Patterns and determinants of plant, butterfly and beetle diversity reveal optimal city grassland management and green urban planning

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Abstract

Urban landscapes are places with high interaction between humans and nature, and the benefit of maintaining their biodiversity to enhance human wellbeing is becoming clear. There is, therefore, an urgent need for understanding what influences biodiversity in cities to inform and influence urban landscape planning.

We used a multi-taxa approach (plants, butterflies, and beetles) to assess the influence of the fragmented landscape of a European city, Pardubice (Czech Republic), on the biodiversity of urban grasslands. We randomly selected 40 urban grasslands and were interested in the influences of site and land-use characteristics on biodiversity. The influence of the land-use around the grasslands was analyzed along a gradient of spatial scales (i.e., the cover of land-use types within circular buffer zones of 250, 500, and 750 m around the study grasslands).

We found that species richness of the three study taxa was positively influenced by the size of the grassland (measured as grassland perimeter). Butterflies were also negatively affected by increasing management intensity. Plants and beetles were influenced by the land-use type, with plant species richness positively affected by the extent of urban greenings (i.e., green areas such as urban parks, gardens, and sport grounds), and beetle species richness negatively affected by the extent of built-up areas in the grassland surroundings.

Biodiversity responses to urbanization partly differed among the studied taxa, indicating different demands of specific groups, but the demands were not conflicting and instead, often complemented each other. Consideration of the three key factors influencing biodiversity identified here (grassland extent, land-use in the surroundings, and management intensity) would provide the optimal options for maintaining city biodiversity. Protecting current urban grasslands from development and restricting construction in their surroundings, restoring city wilderness areas using urban spatial planning, and setting up butterfly-friendly management regimes (e.g., mowing in mosaic) could all be future options to help enhance biodiversity in cities.

Keywords

Built-up areas; Mowing; Semi-natural grassland; Spatial partitioning; Urban landscape

Introduction

Urban landscapes are currently occupied by around half of the human population (United Nations, 2016). Therefore, high competition for space between artificial and natural habitats takes place in these environments. Even though nature is crucial for enhancing human well-being (Brymer et al., 2019), the space available for nature within cities and towns is highly limited because cities occupy only 3% of the land extent on Earth (e.g., Soga et al., 2014). Understanding what influences urban biodiversity has received increasing attention in recent decades, due to the need for providing recommendations for optimal urban planning that satisfy the needs of wildlife in urban areas (Ahern, 2013). Several drivers of urban biodiversity have been suggested in the literature (Fattorini, 2011b; Aronson et al., 2017) – including site structural factors (e.g., area or connectivity), biotic associations, and abiotic factors (Beninde et al., 2015).

Therefore, diversity of green spaces present within urban landscapes is essential, of which grasslands represent important ecosystems for many species (du Toit et al., 2020; Dylewski et al., 2019; Mollashahi et al., 2020). Though grasslands are among the most highly studied habitat types in terms of their biodiversity and conservation value in natural and agricultural landscapes (e.g., Dengler et al., 2014), this is not the case in urban areas (Öckinger et al., 2009; Fischer et al., 2013; du Toit et al., 2020). Thus, it is highly desirable to identify the most important environmental factors that influence biodiversity in grasslands found in urban areas. Specifically, the history of human influence, management intensity, and even grassland distribution within a city area appear to be some of the most influential characteristics (Johansson et al., 2008; Ekroos et al., 2010; Fattorini, 2011a; du Toit et al., 2016) that could help us better manage city grasslands for biodiversity in the future. The grassland landscape context (e.g., reflected by land-use types) is also of high importance (Fahrig, 2003; Öster et al., 2007; Horák et al., 2016) for the sustainability of the natural remnant habitats within the urban landscape. This has the potential for informing urban spatial planning, which is still frequently neglected in efforts to conserve biodiversity (Ahern, 2013; Norton et al., 2016; Nilon et al., 2017).

Urban planners are particularly constrained by how much space could be allocated to green structures within the urban landscape. Therefore, identifying not only the key environmental drivers of biodiversity in cities, but also quantifying threshold values of those factors below which biodiversity significantly decline, could represent a useful tool to maximized co-benefit in urban development (Huggett, 2005; Kato & Ahern, 2011). However, few studies have quantified thresholds in the context of conserving biodiversity in urban landscapes (Snyder & Young, 2020).

In this paper, we focused on grasslands as a frequent, although not the largest, habitat type within many cities – particularly, we focused on freely-accessible urban meadows (urban grasslands mowed for haymaking). We used a multi-taxa approach. Namely, we selected three different taxa: vascular plants, diurnal butterflies, and flower-visiting beetles to study the grassland potential for the conservation of biodiversity in urban landscapes. The species of these three groups are often the most frequent and conspicuous organisms in this type of habitat (Beneš et al., 2002; Münzbergová, 2004). Vascular plants are dominants in grassland ecosystems (Southon et al., 2017) and the two selected insect taxa are their pollinators (Biesmeijer et al., 2006). Furthermore, insect larvae often feed on plant tissues or detritus, which contribute to the dynamics of grasslands (Branson et al., 2006). Therefore, the high dependence of these three groups on grassland ecosystems and their ecological interconnection (Biesmeijer et al., 2006) provide an excellent multitaxa indicator model system for assessing urban grassland biodiversity and their responses to key habitat factors.

Therefore, the main aim of this study was to assess the influence of the highly fragmented environment of a central European city on the diversity of vascular plants, day-active butterflies, and flower-vising beetles in grasslands embedded within the city. We investigated the effects on biodiversity of (1) within-site characteristics and (2) different land-uses in their surroundings. More importantly, we calculated the potential thresholds for these biodiversity drivers (e.g., how small can a grassland be before biodiversity drops significantly?). This should help to provide solutions for optimal urban grassland management. Based on the existing literature on the response of plants and insect to grassland extend and quality, we expected that all three taxa would respond to the same habitat factors, as the three groups are also under ecological interconnection (e.g., Biesmeijer et al., 2006), both butterflies and beetles rely on plants as resources for adult and larval stages. However, we also expected that their responses may differ in strength due to differences in dispersal, behavior and other specific environmental requirements of each group, with some habitat characteristics more important than others depending of the taxa (Sattler et al., 2010). We hypothesized that within-site biodiversity would be positively driven by the temporal continuity and the size of the grassland, and negatively influenced by increased management intensity. We also hypothesized that the amount of grassland and built-up areas in the surrounding landscape would be the most influential land-use types on studied grasslands' biodiversity, with positive and negative effects, respectively.

Materials and methods

Study city and environment

Pardubice is the tenth largest city in the Czech Republic with a population of over 100,000 across the city agglomeration. The city is very flat (highly influenced by the river Labe; 220 m a.s.l.) and has disparate forms of industry. Growing from an initial settlement around Pardubice Castle, Pardubice was first referred to as a city in 1295AD and has been continuously referred to as a city from the mid fourteenth century.

There were more than 100 urban grasslands in the study area (Horák, 2016) of which we randomly selected 40 for this study. All grasslands were managed as meadows – annually mowed for haymaking or mowed in the past (in the case of abandoned sites). They were selected from a circle centered at Pardubice Castle (historical city center) with a diameter of ~ 10 km (Fig. 1).

This diameter was selected to best reflect the current influence of the city area (i.e., its urban character). Current dominant land-use types in our study area include urban arable land (46.4%), followed by built-up areas (36.3%), urban forests (12.1%), urban grasslands (4.7%), and urban water bodies (0.6%).

Study variables

Biodiversity sampling

We selected three taxa for our study: vascular plants (referred to hereafter as: plants), lepidopterans with diurnal activity – i.e., Papilionoidea, Hesperiidae, and Zygaenidae (butterflies), and flower-visiting beetles (beetles).

Butterflies and beetles were sampled from the end of April to the end of August in 2011, and each site was visited six times in optimal weather conditions (Horák et al., 2021). In each visit, surveys were carried out for 15 minutes by walking the grassland and counting all butterflies and beetles seen during this time. We used this method of timed surveys rather than the Pollard's transect, as it has been shown to be the most appropriate for obtaining a comprehensive list of species present at a discrete site (Kadlec et al., 2012). In each visit, we particularly targeted the most suitable places in the site for the taxa studied – e.g., patches with a high number of flowering plants for insects (Kadlec et al., 2012). As each site was visited six times, the total sampling effort for insects per site was 90 minutes. Butterflies and beetles were identified in the field by direct observation. Individuals that could not be easily identified in the field were collected and taken to the lab, where they were identified with the help from specialist taxonomists (mentioned in acknowledgments).

Plants were sampled once in each site, in late spring before the first cut for haymaking. Plants surveys were also standardized by time (15 min) during which all the different species of plants found were recorded. We used equal-stratified sampling (Hirzel and Guisan, 2002), with each site sampled with the same intensity (e.g., Horák et al., 2019). As for insects, areas that looked particularly diverse in flower types were specifically targeted within the site. The idea was to compile a plant list rather than assessing the abundance of each plant species which would be overly time consuming. Although this method may not capture the whole plant community at the site, as sampling effort and searching protocol were the same in all sites, we believe this provides a reasonable assessment of the plant diversity present at the time the insects were surveyed, which is also comparable among sites. Most plants were identified in the field, except for several individuals that were collected, preserved as herbarium samples, and identified later. Due to the loss of plant species data from one site, analyses for plants were done only with 39 sites.

Species richness of each taxon was calculated per site and used as the dependent variable for the analyses. We used species richness because it is the most simple and easy metric for assessing biodiversity for the purpose of providing practical management recommendations. Species abundance matrices were used to assess community compositional changes above and below significant environmental factor’s thresholds (see data analysis), which could aid to inform partitioner, when assessing the success of urban planning in delivering biodiversity gains.

Environmental variables

Two categories of independent variables were analyzed, one related to site characteristics and the other related to landscape variables. Site variables included: grassland temporal continuity, distance to the historic city center, grassland extent, and management intensity. The temporal continuity of each site was measured as a categorical variable with three levels (recent, mid-age, historical). This was calculated by assessing the presence of grassland at each site in three different time periods using aerial photos and topographic maps. All selected grasslands sampled in 2011 were present since 2003 (using aerial photographs, available in www.mapy.cz), we assessed their presence in 1966 (using military topographic maps, S-1952 in www.archivnimapy.cuzk.cz) and in 1834-1844 (using stable cadaster maps, available in www.archivnimapy.cuzk.cz). We classified the sites as recent (present since 2003; 16 sites), mid-age (present since 1966; 13 sites) and historical sites (present since 1844; 11 sites). To assess the impact of the historical settlement, we calculated the distance, in meters, from the Pardubice Castle to each site (mean = 3,542.76 ± 204.17 SE; min = 197.29; max = 5,194.59m). Based on results from our previous study (Horák, 2016), we used the perimeter of each site (rather than area), as a measure of grassland extent (mean = 818.54 ± 100.28 SE; min = 249.30; max = 3,192.00m). Management intensity within the site was measured as a categorical variable, with grasslands classified as 0 = abandoned (13 sites), 1 = mowed only once during the season (5 sites), and 2 = mowed two or more times during the season (22 sites). Management intensity was assessed based on clear evidence during our visits that the grassland has been mowed. As we carried out six visits during the spring and summer when mowing take places, we are confident that this is a robust assessment of the management in the current year. We also classified the sites on grassland managed under the EU Agri-Envi subsidies (12 sites) or not (38 sites), using information from the LPIS (Public register of agricultural land) database (available at www.eagri.cz).

