Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters

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Abstract

Urban growth is a major factor of global environmental change and has important impacts on biodiversity, such as changes in species composition and biotic homogenization. Most previous studies have focused on effects of urban area as a general measure of urbanization, and on few or single taxa. Here, we analyzed the impacts of the different components of urban sprawl (i.e., scattered and widespread urban growth) on species richness of a variety of taxonomic groups covering mosses, vascular plants, gastropods, butterflies, and birds at the habitat and landscape scales. Besides urban area, we considered the average age, imperviousness, and dispersion degree of urban area, along with human population density, to disentangle the effects of the different components of urban sprawl on biodiversity. The study was carried out in the Swiss Plateau that has undergone substantial urban sprawl in recent decades.

Vascular plants and birds showed the strongest responses to urban sprawl, especially at the landscape scale, with non-native and ruderal plants proliferating and common generalist birds increasing at the expense of specialist birds as urban sprawl grew. Overall, urban area had the greatest contribution on such impacts, but additional effects of urban dispersion (i.e., increase of non-native plants) and human population density (i.e., increases of ruderal plants and common generalist birds) were found. Our findings support the hypothesis that negative impacts of urban sprawl on biodiversity can be reduced by compacting urban growth while still avoiding the formation of very densely populated areas.

Key words:

Built-up area; biotic homogenization; imperviousness; human population density; time-lagged effects; urban dispersion.

Introduction

Land-use change is a central component of global change and a major threat to biodiversity (Sala et al. 2000). Urban growth is in turn an important driver of such land-use changes (Grimm et al. 2008; Elmqvist et al. 2013). The growth of urban areas worldwide was especially pronounced during the second half of the 20th century, but rapid urban expansion still continues and is expected to persist in the next decades as the world's population grows and more people live in cities (Grimm et al. 2008; Mcdonald et al. 2008; Elmqvist et al. 2013).

Species richness has frequently been found to peak at moderate levels of urban development (Rebele 1994; Niemelä 1999; Blair 1999; Crooks et al. 2004). However, not all organisms are equally affected, and the impact of urban growth may noticeably vary depending on species characteristics, such as dispersal ability, habitat specialization, or use of resources (Wood and Pullin 2002; Devictor et al. 2007). The peak in species richness at moderate urbanization levels usually results from an increase in common species adaptable to urban environments, such as early successional plants (Deutschewitz et al. 2003) or generalist animals that take advantage of high habitat heterogeneity and resource availability, as well as low competition or predation rates in urban areas (Savard et al. 2000; Crooks et al. 2004; McKinney 2008). At the same time, some species from the original communities that are sensitive to urban conditions may still survive in the remaining natural or semi-natural habitats, adding to the overall species richness (McKinney 2002, 2006, 2008).

Advanced stages of urbanization, however, usually cause a loss of native specialist in favor of a few urban exploiters, such as ruderal and non-native plants, which tolerate high levels of disturbance (Deutschewitz et al. 2003; Kühn and Klotz 2006; Nobis et al. 2009), or synanthropic animals that depend on human-subsidized resources (Crooks et al. 2004; Devictor et al. 2007). As a result, at high levels of urbanization species richness generally decreases and urban biotas tend to become more and more similar – also called biotic homogenization – dominated by a few common native species and some ubiquitous non-native species (McKinney 2002, 2006; Clergeau et al. 2006; Lososová et al. 2012a, b; Le Viol et al. 2012; Aronson et al. 2014; La Sorte et al. 2014).

The spatial scale at which effects of urbanization on biodiversity are analyzed has also been found to be relevant, with impacts like biotic homogenization being more evident at larger spatial scales, both in terms of the extent of the study area and in terms of grain size (Deutschewitz et al. 2003; Kühn and Klotz 2006; La Sorte et al. 2014). However, studies have traditionally focused on particular urban areas, and although some of them have compared urban impacts in different cities across regions, countries, or even continents (see e.g. Pyšek 1993; Pyšek 1998; Aronson et al. 2014; La Sorte et al. 2014), large-scale analyses along broad urbanization gradients are still scarce (Devictor et al. 2007; Lososová et al.2012a, b; Le Viol et al. 2012).

Most previous studies analyzing urban impacts on biodiversity focused on responses of organisms along urbanization gradients that typically consider increasing proportion of urban area or other urban parameters, such as the degree of imperviousness (i.e., soil sealing) or human population density (see McDonnell and Hahs 2008 for a review). However, most studies lacked reliable measures of other components of the so-called urban sprawl (i.e., scattered and widespread urban growth; Jaeger et al. 2010). Specifically, the degree of urban sprawl can be estimated with a combined measure of total urban area, intensity of urban land use (e.g., population density), and degree of urban dispersion (Jaeger and Schwick 2014). Besides built-up area (hereinafter referred to as ‘urban area’) and other characteristics of urban environments, the spatial configuration of urban area, as well as natural or semi-natural areas at the landscape level, may also affect biodiversity (Marzluff and Ewing 2001; Croci et al. 2008; Sattler et al. 2010; Fontana et al. 2011; Latta et al. 2013). Furthermore, time lags may occur before impacts of urban sprawl on biodiversity are apparent (Ramalho and Hobbs 2012). However, such delayed effects of urban development have rarely been explored (but see Soga and Koike 2013).

Here, we present a comprehensive analysis of the effects of different components of urban sprawl on species richness of various species groups in the Swiss Plateau, which represents the largest biogeographic region of Switzerland (ca. 11,200 km^2) and is affected by severe past and current urban sprawl (Schwick et al. 2012). Overall, we aimed to contribute to a better understanding of the impacts driven by the distinct urban sprawl components on species richness and to generate guidelines for biodiversity monitoring and conservation under future urban development. We addressed the following specific questions: (1) Which types of organisms benefit and which suffer most under urban sprawl? (2) Which attributes or components of urban sprawl have the strongest impacts on species richness? And lastly, (3) at which spatial scales are effects of urban sprawl on biodiversity more evident?

