Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale

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Summary

Urbanisation has an important impact on biodiversity, mostly driving changes in species assemblages, through the replacement of specialist with generalist species, thus leading to biotic homogenisation. Mobility is also assumed to greatly affect species' ability to cope in urban environments. Moreover, specialisation, mobility and their interaction are expected to greatly influence ecological processes such as metacommunity dynamics and assembly processes, and consequently the way and the spatial scale at which organisms respond to urbanisation. Here we investigate urbanisation impacts on distinct characteristics of species assemblages – namely specialisation degree in resource use, mobility and number of species, classified according to both characteristics and their combination – for vascular plants, butterflies and birds, across a range of spatial scales (from 1x1 km plots to 5 km-radius buffers around them).

We found that the degree of specialisation, mobility and their interaction, greatly influenced species' responses to urbanisation, with highly mobile specialist species of all taxonomic groups being affected most. Two different patterns were found: for plants, urbanisation induced trait divergence by favouring highly mobile species with narrow habitat ranges. For birds and butterflies, however, it reduced the number of highly mobile specialist species, thus driving trait convergence. Mobile organisms, across and within taxonomic groups, tended to respond at larger spatial scales than those that are poorly mobile. These findings emphasize the need to take into consideration species' ecological aspects, as well as a wide range of spatial scales when evaluating the impact of urbanisation on biodiversity. Our results also highlight the harmful impact of widespread urban expansion on organisms such as butterflies, especially highly mobile specialists, which were negatively affected by urban areas even at great distances.

Key words:
Assembly patterns; Birds; Built-up area; Butterflies; Multi-taxa assessment; Spatial dynamics; Vascular plants

Introduction

The exacerbated growth of urban areas since the second half of the 20th century is considered a main driver of land-use changes and, hence, a major threat to biodiversity worldwide (Grimm et al. 2008, Elmqvist et al., 2013). Urbanisation has been reported to change the composition of biological communities. It can particularly lead to biotic homogenisation through the replacement of non-urban specialist species – which have narrow ranges of habitat and resource use, and are usually hosted in (semi-)natural areas – with urban adapted, typically generalist species, which are able to exploit the wide variety of resources and habitats that urban areas support (Shochat et al. 2006, Lososová et al. 2012, Sol et al. 2014).

Besides the degree of specialisation in the use of resources (i.e., niche width), mobility has been proposed as a relevant trait in disturbed environments like urban areas (Büchi et al. 2009, Öckinger et al. 2010, Schleicher et al. 2011). Species composition of biological communities is greatly affected by dispersal processes and metacommunity dynamics, such as source-sink dynamics, in which species mobility plays a prominent role (see e.g. Dunning et al. 1992, Leibold et al. 2004, Vellend 2010). In the case of plants, highly mobile species able to rapidly colonize open sites after disturbances, usually proliferate in urban areas (Kühn and Klotz 2006, Lososová et al. 2012). Typically, these are pioneer species associated with early successional stages. Mobility is also very important for animals, with highly mobile species being supposed to better cope with urban disturbances (e.g., Devictor et al. 2007). The maintenance of urban communities may actually rely on the immigration of individuals from nearby populations from more natural habitats, in which case species dispersal is even more relevant (Stefanescu et al. 2004, Shochat et al. 2006). This is generally the case in systems that suffer recurrent disturbances, such as agricultural land, where biodiversity levels greatly depend on the species pool hosted by (semi-)natural habitats in their surroundings (Duelli and Obrist 2003, Tscharntke et al. 2005).

Overall, poorly mobile species are assumed to be more intensively affected by habitat loss and fragmentation caused by land-use changes, while more mobile species, able to move among distant habitat fragments, are expected to be less sensitive to this process (Öckinger et al. 2010, Schleicher et al. 2011). However, more mobile animals usually have larger home ranges and rely on larger habitat patches as well, and, as a result, they may be more sensitive to habitat fragmentation (Thomas 2000, Chace and Walsh 2006, Slade et al. 2013). In addition, more mobile organisms tend to be affected by processes acting at larger scales than those influencing poorly mobile or sessile organisms (Merckx et al. 2009, Concepción and Díaz 2011, Braaker et al. 2014). Despite the relevance of selecting a proper range of spatial scales to analyse ecological processes affecting diversity patterns for distinct organism types (Tews et al. 2004, Merckx et al. 2012, Raebel et al. 2012), only a few studies have addressed this question in relation to urbanisation impacts on biodiversity (see e.g. Braaker et al. 2014).

The relevance of spatial dynamics in biological communities greatly varies depending on organisms' degree of specialisation and mobility (Leibold et al. 2004). Every organism may experience the environment in a different way, and the same landscape can hence be perceived as heterogeneous by one species and as fragmented by another. Likewise, a resource-rich patch for one species can be a barrier for another, and this, in addition, depends on the spatial scale we consider (Tews et al. 2004). For instance, specialist species – with narrow ranges of resource and habitat requirements (i.e., niche width) – would typically perceive their habitat as more fragmented than generalists, and would consequently rely more on their mobility to succeed (Öckinger et al. 2010). Responses to ecological processes that shape community assembly also depend on species' degree of specialisation and mobility. This can prevent some species from occurring in certain places, where, for instance, their resource requirements are not fulfilled (i.e., environmental filtering), they are excluded by stronger competitors (i.e., biotic filtering or limiting similarity), or they are not able to reach because of dispersal limitations (Mason et al. 2005, Grime 2006). Moreover, these assembly processes are also expected to be scale-dependent and to act more intensively in disturbed environments, such as managed grasslands (Mason et al. 2011, de Bello et al. 2013). However, studies on how urbanisation affects community assembly patterns have appeared only recently (e.g., Le Viol et al. 2012, Knapp et al. 2012).

Here, we investigate urbanisation impacts on two species characteristics, namely mobility and the degree of specialisation in resource use, which are primarily involved in metacommunity dynamics and community assembly processes, and then supposed to be greatly affected by urbanisation. We explore such impacts for distinct taxonomic groups and across several spatial scales to address the following research questions: (1) Do the degree of specialisation and mobility of species assemblages of different taxonomic groups change along the urbanisation gradient? (2) Which ecological processes are driving these changes? And (3) at which spatial scale are organisms with different degrees of specialisation and mobility affected by urbanisation?

Our study focuses on the Swiss Plateau, the largest biogeographic region of Switzerland, which has undergone significant growth of urban areas in recent decades (Schwick et al. 2012). We considered three taxonomic groups (i.e., birds, butterflies and vascular plants), which were covered in the Swiss biodiversity monitoring programme at the landscape scale (1x1 km plots). For each group, we evaluated urban effects on mean community values of specialisation degree and mobility, as well as on the variation of these characteristics in order to investigate possible changes in community assembly patterns in response to urbanisation

(Mason et al. 2005, Grime 2006). We also examined urban effects on the species richness of distinct ecological groups cross-classified according to specialisation degree and mobility to test for likely interactions between both species characteristics, which has been largely unexplored so far (but see Öckinger et al. 2010, Slade et al. 2013). We adopted a multi-scale approach in our analysis of urbanisation impacts on biodiversity, by considering the proportion of built-up area in a wide range of spatial scales, including 1x1 km plots and a set of surrounding buffer areas of 1 to 5 km radius. This enabled us to investigate the spatial scales at which urbanisation affects diversity most for the different organisms studied.