The second category of independent variables was related to the land-use type and cover (in square meters) within three circular buffer zones of 250, 500, and 750 meters surrounding each grassland. The smallest buffer zone was selected to represent habitat within the daily movement of the studied insects (Sekar, 2012; Horák et al., 2013). Then this value was incremented once or twice to calculate the sizes of the two other buffer zones to reflect longer distance movement (Öckinger et al., 2009). We did not use larger buffer zones due to the potential overlap of landscapes (buffer zones) between sites (Horák et al., 2016). We used the CORINE land cover map (www.eea.europa.eu/publications/COR0-landcover) to calculate the area of different land-use types within each buffer zone. We used the following categories of land-use as described in CORINE: *grasslands*, including any type of grasslands, representing the similar land-use type to our study sites; *built-up area*, buildings including urban fabric with industrial or commercial units, road and rail networks, and associated land, and airports; *agricultural vegetated areas*, mainly arable land; *forests*, forest of any type; and *urban greenings*, described in CORINE as artificial non-agricultural vegetated areas that included urban parks and gardens, sport grounds and leisure parks.

Statistical analyses

All statistical analyses were performed in R 4.1.2 (R Core Team, 2021) unless otherwise stated.

Based on species richness, the autocovariate of species richness was computed to account for the potential statistically significant influence of spatial autocorrelation (Dormann et al., 2007). This variable was computed using the package *spdep* (Bivand & Wong, 2018) and was used in further analyses as an independent variable.

We used *DHARMa* package (Hartig et al., 2021) to assess the appropriate error structure of the dependent variables (species richness of each taxon), all dependent variables were considered Gaussian and no significant problems were detected in residual diagnostics.

All categorical independent variables were transformed to an ordinal scale. We then controlled potential multi-collinearity for all independent variables by using the criterion of variance inflation factor, $VIF < 2$ with the package *HH* (Heiberger & Robbins, 2014). Due to this criterion, the distance to Pardubice Castle was excluded from the site-level variables, and agricultural vegetated areas was excluded from the land-use variables because of $VIF \geq 2$.

The best buffer zone explaining the land-use influence was selected by hierarchical partitioning using the package *hier.part* (Nally & Walsh, 2004). For each taxon, all land-use types (except the above mentioned of agricultural vegetated areas) were included in the analysis, and the buffer zone that explained the highest total variance was used in the final model for the land-use values (for plants: $R^2_{250m} = 0.21$, $R^2_{500m} = 0.10$, $R^2_{750m} = 0.07$; for butterflies: $R^2_{250m} = 0.21$, $R^2_{500m} = 0.19$, $R^2_{750m} = 0.17$; for beetles: $R^2_{250m} = 0.27$, $R^2_{500m} = 0.25$, $R^2_{750m} = 0.23$).

To assess the influence of site characteristics and land-use variables on species richness of each taxonomic group, we performed generalized linear models (GLM) with Gaussian error structure. We first ran the full model including all the nine independent variables and the best model for each taxon was then selected by Δ AICc ≤ 2 using the packages *nlme* (Pinheiro et al., 2021), *pgirmess* (Giraudoux et a., 2021), and *MASS* (Venables & Ripley, 2002). The model with fewer variables was chosen. Hierarchical partitioning was used to calculate total explained variance by individual independent variables in the final best model.

We calculated threshold values of independent variables (i.e., division of values of the variable into significantly different categories for the dependent variable) using the package *party* (Hothorn et al., 2006) with conditional inference tree methods.

Discrimination of species composition by the threshold value of independent variables that were found to be the most influential by conditional inference tree methods, was computed and visualized. Response data were compositional for plants (based on presence-absence data) and beetles (based on the length of gradient = 6.3 SD). Therefore, a unimodal method (CCA – canonical correspondence analysis) was used. In the case of butterflies, we observed a short gradient (1.8 SD), and the linear method (RDA – redundancy analysis) was used. Species composition analyses were performed using the species abundance matrix (total number of individuals counted during the surveys at each site for each species) and implemented in CANOCO 5. We used logarithmic transformation of the data. We also used 9,999 unrestricted permutations with leverage correction of residuals. We did not use detrending.

Results

We observed 310 species of plants (mean = 56.15 ± 2.41 SE per site; min = 38, max = 115), 42 species of butterflies (11.23 ± 0.67; min = 3, max = 27) and 27 species of beetles (3.68 ± 0.38; min = 0, max = 9) during our surveys of grasslands in the city of Pardubice (Table S1, S2, S3).

The final model for plant species richness included grassland perimeter and the extent of urban greenings in 250-m buffer area surrounding the grassland sites (Fig. S1) and the model was highly significant ($F_{2,36} = 10.65$; $P < 0.001$). The extent of urban greenings and grassland perimeter have a significant positive effect on plant species richness (Table 1). Urban greenings explained independently 26.27% and grassland perimeter an additional 10.91% of variation. No other variables had a significant influence on plant species richness (Table S1). We identified a significant threshold value of 1,159 m of grassland perimeter on plant species richness (Statistic = 11.31; $P < 0.05$). A higher number of grasslands (N = 32) were under or equal to this threshold and seven grasslands have a perimeter higher than the threshold. The mean number of plant species in grasslands above the perimeter threshold was 66, while grasslands below the perimeter threshold contained 54 species in average (Fig. 2a). Although urban greening has a positive significant effect on plant species richness, we did not identify a significant threshold value for this factor. The composition of plant species was not significantly discriminated by the threshold value of grassland perimeter (pseudo-F = 0.70; P = 0.99), with an explained variation of 1.88%.

Butterfly species richness was influenced positively by the size of the grassland and negatively by management intensity (Table 1). Specifically, more than one mowing per season on a study site led to a significant reduction in species richness (Fig. S2). The final model was highly significant ($F_{2,37} = 13.32$; $P < 0.001$), with grassland perimeter explaining independently 28.37% of the variance while management intensity explained a further 13.50%. Extent of urban greenings had a positive significant influence on butterfly species richness before best model selection (Table S1). The threshold value for grassland perimeter was 480 m (Statistic = 10.18; $P < 0.01$). Fifteen sites have a perimeter less or equal to this value, with the mean number of species less than nine. A higher number of sites (25 sites) have a perimeter above this threshold, with the mean number of species close to 13 (Fig. 2b). Species composition of butterflies was significantly influenced by the grassland perimeter (pseudo-F = 2.40; $P < 0.01$), with a threshold value of 480m in perimeter and an explained variation of 6.05%. The majority of butterfly species were absent from patches that were below the threshold size. Twenty-nine species of butterflies were associated with grasslands with a perimeter higher than the threshold of 480m and only six species were more abundant in smaller grasslands (Fig. 3, Table S2).

Beetle species richness was influenced negatively by the extent of built-up area surrounding the grassland site within a 250-m buffer zone (Fig. S3). This effect was significant after model selection together with a positive significant effect of grassland perimeter (Table 1). The final model was highly significant ($F_{2,37} = 8.15$; $P < 0.001$), and grassland perimeter explained independently 17.62% of variance while built-up area explained a further 13.89%. No other variables had a significant influence on beetle species richness (Table S1). The threshold value for grassland perimeter was 411.3 m (Statistic = 8.85; $P < 0.01$). The number of sites equal or under the threshold value was 8 and the rest, 32 sites, were above this threshold. The mean number of species at those smaller sites was two, while sites above the threshold containing more than four species on average (Fig. 2c). Although built-up areas has a negative significant effect on beetle species richness, we did not identify a significant threshold value for this factor. The composition of beetle species was not significantly discriminated by the threshold value of grassland perimeter (pseudo-F = 0.60; $P = 0.84$), with an explained variation of 1.82%.

Discussion

Our results, using a multi-taxa approach, revealed that both site-level and landscape-level factors are important for explaining the patterns in species richness in urban grasslands. We found that the size of the grassland, the management of the grassland, and the land-use in the closer surroundings of the study sites (i.e., urban greenings and built-up area) were the most influential factors explaining species richness. Nevertheless, the influence of site and land-use characteristics were partly different among studied taxa, which indicated different demands of specific groups, despite the fact that the three studied taxa are interconnected (e.g., adults of butterflies and beetle species studied here are dependent on flowering plants, while their larvae often feed on disparate plant material). These results highlight the value of using a multi-taxa approach when assessing biodiversity in urban landscapes.

Factors influencing plant diversity in urban grasslands

We found that the influence of land-use on plants was only evident at the 250-m buffer zone, which contrasts with previous findings that plants were the taxon with intermediate distance responses to land-use (Jackson and Fahrig, 2012; 2015), i.e. ≈ 0.5-kilometre buffer area. One potential reason for this difference was the higher habitat isolation we found in urban areas compared to agricultural landscapes, which could affect plant colonization at those short distances (Anderson et al., 2021). The fractal structure (i.e., complex shape of perimeter) of sites in urban landscapes compared to agricultural landscapes are another possible reason (Horák, 2016; du Toit et al., 2021). Moreover, as sampling methodology varied between studies, direct comparisons are not always possible.

We also found that plants were the most demanding group regarding the extent of the grassland. We found that the perimeter threshold was close to 1.2 km, which means that the mean area of these large meadows was close to 20 ha. This resulted to the fact that the conservation of plant diversity appears to be very low toward the city center, which is known also from other European cities (Fischer et al., 2013). The majority of large grasslands are almost located at the peripheries. Nevertheless, above mentioned large urban greenings appears to be a good opportunity as complementary habitats for survival of plants.

Likewise, the fact that only urban greenings in the surroundings and grassland perimeter significantly explained plant species richness in the studied grasslands was unexpected (Öster et al., 2007); if this was the case, one would expect that total area of grassland in the surroundings would be the most important land type (Münzbergová, 2004). Either way, this could be supplemented by the total extent of the grassland itself. However, the land-use type of urban greenings was the most significant factor, even if this type of land-use was relatively scarce in our study area. These greening areas included also urban wilderness (e.g., Rink, 2009), like the semi-natural vegetation of an oxbow lake, and a former military training area. They also included the parkland areas surrounding the city castle. These habitats are likely to act as potential corridors, increasing connectivity, facilitating individual plant species survival, and they are also possible sources of plant propagules that are probably capable of survival in other land-use types (James and Zedler, 2000; Knappová et al., 2012).

Factors influencing butterfly diversity in urban grasslands

Butterflies were influenced by two site-level characteristics, the perimeter of the grassland and the management intensity within the grassland, likely indicators of 'more' and 'better' habitat, respectively.

