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Tree species-rich open oak woodlands within scattered urban landscapes promote biodiversity

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ABSTRACT

It is becoming increasingly evident that cities are important places for biodiversity. Biodiverse urban forests are vital green areas within cities and have favorable impacts on the citizens, including their health. We focused on the effect of the urban forest environment on biodiversity in Prague, the capital of the Czech Republic. We used a multi-taxon approach with five taxa of different ecological demands: butterflies, bees and wasps, vascular plants, mosses, and lichens. We modeled their responses to the various urban forest attributes at four hierarchical levels – plot, permeability, forest, and landscape. Our results revealed that temporally continuous forests dominated by native oaks with open canopies, a high number of admixed and interspersed tree species and shrubs, together with scattered trees in the surrounding landscape, were optimal biodiverse forest environments. The most influential parameter that positively influenced bees and wasps, plants, and lichens at the plot level was canopy openness. We found that the permeability was suitable mainly on 20 m surroundings and increasing coverage of native oaks and tree species richness were the most important parameters. Continuity was the only found parameter that influenced mosses at the forest level. Scattered tree vegetation was the most important landscape parameter and positively drove the species richness of bees and wasps. Forest management methods can relatively easily solve the improvement of the scattered light gap structure within urban forests. Applying traditional forest management (pasture management, controlled burning and/or coppicing) is also an option but requires sensitive communication with the public. The canopy cover has been used as an indicator of urban forest health conditions, now indicating that artificial disturbances could be important issues for urban forest management and planning in the future. Therefore, active forest management is an essential method for biodiversity maintenance. We conclude that urban forests have a high potential for increasing native biodiversity. The response of the studied groups in urban forests was complementary. The resulting biodiverse stages of urban forests are akin to the established idea of the open temperate deciduous woodlands.

1. Introduction

Urban forests are some of the essential ecosystems in green city management. City forests represent an important ecosystem for enhancing the quality of the urban environment and have several ecological benefits for the citizens (Karafakı and Cetin, 2020). The functions and principles of urban forests are diverse (Jaszczak and Wajchman, 2015). They are important for building resilience (Huff et al., 2020), mitigating climate change (Gill et al., 2007), and improving ecosystem services (Escobedo et al., 2011) and biodiversity (Horák, 2018). Many concepts and approaches can be used in the management of urban ecosystems. Practices in urban forestry are diverse not only due to diversified ownership but also due to the stands' diversified species and age structure. Interdisciplinary knowledge

appears to be a key issue in the sustainable development of urban forests, including ecosystem services, green infrastructure, and nature-based solutions (Escobedo et al., 2019).

Modern urban forest management is designed to deliver a wide range of ecosystem services and to conserve biodiversity in cities (Lafortezza et al., 2013). One issue appears to be in the urban planning processes of city forests. Municipalities evaluate the function and structure of urban forest resources to enhance forest management and provide ecosystem services (Alonzo et al., 2016). A frequent question is which forests are appropriate to leave abandoned and which should be managed and how (Horák et al., 2012a). Several ecological opinions argue that it is vital to leave unmanaged forests in urban areas (Tyrväinen et al., 2003). Although abandonment often conflicts with a high density of citizens, it is also questionable whether it is suitable for managing biodiversity (Horák et al., 2016). Thus, active forest management is often required in the case of the commercial use of forests and urban forests. However, there are challenges in managing urban forests using traditional methods (Horák et al., 2012b). In addition to forest management, urban landscape planning is one of the possible tools for implementing these approaches. Urban planning is one of the crucial tools for forest biodiversity in general (Aronson et al., 2017). Thus, urban forests could play an essential role in global biodiversity conservation. Another point of view is that biodiversity in urban areas is often influenced by various socioeconomic and cultural influences (Aronson et al., 2017). Biodiverse environments are positively connected with the emotional well-being of people – there is a vital connection with public mental health (Nghiem et al., 2021).

By focusing on forest organisms, it is known that habitat variability responses are different between and within taxa (Mladenović et al., 2018). A significant factor for biodiversity is the stage in which the forest canopy is disturbed. For example, one study found that the richness and composition of most insect species were positively correlated with canopy openness (Horák et al., 2016). Another study found the opposite effect in areas with dense canopies, where insect dominance was represented by non-native species and pests (Anderson et al., 2021; Véle and Horák, 2018). Forest biodiversity is also influenced by tree species richness and understorey species composition (López-Marcos et al., 2021). Another factor in urban landscapes is forest fragmentation, which highly impacts species richness and abundance (Ye et al., 2021).