Methods

1. Study area

We focused our study on the Swiss Plateau (Fig. 1), the central part of Switzerland between the Alps and the Jura Mountains, delimited according to the definition of Swiss biogeographic regions (Gonseth et al. 2001). This region has a mean altitude of 540 m a.s.l. (range: 300–940 m a.s.l.), a mean annual temperature of 8.5 °C (6.5–9.5 °C) and a mean annual precipitation of 1,140 mm (730–2,000 mm). The Swiss Plateau is the largest biogeographic region in Switzerland, with ca. 11,200 km^2 dominated by agricultural land-uses (around 50% of the area). This region suffers the strongest growth of urban areas in Switzerland, which have tripled since the beginning of the 20th century and now cover around 15% of the region (Schwick et al. 2012).

2. Diversity metrics

We used data on species from three taxonomic groups (vascular plants, butterflies, and birds) regularly collected in the Swiss biodiversity monitoring programme at the landscape scale (BDM - Biodiversity Monitoring in Switzerland Coordination Office 2009). We used data from 109 plots (1x1 km) which are regularly distributed in the study region, where vascular plants, butterflies and breeding birds were surveyed between 2006 and 2011 using standardized methods (i.e., 2.5 km-length transects along paths and roads within 1x1 km plots for plants and butterflies, and in three visits during the breeding season along fixed routes within plots for birds; for additional details see Appendix 1). For plants, we included eight additional plots in the most urbanised areas within the study region, where additional plant surveys were conducted in 2006.

For each taxonomic group, we evaluated urban effects on the degree of specialisation and mobility of the co-occurring species in the 1x1 km plots. Species' characteristics related to the range of resource use (e.g., diet or habitat use) were used to estimate species' degree of specialisation. Specifically, mean standardized range (0-1) of a set of habitat and climatic preferences (e.g., temperature, light, moisture or nutrients), varying from wide (0) to narrow (1) ranges of preferences, was used to estimate plant species specialisation. For birds, we used the mean standardized range of distinct resource use, including food, breeding substrates and habitat requirements (ranging from 0 – wide – to 1 – narrow). Lastly, the standardized range (also varying from 0 – wide – to 1 – narrow) of larval food resources, was used as a proxy of butterflies' degree of specialisation. Mobility was estimated by means of species' morphological or life-history traits (functional traits *sensu* Violle et al. 2007), such as wing load (g/cm^2) for birds and butterflies, and dispersal modes for vascular plants. These metrics have been found to be associated to longer movements or dispersal ability (see e.g., Newton 2008, Meynard et al. 2011, Luck et al. 2012,for birds, Turlure et al. 2009, for butterflies, and Vittoz and Engler 2007, for plants). See Table 1, for a detailed description of species characteristics, and Appendix 2, for specific values of the set of species found in our study.

For each of the two species' characteristics (i.e., mobility and degree of specialisation) and taxonomic groups, we calculated two functional metrics: mean community values (MV) and standard deviations (SD) per plot, that is, mean and SD of mobility and specialisation degree of all the species present in each plot. MV was used to investigate possible shifts in mean dispersal and specialisation values within species assemblages driven by urbanisation (see e.g., Ricotta and Moretti 2010). On the other hand, SD of species characteristics is a metric of functional variability (i.e., functional diversity), and was used to explore the relative role of distinct community assembly processes (e.g., environmental filtering *versus* limiting similarity; Mason et al. 2005) in shaping species assemblages along the analysed urbanisation gradient.

Lastly, richness of distinct groups of species classified according to mobility (i.e., highly and poorly mobile species), degree of specialisation (i.e., specialist and generalist species) and their cross combination (i.e., highly mobile specialists, poorly mobile specialists, highly mobile generalists, and poorly mobile generalists) were also used as dependent variables in subsequent analyses. We thereby tested explicitly for possible interactions between mobility and specialisation affecting species' responses to urbanisation (see Table 1 for group definitions and classification criteria).

3. Urban and non-urban environmental variables

We used proportion of urban area – defined as built-up or sealed area, i.e., houses, industries, roads and other infrastructures, but also gardens, parks and other green areas – in 1x1 km plots and in buffers of 1-, 2-, 3-, 4-, and 5-km radius around those plots to characterize the degree of urbanisation at different spatial scales. We also calculated a set of non-urban environmental predictors, which are known to affect biodiversity, such as climate (i.e., annual precipitation and mean temperature) and topography (i.e., northness and surface roughness) variables (e.g., Wood and Pullin 2002, Nobis et al. 2009, Lososová et al. 2012), and variables related to other land-uses (i.e., agricultural land) and landscape heterogeneity (edge density within plots; see e.g., Duelli and Obrist 2003), to control for possible confounding effects on the distinct diversity metrics (see Table 2 for details).

4. Data analyses

To investigate whether the degree of specialisation, mobility and species richness of the different species groups were significantly affected by urbanisation, and to identify the spatial scale at which this process showed the strongest effects, we used the analytical approach described below.

For each diversity metric and taxonomic group, we used a set of generalised linear models (GLMs), each of which included proportion of urban area at one of the different spatial scales considered (i.e., from 1x1 km plots to 5 km-radius buffers), together with the other environmental predictors (i.e., agricultural land, landscape heterogeneity, climate, and topography) at the plot scale. Response variables for each taxonomic group were mean community values (MV) and standard deviations (SD) of the degree of specialisation and mobility, as well as species richness (SR) of the distinct ecological groups classified according to both features and their cross combination (see above). Then, we used the Akaike information criterion, corrected for finite sample sizes (AICc; Burnham and Anderson 2002), to select the best fitted models (i.e., delta AICc ≤ 2) for each response variable. Percentage of deviance ($\%D^2$) explained by the proportion of urban area at different spatial scales was used to compare the relevance and distance of urbanisation influence for the distinct diversity metrics and taxonomic groups.

Pearson's product-moment correlations between predictors included in models were all below 0.7 (Dormann et al. 2013). Linear and quadratic terms of proportion of urban area at each spatial scale were included in models to account for possible non-linear responses to urbanisation. We used normal distribution of errors for continuous data on mobility and specialisation degree (MV and SD) and Poisson error distribution for count data on species richness of the different species groups. Residuals of GLMs were graphically explored to test for model assumptions (i.e., residual distribution, independence and homoscedasticity). Sites for which the whole set of predictors were not available (12 for plants and six for birds and butterflies) were removed from the analyses. Two overly influential points (Cook's distance >1) were additionally excluded from the analyses for birds and butterflies, which resulted in samples of 105 (90%) plots for plants and 101 (93%) plots for birds. Finally, we used partial residual plots to graphically illustrate significant relationships between distinct diversity variables and the proportion of urban area at the best fitted scales. Partial residual plots of models represent relationships between response variables and the explanatory parameter of interest once the effects of all the other predictors have been accounted for.

All statistical analyses were done with R version 3.0.2 (R Core Team 2014). Urban and other environmental predictors were calculated using the R package *raster* (Hijmans and van Etten 2012) and ArcGIS (ESRI 2011).

Results

Proportion of urban area at different spatial scales explained a substantial part of the variability in mean community values (MV) and variation (SD) of specialisation degree of plants and birds, and of mobility of butterflies and plants (Fig. 2). Our results also showed differences in the responses of species richness (SR) to urban area for the distinct groups of species cross-classified according to the degree of specialisation and mobility. We also found differences in the spatial scales at which those groups were affected most by urban area across and within taxa (see Table 3 and Appendix 3 for details).

1. Plants

MV of plant specialisation significantly increased with the proportion of urban area in the whole range of spatial scales (from 1x1 km plots to the largest 5 km-radius buffers), with the best fitted model being that which included the urban area at the smallest plot scale (Fig. 2a and 3a). SD of plant specialisation also increased with the proportion of urban area at the plot scale (Table 3). SR of specialist plants increased with urban area at a wide range of spatial scales as well, but most at small scales (1 km-radius buffers). In the case of generalist plants, SR showed curvilinear (i.e., hump-shaped) relationships with urban area, and they mostly responded at intermediate spatial scales (3 km-radius buffers).