The influence of patch size and management intensity on species richness in fragmented landscapes has been extensively reported for many groups, including butterflies (e.g., Krauss et al., 2003a), and could result from increasing resource availability, increasing microhabitat heterogeneity, and/or decreasing species competition with increasing patch size. Furthermore, the fact that only habitat generalist species (as classified by Beneš et al., 2002) were associated with smaller grasslands, highlights the importance of maintaining large grasslands rather than just many small ones. The effect of management intensity, however, reflected how the grassland was used and likely influenced the habitat quality and the suitability of the grasslands for the persistence of butterflies (Dennis et al., 2003; Krauss et al., 2003b). Grassland management was predominantly mowing, and most sites were mowed two or more times during the season. Thus, the species richness of butterflies in urban grasslands positively responded to the low-intensity management (e.g., mowing in mosaic or only once a year) as well as to recent abandonment, as it is known that high management intensity often leads to negative effects on butterfly diversity (Ekroos et al., 2010). However, from a long-term perspective, abandonment would lead to the dominance of invasive grasses and woody vegetation resulting in potential negative effects on butterfly richness (Öckinger et al., 2006). The benefits of low-management intensity were not reflected on Agri-Envi subsidies having a positive effect on diversity in the studied grasslands, despite low-intensity management being encouraged in those schemes (Kleijn et al., 2001).

Factors influencing flower-visiting beetle diversity in urban grasslands

As for butterflies, the species richness of flower-visiting beetles increased with the size of the grassland. Their threshold was only a little bit lower than for butterflies, but much lower than for plants. This response was potentially related to resource (e.g., abundance of forbs) and/or microhabitat (e.g., shelters) availability within the grassland. Moreover, beetles were the only studied taxon directly affected by the extent of built-up area in the closer surroundings of grasslands, with a negative effect of increasing built-up area. This result probably reflects the fact that larvae of flower-visiting beetles, unlike butterflies, need for their survival, plant material (e.g., compost heaps or tree cavities) that is found in other habitats in the landscape, rather than in the grassland. Therefore, an increase in built-up area would mean a reduction in the extent of any potentially suitable habitat both for adults and larva. Moreover, increasing built-up area more likely results in lower habitat heterogeneity in the surroundings which could lead to a reduction in the observed species richness. Other studies have reported a decline in beetle richness caused by factors associated with urbanization (Magura et al., 2010; Fattorini, 2011a), including an increase in the built-up area (Fattorini, 2011b, Dylewski et al. 2020) or due to a change in resource availability (Carpaneto et al., 2005). However, other group of beetles may respond differentially to urbanization, as in the case of ground beetles a general negative effect of urbanization has not always been reported (e.g., Niemelä & Kotze, 2009; Magura et al., 2009).

Implications for urban grassland management

The patterns in species richness of the studied taxa observed here, and more importantly the identification of environmental thresholds that significantly affected biodiversity, have management implications for maintaining and enhancing biodiversity in cities. The different observed demands of the three taxa indicate that managing for a single taxon is not necessarily the right way in urban landscapes. Nevertheless, their demands were not completely opposed but rather complementary. Thus, consideration of grassland size, management, and extent of urban green and built-up areas would be the best option to design management plans that maintain high levels of multi-taxa biodiversity in cities.

One of the most important management implications of our results is that efforts should focus on retaining existing grasslands which are above the observed thresholds of approximately 1.5 km perimeter for plants and 0.5 km for insect and increasing the extent of some of the grasslands that are below threshold to enhance connectivity. This is probably best achieved by sharing this information with managers involved with urban spatial planning. A decrease in the perimeter of the grassland to a value below these thresholds would lead to a loss of diversity of all taxa. In our own experience, grassland habitats in the study city, and likely in many other cities, are mostly jeopardized by the construction of residential houses and shopping centers and their associated infrastructure, i.e., parking, road connections, and sidewalks, as well as the temporary use of grasslands as depots and dumping grounds. We can conclude that ensuring that individual grasslands are large, is key for maintaining urban biodiversity, and this seems to be independent of how close a grassland is to the epicenter of the urban development; for example, they could be in the city center, in suburbia or dispersed around former villages recently absorbed by the city. Nevertheless, grasslands that are currently present in the downtown area should be maintained as green spaces under future plans for urban spatial planning, independent of their size, due to the reduced total extent of this habitat within the city center. One of the current problems for grasslands, in terms of urban planning, is the transient nature of local policies.

Pardubice is a good example because in 2010-2014 the local authorities at the time prioritized the use of so-called empty spaces (including urban greenings) for housing and other building developments within the inner city areas; in contrast, local policies since 2014 have moved towards building development to take places in the city's peripheries (Zlínský, 2014).

In addition to maintaining existing grasslands, we conclude that brownfields (e.g., outdoor enclosed factory premises) or wilderness areas (abandoned military training areas) are potentially complementary sites that can help expansion of the urban green infrastructure for both increasing the quantity and quality of urban grasslands in the future.

Our results have shown that biodiversity significantly responded only to land-use variables in the closer surroundings (within a buffer zone of 250-m radius), this is potentially a highly favorable result as active management actions to support biodiversity are surely much easier and practical to implement at smaller than larger landscape scales (Horák et al., 2016). The beneficial effect of urban green spaces on biodiversity should be relatively easily enhanced by the establishment of areas such as playgrounds, places for dog walking, new parks in city outskirts, as well as restoration of traditional orchards (Horák et al., 2018).

We also identified negative effect of built-up area in the surroundings. When the extent of built-up area exceeded in the closer vicinity of a grassland, it resulted in a significant decrease in beetle species richness. Although the negative effect of already built-up areas on biodiversity in urban landscapes has no immediate solution, this information provides a useful tool for future urban planning. Namely, the avoidance of often slow but gradual suburbanization of green urban infrastructure. Therefore, a combined approach of protecting existing grasslands from urban development, increase in urban greenings and maintaining the extent of urban build-up, using legal constraints in spatial urban planning, is highly desirable. Our assessment of the critical threshold values assumed that the species that are currently present in the grasslands have viable populations and does not consider the potential for an extinction debt (Kuussaari et al., 2009). Furthermore, we found no significant effect of temporal continuity of the grassland on species richness of any of the study taxa.

Finally, the intensity of management of the grasslands should be reduced to increase biodiversity levels, including partial temporal abandonment of some sites and/or single mowing regimes. One of the simplest, but still only rarely used, biodiversity management options is mowing city grasslands (including lawns) in mosaic (Morris and Herzog, 1995). This means that the grassland is partly mowed and partly abandoned during the annual mowing regime. This can be done in strips, blocks, or irregular shape areas, which means the mowing regime is diversified (Cizek et al., 2012). Such management could be part of the so called, butterfly gardening or ButterflyScaping (e.g., Malone et al., 2010) – which especially means leaving unmowed strips in lawns and maintaining or planting areas with nectar plants. This could also be used for the grasslands located in the city center because it not only has biodiversity benefits but also has aesthetic value (Southon et al., 2017), which is provided by flowering plants and conspicuous day-flying butterflies.

Conclusions

This study illustrates that the effect of a highly fragmented city landscape on biodiversity within urban grasslands is driven by a combination of site-level factors and the land-uses in the immediate surroundings. Though the three taxa studied (plants, butterflies, and beetles) partly revealed different demands, the demands were not conflicting and instead, often complemented each other. We can conclude that there are several ways in which biodiversity can be enhanced using urban planning: preservation of existing urban grasslands, restrictions on construction in their closer surroundings, restoration or retention of city wilderness areas, and insect friendly mowing regimes are some of the many options available for enhancing biodiversity in cities.

References

Ahern, J., 2013. Urban landscape sustainability and resilience: the promise and challenges of integrating ecology with urban planning and design. Landscape Ecology 28, 1203-1212. https://doi.org/10.1007/s10980-012-9799-z.

Anderson, P. M., Potgieter, L. J., Chan, L., Cilliers, S. S., Nagendra, H. 2021. Urban plant diversity: understanding informing processes and emerging trends. Urban ecology in the Global South. Springer, Cham.

Aronson, M.F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., Vargo, T., 2017. Biodiversity in the city: key challenges for urban green space management. Frontiers in Ecology and the Environment 15, 189-196. https://doi.org/10.1002/fee.1480.

Beninde, J., Veith, M., Hochkirch, A., 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecology Letters 18, 581-592. https://doi.org/10.1111/ele.12427.

Beneš, J., Konvička, M., Dvořák, J., Fric, Z., Havelda, Z., Pavlíčko, A., Weidenhoffer, Z., 2002. Motýli České republiky. Rozšíření a ochrana I., II. SOM, Praha.

Biesmeijer, J.C., Roberts, S.P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Settele, J., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313, 351-354. https://doi.org/10.1126/science.1127863.

Bivand, R., Wong, D.W.S. 2018. Comparing implementations of global and local indicators of spatial association. Test, 27, 716–748. https://doi.org/10.1007/s11749-018-0599-x.

Branson, D.H., Joern, A., Sword, G.A., 2006. Sustainable management of insect herbivores in grassland ecosystems: new perspectives in grasshopper control. Bioscience 56, 743-755. https://doi.org/10.1641/0006-3568(2006)56[743:SMOIHI]2.0.CO;2.

Brymer, E., Freeman, E., Richardson, M., 2019. One health: the well-being impacts of Human-Nature relationships. Frontiers in Psychology 10, 1611.

Carpaneto, G.M., Mazziotta, A., Piattella, E., 2005. Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). Biological Conservation 123, 547-556. https://doi.org/10.1016/j.biocon.2004.12.007.

Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P., Konvicka, M. 2012. Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. Journal of Insect Conservation, 16, 215-226.

Cizek, O., Vrba, P., Benes, J., Hrazsky, Z., Koptik, J., Kucera, T., Konvicka, M., 2013. Conservation potential of abandoned military areas matches that of established reserves: plants and butterflies in the Czech Republic. PLoS One 8, e53124. https://doi.org/10.1371/journal.pone.0053124

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: a synthesis. Agriculture, Ecosystems & Environment 182, 1-14. https://doi.org/10.1016/j.agee.2013.12.015.

Dennis, R.L., Shreeve, T.G., Van Dyck, H., 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos, 417-426.

Dormann, C., McPherson, J., Araújo, M., Bivand, R., Bolliger, J., Carl, G., Davies, R., Hirzel, A., Jetz, W., Kissling, W., Kühn, I., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609-628. https://doi.org/10.1111/j.2007.0906-7590.05171.x.

du Toit, M. J., Kotze, D. J., Cilliers, S. S., 2016. Landscape history, time lags and drivers of change: urban natural grassland remnants in Potchefstroom, South Africa. Landscape Ecology 31, 2133-2150.

du Toit, M. J., Kotze, D. J., Cilliers, S. S. 2020. Quantifying long-term urban grassland dynamics: biotic homogenization and extinction debts. Sustainability, 12, 1989.

du Toit, M. J., Du Preez, C., Cilliers, S. S. 2021. Plant diversity and conservation value of wetlands along a rural-urban gradient. Bothalia-African Biodiversity & Conservation, 51, 1-18.

Dylewski, Ł., Maćkowiak, Ł., Banaszak-Cibicka, W. 2019. Are all urban green spaces a favourable habitat for pollinator communities? Bees, butterflies and hoverflies in different urban green areas. Ecological Entomology, 44, 678-689.

