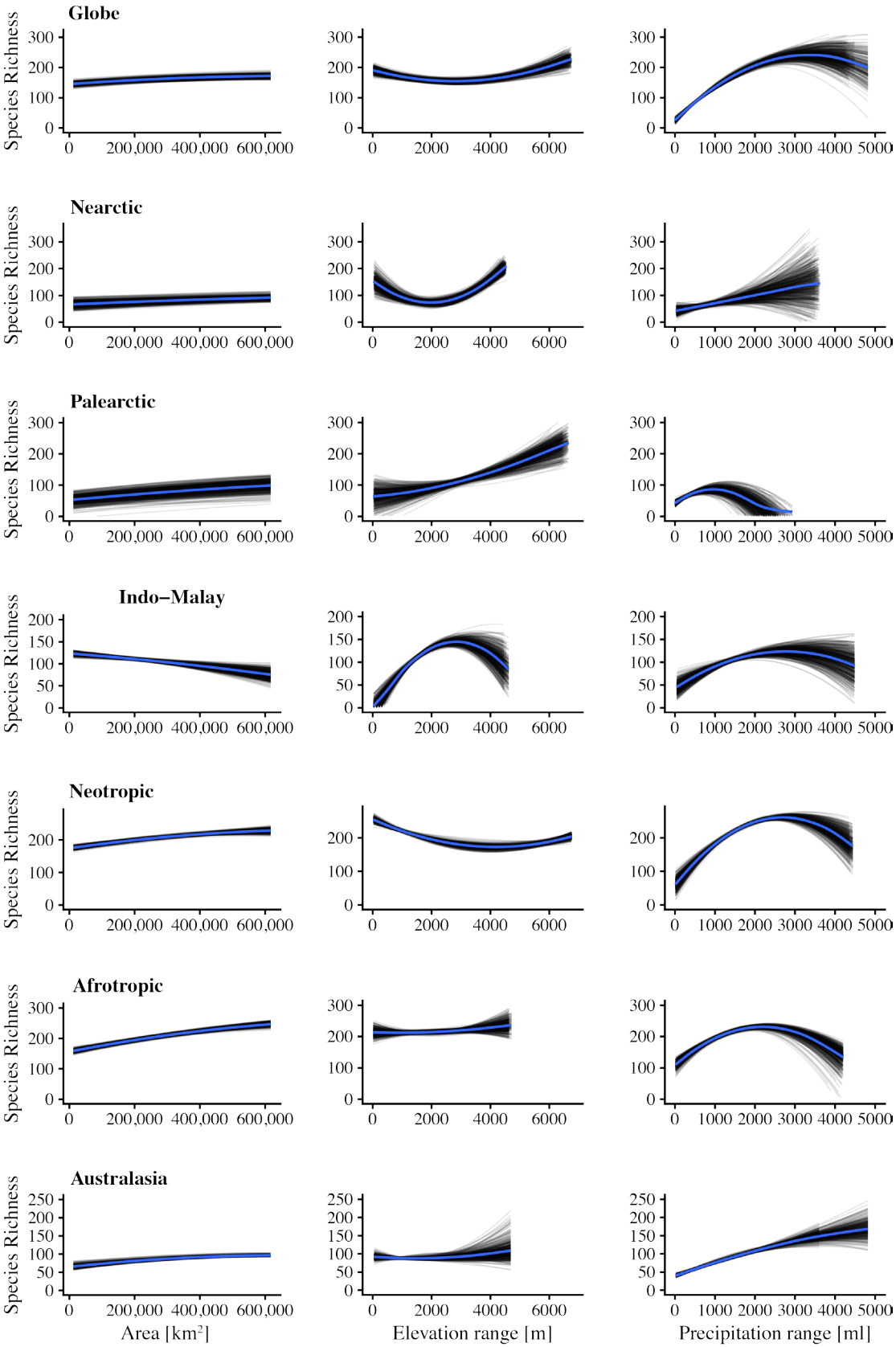


Fig. 2: Species richness relationships (SR) dependent on area and ranges of elevation and precipitation, based on predictions calculated from multivariate models where all variables were present, for the globe and biogeographic regions. Blue lines represent the mean of 500 iterations and each black line represents one of these iterations from polynomial models bootstrapped over focal cells.