Nevertheless, further research on different taxa is vital for gaining necessary knowledge on biodiversity dynamics within forest ecosystems (Horák et al., 2019). Focusing on information on urban planning and forest management, it is also essential to study responses at different hierarchical levels. It can be predicted that more sedentary organisms will be more influenced at small spatial scales than mobile taxa. By focusing on bees, we can see that forest fragments are a critical conservation factor of exclusive forest bee communities (Landsman et al., 2019). A forest management approach that preserves aboveground deadwood can provide nest sites for wood-nesting bees (Urban-Mead et al., 2021). Sedentary organisms such as mosses and lichens have been used for monitoring urban biota under air pollution stress (Insarov and Insarova, 2013). An important fact in studying urban forest biodiversity is the interconnection of the studied taxa. An example is the dependency of insects on diversified nectar sources and plant diversity on pollination services.

In this study, we aimed to determine the effect of the urban forest environment on biodiversity. We used a multi-taxon approach with the species richness of five taxa (butterflies, bees and wasps, vascular plants, mosses, and lichens). We focused on their relationship with the environment at four hierarchical levels (plot, permeability, forest and landscape). We predicted that the response would differ among taxa with their different sensitivity to studied environmental levels of selected variables. Namely, we predicted that taxa with lower dispersal ability would be more sensitive to small-scale levels conversely. We were also interested if the responses would be contrasting or complementary, which enable us for biodiversity management

recommendations.

2. Methods

2.1. Study area

We studied forests in Prague (area of 496 km^2 and population of 1.31 million people) in the Czech Republic. Prague's forests cover more than 10% of the city area (Lesy, 2020). The mean altitude is 235 m a.s.l. The city has a temperate oceanic climate (relatively warm summers and chilly winters) with an average temperature of 9.8 °C and rainfall of 500–550 mm. The forests are mainly located in the outer parts of the city area, with several wooded areas in less accessible places in the center (Fig. S1). All forests are managed in the Czech forest law category called special-purpose forests (namely, urban or recreational forests). The cover of Prague's forests has increased by more than 30% during the last 100 years (Hlavní město Praha, 2013). Prague's forests are dominated by native oaks (Pedunculate and Sessile), and deciduous trees are represented in 75% (Lesy, 2020). Prague forests are the largest area of urban forests in the Czech Republic. Their location is not spatially clustered, with many forest islands within the most urbanized landscape in the Czech Republic.

We selected ten large forests (Bohnice, Hostivař, Chuchle, Kunratice, Petřín, Přední Kopanina, Satalice, Xaverov, Cibulka and Ďáblice; Fig. S1). Their selection was based on their scattered distribution within the city, corresponding with the actual state of forests and sufficient area. We used equal-stratified sampling (Hirzel and Guisan, 2002) with 10 study plots in each forest. All study plots were selected in 2019 based on Prague's Forest Management Plans and placed only in mature forest stands – i.e., randomly stratified selection with a distance limit – at least 50 m apart and from the forest's edge (mean = 434.9 m ± 12.9 SE). We used this distance limit due to no overlap between and among plots, no contact with the forest edge, and no contact with stands where the plot was located (Loskotová and Horák, 2016). This design resulted in 100 studied plots in 2020.

2.2. Study taxa and sampling

We studied five different taxa: (i) butterflies, (ii) bees and wasps, (iii) vascular plants, (iv) lichens, and (v) mosses.

We recorded all studied plot centers in the field with the Garafa GIS-Pro application (Garafa, LLC, version 3.21.1). The studied plots were then established as circular plots with 10 m diameters.

Butterflies (namely, diurnal) were counted during time-limited survey walks from mid-May to mid-August. During each survey, the observer spent 15 min of slow walking at each study plot (see 2.3.) and counted every butterfly that took off or arrived within the plot. For species identification, we used visual observations, with occasional catches by aerial insect nets for species difficult to identify. We identified the majority of individuals in the field. Individuals who could not be recognized in the field were stored in waxed bags and identified later in the laboratory. Each site was visited five times between 9:30 and 16:30 CEST under suitable weather conditions (Horák et al., 2021).