Dylewski, Ł., Maćkowiak, Ł., Banaszak-Cibicka, W. 2020. Linking pollinators and city flora: How vegetation composition and environmental features shapes pollinators composition in urban environment. Urban Forestry & Urban Greening, 56, 126795.

Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. Journal of Applied Ecology 47, 459-467. https://doi.org/10.1111/j.1365-2664.2009.01767.x.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487-515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419.

Fattorini, S., 2011a. Insect extinction by urbanization: a long term study in Rome. Biological Conservation 144, 370-375. https://doi.org/10.1016/j.biocon.2010.09.014.

Fattorini, S., 2011b. Insect rarity, extinction and conservation in urban Rome (Italy): a 120-year-long study of tenebrionid beetles. Insect Conservation and Diversity 4, 307-315. https://doi.org/10.1111/j.1752-4598.2010.00129.x.

Fischer, L. K., Von der Lippe, M., Kowarik, I., 2013. Urban land use types contribute to grassland conservation: The example of Berlin. Urban Forestry & Urban Greening 12, 263-272.

Giraudoux, P., Antonietti, J.P., Beale, C., Lancelot, R., Pleydell, D., Treglia, M. 2021. pgirmess: spatial analysis and data mining for field ecologists. https://CRAN.R-project.org/package=pgirmess.

Hartig, F. 2021. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html.

Heiberger, R.M., Robbins, N.B. 2014. Design of diverging stacked bar charts for likert scales and other applications. Journal of Statistical Software, 57, 1–32. https://www.jstatsoft.org/v57/i05/.

Heneberg, P., Bogusch, P., Řezáč, M., 2016. Off-road motorcycle circuits support long-term persistence of bees and wasps (Hymenoptera: Aculeata) of open landscape at newly formed refugia within otherwise afforested temperate landscape. Ecological Engineering 93, 187-198. https://doi.org/10.1016/j.ecoleng.2016.05.026.

Hirzel, A., Guisan, A., 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecological Modelling 157, 331-341.

Horak, J. 2014. Insect taxa with similar habitat requirements may differ in response to the environment in heterogeneous patches of traditional fruit orchards. Journal of Insect Conservation, 18, 637-642.

Horák, J., 2016. Suitability of biodiversity-area and biodiversity-perimeter relationships in ecology: a case study of urban ecosystems. Urban Ecosystems 19, 131–142. https://doi.org/10.1007/s11252-015-0492-2.

Horák, J., Brestovanská, T., Mladenović, S., Kout, J., Bogusch, P., Halda, J. P., Zasadil, P., 2019. Green desert?: Biodiversity patterns in forest plantations. Forest Ecology and Management 433, 343-348.

Horák, J., Holuša, J., Nováková, P., Lukášová, K., Loskotová, T., Romportl, D., 2016. Agricultural landscapes with prevailing grasslands can mitigate the population densities of a tree-damaging alien species. Agriculture, Ecosystems and Environment 230, 177–183. https://doi.org/10.1016/j.agee.2016.06.013.

Horak, J., Peltanova, A., Podavkova, A., Safarova, L., Bogusch, P., Romportl, D., Zasadil, P., 2013. Biodiversity responses to land use in traditional fruit orchards of a rural agricultural landscape. Agriculture, Ecosystems and Environment 178, 71–77. https://doi.org/10.1016/j.agee.2013.06.020.

Horák, J., Rom, J., Rada, P., Šafářová, L., Koudelková, J., Zasadil, P., Halda, J.P., Holuša, J., 2018. Renaissance of a rural artifact in a city with a million people: biodiversity responses to an agro-forestry restoration in a large urban traditional fruit orchard. Urban Ecosystems 21, 263-270. https://doi.org/10.1007/s11252-017-0712-z.

Horák, J., Rada, P., Lettenmaier, L., Andreas, M., Bogusch, P., Jaworski, T., 2021. Importance of meteorological and land use parameters for insect diversity in agricultural landscapes. Science of the Total Environment 791, 148159. https://doi.org/10.1016/j.scitotenv.2021.148159.

Hothorn, T, Hornik, K, Zeileis, A 2006. Unbiased recursive partitioning: a conditional inference framework. Journal of Computational and Graphical Statistics, 15, 651–674.

Huggett, A.J. (2005) The concept and utility of 'ecological thresholds' in biodiversity conservation. Biological Conservation 124, 301-310.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Global Ecology and Biogeography 24, 52-63. https://doi.org/10.1111/geb.12233.

Jackson, H.B., Fahrig, L., 2012. What size is a biologically relevant landscape? Landscape Ecology 27, 929–941.

James, M.L., Zedler, J.B., 2000. Dynamics of wetland and upland subshrubs at the salt marsh-coastal sage scrub ecotone. The American Midland Naturalist 143, 298-311. https://doi.org/10.1674/0003-0031(2000)143[0298:DOWAUS]2.0.CO;2.

Johansson, L.J., Hall, K., Prentice, H.C., Ihse, M., Reitalu, T., Sykes, M.T., Kindström, M., 2008. Semi-natural grassland continuity, long-term land-use change and plant species richness in an agricultural landscape on Öland, Sweden. Landscape and Urban Planning 84, 200-211. https://doi.org/10.1016/j.landurbplan.2007.08.001.

Kadlec, T., Tropek, R., Konvicka, 2012. Timed surveys and transect walks as comparable methods for monitoring butterflies in small plots. Journal of Insect Conservation 16, 275-280.

Kato, S. & Ahern, J. (2011) The concept of threshold and its potential application to landscape planning. Landscape and Ecological Engineering 7, 275-282.

Kleijn, D., Berendse, F., Smit, R., Gilissen, N., 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413, 723-725. https://doi.org/10.1038/35099540.

Knappová, J., Hemrová, L., Münzbergová, Z., 2012. Colonization of central European abandoned fields by dry grassland species depends on the species richness of the source habitats: a new approach for measuring habitat isolation. Landscape Ecology 27, 97-108. https://doi.org/10.1007/s10980-011-9680-5.

Krauss, J., Steffan-Dewenter, I., Tscharntke, T., 2003a. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography 30, 889-900. https://doi.org/10.1046/j.1365-2699.2003.00878.x.

Krauss, J., Steffan-Dewenter, I., Tscharntke, T., 2003b. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia 137, 591-602. https://doi.org/10.1007/s00442-003-1353-x.

Kuussaari, M., Bommarco, R., Risto K. Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Ockinger, E., Partel, M.,Pino, J., Roda, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewente, I., 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology and Evolution 24, 564-571.

Kuussaari, M., Toivonen, M., Heliölä, J., Pöyry, J., Mellado, J., Ekroos, J., Tiainen, J. 2021. Butterfly species' responses to urbanization: differing effects of human population density and built-up area. Urban Ecosystems, 24, 515-527.

Magura, T., Lövei, G.L., Tóthmérész, B., 2010. Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? Global Ecology and Biogeography 19, 16-26. https://doi.org/10.1111/j.1466-8238.2009.00499.x.

Malone, K. C., Wilber, W., Hansen, G., Daniels, J. C., Larsen, C., Momol, E. 2010. Community ButterflyScaping: How to Move Beyond Butterfly Gardening to Create a Large-Scale Butterfly Habitat. University of Florida IFAS Extension.

Mollashahi, H., Szymura, M., Szymura, T. H. 2020. Connectivity assessment and prioritization of urban grasslands as a helpful tool for effective management of urban ecosystem services. Plos One, 15, e0244452.

Morris, J., Herzog, C., 1995. Butterfly gardening for education, recreation & therapy. Proceedings-Florida State Horticultural Society, Vol. 108, Florida State Horticultural Society, pp. 391-392.

Münzbergová, Z., 2004. Effect of spatial scale on factors limiting species distributions in dry grassland fragments. Journal of Ecology 92, 854-867. https://doi.org/10.1111/j.0022-0477.2004.00919.x.

Nally, R.M., Walsh, C.J. 2004. Hierarchical partitioning public-domain software. Biodiversity and Conservation, 13, 659–-660. https://search.proquest.com/openview/6f19c4d612b6cf75b106c479e7084a58/1.

Nilon, C.H., Aronson, M.F., Cilliers, S.S., Dobbs, C., Frazee, L.J., Goddard, M.A., Winter, M., 2017. Planning for the future of urban biodiversity: a global review of city-scale initiatives. BioScience 67, 332-342. https://doi.org/10.1093/biosci/bix012.

Norton, B.A., Evans, K.L., Warren, P.H., 2016. Urban Biodiversity and Landscape Ecology: Patterns, Processes and Planning. Current Landscape Ecology Reports 1, 178-192. https://doi.org/10.1007/s40823-016-0018-5.

Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biological Conservation 133, 291-300. https://doi.org/10.1016/j.biocon.2006.06.009.

Öckinger, E. Dannestam, H., Smith, G., 2009 The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. Landscape and Urban Planning 93, 31-37.

Öster, M., Cousins, S.A., Eriksson, O., 2007. Size and heterogeneity rather than landscape context determine plant species richness in semi-natural grasslands. Journal of Vegetation Science 18, 859-868. https://doi.org/10.1111/j.1654-1103.2007.tb02602.x.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. 2021. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-153, https://CRAN.R-project.org/package=nlme.

Pyle, R.M., 1993. The Thunder Tree: Lessons from an Urban Wildland. Oregon State University Press, Corvallis, USA.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rink, D., 2009. Wilderness: The nature of urban shrinkage? The debate on urban restructuring and restoration in Eastern Germany. Nature and Culture 4, 275-292. https://doi.org/10.3167/nc.2009.040304.

Sekar, S., 2012. A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? Journal of Animal Ecology 81,174-184.

Silvertown, J., 2009. A new dawn for citizen science. Trends in Ecology & Evolution 24, 467-471. https://doi.org/10.1016/j.tree.2009.03.017.

Sjödin, N. E., Bengtsson, J., Ekbom, B. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. Journal of Applied Ecology, 45, 763-772.

Snyder, C.D. & Young, J.A. (2020) Identification of management thresholds of urban development in support of aquatic biodiversity conservation. Ecological Indicators 112, 106124.
Soga, M., Yamaura, Y., Koike, S., Gaston, K.J., 2014. Woodland remnants as an urban wildlife refuge: a cross-taxonomic assessment. Biodiversity and Conservation 23, 649-659. https://doi.org/10.1007/s10531-014-0622-9.

Southon, G.E., Jorgensen, A., Dunnett, N., Hoyle, H., Evans, K.L., 2017. Biodiverse perennial meadows have aesthetic value and increase residents' perceptions of site quality in urban green-space. Landscape and Urban Planning 158, 105-118. https://doi.org/10.1016/j.landurbplan.2016.08.003.

United Nations, 2016. Department of Economic and Social Affairs, Population Division. The World's Cities in 2016-Data Booklet (ST/ESA?SER.A/392). Accessible from: https://digitallibrary.un.org/record/1634928.

Venables, W.N., Ripley, B.D. 2002. Modern applied statistics with S, Fourth edition. Springer, New York. https://www.stats.ox.ac.uk/pub/MASS4/.