We considered five taxonomic groups (i.e., birds, butterflies, terrestrial gastropods, vascular plants, and mosses) that were covered in Swiss biodiversity monitoring programs at varying spatial scales from 10 m^2 (habitat level) to 1 km^2 (landscape level). We evaluated effects of urban sprawl on the species richness of each taxonomic group and of distinct ecological groups defined according to species characteristics that were expected to be sensitive to urban development (e.g., habitat and resource specialization, commonness, dispersal ability). We investigated urban effects along with other environmental variables (climate, topography, and land use) that are known to affect biodiversity. In addition, we used a wide set of urban predictors to disentangle relationships between different components of urban sprawl and species richness. Besides urban area, which was expected to strongly affect species richness, we analyzed the impact of additional urban attributes of likely influence, such as the degree of imperviousness, human population density, urban dispersion, and average age of urban area.

Methods

1) Study area, species richness, and ecological groups

Our study focused 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 1140 mm (730–2000 mm). In the Swiss Plateau, agricultural land use predominates (around 50% area), followed by forests (24%) and urban areas (15%). Total urban area has tripled since the beginning of the 20th century, especially between 1960 and 1980 when an increase of around 50% occurred, and is still expected to grow in the future, though at lower rates (Schwick et al. 2012). We analyzed data on species richness of five taxonomic groups (mosses, vascular plants, terrestrial gastropods, butterflies, and birds) regularly collected using a systematic sampling design in the biodiversity monitoring programs of Switzerland (BDM – Biodiversity Monitoring in Switzerland Coordination Office 2009) and of the Canton of Aargau (LANAG; Kanton Aargau 1996). From the BDM program, we used species lists of all available plots in the Swiss Plateau, that is, 109 plots at the landscape level (each 1 km^2 in area; including vascular plants, butterflies, and birds; BDM Z7 indicator) and 473 circular plots at the habitat level (each 10 m^2 in area; including mosses, vascular plants, and gastropods; BDM Z9 indicator; Table 1, Fig. 1). From the LANAG program, we analyzed 436 plots at the habitat level located within the Swiss Plateau (10 m^2 plots for vascular plants and gastropods, 100 m radius-plots for birds, and 250 m transects for butterflies). From both programs, we used data of surveys performed between 2007 and 2011 (see Table A.1 for further details about sampling designs of the different biodiversity monitoring programs).

For each taxonomic group and monitoring program, we calculated overall species richness per plot as well as species richness of a variety of ecological groups classified according to species-specific characteristics that we expected to influence species' responses to urban sprawl. Species characteristics were morphological, physiological, or phenological features (functional traits sensu Violle et al. 2007), such as dispersal ability, growth form, and resource use (e.g., diet, habitat use and specialization). Species were additionally classified according to their commonness or rarity (calculated as frequency of occurrence in the dataset), and in the case of vascular plants as native and non-native species. We further classified non-native vascular plant species according to time of introduction (archeophytes and neophytes, i.e., species introduced in Switzerland by humans before or after 1500 A.D.). Resource range and habitat requirements were used to classify species as specialists or generalists (for a detailed description of species characteristics and classification see Table A.2). To explicitly test for a qualitative shift in species composition along the urbanization gradient, we calculated ratios of generalist to specialist species, very common to rare species, and native to non-native plant species. Threatened species according to Swiss Red Lists were also considered.

2) Urban sprawl data

To describe urban sprawl, we calculated a set of explanatory variables at the different plot scales of the distinct biodiversity monitoring programs (see Table 1 for details). As urban variables, we used urban area (defined as built-up area, i.e., houses, industries, roads, and other infrastructures, but also gardens, parks, and other recreational areas), degree of imperviousness (i.e., soil-sealing), average age of urban area (considered over a period of 125 years, i.e. 1885–2010), human population density (number of inhabitants per area), and the spatial dispersion of urban areas. This last variable was quantified using the mean proximity index of urban areas (MPI, with low MPI values meaning high urban dispersion) for larger plot sizes, or the nearest distance to urban areas in the case of the small plots at the habitat level. Overall, we investigated urban sprawl impacts along a broad urbanization gradient, which covers a range from 0% up to 66% of urban area at the landscape scale (see Table 2 for a detailed description of urban sprawl variables).

We also used other environmental predictors known to affect biodiversity, like climatic, topographic, and additional land use variables (see e.g. Blair 1999; Wood and Pullin 2002; Nobis et al. 2009; Lososová et al. 2012a), which were calculated at the same spatial scale as species richness data to control for possible confounding effects (see Tables 1 and 2 for details).

3) Data analyses

We followed a hierarchical approach to analyze the relationships between urban sprawl and species richness. In a first step, we compared the overall importance of all urban versus all non-urban predictors to explain the variability in species richness for the different taxonomic and ecological groups. Second, for those groups for which urban predictors explained a substantial amount of variability, independently from non-urban predictors, we looked at the effects of individual urban predictors.

For the first step, we performed generalized linear models (GLMs) with species richness of the different taxonomic and ecological groups as response and a Poisson error distribution for count data. For the ratios of generalist to specialist species, very common to rare species, and non-native to native plant species, we applied GLMs with a normal distribution of errors. We used two sets of predictors: (1) all urban variables and (2) all environmental variables other than urban ones (Tables 1 and 2). Pearson's product-moment correlations between single predictors were all below 0.8. To control for possible bias caused by collinearity, we compared results of models both excluding and including human population density, the only predictor that showed noticeable correlations with other urban predictors ($0.8 \geq r \geq 0.7$; Dormann et al. 2013). Linear and quadratic terms of urban predictors were included in models to account for possible non-linear effects. For every response variable, we then calculated the percentage of null deviance explained by full models (i.e., including the whole set of urban and non-urban predictors; D^2_{full}), the percentage of null deviance (D^2) explained by the two sets of environmental predictors independently ($D^2_{I.Urban}$ and $D^2_{I.Non\text{-}urban}$), as well as their joint contribution to deviance explanation (D^2_J).