With respect to plant mobility, MV per plot also increased with the proportion of urban area, especially at the plot scale (Figs. 2b and 3b), but no significant effects were found on SD (Table 3). Although SR of both highly and poorly mobile plants responded best to urban area at intermediate spatial scales (3 km-radius buffers), highly mobile species showed significant curvilinear responses in a wider range of spatial scales (from plots to the largest buffers) than poorly mobile plant species (Table 3). Likewise, SR of highly mobile specialist plants, though responding best at small spatial scales (plots and 1 km-radius buffers), significantly increased with urban area over the whole range of spatial scales (Figs. 2c and 5a). In contrast, SR of poorly mobile specialist plants only showed significant positive responses at the smallest scales (plots and 1 km-radius buffers). In the case of generalist plants, the differences between highly and poorly mobile species were less clear, and SR of both responded best to urban area at intermediate spatial scales (3 km-radius buffers, hump-shaped responses), though SR of poorly mobile generalists also showed significant responses at smaller scales (plots and 1 km-radius buffers; Table 3).

2. Birds

MV of bird specialisation degree decreased with the proportion of urban area over a wide range of spatial scales (from plots to the largest buffers; Fig. 2a). However, similar to plants, they responded best to urban area at small spatial scales (plots and 1 km-radius buffers; Table 3, Fig. 4a). SD of bird specialisation also decreased most with urban area at the plot scale, but also in small buffers of 1-2 km radius. SR of specialist birds showed similar responses, being negatively affected by the proportion of urban area in plots and small buffers around them, whereas SR of generalists showed no significant responses to urban area at any scale (Table 3). Neither MV nor SD of bird mobility were significantly affected by urban area. SR of both highly and poorly mobile birds did not show significant responses to urban area at any scale. In addition, only highly mobile specialist birds were negatively affected by the proportion of urban area at small spatial scales, especially in plots (Table 3, Fig. 5b).

3. Butterflies

The degree of specialisation of butterflies was not significantly affected by urban area, with SR of both specialist and generalist species decreasing with rising urban area. However, while specialist butterflies responded to urban area over a range of spatial scales, mostly from intermediate to the largest buffers (2 to 5 km radius; Table 3), generalist species only showed significant responses at intermediate scales (2 and 3 km radius). MV of mobility, in contrast, significantly decreased with the proportion of urban area at a wide range of spatial scales (from the smallest to the largest buffers around plots, Fig. 2b), but the best-fitted model included urban area at intermediate scale (3 km-radius buffers; Fig 4b). SD of butterfly mobility also decreased with the proportion of urban area at this scale (Table 3).

SR of highly mobile butterflies was negatively affected by urban area at a wide range of spatial scales (from the smallest to the largest buffers around plots), but responded best at large spatial scales (i.e., 3 to 5 km-radius buffers; Fig. 2c). In contrast, SR of poorly mobile butterflies only showed significant negative responses to urban area at a smaller spatial scale (i.e., 2 km-radius buffers; Table 3). Similarly to birds, highly mobile specialist butterflies were the only group among combined classes of mobility and specialisation degree that showed significant negative responses to urban area, especially at the largest spatial scale (Fig. 5c).

4. Effects of non-urban predictors

Besides urbanisation effects, significant responses to non-urban environmental predictors were found for the different diversity metrics. Overall, topography and climate had a large influence on the different diversity metrics, especially for plants, with SR of the distinct groups of plants decreasing with northness, precipitation and temperature, while increasing with surface roughness. Proportion of agricultural land in the landscape negatively affected SR of distinct groups of plants and highly mobile specialist birds and butterflies. In contrast, landscape heterogeneity (i.e., edge density) increased SR of the different groups analysed, particularly for birds (see Appendix 4 for details).

Discussion

Overall, our results show the considerable influence that species degree of specialisation and mobility, as well as their interaction, have on species assemblage responses to urbanisation. We found different relationships between urbanisation and species richness (SR) of the distinct ecological groups classified according to specialisation degree, mobility and their combination, as well as differences in the spatial scales at which those groups responded most to urbanisation.

1. Degree of specialisation and mobility

Although SR of all functional groups of plants was significantly and positively related to urbanisation, highly mobile (i.e., able to rapidly colonize cleared sites after disturbances) and specialist plants (i.e., with a narrow range of habitat preferences), benefitted most. This led to an increase of specialisation degree and mobility of plant assemblages with a rising urbanisation level. The positive response of specialist plants to urbanisation was most likely driven by species within this group that prefer eutrophic habitats, such as early successional species that are highly mobile as well (Kühn and Klotz 2006, Lososová et al. 2012), rather than rare or threatened specialists from (semi-)natural habitats. Most specialist plants in our study were actually common species that inhabit eutrophic places (around 73% of species occurrences *vs.* 44% for generalist species), many of them non-natives (28% *vs.* 9% for generalists), while red-listed species only represented 4% of specialist plants (in contrast to 1% for generalist plants).

In the case of birds, urbanisation decreased specialisation degree of species assemblages, as SR of specialists decreased, while generalist species were not affected. This confirms previous studies showing the homogenisation of urban bird communities due to the prevalence of generalist species (Chace and Walsh 2006, Devictor et al. 2007, Le Viol et al. 2012, Sol et al. 2014). In contrast, for butterflies specialisation degree was not affected. In fact, SR of both specialist and generalist butterflies decreased with urbanisation, which stresses the generally high sensitivity of this taxon to the loss of (semi-)natural habitats (e.g. Wood and Pullin 2002, Stefanescu et al. 2004, Casner et al. 2014). Nonetheless, the stronger decrease in SR of highly mobile butterflies compared to less mobile ones resulted in urban species assemblages that were on average less mobile. Potentially, this indicates that urbanisation might make butterfly assemblages not only less diverse but also more prone to be affected by isolation, and thus more likely to suffer local extinctions (Öckinger et al. 2010).

In the cross combination of mobility and specialisation degree, only SR of highly mobile specialist birds and butterflies showed significant decreases as urbanisation level grew. This indicates a likely interaction between specialisation degree and mobility influencing organisms' responses to urbanisation. In particular, these results indicate that highly mobile and specialist species are more sensitive to the fragmentation of their original habitats, which contrast with the traditional view that low mobile specialists are likely to be more intensively affected by habitat fragmentation (Öckinger et al. 2010, Schleicher et al. 2011).

However, Slade et al. (2013) found similar results of forest fragmentation on mobile forest specialist moths. Highly mobile specialists might be more vulnerable to habitat loss since they have larger home ranges and, as a result, would depend on the conservation of larger patches of suitable habitat (Stefanescu et al. 2004, Chace and Walsh 2006, Slade et al. 2013). This appears to be the case for the highly mobile specialist birds in our study, which were mostly forest species (78% of species occurrences; e.g., *Dendrocopos major* and *Buteo buteo*). Among poorly mobile specialist birds, there were also forest species, however, they were less abundant (54% of species occurrences) and tended to be smaller (e.g., *Sitta europaea* and *Regulus regulus*). Hence, poorly mobile specialist birds are likely to rely on smaller habitat patches and, in turn, to be less sensitive to fragmentation caused by urbanisation (Chace and Walsh 2006). Besides forest species, some urban-adaptable species (e.g., *Apus apus*) or more rural species, although still linked to human presence (e.g., *Hirundo rustica*), were frequent among poorly mobile specialist birds as well (33% of species occurrences), which also contributes to explain their lower vulnerability to urbanisation.