Zlínský, M., 2014. Noví vládci Pardubic pustí stavbaře na zatím zelená místa. iDnes. Accessed February 25nd, 2021 from http://pardubice.idnes.cz/tam-kde-se-v-pardubicich-stavet-nemohlo-uz-to-pujde-fwn-/pardubice-zpravy.aspx?c=A141025_2110878_pardubice-zpravy_jah.

Figures:

Fig. 1. The study area and grasslands in the Pardubice city (Czech Republic). (A) despite the localization of the Czech Republic in Europe, (B) the localization of Pardubice city in the Czech Republic, and (C) location of the study grassland sites within a 10 km circle centered at the city castle, showing in grey the build-up areas.

Fig. 2. Significant threshold values of grassland perimeter for (a) plant, (b) butterfly and (c) beetle species richness in grasslands in the city of Pardubice.

Fig. 3. Species composition of butterfly communities in grasslands in the city of Pardubice discriminated by the threshold value of grassland perimeter, represented as the first RDA axis. Abbreviations and full name for butterfly species are presented in Table S2.

Figure 1

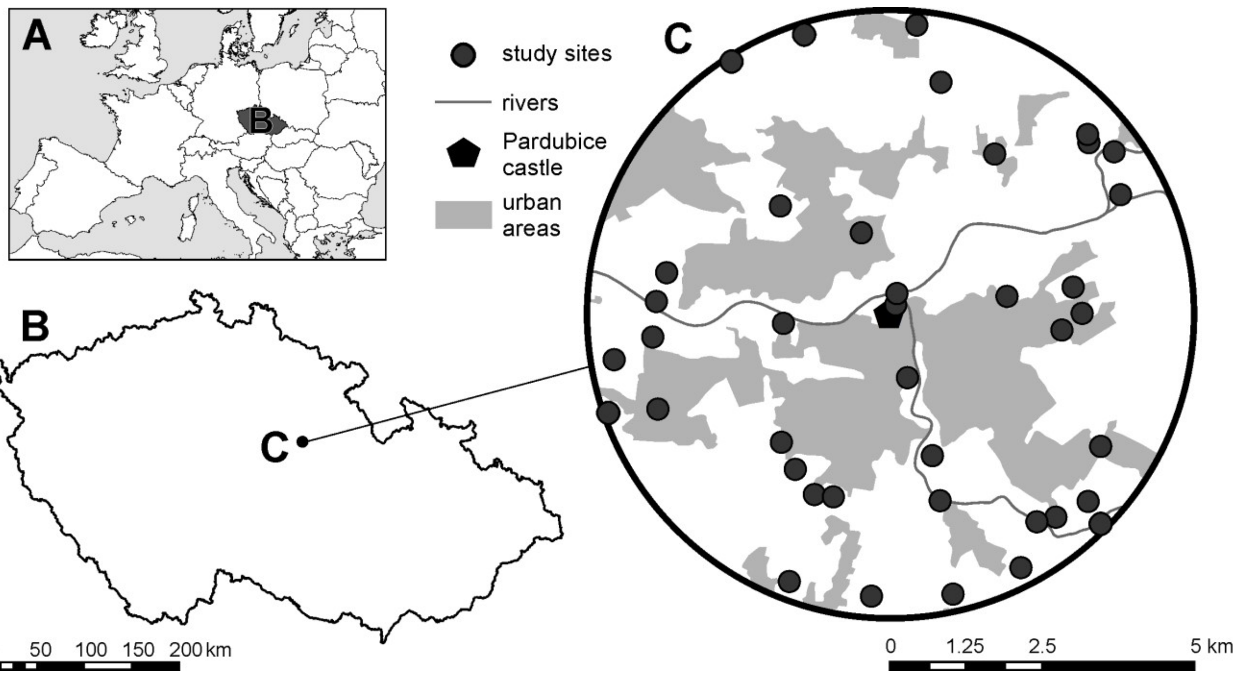
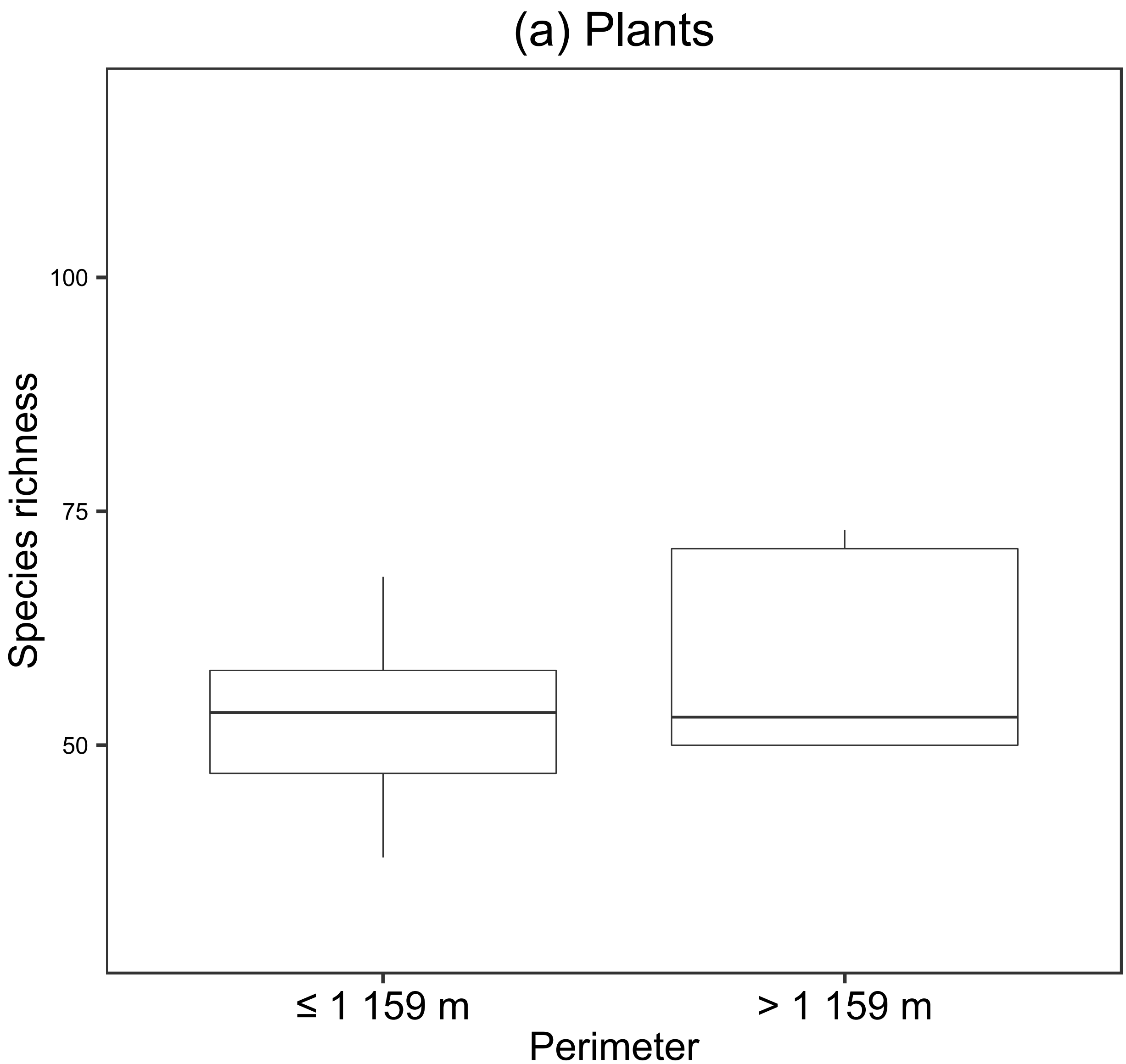
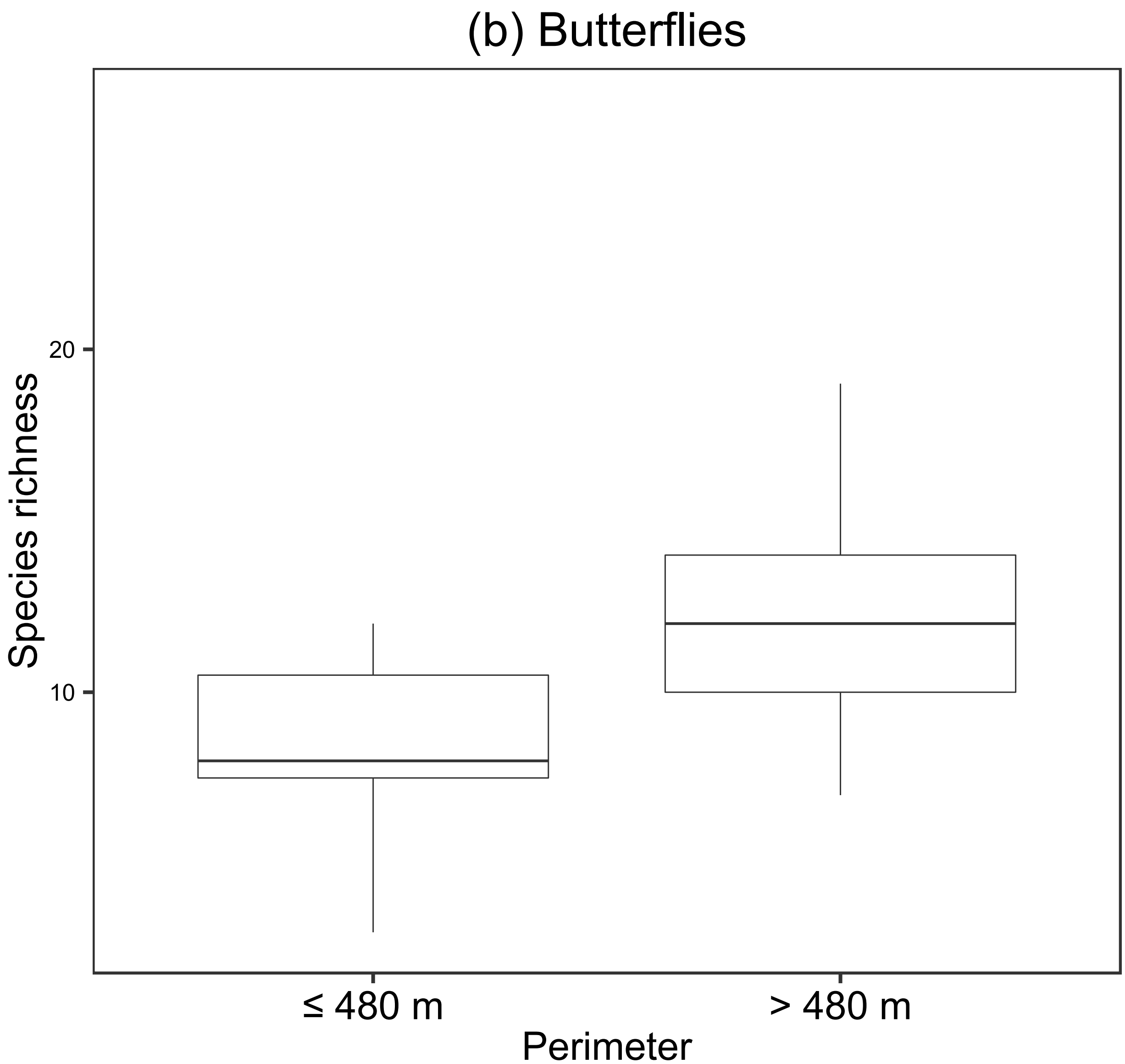