In a second step, we examined the individual effects of urban predictors on species richness for those taxonomic and ecological groups that were substantially affected by urban predictors, independent from non-urban predictors ($D^2_{I.Urban} \geq 15\%$). We selected this threshold because it coincided with significant effects ($p \leq 0.05$) of single urban predictors included in full models. We used multi-model inference based on model averaging in order to calculate more robust estimates of the coefficients of urban predictors (Burnham and Anderson 2002). For each response variable, we performed GLMs with all possible combinations of predictors (including both urban and other environmental variables) and ranked them according to the second-order Akaike's information criterion (AICc), or its quasi-likelihood counterpart (QAICc) in cases where over-dispersion occurred. We then selected the most plausible models according to these criteria (delta AICc or QAICc ≤ 4) and calculated averaged parameter estimates using Akaike's weights. To assess the relative contribution of each urban predictor to the overall effects of urban sprawl on species richness, we calculated the relative variable importance (RVI), that is, the sum of Akaike weights that measures the overall likelihood of the selected models in which the parameter of interest appears. RVI values range from 0 (for predictors excluded in all selected models) to 1 (for predictors included in all selected models; Burnham and Anderson 2002). Finally, we used partial residual plots of best-fit models (AIC-based) to graphically illustrate and explore the direction of significant relationships between distinct urban predictors and species richness. Partial residuals plots of models represent relationships between response variables and an explanatory variable of interest once the effects of all the other predictors have been accounted for.

All statistical analyses were done in R 3.0.2 (R Core Team 2014), using the package MuMIn (Bartón 2013) for model averaging. Urban and non-urban predictors were calculated using the R package raster (Hijmans 2015), as well as ArcGIS and its extension Patch Analyst (ESRI 2011).

Results

Urban predictors explained together and independently of other environmental predictors a substantial proportion of the variability ($D^2_{I.Urban} \geq 15\%$) in species richness of distinct ecological groups of vascular plants and birds. For these groups urban predictors were slightly more relevant than the other environmental variables (23% $D^2_{I.Urban}$ and 20% $D^2_{I.Non\text{-}urban}$ on average; see Table 3 for details). These responses were found almost exclusively at the landscape level (BDM Z7; with 16 responding groups out of 80), with only a few groups of bird species being affected also at the habitat level (LANAG; 3 responding groups out of 82). All these species groups showed significant responses to specific urban predictors (Table 3; for additional details see Tables A.3 and A.4).

Urban area had on average the highest relative variable importance (RVI), followed by human population density, degree of urban dispersion (i.e., mean proximity index of urban areas [MPI] or nearest distance to urban areas), degree of imperviousness, and average age of urban areas (Table 3, Fig. 2). Models excluding human population density as a predictor to control for slight collinearity with other predictors showed consistent results for the remaining urban variables, and therefore we only present the models including the complete set of predictors.

For vascular plants, partial regression plots showed along the gradient of increasing urban area a considerable increase in species richness of non-natives, in particular neophytes (Table 3, Fig. 3a), specific growth forms (phanerophytes and chamaephytes), and human-dispersed (anthropochorous) plants. In addition, species richness of plants inhabiting eutrophic habitats (Fig. 3b), non-native, habitat specialist, and annual (therophytes) plants increased together with human population density. The degree of urban dispersion had additional positive effects on the ratio between non-native and native plant species and on the species richness of neophytes, phanerophytes, and chamaephytes (i.e., negative effects of MPI; Table 3 and Fig. 3c). Last, the degree of imperviousness of urban areas mostly increased species richness of highly dispersive and wind-dispersed (anemochorous) plants (Table 3 and Fig. 3d).

Among birds, species groups showing responses relevant to urban sprawl variables were urban, zoophagous, ground breeding, and breeding generalist birds as well as the ratio of breeding generalist to specialist birds. All these groups showed positive responses to urban area and human population density, except ground breeding birds whose species richness significantly decreased with the amount of urban area (see Fig. 4 for examples of the most relevant effects of these variables on birds). When considered at the habitat level, species richness of zoophagous and urban birds and the ratio of breeding generalist to specialist birds significantly decreased as the nearest distance to urban areas increased, whereas the ratio of breeding generalists to specialists increased with the average age of urban areas (Table 3).

Species richness of all other ecological and taxonomic groups (i.e., mosses, gastropods and butterflies), including endangered species of the different taxa, showed only weak ($D^2_{\mathrm{I.Urban}} <$ 15 %) or non-significant responses to urban sprawl variables, and were more strongly affected by non-urban variables (7% $D^2_{I.Urban}$ and 15% $D^2_{I.Non\text{-}urban}$ on average; see Tables A.3 and A.4 for details).

Discussion

Overall, our study showed important impacts of urban sprawl on species richness of distinct taxonomic and ecological groups. As we hypothesized, these impacts considerably varied depending on the species groups, urban sprawl components and spatial scales considered.

1) Taxonomic and ecological groups

Time of introduction, dispersal mode, growth form and habitat specialization were the species characteristics that mainly affected the responses of plant species richness to urban sprawl. Non-native species, especially neophytes, benefitted most from urban sprawl, which confirms results of previous studies for our study area (Kühn and Klotz 2006; Nobis et al. 2009; Lososová et al. 2012a).

Species richness of plants inhabiting eutrophic places, as well as annual, highly dispersive, wind- and human dispersed plants, also benefitted from urban sprawl (see e.g. Knapp et al. 2009). These results are in line with previous findings revealing that native common generalists still predominate in most urban areas (Lososová et al. 2012a, b; Schmidt et al. 2013; Aronson et al. 2014).