Poorly mobile specialist butterflies were, however, less frequent (average species richness per plot: 5.8 ± 2.0 [SE]) than highly mobile specialists (7.8 ± 3.1). It is likely that the most vulnerable butterfly species may have already disappeared from the Swiss Plateau after the severe loss of their original habitats due to the intensive land-use changes that took place in this region between 1950 to 1980 (Lachat et al. 2010) or even before, and consequently would not be included in our analyses. Interestingly, among the poorly mobile specialist butterflies found in our study, a higher proportion was able to feed on evergreen plants during the larval stage compared to highly mobile species (84% of species occurrences for poorly mobile species *vs.* 33% for highly mobile specialists). Hence, poorly mobile specialist butterflies still remaining in our study region could be those that are able to exploit resources provided by alternative habitats, such as evergreen – usually ornamental – vegetation from urban gardens and parks (Pearse and Altermatt 2013). In contrast, highly mobile specialists, which are able to move across suitable habitat patches at farther distances in the landscape (Stefanescu et al. 2004), may still rely on (semi-)natural habitats outside urban areas, rather than on ornamental vegetation. This would explain their higher vulnerability to urbanisation compared to poorly mobile specialists detected in our study.

Most urbanisation impacts on birds and butterflies can be considered indirect effects of the elimination of the original vegetation in urban areas (Devictor et al. 2007, Casner et al. 2014). Groups of birds and butterflies that showed clear decreases with increasing urbanisation (i.e., highly mobile specialists) were those that appear to rely more on (semi-) natural vegetation (i.e., forest specialist birds and butterfly species unable to exploit evergreen vegetation). Hence, besides likely interactions between mobility and specialisation degree, our results suggest some kind of overlap or association between both species characteristics.

In addition to urbanisation impacts, species richness of the different groups of organisms analysed, tended to be negatively affected by the percentage of agricultural land in the landscape, but positively affected by its degree of heterogeneity (Appendix 4). Altogether, these results point to the likely joint impact of generalised land-use changes on biodiversity, including the expansion of both urban areas and intensive agriculture (Wood and Pullin 2002, Stefanescu et al. 2004, Chace and Walsh 2006, Casner et al. 2014).

2. Community assembly patterns

Shifts in community assembly patterns in response to urbanisation were assessed by examining the variation (SD) in mobility and specialisation degree of the focal taxonomic groups along the urbanisation gradient (Mason et al. 2005). Besides mean values, urbanisation slightly increased the variation in specialisation degree of plant assemblages, that is, it drove trait divergence. Such an assembly pattern is often attributed to niche differentiation due to biotic interactions (mainly species competition) in local communities (Mason et al. 2005). However, our results confirm recent studies that show that divergence patterns may also arise at large spatial scales like those considered here (i.e., 1x1 km plots), likely due to the increased environmental heterogeneity (see e.g., de Bello et al. 2013) that favoured species with a variety of particularly narrow habitat preferences. Plant species diversification, rather than homogenisation, has generally been found in urban areas due to the increase in non-native species, in particular neophytes (species introduced by humans after 1500 A.D.), which are functionally a very diverse group (Kühn and Klotz 2006, Knapp et al. 2012, Ricotta et al. 2012). Neophyte richness has actually been found to increase with urbanisation in Switzerland (Nobis et al. 2009).

For birds, our results clearly indicate that increased urbanisation filtered out specialist species, and thus decreased mean values and variation of specialisation degree in bird assemblages. Likewise, urbanisation filtered out highly mobile species of butterflies, thus decreasing mean values and variation of mobility in butterfly assemblages. These results suggest that urbanisation induced convergence in bird specialisation degree and butterfly mobility (Mason et al. 2005). This is in agreement with the general expectation of environmental filtering to predominate at broad spatial scales (de Bello et al. 2009, 2013).

Differences in the predominant assembly patterns found for birds and butterflies in contrast to plants might arise from an ‘organism-scaled’ environmental perception, which in turn is related to the degree of specialisation and mobility of organisms (Leibold et al. 2004, Tews et al. 2004, Öckinger et al. 2010). In our study, the same 1x1 km plot is probably perceived as larger, in relative terms, for sessile organisms like plants than for mobile organisms, such as birds or butterflies. Thus, ecological patterns that are expected to occur at large scales for some organisms (e.g., divergence patterns driven by increased habitat heterogeneity at landscape or regional scales) may arise at smaller spatial scales for organisms with lower mobility.

Likewise, urbanisation might drive different ecological patterns for plants on the one hand, and birds and butterflies on the other one, since most urban impacts on the latter can be considered as indirect effects caused by the alteration of the original vegetation cover. Urbanisation may drive ecological divergence in plant assemblages by favouring species with specific characteristics that enable them to settle in newly created urban habitats (typically ruderal and non-native species; Kühn and Klotz 2006, Lososová et al. 2012), while causing ecological convergence in bird and butterfly assemblages by filtering most specialist and sensitive species from the original communities after the depletion of their (semi-)natural habitats (Devictor et al. 2007, Casner et al. 2014).

It should also be noted that differences in assembly patterns found for the distinct taxonomic groups might also be due to the different proxies that were used to estimate mobility (i.e., wing load for birds and butterflies, and dispersal modes for plants) and specialisation degree (i.e., local habitat and climatic ranges for plants, food resources, breeding substrates and habitat types for birds, and host plants for butterflies) of each taxon. The development of standardized metrics related to species' ecological or functional traits, especially for animals, will facilitate comparisons among taxa.

3. Impact of urbanisation at different spatial scales

In general, although plants and birds responded significantly to urbanisation at a wide range of spatial scales, they responded better at smaller scales (i.e., plots to intermediate buffers) than butterflies (i.e., intermediate to large buffers). These results partially (i.e., except for birds) confirm our expectations of highly mobile organisms (i.e., butterflies) being affected by factors acting at larger spatial scales than poorly mobile or sessile organisms (i.e., plants; see e.g., Concepción and Díaz 2011, Braaker et al. 2014). Furthermore, differences in the spatial scale at which highly and poorly mobile species within taxonomic groups responded to urbanisation also became evident for plants and butterflies and, in addition, varied with species degree of specialisation.

In the case of plants, SR of both highly and poorly mobile species tended to respond best to urbanisation at intermediate spatial scales, but highly mobile plants showed significant responses at a wider range of scales. Interestingly, SR of specialists showed stronger responses at smaller spatial scales than generalist species, likely because they rely more on the presence of patches of suitable habitat (Schleicher et al. 2011). Moreover, our results suggest a likely interaction between specialisation degree and mobility (Öckinger et al. 2010) since clearer differences between highly and poorly mobile species were found for specialist than for generalist plants. SR of generalists, both highly and poorly mobile, as well as highly mobile specialists responded significantly to urbanisation at a wider range of scales than poorly mobile specialists, which only reacted at smaller scales.

Butterflies, in contrast, responded best to urbanisation at large spatial scales. This is most likely related to the high relevance of metapopulation dynamics for this taxonomic group that relies on source-sink movements of individuals among distant habitat patches across landscapes and even regions (Hanski 1998). We additionally found differences in the spatial scale at which SR of highly and poorly mobile butterflies responded best to urbanisation. As expected, highly mobile species responded most to the proportion of urban area in the largest buffers, while poorly mobile species responded best at intermediate scales.

For birds, however, no differences in the spatial scale at which SR of highly and poorly mobile species responded to urbanisation were found, and both were affected most at small spatial scales. These results are likely due to the importance of local conditions for the selection of nesting sites, especially for breeding birds that we considered and, in accordance with previous studies (e.g., Clergeau et al. 2002), indicate that although birds may be affected by urbanisation at great distances, they tend to respond most to what is occurring in close proximity.