A
B
C
study sites
rivers
Pardubice castle
urban areas
0 50 100 150 200 km
0 1.25 2.5 5 km

Figure 2




(b) Butterflies
Species richness
20
10
≤ 480 m
> 480 m
Perimeter

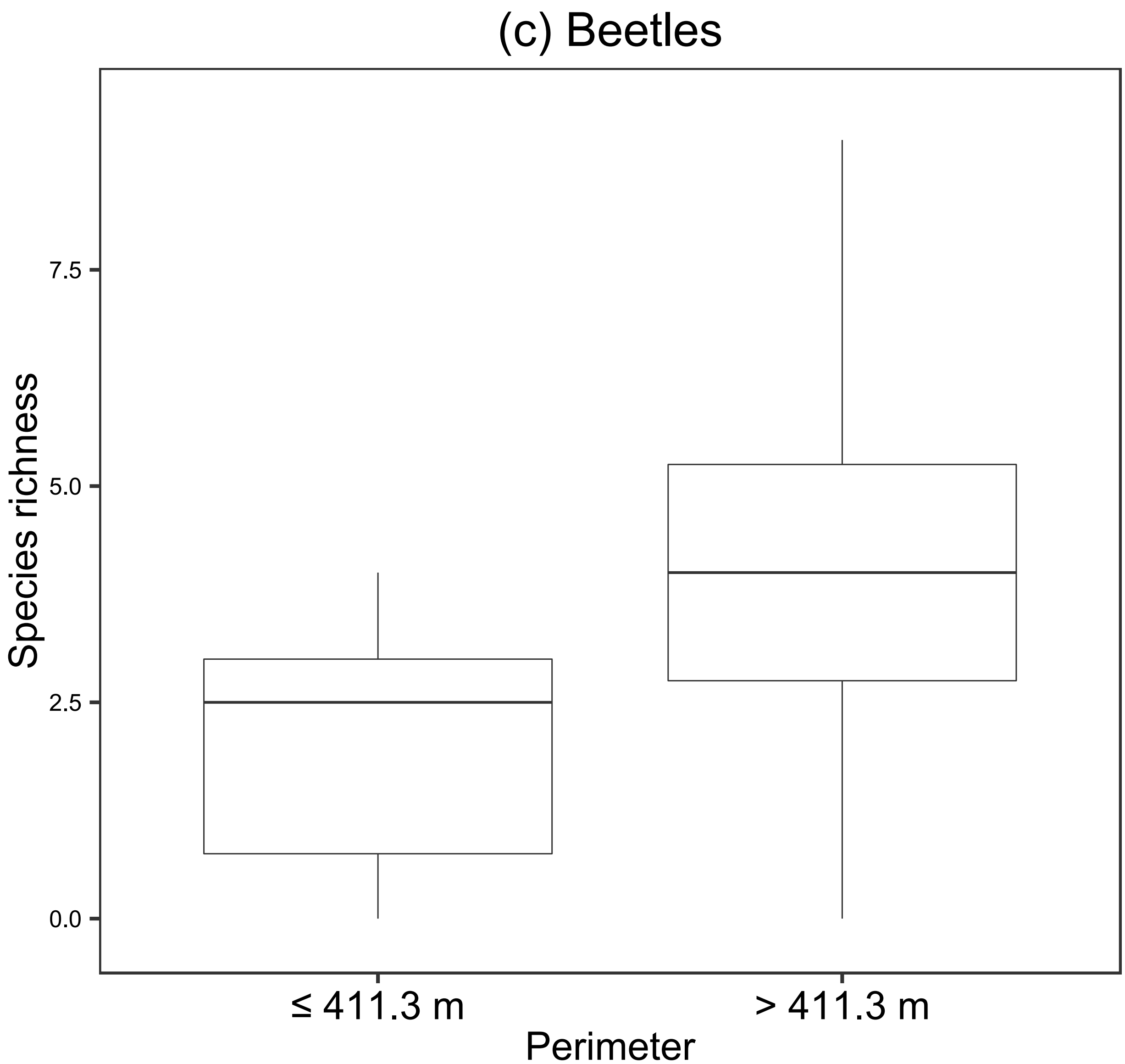
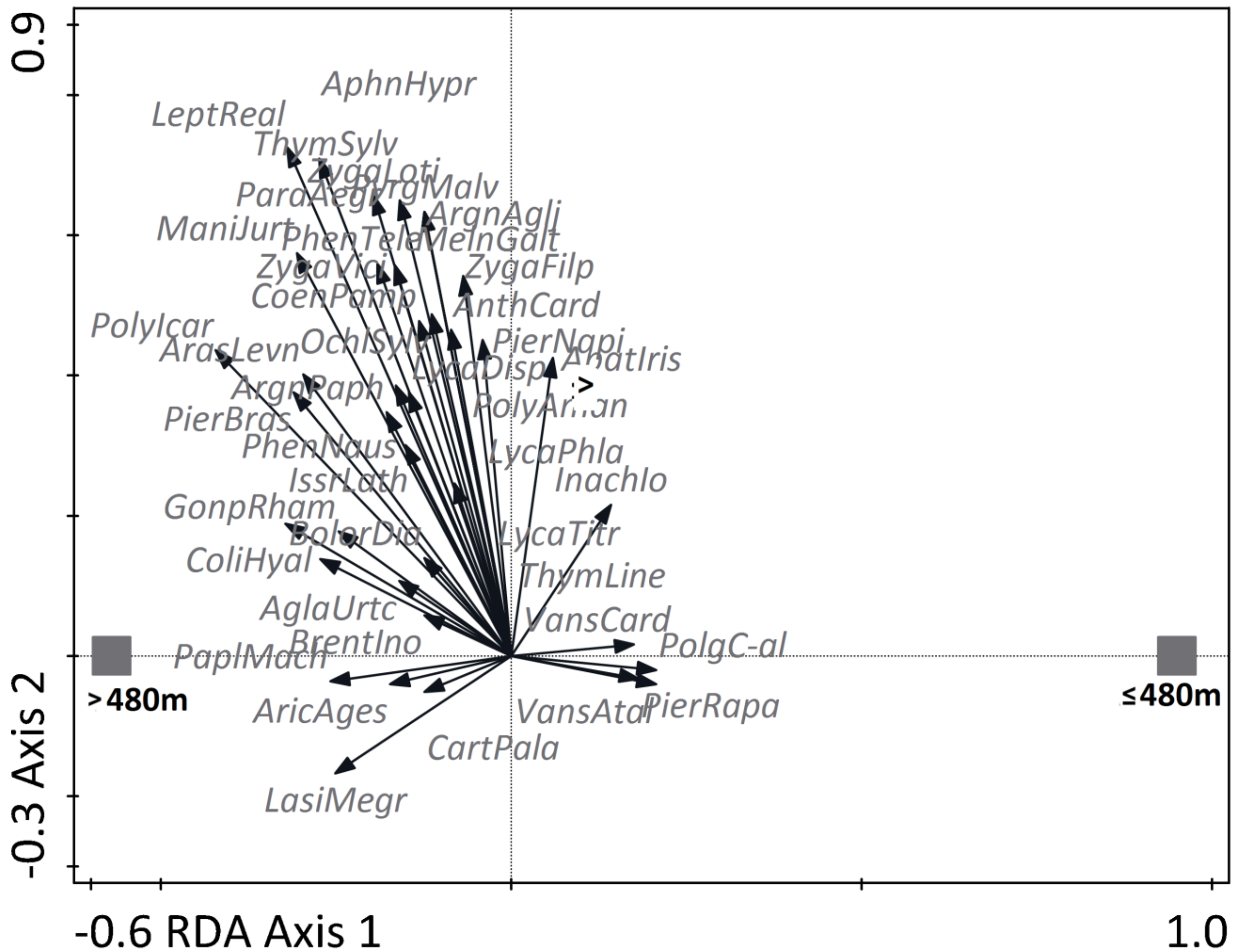

(c) Beetles
Species richness
7.5
5.0
2.5
0.0
≤ 411.3 m
> 411.3 m
Perimeter

Figure 3



0.9
-0.3 Axis 2
-0.6 RDA Axis 1
1.0
AphnHypr
LeptReal
ThymSylv
ZygaLoti
PyrgMalv
ManiJurt
ArgnAgli
PhenTela
MelnGalt
ZygaVici
ZygaFilp
CoenPamp
AnthCard
PolyIcar
ArasLevn
OchlSylv
PierNapi
LycaDisp
ApatIris
ArgnPaph
PierBras
PhenNaus
LycaPhla
IssrLath
InachIo
GonpRham
BolorDia
LycaTitr
ColiHyal
ThymLine
AglaUrtc
VansCard
BrentIno
PolgC-al
PaplMach
>480m
≤480m
AricAges
VansAtal
PierRapa
CartPala
LasiMegr

Tables:

Table 1 Final models (based on GLM selection) for the effect of site-level and land-use characteristics on species richness of the three studied taxa in grasslands in the city of Pardubice. Land-use categories were significant for the 250m buffer zone.

Response variable	Independent variable	Estimate	SE	t	P
Plant species richness	Intercept	4.84E+01	3.21E+00	15.06	<0.001
	Grassland perimeter	6.52E-03	3.16E-03	2.06	0.046
	Cover of urban greenings	1.94E-04	5.36E-05	3.61	<0.001
Butterfly species richness	Intercept	1.04E+02	1.07E+00	9.73	<0.001
	Grassland perimeter	3.73E-03	8.45E-04	4.42	<0.001
	Grassland management intensity	-1.85E+00	5.83E-01	-3.17	0.003
Beetle species richness	Intercept	3.12E+00	6.73E-01	4.63	<0.001
	Grassland perimeter	1.41E-03	5.42E-04	2.60	0.013
	Cover of built-up area	-1.26E-05	5.76E-06	-2.18	0.036

Supporting data:

Figures

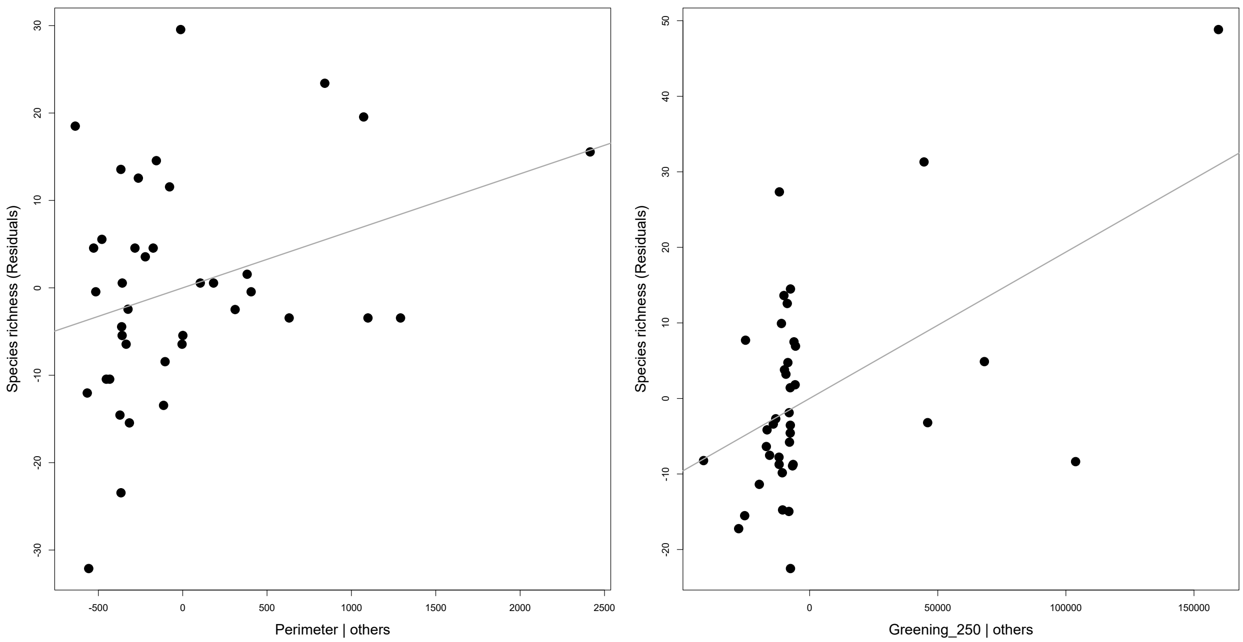


Figure S1. The effect of grassland size (perimeter) and total area of urban greenings on species richness of plants in grasslands in the city of Pardubice. The results of partial regression of best-subset model selection are visualized by Pearson residuals and a grey regression line (for P < 0.05). Greening_250 is an abbreviation for urban greenings in a 250-m buffer zone.

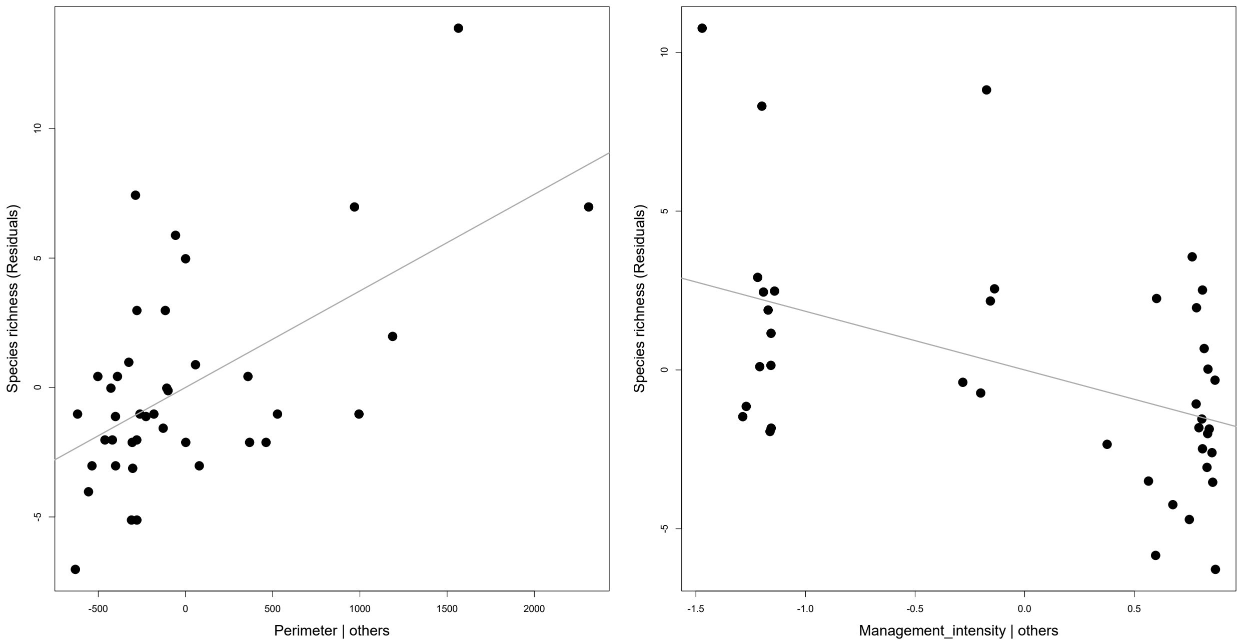


Figure S2. The effect of grassland size (perimeter) and management intensity (mowing) on species richness of butterflies in grasslands in the city of Pardubice. The results of partial regression of best-subset model selection are visualized by Pearson residuals and grey regression lines (for $P < 0.05$).

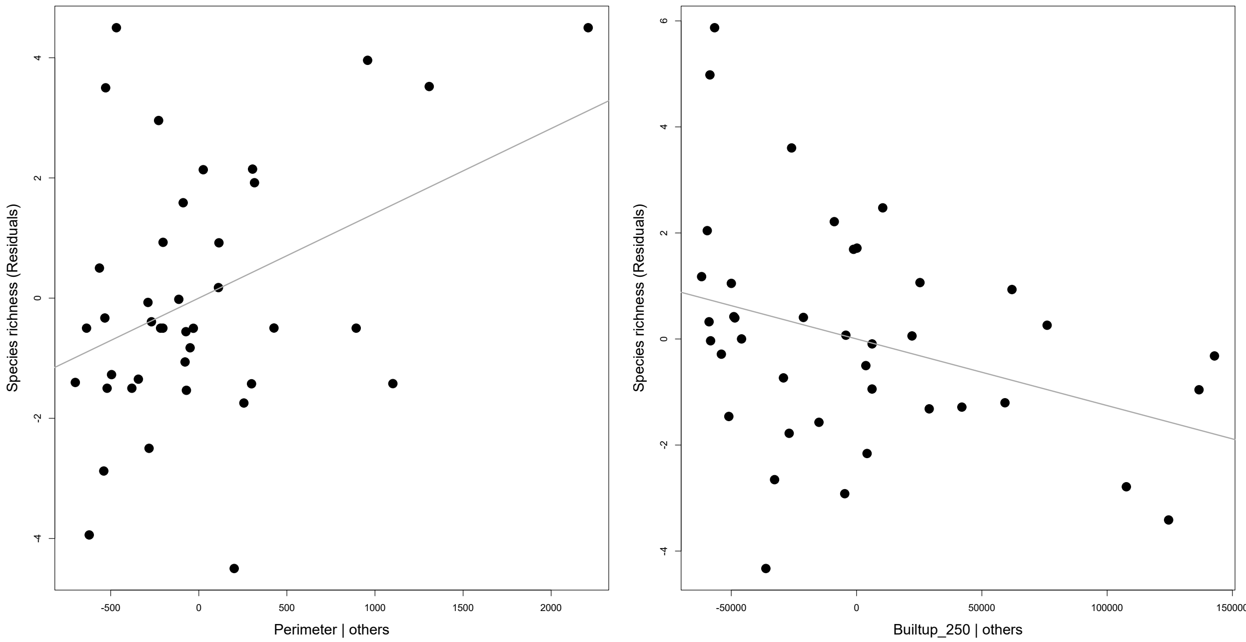


Figure S3. The effect of grassland size (perimeter) and the extent of built-up areas on species richness of beetles in grasslands in the city of Pardubice. The results of partial regression of best-subset model selection are visualized by Pearson residuals and grey regression lines (for $P < 0.05$). Builtup_250 is an abbreviation for built-up areas in the 250-m buffer zone.

Tables

Table S1. Checklist of observed plants in Pardubice.

Latin name	Number of sites
Acer campestre	1
Acer negundo	3
Acer pseudoplatanus	1
Aegopodium podagraria	9
Agrimonia eupatoria	1
Agrostis capillaris	8
Agrostis stolonifera	10
Achillea millefolium agg.	34
Ajuga reptans	1
Alchemilla monticola	1
Alchemilla sp.1	3
Allium angulosum	2
Alopecurus geniculatus	1
Alopecurus pratensis	20
Amaranthus retroflexus	7
Anemone nemorosa	1
Angelica sylvestris	1
Anthemis arvensis	1
Anthoxanthum odoratum	10
Anthriscus sylvestris	7
Apera spica-venti	1
Arctium lappa	8
Arctium minus	1
Arctium sp.1	11
Arctium tomentosum	7
Arctium ambiguum	3
Arenaria serpyllifolia	2
Armoracia rusticana	2
Arrhenatherum elatius	36
Artemisia vulgaris	29
Astragalus glycyphyllos	5
Atriplex sagittata	2
Atriplex sp.1	1
Avenula pubescens	2
Ballota nigra	3
Barbarea vulgaris	2
Bellis perennis	11
Berteroa incana	2
Betonica officinalis	4

Latin name	Number of sites
Betula pendula	3
Bidens frondosa	1
Brassica napus	1
Briza media	1
Bromus erectus	1
Bromus hordeaceus	17
Bromus inermis	2
Bromus sterilis	2
Bunias orientalis	1
Calamagrostis epigejos	19
Calendula officinalis	1
Calystegia sepium	5
Campanula patula	14
Campanula rotundifolia agg.	1
Capsella bursa-pastoris	15
Cardamine amara	1
Cardamine pratensis	4
Cardaria draba	1
Carduus crispus	2
Carex acuta	5
Carex brizoides	1
Carex hirta	9
Carex ovalis	1
Carex nigra	1
Carex otrubae	1
Carex vesicaria	1
Carex vulpina	3
Carpinus betulus	1
Centaurea jacea	16
Centaurea scabiosa	1
Centaurea stoebe	1
Centaurium erythraea	1
Cerastium arvense	1
Cerastium glomeratum	1
Cerastium holosteoides	28
Cichorium intybus	17
Cirsium arvense	31
Cirsium canum	5
Cirsium oleraceum	1
Cirsium vulgare	12
Convolvulus arvensis	14
Conyza canadensis	19
Cornus sanguinea	6

Latin name	Number of sites
Coronilla varia	5
Crataegus spp.	6
Crepis biennis	36
Cruciata laevipes	1
Cynosurus cristatus	1
Dactylis glomerata	35
Daucus carota	19
Descurainia sophia	2
Deschampsia cespitosa	6
Digitaria sanguinalis	2
Dipsacus fullonum	3
Echinochloa crus-galli	8
Echium vulgare	6
Eleocharis palustris ssp. vulgaris	1
Elytrigia repens	3
Epilobium ciliatum	1
Epilobium hirsutum	3
Equisetum arvense	15
Eragrostis minor	3
Erigeron acris	2
Erigeron annuus	21
Erodium cicutarium	5
Eupatorium cannabinum	4
Euphorbia cyparissias	4
Euphorbia helioscopia	3
Euphorbia peplus	2
Fagus sylvatica	1
Fallopia convolvulus	2
Fallopia dumetorum	1
Festuca arundinacea	13
Festuca brevipila	1
Festuca gigantea	1
Festuca pratensis	20
Festuca rubra	22
Festuca rupicola	1
Filipendula ulmaria	2
Fragaria moschata	2
Fragaria viridis	2
Fraxinus excelsior	2
Galeopsis bifida	1
Galeopsis pubescens	1
Galeopsis tetrahit	2
Galinsoga parviflora	1