Habitat specialist plants also benefitted from intermediate levels of urbanization covered in our study, probably because of the wide variety of habitats and more extreme environmental conditions in urban areas (Rebele 1994; Niemelä 1999). According to our definition (Table A.2), this group of plants consists of species with narrow ranges of habitat preferences, that is, preferring habitat extremes with respect to temperature, continentality, light, or moisture, pH, nutrients, humus, or aeration of soils. Valued species like native specialist or endangered species are still known to inhabit less-disturbed urban sites (e.g. Kühn and Klotz 2006; Sattler et al. 2010; Fontana et al. 2011; Lososová et al. 2012a; Schmidt et al. 2013). However, we did not find significant responses of these valued species to urban sprawl, likely because they are affected by factors related to local habitat characteristics that were not included in our set of predictors. Likewise, specialist species from rare natural habitats are hardly covered in the distinct biodiversity monitoring programs used in this study, given the broad extension they cover and their regular sampling designs. In addition, whereas colonization by highly dispersive species may more directly track environmental change caused by urban sprawl, species that are negatively affected by urban sprawl may show less clear or direct responses due to the delay in the manifestation of such effects in species richness (i.e., extinction debt; Ramalho and Hobbs 2012; Soga and Koike 2013). Therefore, the positive response of habitat specialists in our study was most probably driven by species occurring in disturbed eutrophic or dry habitats, such as early successional plants, rather than specialist species from rare natural habitats (Knapp et al. 2009). Most habitat specialist plants in our study actually were common species inhabiting eutrophic places (around 70% of species occurrences), and both groups of plants in fact showed similar responses to urban sprawl, being affected most by population density (i.e., intensity of urban land use).

Habitat specialization, together with foraging and breeding traits, also had a large influence on birds' responses to urban sprawl. As expected, birds pre-defined as urban benefitted most, confirming the classification developed by the Swiss Ornithological Institute (http://www.vogelwarte.ch/). More interestingly, our results indicate a shift towards breeding generalists, while species richness of ground breeding birds decreased as urban sprawl grew. Breeding specialists, especially ground-nesting birds, tend to be highly sensitive to urban development (McKinney 2002, 2006; Clergeau et al. 2006), whereas birds able to nest in buildings and on other artificial substrates such as cavity and cliff nesters (e.g., swifts, doves, or falcons) benefit from urban areas (Blair 1996; Savard et al. 2000; Chace and Walsh 2006).

Species richness of zoophagous birds was also positively affected by urban sprawl, probably driven by ground foragers and aerial insectivores that benefit from the high food availability and the variety of open spaces at the still moderate levels of urbanization gathered in our study (Beissinger 1982; Clergeau et al. 1998; McKinney 2002, 2006; Chace and Walsh 2006).

According to additional data from the Swiss Ornithological Institute, the groups of birds that benefitted from urban sprawl hold larger population sizes in Switzerland than those that were negatively affected. Breeding generalist species have on average ca. 122,000 (± 32,000 [SE]) breeding pairs, whereas breeding specialists and especially ground breeding specialists in our study have on average only ca. 34,000 (± 7,000) breeding pairs. Birds pre-defined as urban (ca. 90,000 ± 43,000 breeding pairs) or zoophagous (ca. 64,000 ± 12,000 pairs) also exceed the mean population size of the overall set of bird species in our study (ca. 62,000 ± 12,000 pairs). Consequently, urban sprawl clearly favored more common generalist birds at the expense of less-abundant specialist species and thus tended to homogenize bird communities (see e.g. Savard et al. 2000; Devictor et al. 2007).

Surprisingly, all species groups of mosses, gastropods, and butterflies showed only marginal responses to urban sprawl in our analyses. Lack of response of these groups is probably due to either spatial or temporal constraints in our study that are discussed in depth in the last section of the discussion, and therefore cannot directly be interpreted as a signal of insensitivity to urbanization of these species groups.

2) Components of urban sprawl

As expected, urban area had the largest effects, but the other components of urban sprawl also had a great influence. Besides urban area, relevant changes in species richness were also driven by human population density and the degree of urban dispersion.

Human population density in urban areas can be related to the intensity of urban land use and was positively related to groups of birds that are more tolerant of human disturbances. These groups include common generalists with respect to both breeding and foraging requirements, in contrast to more sensitive and specialist species (Blair 1996; Clergeau et al. 1998; Savard et al. 2000; McKinney 2002, 2006). For plants, increased human population density mostly favored species associated with eutrophic habitats. Likewise, degree of imperviousness, which is related to the extent of modification of the previous habitats, favored highly dispersive and wind-dispersed plant species. These species thus tend to occur in intensively used (i.e., human-populated) or altered (i.e., impervious) urban sites and take advantage of modified urban habitats that are maintained at early successional stages by recurrent urban disturbances (Deutschewitz et al. 2003; Kühn and Klotz 2006; Nobis et al. 2009; Lososová et al. 2012a, b).

The spatial configuration of urban areas also had relevant effects on species richness. Increased urban dispersion (measured as mean proximity index [MPI] of urban area) mostly favored the proliferation of non-native plant species, in particular neophytes. Neophytes tend to proliferate in highly dispersed urban areas probably because these regions offer more opportunities for species spread, with the consequent risk of dispersal into rural or semi-natural areas.

With respect to the temporal component of urban sprawl, increased age of urban areas augmented the ratio of breeding generalist to specialist birds at the habitat level. Despite possible effects of building typology and structure related to the age of urban areas, this result might indicate a time lag in the shift from breeding specialists to generalists related to urban sprawl. Longer (i.e., more delayed) time-lagged effects of urbanization are usually expected for organisms with lower turnover rates, such as birds or perennial plants, compared to short-lived organisms like annual plants (Ramalho and Hobbs 2012; Soga and Koike 2013). Our results partially support this postulate since birds behaved as expected, but we only found marginally significant age-related effects for perennial plants.

3) Spatial scales and constraints

Most effects of urban sprawl on species richness were found at the landscape scale, and only a few groups of birds significantly responded at the habitat scale, demonstrating that larger spatial scales are more appropriate for monitoring impacts of urban sprawl on biodiversity. This is probably due to the small size of plots at the habitat level, especially the 10 m^2 plots, where factors related to local habitat characteristics or land-use intensity and history might be more important than our set of urban predictors, which describe a process occurring at the landscape level. Species groups that showed strong responses at the landscape level, like vascular plants, exhibited no clear responses at the habitat level at all. Hence, the lack of responses of those taxonomic groups that were exclusively surveyed at the habitat level (i.e., mosses and gastropods) may be partly due to the unsuitability of this spatial scale to explore impacts of urban sprawl. This is supported by the fact that birds that were surveyed at a larger habitat scale (3.14 ha plots) in the Canton of Aargau (LANAG) responded similarly to those sampled at the landscape scale (BDM Z7). Together with the typically large home ranges of birds, this finding suggests that responses of birds at the habitat level also reflect what occurs in the surrounding landscape (see e.g. Chace and Walsh 2006).