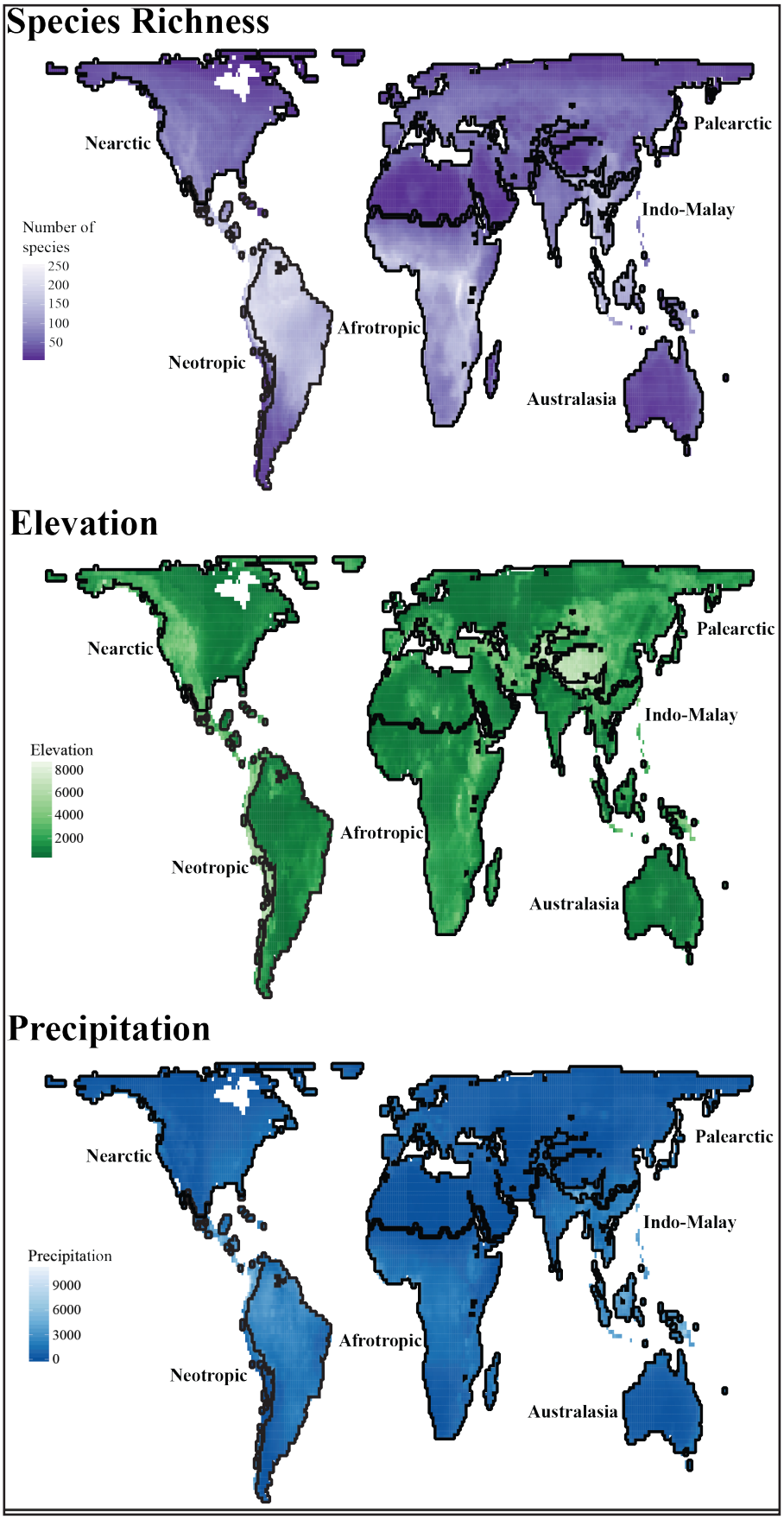


Fig. 3: Species richness, maximum elevation and maximum precipitation across the globe with biogeographic region boundaries based on (Olson et al. 2001) outlined in black (excluding areas with no native terrestrial mammals and bats). .

## Discussion

In this study, we tested for the explanatory power of area, as well as precipitation and elevation range on species richness in an area. The two environmental heterogeneity variables explained a larger share of the species richness relationships than area, supporting the idea that diversity is structured by niches at large scales (Fig. 1). Although, with some complex patterns that might derive from other processes, for example areas of particular low or high species richness (e.g. the tropics vs. the Siberian tundra). These results were consistent at the global scale and at the level of the biogeographical regions. This is because environmental heterogeneity enhances species richness through increased variation in resources, structural complexity or environmental conditions (Tews et al. 2004). This may relate to increased probability of species diversification through isolation or adaptation, which promote species coexistence, persistence and diversification (Stein et al. 2014). Furthermore, range measures of environmental variables capture the length of environmental gradients and relate spatial turnover of mammal species with different environmental requirements at coarse scales (Kallimanis et al. 2010; Stein et al. 2015). Species richness patterns differ in the biogeographic regions as these areas have different climatic and geomorphological characteristics that influence the origins of species distributions (Hortal et al. 2008; Buckley et al. 2010).