Conclusions

Our study shows that specialisation degree and mobility of species assemblages of plants, birds and butterflies clearly changed with the level of urbanisation. Both species characteristics, in addition, interacted with each other in their influence on species responses to urbanisation. Two different ecological patterns were found. Trait divergence increased along the urbanisation gradient in the case of plants, likely caused by the increased variability in urban environments that favoured highly mobile species with narrow habitat ranges. Trait convergence, in contrast, predominated for birds and butterflies, most likely driven by environmental filtering through the exclusion of specialist and highly mobile species from urban areas, thus favouring the homogenisation of species assemblages. These findings emphasise the need to take into account species' characteristics related to ecological processes that shape biological communities in order to better understand the extent of human-induced impacts on biodiversity (Öckinger et al. 2010, Schleicher et al. 2011).

Our results also emphasize the need to consider an appropriate range of spatial scales to address ecological questions based on and in line with the organisms and processes studied (Tews et al. 2004, de Bello et al. 2013). Here, we found substantial differences in the range of spatial scales at which organisms with distinct mobility, and even specialisation degree, within and across taxa, responded to urbanisation. Our results also emphasise the urgent need to halt the widespread expansion of urban areas (i.e., urban sprawl; Schwick et al. 2012) for the conservation of some organisms such as butterflies, since they as a whole, and the most mobile and specialist species in particular, were strongly negatively affected by urbanisation at great distances from the places they inhabit. This is even more important when considering the joint impacts of other land-use changes (e.g., agricultural intensification) that take place simultaneously and greatly affect biodiversity as well.

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Table 1. Species characteristics and classification criteria used for the definition of the degree of specialisation, mobility, and the set of species groups classified according to both features for the different taxonomic groups analysed. Species characteristics were extracted from information provided by the Swiss Ornithological Institute (http://www.vogelwarte.ch/) for birds, from the authors' own expertise for butterflies (FA; Altermatt and Pearse 2011), and from Landolt et al. (2010) for vascular plants.

Species characteristics	**Classification criteria**
Birds	
Degree of specialisation: Mean value of specialisation in the following ecological aspects: • Feeding specialisation: 1/number of items named as food (e.g., insects, vertebrates, seeds, fruits, and plants) • Breeding specialisation: 1/number of items named as breeding substrate (e.g., ground, shrubs, trees, rocks, and buildings) • Habitat specialisation: 1/number of items named as habitat (e.g., grassland, crops, woodlands, settlements, and wetlands)	▪ Specialist (if ≥ median) ▪ Generalist (if < median)
Mobility: Wing load (weight/wing area; g/cm^2)	▪ Highly mobile (if ≥ median) ▪ Poorly mobile (if < median)
Butterflies	
Degree of specialisation: 1/number of items named as food • Larval feeding: number of plant species on which larva feeds grouped in four categories: monophagous (one plant species), narrow oligophagous (several plant species of one plant genus), oligophagous (several plant genera of one plant family), and poliphagous (different plant families) • Type of food resource (e.g., feeding on trees and shrubs or evergreen plants)	▪ Specialist (if ≥ median) ▪ Generalist (if < median)
Mobility: Wing load (weight/wing area; g/cm^2)	▪ Highly mobile (if ≥ median) ▪ Poorly mobile (if < median)
Vascular plants	
Degree of specialisation: Mean standardized range (0-1) of the following set of habitat and climatic variables that varied from wide (0) to narrow (1) ranges of preference: Temperature, continentality, light, moisture, reaction, nutrients, humus and aeration	▪ Specialist (if ≤ median) ▪ Generalist (if > median)
Mobility: Classification based on dispersal modes (adapted from Vittoz and Engler, 2007): ▪ Poorly mobile plants (mobility=0): o Authochorous (self-dispersal) o Ombrochorous (dispersed by rain drops) o Myrmerchorous (dispersed by ants) o Boleochorous (dispersed by wind gusts) ▪ Highly mobile plants (mobility=1): o Dyszoochorous (seeds caught by animals, afterwards lost or forgotten) o Endozoochorous (seeds eaten and afterwards deposited by animals) o Epizoochorous (seeds clung to fur, feathers or hooves of animals) o Anthropochorous (dispersed by man) o Bythisochorous and nautochorous (dispersed by water courses and surfaces) o Meteorochorous (diaspores with special features that facilitate wind transportation)	

Table 2. Definitions and data sources of environmental predictors, including variables describing degree of urbanisation, other land-use types, landscape heterogeneity, climate, and topography parameters which were included in the analyses.

Explanatory Parameters	Definition	Data source
Urbanisation:		
Built-up area	Proportion of area occupied by houses (including gardens), roads and other infrastructures, industries, parks and recreational areas	Die Geographen schwick + spichtig http://www.zersiedlung.ch (2010, 15 m resolution)
Other land uses:		
Agricultural area	Proportion of area occupied by agricultural land	Federal Statistical Office (FSO) Land use statistics http://www.bfs.admin.ch/ (2004/09, 100 m resolution)
Landscape heterogeneity:		
Edge density	Length of edges –contacts between patches of distinct land-use types – relative to the plot area; m/ha	Federal Statistical Office (FSO) Land use statistics http://www.bfs.admin.ch/ (2004/09, 100 m resolution)
Climate:		
Mean annual temperature	Average value of monthly mean temperatures (°C)	Swiss Federal Office of Meteorology and Climatology http://www.meteoswiss.ch/ (Data averaged for the period 1961–1990, 25–100 m resolution)
Annual precipitation	Sum of monthly precipitation (mm)	
Topography:		
Northness (aspect)	Northness = cosine(aspect) Orientation or direction to which slope faces. Values range from 1 (North facing slope) to -1 (South facing slope) based on the transformation of aspect (range: 0-360°)	Swiss Federal Office of Topography http://www.swisstopo.ch/ (100 m resolution)
Surface roughness	Standard deviation (SD) of altitude (m a.s.l.)	

Table 3. Results of generalised linear models (GLMs) testing the effects of proportion of urban area at different spatial scales (i.e., from 1x1 km plots to 5 km-radius buffers around plots) on the distinct diversity metrics of vascular plants, birds and butterflies. Sign and shape of effects (↗ positive, ↘ negative, and ↗↘ hump- or ↘↗ through-shaped), percentage of deviance explained by urban area ($\%D^2$ urban), overall goodness of fit (GOF) expressed as percentage of deviance ($\%D^2$) explained by the full model, and 2nd-order Akaike's information criterion (AICc) are provided for models with significant urban effects (P<0.05). For each response variable, best fitted models according to AICc (delta ≤ 2) are highlighted. See also Appendix 3.