The absence of a significant impact of urban sprawl for some groups of organisms (mosses, gastropods, butterflies, or endangered species), however, might also be due to strong declines in species richness of these groups between 1950 to 1980 due to large-scale changes and intensification of land uses in our study region (Lachat et al. 2010). Hence, past large-scale declines of these taxonomic groups are likely to be masking potential urbanization signals in the present. Specifically in the case of butterflies, we did not find clear responses to urban variables at the landscape or at the habitat level. These results contradict previous studies that have found this taxon to be highly sensitive to the loss of natural and semi-natural habitats due to the expansion of urban areas and intensive agriculture (e.g. Blair 1999; Wood and Pullin 2002; Stefanescu et al. 2004; Altermatt 2012; Casner et al. 2014). However, contemporary levels of butterfly species richness in our study region are likely so low that no further urbanization impacts are detectable. Mean species richness of butterflies per plot in our dataset (22.4 species in landscape plots) was indeed lower than for those groups that markedly responded to urban sprawl (i.e., plants and birds, with 248.4 and 40.2 species per plot, respectively).

Meta-community dynamics of butterflies that move across dispersed patches of suitable habitat in the landscape are probably influencing their responses to urban sprawl as well, so that urban impacts may only be evident at even larger spatial scales than those considered in our study (1 km^2). Most studies showing urban impacts on butterfly diversity actually measured urbanization levels in large areas around the sites where diversity data were gathered (e.g., 5–10 km radius buffers; Stefanescu et al. 2004; Casner et al. 2014).

Lastly, due to the fact that our study did not cover a whole urban gradient our survey, reaching only maxima of 66% urban area at the landscape scale (see Table A.5 for details), impacts of urban sprawl on species richness at the end of the urban gradient (i.e., completely urbanized areas) were not explored and may have been unnoticed. Nevertheless, our approach allowed us to investigate the impacts of urban sprawl in the transition from rural to urban landscapes, where most relevant impacts on biodiversity are expected to occur (Miller and Hobbs 2002; Mcdonald et al. 2008). The absence of response of some groups of organism, probably because of either spatial (i.e., unsuitable scale of analysis) or temporal (i.e., remarkable impacts happened in the past) constraints, also suggests that some impacts of urbanization may have gone undetected. These facts compel us to be cautious in the interpretation of our results, even more so if we consider possible time-lagged effects. A broader spatio-temporal perspective might thus be required to find relevant impacts of urban sprawl for groups that seemed to be unaffected in our analyses.

Conclusions

Urban sprawl was a strong predictor of species richness for distinct groups of plants and birds in the Swiss Plateau. It mostly related to the proliferation of non-native, especially neophyte, and ruderal plant species, as well as to the replacement of specialist birds with more common and generalist species, and thus to the homogenization of species assemblages. Moreover, we found that most impacts of urban sprawl were driven by the increase in urban area, but interestingly other components of this process greatly contributed to these impacts as well. In particular, the increases of ruderal plants and common generalist birds were highly related to the intensity of urban land use, whereas the spread of non-native plants was strongly related to urban dispersion. These results pointed out the negative impacts of urban spreading into natural or semi-natural areas on biodiversity. In the context of the current discussion on urban dispersion versus densification, the latter seems preferable (see also Soga et al. 2014). Hence, new urban areas should be developed close to already urbanized areas rather than dispersed into rural landscapes. However, such new developments should also provide enough high-quality open spaces (i.e., parks, gardens and other green areas) that soften urban land use intensity in order to support biodiversity and concurrently foster residents' welfare (e.g., Miller and Hobbs 2002; Sattler et al. 2010; Fontana et al. 2011). Even though dense urban development may reduce opportunities for people to live close to nature, it facilitates public access (Sushinsky et al. 2013). Finally, if we consider present rates of land consumption by urban development, both worldwide (Grimm et al. 2008; Mcdonald et al. 2008) and particularly in our study region (Schwick et al. 2012), and the likely time lag in the manifestation of some impacts of urban sprawl on biodiversity (Ramalho and Hobbs 2012), the balance inclines towards an urban densification. Upper limits of urban densification have however to be carefully investigated taking together into account biodiversity conservation and human quality of life.

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Table 1. Details on species data from the different monitoring programs operating in the study areas at the habitat and landscape scales. The set of urban and other environmental predictors (i.e., climate, topography and land use) tested for each taxonomic group and monitoring program is provided. See also Table 2.

Spatial scale	**Biodiversity monitoring program**	**Study area**	**Plot size**	**Taxonomic group**	**Urban variables**	**Other environmental variables**
Habitat	BDM Z9	Swiss Plateau	10 m^2	Mosses Vascular plants Gastropods	Urban area Age of urban area Imperviousness Human population density Nearest distance to urban areas (urban dispersion)	Mean annual temperature Mean annual precipitation Aspect Slope (surface roughness) Forest area
	LANAG	Swiss Plateau of the Canton of Aargau	10 m^2	Vascular plants Gastropods		
			3.14 ha (100 m-radius buffers)	Birds		
			78.54 ha (250 m-transects around plot centers within 500 m-radius buffers)	Butterflies	Urban area Age of urban area Imperviousness degree Human population density Mean proximity index (MPI) of urban area (urban dispersion)	Mean annual temperature Mean annual precipitation Aspect Standard deviation ofaltitude (surface roughness) Forest area
Landscape	BDM Z7	Swiss Plateau	1 km^2	Vascular plants Butterflies Birds		

Table 2. Definitions and data sources of environmental predictors, including variables describing urban sprawl and other environmental variables for the plots of the distinct biodiversity monitoring programs at the habitat level (BDM Z9 and LANAG) and landscape level (BDM Z7). See also Table 1.