Latin name	Number of sites
Galinsoga quadriradiata	1
Galium album s.lat.	37
Galium aparine	8
Galium boreale	2
Galium verum	4
Galium wirtgenii	2
Geranium pratense	27
Geranium pusillum	3
Geum urbanum	15
Glechoma hederacea	11
Glyceria maxima	2
Gnaphalium uliginosum	1
Heracleum sphondylium	21
Herniaria glabra	1
Hieracium pilosella	4
Holcus lanatus	18
Holcus mollis	1
Humulus lupulus	7
Hyoscyamus niger	1
Hypericum maculatum	1
Hypericum perforatum	15
Hypochaeris radicata	8
Chaerophyllum aromaticum	4
Chaerophyllum bulbosum	3
Chaerophyllum temulum	1
Chelidonium majus	1
Chenopodium album agg.	1
Chenopodium sp.1	11
Chenopodium strictum	1
Impatiens glandulifera	1
Impatiens parviflora	5
Inula britannica	1
Iris pseudacorus	2
Juglans regia	1
Juncus articulatus	3
Juncus bufonius	1
Juncus conglomeratus	1
Juncus effusus	3
Juncus inflexus	5
Juniperus communis	1
Knautia arvensis	4
Lactuca serriola	10
Lamium album	11

Latin name	**Number of sites**
Lamium amplexicaule	2
Lamium maculatum	2
Lamium purpureum	2
Lapsana communis	2
Lathyrus pratensis	18
Lathyrus tuberosus	2
Leontodon autumnalis	4
Leontodon hispidus	11
Leucanthemum vulgare agg.	4
Linaria vulgaris	4
Lolium perenne	18
Lotus corniculatus	20
Luzula campestris	2
Lychnis flos-cuculi	10
Lysimachia nummularia	7
Lysimachia vulgaris	1
Lythrum salicaria	7
Malva neglecta	2
Malva sylvestris	2
Matricaria discoidea	6
Matricaria chamomilla	1
Medicago falcata	1
Medicago lupulina	23
Medicago sativa	18
Medicago varia	1
Melilotus albus	8
Melilotus officinalis	1
Mentha aquatica	2
Mentha arvensis	1
Mentha sp.1	1
Molinia sp.1	1
Myosotis arvensis	8
Myosoton aquaticum	1
Odontites vernus	4
Oenothera biennis agg.	1
Onobrychis viciifolia	1
Ononis spinosa	2
Ornithogalum kochii	1
Papaver rhoeas	4
Pastinaca sativa	21
Persicaria amphibia	12
Persicaria hydropiper	1
Persicaria lapathifolia	1

Latin name	Number of sites
Petroselinum crispum	1
Phalaris arundinacea	16
Phleum pratense	14
Phragmites australis	7
Picris hieracioides	3
Pinus sylvestris	1
Plantago lanceolata	36
Plantago major	21
Plantago media	4
Poa annua	13
Poa compressa	5
Poa pratensis	36
Poa trivialis	1
Polygala comosa	2
Polygonum aviculare agg.	15
Bistorta major	5
Populus tremula	4
Populus x canadensis	1
Potentilla anserina	15
Potentilla argentea	14
Potentilla reptans	16
Potentilla supina	2
Prunella vulgaris	11
Prunus spinosa	2
Puccinellia distans	1
Quercus robur	6
Ranunculus acris	24
Ranunculus auricomus agg.	1
Ranunculus repens	25
Reynoutria japonica	1
Robinia pseudoacacia	3
Rosa canina	1
Rosa sp.1	6
Rubus spp.	14
Rudbeckia laciniata	4
Rumex acetosa	24
Rumex acetosella s.lat.	3
Rumex aquaticus	1
Rumex crispus	3
Rumex obtusifolius	17
Rumex thyrsiflorus	12
Salix caprea	1
Salix sp.1	5

Latin name	Number of sites
Sambucus nigra	4
Sanguisorba officinalis	15
Saponaria officinalis	3
Scleranthus annuus	1
Sedum acre	1
Senecio aquaticus	1
Senecio jacobaea	9
Senecio vulgaris	3
Libanotis pyrenaica	9
Setaria pumila	8
Setaria verticillata	4
Silene latifolia subsp. alba	13
Silene vulgaris	6
Sisymbrium officinale	2
Solanum lycopersicum	1
Solanum nigrum	3
Solidago canadensis	22
Solidago gigantea	4
Sonchus oleraceus	5
Spergularia rubra	2
Stachys palustris	3
Stellaria graminea	6
Stellaria media	3
Symphytum officinale	17
Tanacetum vulgare	14
Taraxacum sect. *Ruderalia*	38
Thlaspi arvense	4
Thymus pulegioides	2
Tilia cordata	3
Torilis japonica	6
Tragopogon orientalis	9
Trifolium arvense	10
Trifolium campestre	8
Trifolium dubium	3
Trifolium hybridum	18
Trifolium medium	1
Trifolium pratense	28
Trifolium repens	28
Tripleurospermum inodorum	17
Trisetum flavescens	19
Tussilago farfara	3
Typha angustifolia	2
Typha latifolia	2

Latin name	Number of sites
Urtica dioica	26
Valeriana officinalis	2
Verbena officinalis	1
Veronica arvensis	14
Veronica chamaedrys	20
Veronica persica	1
Vicia cracca	25
Vicia hirsuta	6
Vicia lathyroides	2
Vicia sativa	9
Vicia sepium	12
Vicia tetrasperma	16
Vicia villosa	2

Table S2. Checklist of observed butterflies in Pardubice. Species associated with grassland above the (*) and below ($) the threshold perimeter of 480m.

Latin name	**Abbreviation**	**Number of sites**
*Aglais urticae**	AglaUrtc	19
Anthocharis cardamines	AnthCard	4
Apatura iris$	ApatIris	2
*Aphantopus hyperantus**	AphnHypr	24
*Araschnia levana**	AracLevn	21
*Argynnis aglaja**	ArgnAglj	1
*Argynnis paphia**	ArgnPaph	2
*Aricia agestis**	AricAges	2
*Boloria dia**	BolorDia	1
*Brenthis ino**	BrentIno	1
*Carterocephalus palaemon**	CartPala	1
*Coenonympha pamphilus**	CoenPamp	40
*Colias hyale**	ColiHyal	8
*Gonepteryx rhamni**	GonpRham	10
Inachis io$	InachIo	12
*Issoria lathonia**	IssrLath	12
*Lasiommata megera**	LasiMegr	4
*Leptidea reali**	LeptReal	12
Lycaena dispar	LycaDisp	14
Lycaena phlaeas	LycaPhla	10
*Lycaena tityrus**	LycaTitr	1
*Maniola jurtina**	ManiJurt	38
*Melanargia galathea**	MelnGalt	17
*Ochlodes sylvanus**	OchlSylv	14
*Papilio machaon**	PaplMach	4
*Pararge aegeria**	ParaAegr	1
*Phengaris nausithous**	PhenNaus	2
*Phengaris teleius**	PhenTele	1
*Pieris brassicae**	PierBras	35
Pieris napi	PierNapi	40
Pieris rapae$	PierRapa	30
Polygonia c-album$	PolgC	1
Polyommatus amandus	PolyAman	2
*Polyommatus icarus**	PolyIcar	32

*Pyrgus malvae**	PyrgMalv	1
Thymelicus lineola	ThymLine	3
*Thymelicus sylvestris**	ThymSylv	11
Vanessa atalanta$	VansAtal	1
Vanessa cardui$	VansCard	4
Zygaena filipendulae	ZygaFilp	6
*Zygaena loti**	ZygaLoti	3
*Zygaena viciae**	ZygaVici	2

Table S3. Checklist of observed beetles in Pardubice.

Latin name	Number of sites
Agriotes ustulatus	6
Agrypnus murinus	1
Anthaxia nitidula	3
Anthaxia similis	1
Byturus ochraceus	3
Cantharis pellucida	4
Cetonia aurata	1
Cidnopus pilosus	4
Clanoptilus marginellus	1
Clythra quadripunctata	1
Coccinela septempunctata	13
Cryptocephalus sericeus	7
Cteniopus sulphureus	1
Harmonia axyridis	1
Julodia erratica	5
Larinus turbinatus	6
Leptura quadrifasciata	1
Mordellochroa abdominalis	3
Oedemera femorata	6
Oedemera virescens	8
Oxythyrea funesta	18
Pseudovadonia livida	13
Rhagonycha fulva	22
Stenurella bifasciata	1
Strangalia attenuata	1
Tomoxia bucephala	7
Trichodes apiarius	9

Table S4 Results of GLMs assessing the effect of site and land-use characteristics on the species richness of studied taxa in grasslands in the city of Pardubice. The results are for the full models including all the independent variables.

Taxon	Variable	Estimate	SE	t	P
Plants	Intercept	5.93E+01	2.18E+02	0.27	0.787
	Perimeter	7.37E-03	4.21E+02	1.757	0.091
	Management intensity	-7.88E-01	2.99E+00	-0.26	0.794
	AgriEnvi	-4.43E+00	6.08E+00	-0.73	0.473
	Continuity	6.44E-02	3.18E+00	0.02	0.984
	Built-up areas_250	-1.20E-05	4.05E-05	-0.30	0.770
	Urban greenings_250	1.80E-04	6.39E-05	2.82	0.009
	Grasslands_250	2.95E-05	7.63E-05	0.39	0.702
	Forests_250	7.15E-06	9.80E-05	0.07	0.942
	Autocovariate	-5.11E+00	1.25E+02	-0.04	0.968
Butterflies	Intercept	1.74E+01	3.97E+00	4.37	< 0.001
	Perimeter	2.44E-03	1.03E-03	2.36	0.025
	Management intensity	-1.47E+00	6.75E-01	-2.18	0.037
	AgriEnvi	-2.63E-01	1.50E+00	-0.18	0.863
	Continuity	9.97E-02	6.66E-01	0.15	0.882
	Built-up areas_250	-8.98E-06	9.99E-06	-0.90	0.376
	Urban greenings_250	3.11E-05	1.48E-05	2.10	0.044
	Grasslands_250	-1.16E-05	1.86E-05	-0.62	0.539
	Forests_250	1.24E-05	2.64E-05	0.47	0.642
	Autocovariate	-5.34E-04	2.97E-04	-1.80	0.082
Beetles	Intercept	3.65E+00	2.18E+00	1.67	0.105
	Perimeter	1.34E-03	6.68E-04	2.00	0.054
	Management intensity	2.54E-01	4.44E-01	0.57	0.572
	AgriEnvi	-1.44E+00	9.51E-01	-1.51	0.141
	Continuity	3.86E-02	4.33E-01	0.09	0.930
	Built-up areas_250	-1.57E-05	6.54E-06	-2.41	0.022
	Urban greenings_250	1.01E-06	9.10E-06	0.11	0.913
	Grasslands_250	1.39E-06	1.22E-05	0.11	0.910
	Forests_250	1.43E-05	1.69E-05	0.84	0.405
	Autocovariate	-1.02E-04	4.69E-04	-0.22	0.829