GLMs results	Urban area:	1x1 km				1 km radius				2 km radius				3 km radius				4 km radius				5 km radius			
		Sign	$\%D^2$ urban	GOF ($\%D^2$)	AICc	Sign	$\%D^2$ urban	GOF ($\%D^2$)	AICc	Sign	$\%D^2$ urban	GOF ($\%D^2$)	AICc	Sign	$\%D^2$ urban	GOF ($\%D^2$)	AICc	Sign	$\%D^2$ urban	GOF ($\%D^2$)	AICc	Sign	$\%D^2$ urban	GOF ($\%D^2$)	AICc
Plants	MV specialization	↗	20.5	58.1	-603.5	↗	21.3	56.6	-599.7	↗	15.5	50.8	-586.5	↗	11.5	48.8	-582.4	↗	8.9	47.7	-580.2	↗	7.7	47.1	-578.8
	SD specialization	↗	2.2	36.5	-809.7	n.s.				n.s.				↗↘	4.8	35.7	-808.5	n.s.				n.s.			
	MV mobility	↗	7.1	14.1	-566.9	↗	7.0	13.7	-566.5	n.s.				n.s.				n.s.				n.s.			
	SD mobility	n.s.				n.s.				n.s.				n.s.				n.s.				n.s.			
	Species richness:																								
	Highly mobile species	↗↘	5.8	36.2	1172.5	↗↘	7.1	37.4	1164.7	↗↘	8.6	39.1	1154.0	↗↘	10.9	41.5	1139.5	↗↘	7.9	39.4	1152.2	↗↘	5.2	37.5	1164.7
	Poorly mobile species	n.s.				n.s.				n.s.				↗↘	6.6	38.0	694.2	↗↘	5.0	36.9	695.7	n.s.			
	Specialist species	↗↘	13.5	45.4	989.3	↗↘	14.3	45.9	987.0	↗↘	11.1	43.5	999.3	↗↘	11.1	44.1	996.3	↗↘	7.6	42.0	1007.0	↗↘	5.1	40.3	1012.2
	Generalist species	n.s.				n.s.				↗↘	4.6	36.4	953.3	↗↘	8.3	39.6	942.0	↗↘	6.8	38.4	946.3	↗↘	4.8	36.8	951.7
	Highly mobile specialists	↗	13.5	45.2	947.3	↗↘	14.4	45.6	945.4	↗↘	12.1	43.9	953.4	↗↘	11.9	44.5	950.8	↗↘	8.2	42.3	961.3	↗↘	5.7	40.5	969.8
	Poorly mobile specialists	↗	8.0	30.5	590.1	↗	7.8	30.5	590.1	n.s.				n.s.				n.s.				n.s.			
	Highly mobile generalists	n.s.				n.s.				↗↘	4.6	34.1	897.2	↗↘	7.7	36.9	889.3	↗↘	6.1	35.6	892.7	↗↘	4.1	34.0	897.3
	Poorly mobile generalists	↘	3.2	37.7	611.3	↘	3.4	37.2	611.8	n.s.				↗↘	7.6	38.6	610.3	↗↘	6.9	37.9	611.1	↗↘	5.9	37.1	611.9
Birds	MV specialization	↘	12.6	26.3	-559.7	↘	13.4	27.3	-561.1	↘	10.0	24.8	-557.7	↘	6.5	20.7	-552.3	↘	4.8	18.5	-549.6	↘	5.1	19.1	-550.3
	SD specialization	↘	20.4	56.6	-907.9	↘	12.6	49.2	-892.2	↘↗	3.8	42.8	-880.2	n.s.				n.s.				n.s.			
	MV mobility	n.s.				n.s.				n.s.				n.s.				n.s.				n.s.			
	SD mobility	n.s.				n.s.				n.s.				n.s.				n.s.				n.s.			

GLMs results	Urban area:	1x1 km				1 km radius				2 km radius				3 km radius				4 km radius				5 km radius			
		Sign	%D^2 urban	GOF (%D^2)	AICc	Sign	%D^2 urban	GOF (%D^2)	AICc	Sign	%D^2 urban	GOF (%D^2)	AICc	Sign	%D^2 urban	GOF (%D^2)	AICc	Sign	%D^2 urban	GOF (%D^2)	AICc	Sign	%D^2 urban	GOF (%D^2)	AICc
	Species richness:																								
	Highly mobile species		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	Poorly mobile species		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	Specialist species	↘	9.0	27.3	530.0	↘	10.0	27.7	529.6	↘	7.3	23.6	533.0		n.s.				n.s.				n.s.		
	Generalist species		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	Highly mobile specialists	↘	13.3	31.3	432.2	↘	8.1	25.9	435.8		n.s.				n.s.				n.s.				n.s.		
	Poorly mobile specialists		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	Highly mobile generalists		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	Poorly mobile generalists		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
Butterflies	**MV specialization**		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	SD specialization		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	MV mobility		n.s.			↘	7.2	13.9	-417.0	↘	6.8	13.4	-416.4	↘↗	10.9	17.1	-420.8	↘	9.1	15.1	-418.4	↘	9.2	15.2	-418.6
	SD mobility		n.s.			↘	4.5	19.8	-543.5		n.s.			↘↗	8.8	21.2	-545.2		n.s.				n.s.		
	Species richness:																								
	Highly mobile species		n.s.			↘	7.1	22.4	552.7	↘	9.7	24.8	548.9	↘	10.9	25.5	547.9	↘	12.3	25.8	547.4	↘	13.4	26.7	546.0
	Poorly mobile species		n.s.				n.s.			↘	7.3	31.3	497.5		n.s.				n.s.				n.s.		
	Specialist species	↘	3.5	23.7	589.6	↘	5.9	26.0	585.9	↘	8.6	28.3	582.1	↘	8.4	27.4	583.6	↘	9.2	27.4	583.7	↘	10.4	28.2	582.2
	Generalist species		n.s.				n.s.			↘	8.7	26.0	446.6	↘	10.7	27.5	445.5		n.s.				n.s.		
	Highly mobile specialists	↘	3.8	21.0	508.8	↘	7.6	24.5	504.2	↘	8.8	25.6	502.8	↘	8.9	25.3	503.2	↘	10.0	25.8	502.6	↘	11.2	26.9	501.0
	Poorly mobile specialists		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	Highly mobile generalists		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		
	Poorly mobile generalists		n.s.				n.s.				n.s.				n.s.				n.s.				n.s.		

Figure 1. Delineation of study area within Switzerland (left), i.e. the Swiss Plateau (thick solid line; delimited according to the definition of Swiss biogeographic regions; Gonseth et al., 2001). Degree of urbanisation in the study area is represented with a grid (1 km resolution) in colored scale, from white (no urban area within cells) to red (entire cell area urbanised). The location of the biodiversity survey plots, including data on vascular plants, butterflies, and birds in 109 square plots (1x1 km) is indicated (empty squares), together with the position of eight additional plots, with data on vascular plants, in highly urbanised areas of the Swiss Plateau (crossed squares). A zoomed view of the surroundings of the city of Zürich is shown to the right of the map.