Predictor	Definition	Data source
Urban variables:		
Urban area	Proportion of plot area occupied by houses (including gardens), roads and other infrastructures, industries, parks and recreational areas, used for BDM Z7 plots and for butterflies in LANAG plots. Location in urban area, used for BDM Z9 plots and for LANAG plots (except butterflies)	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung/ (2010, 15 m resolution)
Age of urban area	Average age (weighted by area) of urban areas (in years) using 2011 as reference year, calculated from data on urban areas at different time points (1885, 1935, 1960, 1980, 2002 and 2010)	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung/ (time series: 1885–2010; 15 m resolution)
Imperviousness of urban area	Degree of soil-sealing of urban area (%)	Pan-European Copernicus Land Monitoring Services http://www.copernicus.eu/ (2009, 20 m resolution)
Human population density in urban area	Number of human inhabitants (residents) per ha of urban area	Swiss Federal Statistical Office http://www.statistics.admin.ch/ (2011, 100 m resolution)
Mean proximity index (MPI) of urban area	Degree of dispersion of urban area (low MPI values = high dispersion), calculated as the ratio between the mean size of urban patches and the nearest neighbor distance to other urban patches (dimensionless). Used for BDM Z7 plots and for butterflies from LANAG plots	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung/ (2010, 15 m resolution)
Nearest distance to urban areas	Distance from plots to the nearest neighbor urban area (m). Used for BDM Z9 plots and for LANAG plots (except butterflies)	
Non-urban variables:		
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, at 25 and100 m resolution for the habitat and landscape scales, respectively)
Annual precipitation	Sum of monthly precipitation (mm)	
Northness (aspect)	Orientation or direction to which slope faces, ranges from 1 (north-	Swiss Federal Office of Topography

	facing slope) to -1 (south-facing slope)	http://www.swisstopo.ch/ (Data at 25and100 m resolution for the habitat and landscape scales, respectively)
Surface roughness	Standard deviation (SD) of altitude (m a.s.l.), used for BDM Z7 plots and for butterflies in LANAG plots. Slope (surface inclination relative to horizontal, 0–90°), used for BDM Z9 plots and for LANAG plots (except butterflies)	
Forest area	% plot area occupied by forest, used for BDM Z7 plots and for butterflies in LANAG plots. Location in forest area, used for BDM Z9 plots and for LANAG plots (except butterflies)	Federal Statistical Office (FSO) Land use statistics (2004/09, 100 m resolution) http://www.bfs.admin.ch/

Table 3. Results of the two steps of analysis. Step 1: Model performance D^2_{full} of the full models, i.e., percentage of null deviance explained by urban and non-urban predictors, and the corresponding values $D^2_{I.Urban}$, i.e., the percentage of null deviance independently explained by urban predictors based on hierarchical partitioning. All species groups with $D^2_{I.Urban} \geq 15\%$ are shown. Step 2: Relative variable importance (RVI) of single urban predictors from multi-model averaging. Values are provided for urban predictors included in best fitted models (delta AICc or QAICc ≤ 4) for each diversity variable. Arrows indicate the direction of effects (positive ↗ and negative ↘) based on partial regression plots of the best fitted model (AIC-based) and coefficients estimates which are significantly different from zero ($P<0.05$; values in bold).

	Step 1: Deviance partitioning		**Step 2: Multi-model averaging & partial regressions**				
Species group (Monitoring program)	**D^2_{full} (%)**	**$D^2_{I.Urban}$ (%)**	**Urban area**	**Population density**	**Dispersion**	**Imperviousness**	**Average age**
Vascular plants							
Non-native plants (BDM Z7)	64.2	28.4	**0.45 (↗)**	**0.97 (↗)**	0.22	**0.42 (↗)**	0.03
Neophytes (BDM Z7)	61.8	41.9	**1.00 (↗)**	**0.97 (↗)**	**1.00 (↘)**	0.12	0.07
Ratio non-native *vs.* native plants (BDM Z7)	66.4	17.7	**0.67 (↗)**	**0.69 (↗)**	**0.64 (↘)**	0.07	-
Habitat-specialist plants (BDM Z7)	43.8	15.7	-	**0.67 (↗)**	0.03	**0.43 (↗)**	0.02
Phanerophytes (BDM Z7)	42.6	19.3	**0.98 (↗)**	0.07	**1.00 (↘)**	**0.13 (↗)**	0.17
Chamaephytes (BDM Z7)	29.8	24.5	**0.51 (↗)**	0.01	**0.83 (↘)**	0.03	0.07
Therophytes (BDM Z7)	61.9	16.9	**0.24 (↗)**	**0.49 (↗)**	-	**0.41 (↗)**	0.02
Eutrophic-habitat plants (BDM Z7)	52.9	24.1	-	**0.97 (↗)**	0.04	**0.41 (↗)**	**0.05 (↘)**
Anemochorous plants (BDM Z7)	42.0	17.4	-	-	0.07	**1.00 (↗)**	0.10
Anthropochorous plants (BDM Z7)	45.2	29.7	**1.00 (↗)**	-	0.05	0.18	-
Highly dispersive plants (BDM Z7)	42.0	16.1	0.05	**0.11 (↗)**	0.05	**0.95 (↗)**	0.12
Birds							
Zoophagous birds (BDM Z7)	36.2	23.4	-	**1.00 (↗)**	0.03	-	-
(LANAG)	27.3	18.5	**0.96 (↗)**	0.03	**0.96 (↘)**	0.07	0.03
Ground-breeding birds (BDM Z7)	28.6	15.0	**0.92 (↘)**	0.06	0.12	-	0.04
Urban birds (BDM Z7)	39.2	29.5	**0.76 (↗)**	**0.29 (↗)**	0.02	-	0.05
(LANAG)	37.9	31.7	**1.00 (↗)**	0.03	**1.00 (↘)**	0.05	0.04
Breeding-generalist birds (BDM Z7)	25.7	15.4	0.05	**0.54 (↗)**	0.02	0.04	0.05
Ratio breeding-generalist vs. specialist birds (BDM Z7)	31.0	24.2	**1.00 (↗)**	0.02	0.21	0.02	-
(LANAG)	41.7	28.9	0.02	**1.00 (↗)**	**0.75 (↘)**	0.14	**1.00 (↗)**

Figure 1. Delimitation of study area within Switzerland (thin boundary line), i.e. the Swiss Plateau (thick solid boundary line; Gonseth et al. 2001), and the location of plots from the different monitoring programs are shown: BDM Z7 indicator *Species Diversity in Landscapes* (large dots; 109 plots of 1 km^2); BDM Z9 indicator *Species Diversity in Habitats* (small dots; 473 circular plots of 10 m^2); and LANAG program of the canton of Aargau (denser small dots; 436 plots of different sizes at the habitat level in the Swiss Plateau). The location of the main cities within the study area are indicated in grey.