### Species richness patterns

For the global species richness patterns, precipitation range was the strongest predictor. This finding is supported by Field et al. (2009) and Hawkins et al. (2003), who also found that climate variables are the strongest driver of species richness at large scales, as it defines species richness capacity. This could be because climate varies more over large geographic areas than other heterogeneity variables, such as altitude (Hawkins et al. 2003; Field et al. 2009).

In the Neotropic biogeographic region precipitation range was the strongest explanatory variable, most likely because of a strong gradient from desert and temperate regions to tropical regions all within this single biogeographic region (Fig. 3; Hawkins et al. 2003). Elevation range strongly influenced species richness patterns in both the Nearctic and Indo-Malay biogeographic regions as these regions include large mountain ranges (Fig. 3). This pattern agrees with findings from Kerr and Packer (1997) and Davies et al. (2007) who also found that elevation range is an important predictor of mammal richness in the Indo-Malay and in parts of the Nearctic biogeographic regions. Species

richness increased most strongly at intermediate elevation ranges (Fig. 2), yielding a hump-shaped relationship between species richness and elevation range. The strength of this hump-shaped pattern could be driven by the proportion of mountainous regions in the biogeographic regions. Mountains cover a large proportion of the Nearctic and Indo-Malay regions (Fig. 3). The lower species richness at high elevation ranges is most likely due to extreme conditions at high altitudes restricting the maximum altitude mammals can live at (Storz et al. 2010), therefore iterations of our algorithm that exceeded this border would not have increased in species richness. Additionally, in the Indo-Malay region, iterations of our algorithm that reached an elevational range of 8,000 m covered a huge amount of environmental heterogeneity and with such high habitat heterogeneity over a limited space (up to 50 neighboring grid cells; 605,000 km2) the species richness found could be limited (Allouche et al. 2012). Topographical isolation through elevational heterogeneity that led to evolutionary species diversification (Kay et al. 2005; Hughes & Eastwood 2006) could also explain why elevation range has a large influence on species richness in mountainous biogeographic regions. But species diversification through topographical isolation occurs at regional scales and, while important, probably does not have a large influence at the scales we investigated (REF).

Combinations of explanatory variables explained species richness patterns better than individual variables in several biogeographic regions. In the Palearctic and Australasia biogeographic regions, elevation range and precipitation range together had the largest effect on richness (Fig. 1). In the Palearctic, change in species richness increased with increasing elevation range and formed a hump-shaped relationship with precipitation range (Fig. 2). This could be due to high spatial heterogeneity in elevation and precipitation and because high values of both variables often overlapped (Fig. S2). In Australasia, areas of high elevation range and high precipitation range supported highest species richness (Fig. 2). This makes sense as the east coast of Australia has the highest elevation range on the continent due to the presence of mountains and also higher levels of precipitation with correspondingly higher species richness. Furthermore, the Australasia biogeographic region includes Papua New Guinea, which also has corresponding patterns of elevation and precipitation, as precipitation is lowest in the mountains (Fig. 3). Papua New Guinea therefore has large heterogeneity of both elevation and precipitation from the lowlands towards the island centre. In the Afrotropic biogeographic region all three variables combined (area, elevation and precipitation) explained species richness patterns

the best (Fig. 1). This could be due to low environmental heterogeneity throughout large regions of Africa and weak elevation and precipitation gradients (Fig. 3).

**Niche and neutral processes**

Species richness patterns can be produced by both neutral and niche processes, but niche processes, through environmental heterogeneity, had the larger influence. Therefore, we advocate using environmental heterogeneity variables as they more accurately predict global species richness relationships, especially as these relationships better reflect the environmental conditions in each biogeographic region. The relationships are not always simple as biodiversity for the globe increased sharply until precipitation range exceeded 6,000 ml and then species richness decreased. A similar hump-shaped relationship was found in several of the biogeographic regions. It is important to note that high ranges of elevation and precipitation did not have a negative effect on species richness rather that at high ranges of heterogeneity, species richness was lower compared with intermediate ranges of heterogeneity.