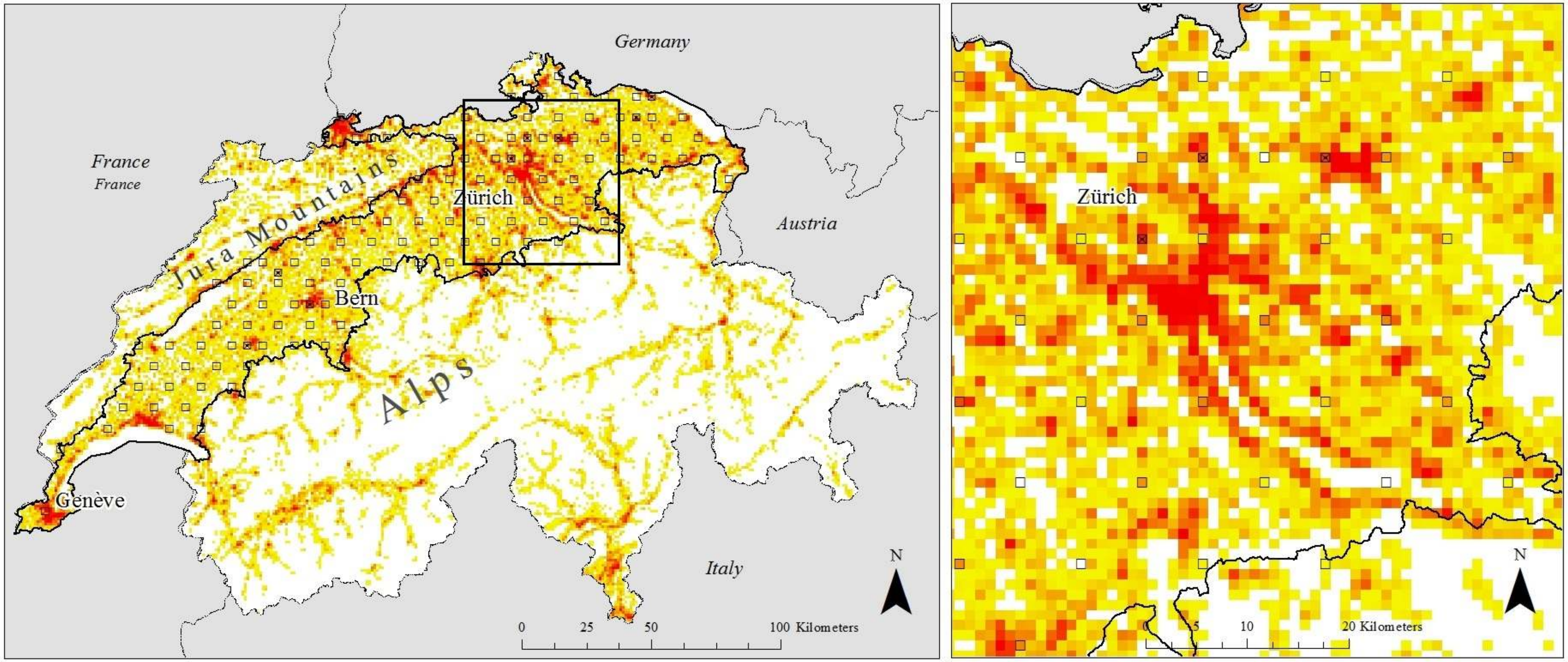
Figure 2. Percentage of deviance (%D^2) of mean values of (a) degree of specialisation and (b) mobility, and (c) species richness of highly mobile specialists explained by the proportion of urban area at different spatial scales (i.e., from 1x1 km plots to 5 km-radius buffers around plots) for the distinct taxonomic groups studied: vascular plants (grey), butterflies (black) and birds (white). Negative values of %D^2 represent negative effects of urban predictors on response variables.

Figure 3. Partial residual plots of significant responses of mean values of (a) plant degree of specialisation and (b) mobility to the proportion of urban area in 1x1 km plots, according to best fitted models for each of these variables. Partial residual plots represent estimated relationships between response variables and the explanatory parameter of interest (solid lines; ±SE, dashed lines) once the effects of all the other explanatory parameters have been accounted for. Mean values per plot (±SD) of response variables are provided to contextualise the size of effects.

Figure 4. Partial residual plots (solid lines; ±SE, dashed lines) of significant responses of mean values of (a) bird degree of specialisation and (b) butterfly mobility to the proportion of urban area in 1- and 3 km-radius buffers, respectively, according to best fitted models for each of these variables. Mean values per plot (±SD) of response variables are provided.

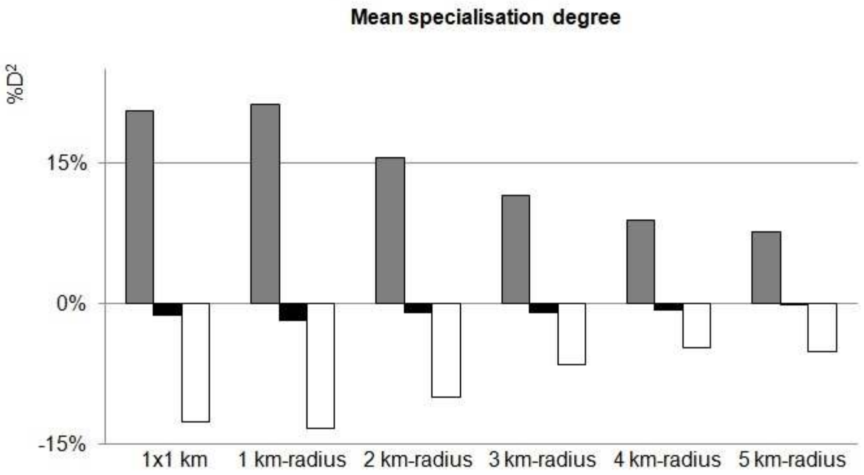
Figure 5. Partial residual plots (solid lines; ±SE, dashed lines) of significant responses of species richness of highly mobile specialists of (a) plants, (b) birds and (c) butterflies to the proportion of urban area in 1 km-radius buffers, 1x1 km plots and 5 km-radius buffers, respectively, according to best fitted models for each of these variables. Mean values per plot (±SD) of response variables are provided.

Concepción et al., Figure 1

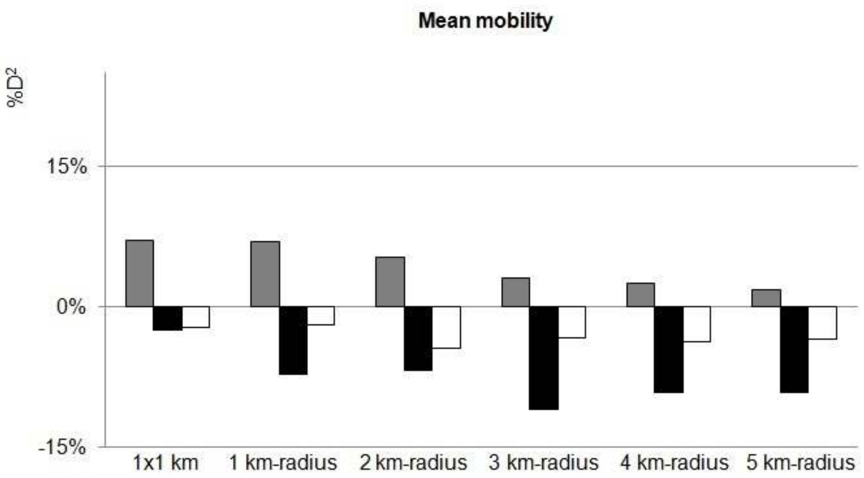


Concepción et al., Figure 2

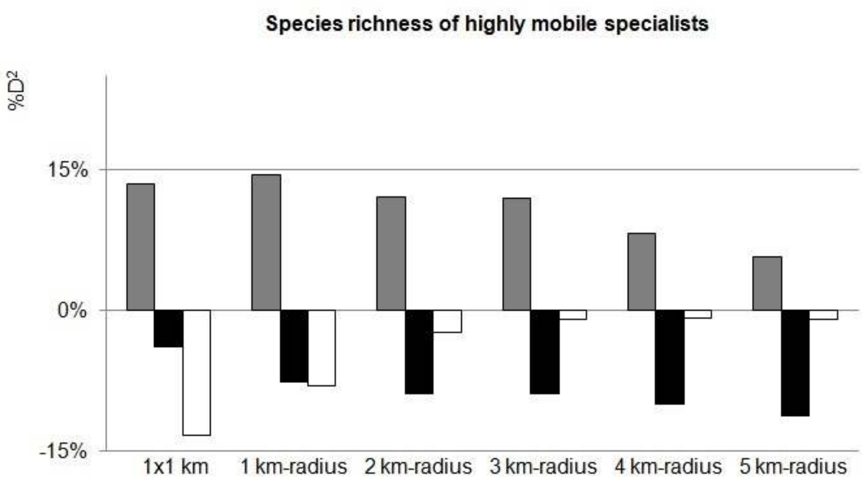
a)



b)