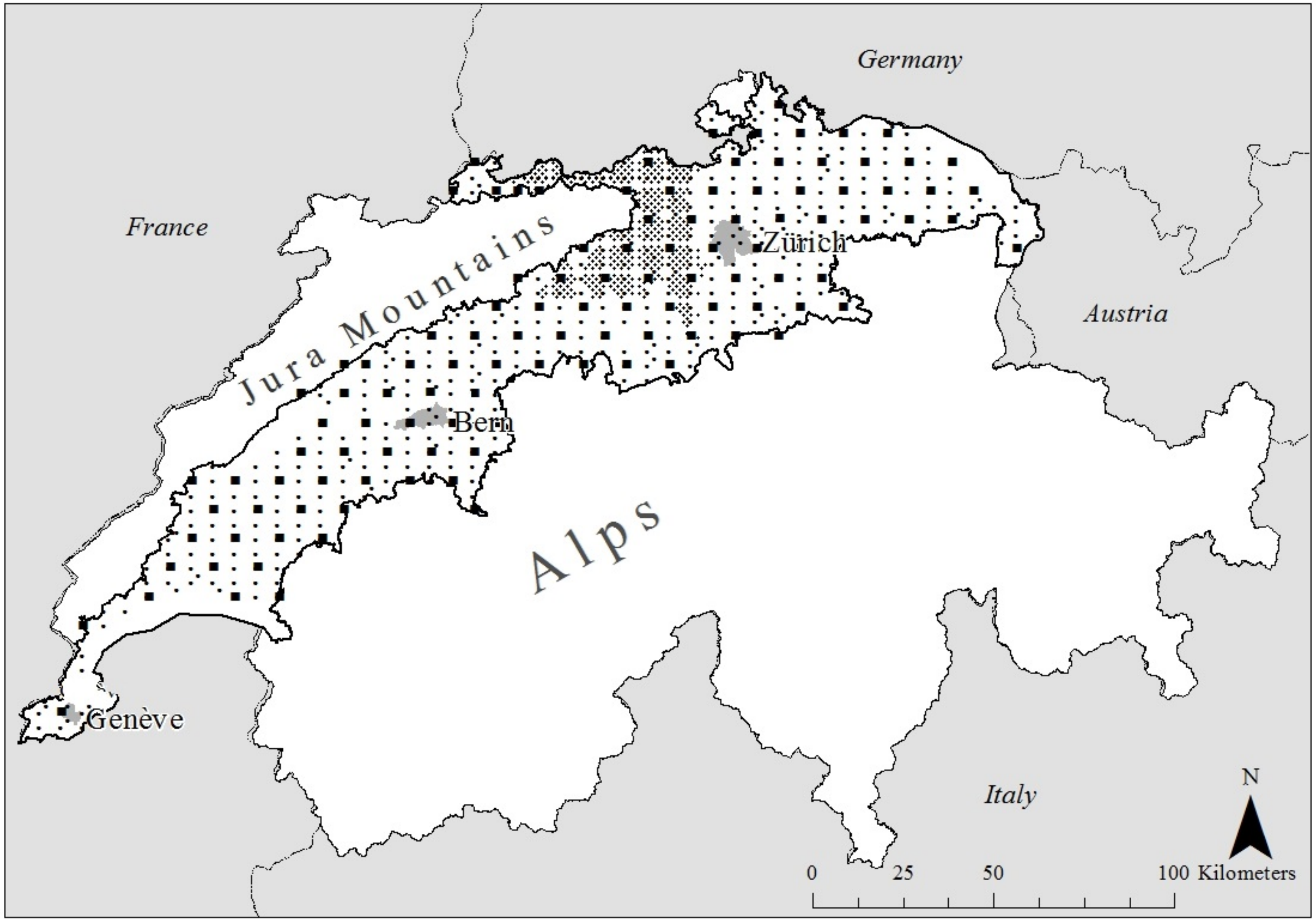
Figure 2. Average (±SE) relative variable importance (RVI) of the different urban predictors (i.e., urban area, population density, dispersion, imperviousness, and average age of urban area) to explain the variation in species richness variables for all species groups that showed relevant responses to urban sprawl ($D^2_{\mathrm{I.Urban}} \geq 15\%$) independent from other environmental predictors (see Table 3). Averaged-values are shown for all these groups (grey) and for the subsets of groups for vascular plants (white) and birds (black).

Figure 3. Partial residual plots of significant responses of species richness to single components of urban sprawl at the landscape scale for (a) neophytes and urban area (linear term), (b) plants from eutrophic habitats and human population density of urban area (linear and quadratic terms), (c) neophytes and urban disperson (MPI) (linear term), and (d) highly dispersive plants and imperviousness (linear term). Partial residual plots represent the estimated relationships between response variables and a predictor of interest (solid lines; ±1 SE, dotted lines) once the effects of other predictors have been accounted for. Mean values of species richness per plot (avg.sr) are provided to contextualize the size of effects.