In our study we found that area alone had a weak predictive influence on species richness patterns, probably because it does not contain ecological mechanisms that structure animal communities (Rosenzweig 1995; Field et al. 2009). However, area is definitely an important factor that influences species richness relationships as it interacts with environmental heterogeneity in the form of an area-heterogeneity tradeoff (Allouche et al. 2012). There is an area-heterogeneity tradeoff when environmental heterogeneity is high, as area becomes a limiting factor and the number of species decreases through mechanisms such as stochastic extinctions due to reduced population size and the loss of species with specific niche requirements (Allouche et al. 2012). This means that as, for example, elevation increases, the species present were replaced by those with different niche requirements to those at lower elevational levels (i.e. vegetation requirements and cold tolerance). This helps explain our hump-shaped relationships with elevation range in the Nearctic and Indo-Malay biogeographic regions as when iterations covered large ranges of elevation, species richness was low.

Identifying ranges of elevation or precipitation where change in species richness is highest offers a fresh perspective over the factors shaping species' richness in different regions. For instance, elevation is known to be a strong predictor of species' richness globally, with particularly high richness at mid-elevation along elevation

gradients (McCain & Grytnes 2010). The patterns of change in species richness with heterogeneity in elevation and precipitation were more complex than species-area curves are, but do improve our understanding and predictions of how species richness patterns are structured in different areas of the globe. This approach may be particularly useful in light of large-scale homogenization of Earth's environments and species - be it due to vast homogeneous landscapes or the mobilization of species across the globe (Davies et al. 2008). Under such conditions, the species-area relationship is limited to examining the potential impacts of habitat loss and fragmentation, but examining environmental heterogeneity instead may be the best way to accurately predict how patterns in species richness will change with climate change and further habitat loss.

**Conclusion**

The importance of environmental heterogeneity for the conservation of biodiversity has been stressed by a range of studies. In line with these earlier results, our findings indicate that environmental heterogeneity is more important than area for predicting species richness up to the global level. Our results support the concern that the global decline in landscape heterogeneity, primarily due to agricultural expansion, intensification and specialization (– leading to landscape homogenization) has detrimental effects on biodiversity at all scales from local to global.

## Acknowledgements

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## Supplementary Material

### S1: Random walk algorithm

We applied a burning algorithm to create sets of nested areas for seven datasets: The global dataset with 10,704 grid cells, Nearctic with 1,731 grid cells, Palearctic with 4,257 grid cells, Indo-Malay with 690 grid cells, Neotropic with 1,553, Afrotropic with 1,771 and Australasia with 702 grid cells. Absolute values of variables per grid cell ranged from: species richness of 5-463, elevation ranges of 10 m - 8,235 m and precipitation ranges of 0 ml -11210.0 ml. To calculate species richness and environmental heterogeneity across spatial scales, we developed a new algorithm in R 3.3.0 (R Core Team 2016). Our algorithm worked well on both spatially contiguous and multi-part grids (Fig. S1.1). The design included the ability to adapt to any given spatial configuration of cells through a flexible neighbor selection, stochasticity through randomized selection of neighbors and a dynamic sampling window that allows observations of all possible realizations of a given spatial dataset including edge/peripheral grid cells. However, the observations were autocorrelated as the observed values at larger spatial scales depended on those at smaller spatial scales, similar to the strictly nested quadrat construction encountered by Storch et al. (2012).

The procedure followed three steps: (1) identification of direct neighbors to all grid cells in the dataset, (2) iterative selection of k-neighbors at each focal grid cell and (3) computation of cumulative species richness and environmental heterogeneity measures for expanding spatial scales centered at a focal grid cell.

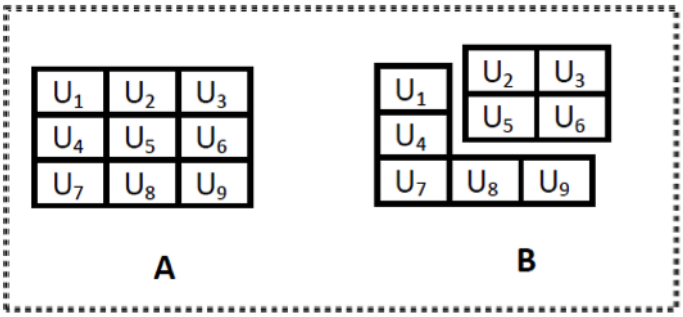


Fig. S1.1: Gridded datasets A and B. A is contiguous, B is multi-part as can arise on islands or at continental boundaries.