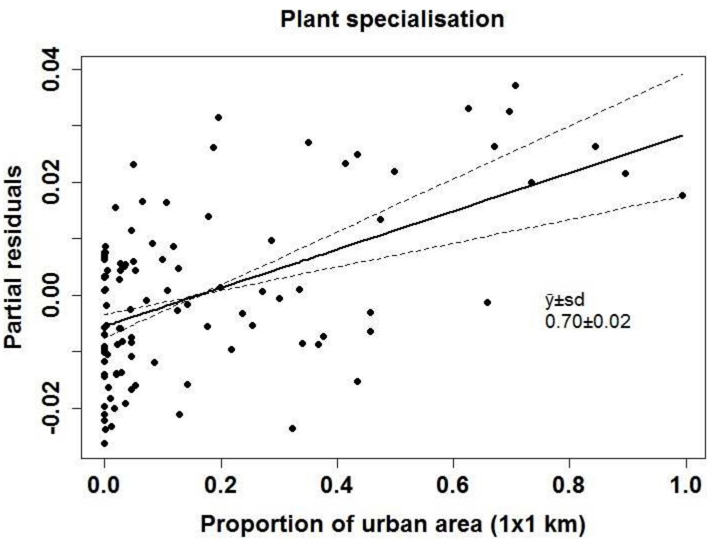


c)

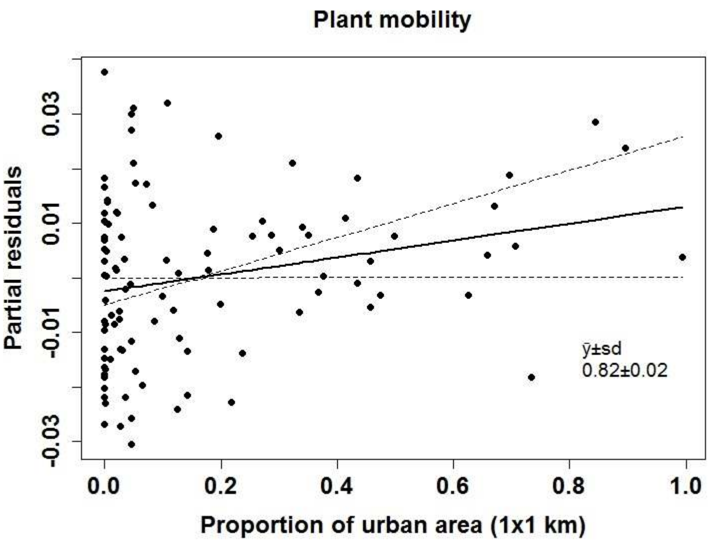


Concepción et al., Figure 3

a)

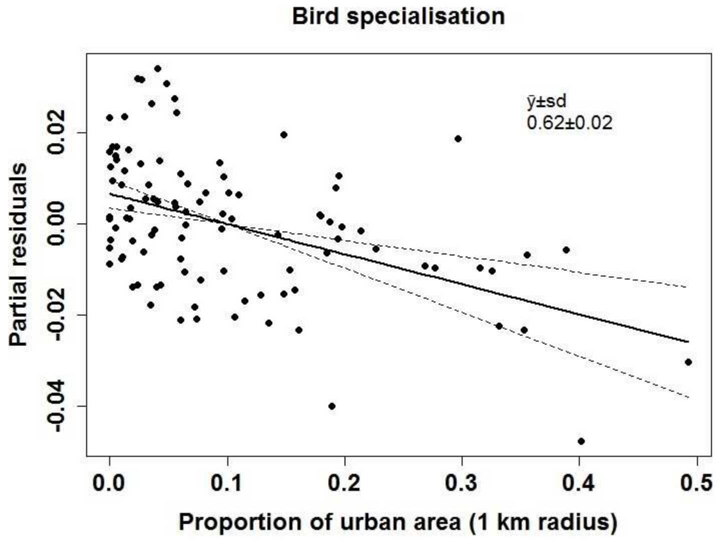


b)

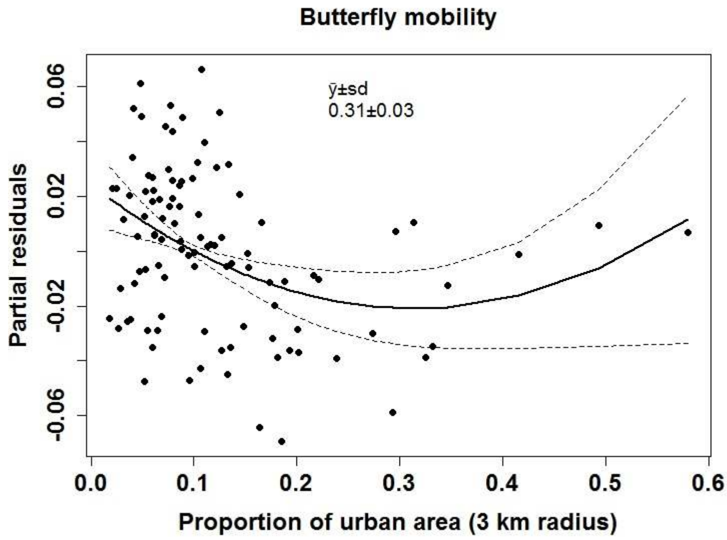


Concepción et al., Figure 4

a)

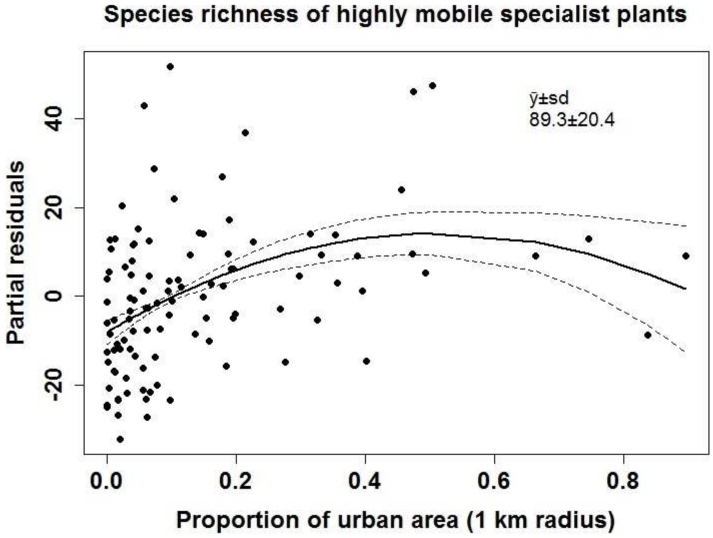


b)

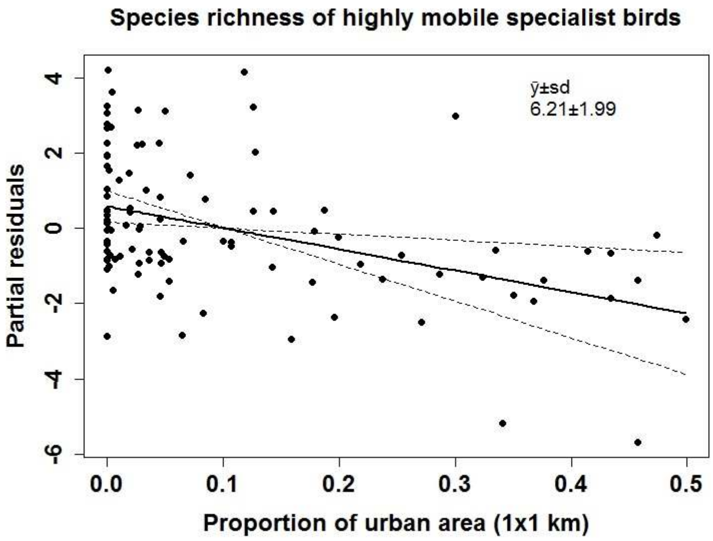


Concepción et al., Figure 5

a)



b)



c)