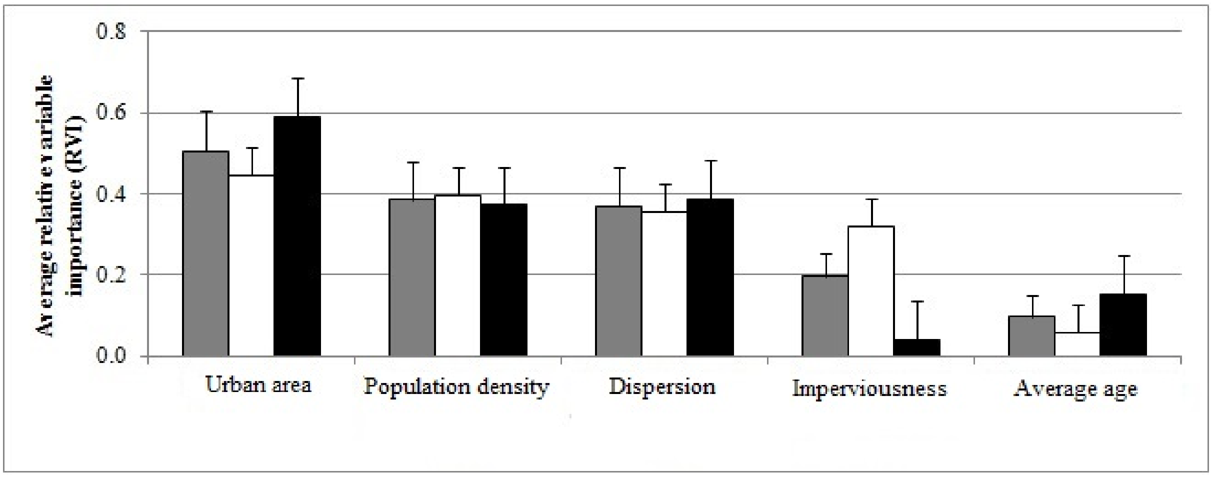
Figure 4. Partial residual plots of significant responses of birds to single components of urban sprawl at the landscape scale for (a) species richness of ground breeding birds to urban area,

and (b) the ratio of breeding generalist to specialist bird species to urban area (linear terms). For further details on partial residual plots see Figure 3.

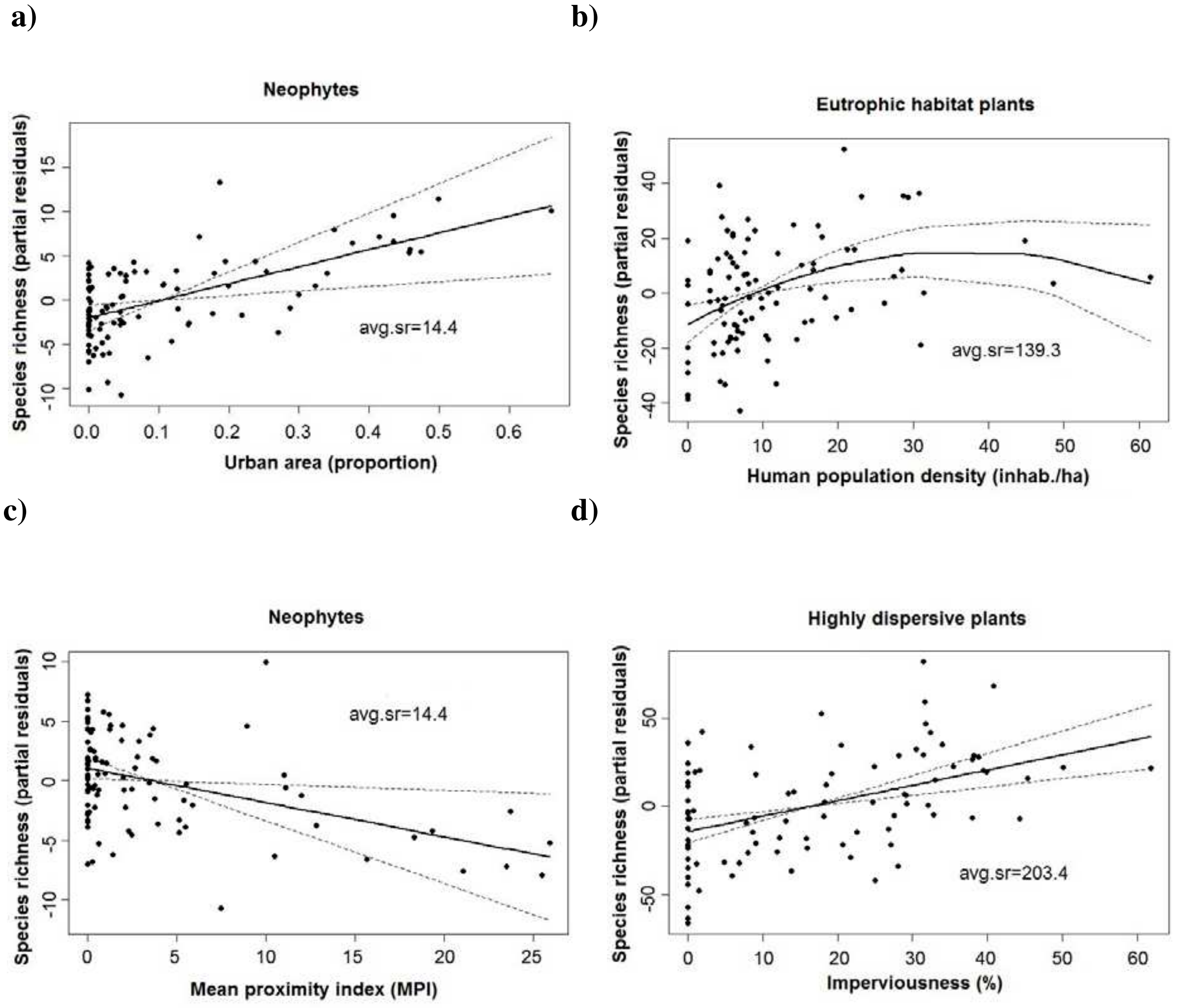
Concepción et al., Figure 1



Concepción et al., Figure 2



Concepción et al., Figure 3



Concepción et al., Figure 4