Step One:

We first identified all direct neighbours to each grid cell ($DN_f$) in the eight directions. Neighbour identification was as follows; consider $U$ = {1, …, i, …, N}, a finite population of grid cells in dataset A or B as shown in Fig. 1. In Fig. 1, the direct neighbour subset of focal cell $U_5$ in dataset A $DN_{f=5}$= ($U_1$,$U_2$,$U_3$,$U_4$,$U_6$,$U_7$,$U_8$,$U_9$)' and in dataset B, is $DN_{f=5}$ = ($U_2$,$U_3$,$U_6$)'. Their respective subset sizes are; $n(DN_{f=5})$ = 8 and $n(DN_{f=5})$ = 3. This neighbour selection procedure was repeated across all grid cells in the biogeographic region to identify all direct neighbours to each grid cell.

Step two:

We iteratively selected k-neighbours at each focal grid cell. For a focal grid cell (say, $U_5$ in dataset A), the respective direct neighbour subset ($DN_{f=5}$= ($U_1$,$U_2$,$U_3$,$U_4$,$U_6$,$U_7$,$U_8$,$U_9$)') was sampled randomly with a fixed sample size of one. The selected neighbour to the focal grid cell was then added to a vector of neighbours, k, which has the focal grid cell as the first element. Consider that $U_4$ in dataset A is the first selected direct neighbour of $U_5$ to k. For the next iteration, the neighbour subset $DN_f$ is updated (i.e. all direct neighbours $DN_f$ for each cell in k are merged and filtered for already selected cells). A new random selection of a grid cell is made, say $U_7$, and added to k making the following vector; k = ($U_5$,$U_4$,$U_7$)'. This successive sampling without replacement continued until a predefined number of neighbours n(50) was reached or no other contiguous neighbour was found ($DN_f$ is exhausted). By running 50 iterations centered at the focal grid cell, different combinations of selected neighbours to the focal grid cell were realised. For multi part grids with small 'islands' with fewer grid cells than the predetermined length of k (number of neighbours (n(50)), k becomes a vector of dynamic length dependent on the number of contiguous neighbours encountered on the grid.

Step three:

In the last step, we computed cumulative species richness and environmental heterogeneity measures for expanding spatial scales (areas) pivoted at each cell in the dataset as a focal grid cell. Area was calculated as the product of the grid resolution and the number of selected neighbours. Species richness was computed as the number of unique species per grid cell. Elevation and precipitation ranges were computed as the cumulative difference between the maximum and minimum grid cell value in the pool, thus capturing the

length of the environmental gradient. To analyse influences of area, elevation range and precipitation range on species richness, a mean was calculated over 50 iterations per focal cell at the scale of the observation/number of neighbours. An example of these results is shown in Fig S1.2. All results including all grid cells in the dataset as focal cells and at all scales of observation were stored in a large database for further statistical analyses.

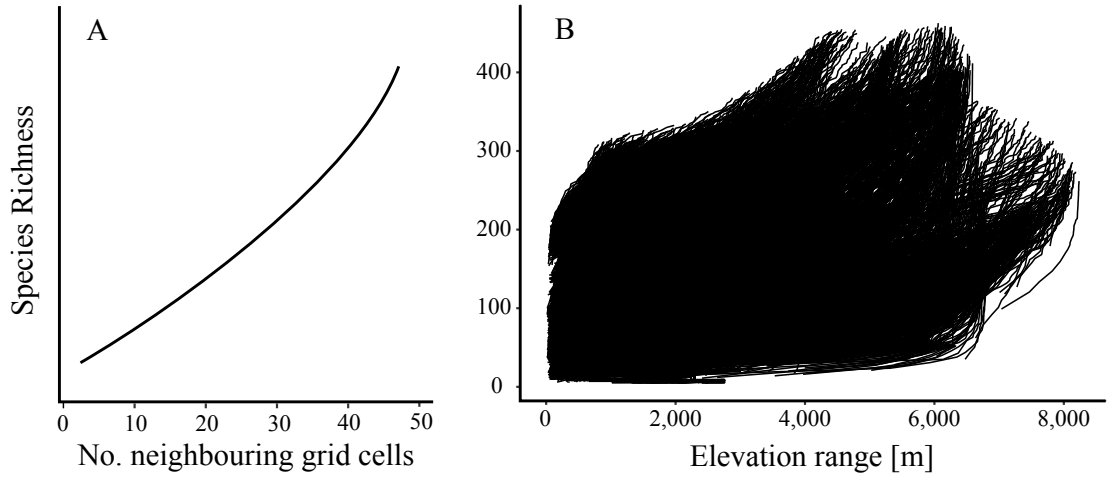


Fig S1.2: Species richness pattern against environmental variables. (a) hypothetical iteration of species richness increasing with area (No. neighboring grid cells), iteration starts at a focal grid cell with species richness increasing as grid cells are added. (b) results of algorithm for the globe where species richness is plotted against elevation range, iterations all begin at a focal cell.