Bees and wasps (Aculeata Hymenoptera except for Formicidae) were studied using flight-interception traps. We installed each trap in the center of the studied plot. We used crossed panel traps consisting of three transparent plastic panels (trap height 50 cm and width 40 cm) with a protective brown-red top cover 45 cm in diameter. At the bottom of the trap, the funnel was led down into a container with saturated brine containing several drops of detergent to reduce the surface tension. This solution fully preserved captured invertebrates but did not attract them (e.g., Horák et al., 2014). Traps were installed in mid-May and deactivated in mid-August. We checked the traps every two weeks, collected the brine with the sample material, and replenished containers with new brine. We then stored collected samples in a cooler (−15 °C). After this, we sorted the collected insects, put them in a solution

containing 96% ethanol and 8% vinegar (1:1), and placed them in a refrigerator (5 °C). This solution cleaned individuals from salt and left them in perfect condition for identification. All individuals were then identified to the species level in the laboratory.

All butterflies, and bees and wasps records were imported into the Excel (Microsoft) application database. We categorized the threatened species according to Hejda et al. (2017).

Vascular plants (plants thereinafter), mosses, and lichens were surveyed with a time-limited survey (15 min per visit; Horák et al., 2022) in each study plot (see 2.3.). We recorded plants three times during the vegetation season (late spring, summer, and early autumn). We identified species in the field and some in the laboratory using an Arsenal SZP 1102-T ZOOM stereomicroscope. The nomenclature was unified according to Kaplan et al. (2019). Categorization of the threatened species was according to Grulich (2017).

Mosses were observed on all available substrates (soil, stones, dead wood, and tree trunks). We identified all species by observation at the sites, while some species were identified in the laboratory using an Olympus CX 31 microscope. The nomenclature of bryophytes was unified according to the work of Kučera and Váňa (2005). We categorized them again according to Grulich (2017).

We also studied lichens on all available substrates (trees, rocks, dead wood, and humus). Lichens were identified at the species level. Some species were then identified using observations and measurements of thallus and apothecium anatomy, asci and ascospores were made on hand-cut sections mounted in water and diluted with KOH (K) and were observed on an Olympus BX41 DIC microscope. Thin-layer chromatography (TLC) was carried out according to Orange et al. (2001). The nomenclature of the lichens was unified according to the work of Liška and Palice (2010).

Plants, mosses, and lichens were recorded with numbers (Apple) application in the field and then imported to the MySQL (Oracle Corporation) database table.

2.3. Study environmental variables

2.3.1. Plot level

We studied the plot level (inner forest) independent variables that were potentially the most important to our chosen taxa of study. We used circular study plots (Horák et al., 2014). Therefore, we measured plot level variables in a 10 m radius (Table S1).

We took Canopy openness under the full foliage under similar weather conditions in the middle of summer. We used fisheye (180°) photographs taken from the center of a particular plot. We evaluated all photographs using Gap Light Analyser 2.0 as a percentage of the open sky. Canopy openness reflected the microclimatic and light conditions of the study site for all studied taxa.

All types of dead wood except for twigs and dead crown branches (diameter under 7 cm) were estimated in cubic meters. We did the estimation based on a comparison with a measured real 1 m^3 tree. The amount of dead wood represented important microhabitats and nutrient sources in the study site for taxa with saproxylic species (i.e., except butterflies).

We counted all stumps with the presence of bark (approximately five years old). We analyzed them as specific microhabitats for mosses and lichens. The stump number also reflected the actual management intensity, which could not be found in the management plans.

We estimated native oak (*Quercus*) coverage in the canopy as a percentage. It was used as a reflection of native vegetation for non-insect taxa.

We counted the number of large trees (i.e., with DBH > 50 cm) and considered this a reflection of the potential veteran tree conditions for non-insect taxa.

We used the number and coverage of herbs as two independent variables for insect taxa. We used the species data mentioned above for the number of herbs. Coverage was estimated in the understorey. The number and coverage of herbs indicate potential food sources.