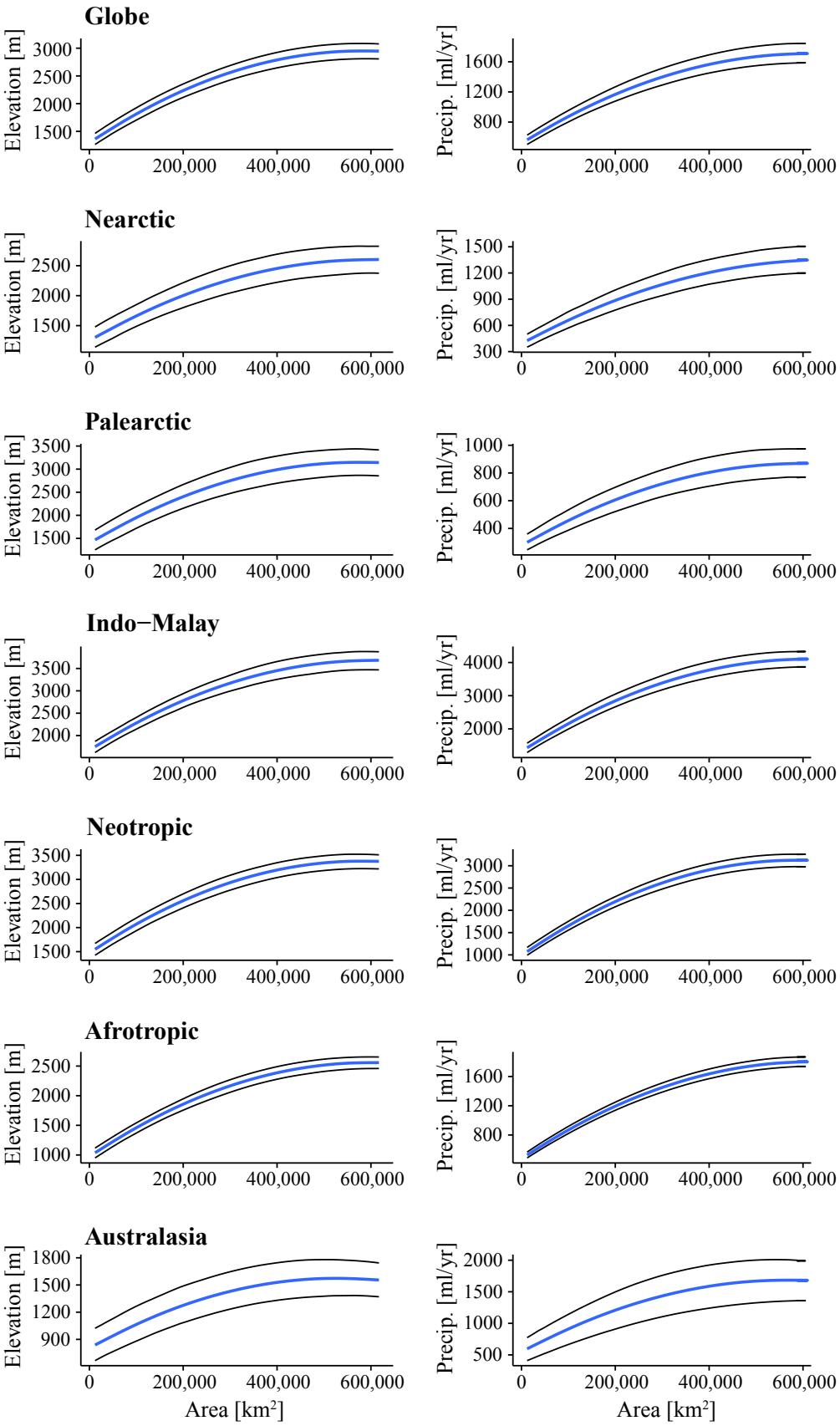


Fig. S1: Environmental heterogeneity relationships for the globe and biogeographic regions plotted against area (number of adjacent grid cells) for ranges of elevation and precipitation (precip.). Blue lines represent the average relationships and black lines represent the 2.5 and 97.5 quantiles from the polynomial models predictions.

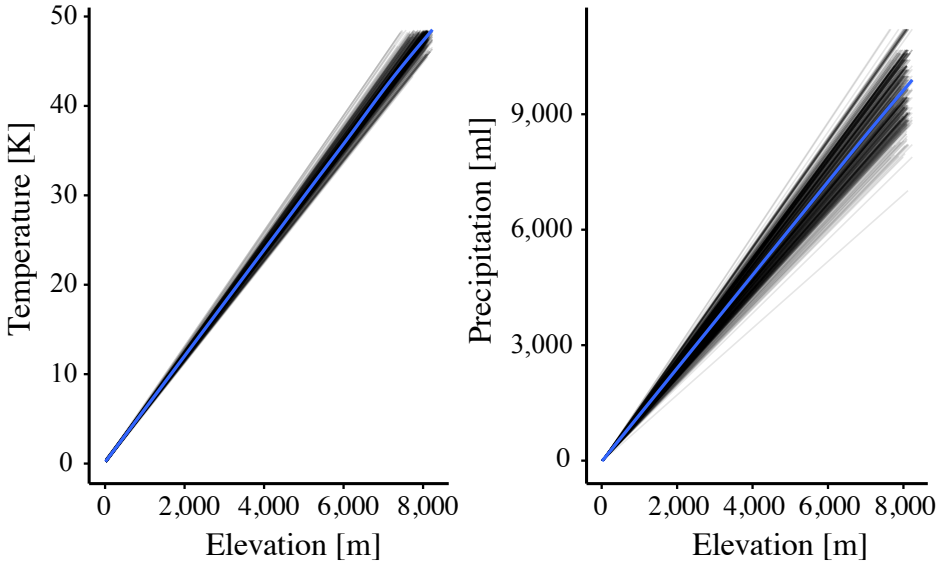


Fig. S2: Fitted bootstrapped polynomial models for temperature range and precipitation range against elevation range for the entire globe. Lines are from the based on focal cells and iterated 500 times, the blue line denotes average relationship. Because of the high colinearity, temperature was excluded from all analyses (Table S1).

Table S1: Variance Inflation Factor for all predictors used in the linear models and split by dataset; supports Fig. S2. Bold values indicate which predictors are correlated. Elevation, temperature and precipitation are all ranges.

| Dataset | Area | Elevation | Temperature | Precipitation |
|---|---|---|---|---|
| **Globe** | 1.313 | **9.319** | **9.364** | 1.413 |
| **Nearctic** | 2.026 | 4.341 | **5.309** | 1.762 |
| **Palearctic** | 1.367 | **8.459** | **9.483** | 1.785 |
| **Indo-Malay** | 1.555 | **109.11** | **108.044** | 1.725 |
| **Neotropic** | 1.209 | **67.585** | **78.567** | 2.669 |
| **Afrotropic** | 1.456 | **31.2** | **32.648** | 1.662 |
| **Australasia** | 1.805 | **18.692** | **12.407** | **6.228** |

Table S2: AIC values for environmental heterogeneity model selection with area and area squared as factors. Two models were run per environmental heterogeneity variable, one with and the other without the quadratic term for area (i.e. lm(elevation ~ area + poly(area)); lm(elevation ~ area)). Columns titled elevation and precipitation show values from models where these variables were tested against just area, columns with 'sq' after the name show values from models where these variables were tested against area + poly(area). Bold values indicate models with best fit.

| Dataset | Elevation | Elevation sq | Precipitation | Precipitation sq |
|---|---|---|---|---|
| **Globe** | 475243 | **475028.9** | 464559.9 | **464426.8** |
| **Nearctic** | 103225.2 | **103186.6** | 96656.6 | **96616.96** |
| **Palearctic** | 95240.02 | **95188.66** | 83667.61 | **83626.26** |
| **Indo-Malay** | 183739.6 | **183624.7** | 188112.6 | **187972.9** |
| **Neotropic** | 103225.2 | **103186.6** | 96656.6 | **96616.96** |

| | | | | |
|---|---|---|---|---|
| **Afrotropic** | 268031.7 | **267804.7** | 249599.5 | **249159.2** |
| **Australasia** | 74954 | **74928.18** | 78569.12 | **78551.28** |

Table S3: AIC values for species richness model selection with area, elevation and precipitation and their polynomials as factors in the linear models. Models were setup as follows: full model: variables + their polynomial terms (area + poly(area) + elevation + poly(elevation) + precipitation + poly(precipitation); subset models: with all variables + all combinations of polynomial terms (both one and two polynomial term combinations); basic model: all variables (no polynomial terms)). Bold values indicate models with best fit. 'sq' indicates polynomial term; names of columns indicate combinations of polynomial terms. 'Elev' = elevation and 'Precip' = precipitation.

| **Dataset** | **Full model** | **Area sq + Elev. sq** | **Area sq + Precip. sq** | **Elev. sq + Precip. sq** |
|---|---|---|---|---|
| **Globe** | **300287.4** | 303699.6 | 300634.7 | 300543 |
| **Nearctic** | **61431.86** | 61720.8 | 61875.83 | 61586 |
| **Palearctic** | **51297.41** | 52253.61 | 52065.9 | 51402.94 |
| **Indo-Malay** | **107175.2** | 111553.6 | 113899.8 | 107632.4 |
| **Neotropic** | **245490.7** | 246690.7 | 247918.5 | 245822 |
| **Afrotropic** | **170023.4** | 171775.8 | 171395.5 | 170155.3 |
| **Australasia** | **31571.02** | 32405.49 | 31750.22 | 32220.18 |
| **Single terms** | **Area sq** | **Elev. sq** | **Precip. sq** | **Basic model** |
| **Globe** | 303804.6 | 303775.8 | 300918.5 | 303812.6 |
| **Nearctic** | 62097.02 | 61814.05 | 61896.69 | 62101.1 |
| **Palearctic** | 52531.16 | 52302.37 | 52250.73 | 52531.21 |
| **Indo-Malay** | 114267.3 | 111999.2 | 113950 | 114300 |
| **Neotropic** | 247996.4 | 246897.4 | 247974.3 | 248052.4 |
| **Afrotropic** | 172483.5 | 171969.1 | 171582.6 | 172560.4 |
| **Australasia** | 32591.98 | 32507.78 | 32293.01 | 32656.98 |

Table S4: Scaled coefficients for species richness models with area, elevation and precipitation and their polynomials as factors in the linear models. Models were setup as following: full model: variables + their polynomial terms (area + poly(area) + elevation + poly(elevation) + precipitation + poly(precipitation); subset models: with all variables + all combinations of polynomial terms (both one and two quadratic term combinations); basic model: all variables (no polynomial terms)). 'sq' indicates polynomial term; names of columns indicate combinations of polynomial terms. 'Elev' = elevation and 'Precip' = precipitation.

| **Dataset** | **Intercept** | **Area** | **Area sq** | **Elev.** | **Elev. sq** |
|---|---|---|---|---|---|
| **Globe** | 135.82 | 8.08 | -7.85 | -13.91 | 4.64 |
| **Nearctic** | 85.56 | 3.24 | -5.37 | 34.14 | -39.64 |
| **Palearctic** | 89.29 | 10.36 | -7.13 | -8.35 | 11.39 |
| **Indo-Malay** | 188.6 | -9.77 | -1.3 | 119.85 | -205.37 |
| **Neotropic** | 233.01 | 46.03 | -11.54 | -86.11 | 53.53 |
| **Afrotropic** | 209.73 | 38.62 | -11.83 | -36.24 | 17.26 |
| **Australasia** | 81.75 | 13.09 | -5.91 | 5.83 | -6.64 |
| | **Precip.** | **Precip. sq** | **Area*Elev.** | **Area*Precip.** | **Elev.*Precip.** |

| | | | | | |
|---|---|---|---|---|---|
| **Globe** | 94.73 | -68.83 | -8.6 | 13.05 | 14.93 |
| **Nearctic** | 22.73 | -32.91 | 23.24 | -3.45 | 14.11 |
| **Palearctic** | 31.59 | -49.3 | -0.73 | 10.67 | 36.32 |
| **Indo-Malay** | 45.94 | -165.49 | 18.55 | 19.27 | 193.84 |
| **Neotropic** | 57.34 | -54.76 | -19.07 | 0.6 | 79.32 |
| **Afrotropic** | 52.89 | -60.56 | -13.6 | 7.37 | 56.9 |
| **Australasia** | 39.39 | -24.23 | -8.56 | 15.43 | 18.73 |

Table S5: Summary of terrestrial mammal species richness for each dataset.

| **Dataset** | **Minimum** | **1st Quartile** | **Median** | **Mean** | **3rd Quartile** | **Maximum** |
|---|---|---|---|---|---|---|
| **Globe** | 5 | 33 | 53 | 68.23 | 89 | 250 |
| **Nearctic** | 5 | 27 | 44 | 43.27 | 57 | 137 |
| **Palearctic** | 7 | 27 | 42 | 43.54 | 57 | 187 |
| **Indo-Malay** | 40 | 67 | 95 | 103.5 | 138 | 202 |
| **Neotropic** | 11 | 100 | 144 | 134 | 179 | 246 |
| **Afrotropic** | 14 | 70 | 101 | 101.7 | 133 | 250 |
| **Australasia** | 7 | 26 | 30 | 38.64 | 45 | 128 |

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