We also measured the conditions in the understorey with a focus on the total coverage of shrubs and used it as an index for the potential food source availability for herbivores.

2.3.2. Permeability level

We used two different spatial scales extending from the circular plots to reflect best the permeability of the forest's surroundings influencing the studied taxa – i.e., 20 m and 40 m radii from the center of the studied plot (Table S1). The permeability reflected the influence of the closer surrounding of the study plots and its suitability for studied taxa (e.g., Zasadil et al., 2020). We analyzed six independent variables that describe the forest environment, namely, five similar to the plot level: dead wood, native oak coverage, number of large trees, number of stumps, and coverage of shrubs.

The number of tree species was added. This independent variable reflected the fact that diverse tree species support different numbers of studied taxa species.

2.3.3. Forest level

The conditions of each of the ten studied forests were reflected by two independent variables (Table S1). We studied the spatial-temporal continuity of the studied forests as an important parameter for the establishment of forest communities. We described this variable by the year of planting for each forest. The oldest aerial maps were from 1938, so we used this value as the first threshold. Forest cover on maps from 1938 until the present was categorized as continuous (N = 7). We categorized forests not presented on the 1938 maps (N = 3) with no continuity.

The second variable was the total area of permanent non-forest land inside the studied forests. This variable reflects the fragmentation of the forest. We calculated the area in QGIS 3.10.7 from vectorized actual aerial maps of Prague (see Landscape level).

2.3.4. Landscape level

We analyzed the landscape-level variables that described landscape composition in three radii of 100, 250, and 500 m from the studied forest (Table S1). We calculated land uses in QGIS from actual aerial maps. Vectorization of their area was based on Corine Land Cover classes (Kosztra et al., 2017) under a map scale of 1:1500. As landscape requirements may differ among the studied taxa, we used six landscape types in our study: (1) agriculture; (2) grasslands; (3) urban fabric (combined continuous and discontinuous fabric with industrial and commercial units); (4) forests; (5) water surfaces (combined both water bodies and courses) and (6) scattered trees (combined orchards, shrublands, and green urban areas).

2.4. Statistical analyses

We performed statistical analyses in R 4.1.2.

Dependent variables were tested for the effect of spatial autocorrelation using Geary's C with package spdep (Bivand and Wong, 2018). We found a statistically significant effect of spatial autocorrelation for butterflies (C = 0.84; P = 0.014), plants (C = 0.75; P < 0.001), mosses (C = 0.68; P < 0.001), and lichens (C = 0.57; P < 0.001). Bees and wasps were not significantly influenced (C = 1.04; P = 0.70). As butterflies, plants, mosses, and lichens species richness was not spatially independent, we used autocovariates of the dependent variable for further analyses with the plot level as the control as recommended (Dormann et al., 2007).

We tested independent variables for multicollinearity with the package HH (Heiberger, 2020). We set the criterion for the effect of multicollinearity on a variance inflation factor (VIF) equal to or higher than 2. These independent variables (agriculture and grassland at the landscape level) were excluded from the final analyses.

Plot parameters were analyzed using generalized linear mixed

models (GLMM) with the package MASS (Venables and Ripley, 2002). The locality was used as a random factor.

Permeability parameters were analyzed using GLMM with the package glmmTMB (Brooks et al., 2017). The locality was used as a random factor. We used two radii – 20 and 40 m – to select the optimal ambient permeability. The best radius was then selected based on the AIC for the final GLMM. Only the results of the final GLMM at the radius with a lower AIC were visualized and discussed.

Forest parameters were analyzed using GLMM with the package MASS. The forest fragment area was used as a random factor.

Landscape parameters were analyzed using generalized linear models (GLM). The best radius at the landscape level was selected based on the Akaike information criterion (AIC). We computed the final GLM at the radius with the lowest AIC.

The percentage of independently explained variance of all parameters in GLM and GLMM (including random factor) was computed by hierarchical partitioning with the package hier.part (Walsh and Nally, 2020). We used the root-mean-square prediction error as the goodness-of-fit measure and logistic link function.

We tested all significant independent variables for potential thresholds (for each hierarchical level separately). We calculated threshold values (i.e., division of values of the variable into significantly different categories for the dependent variable) using the package party with conditional inference tree methods (Hothorn et al., 2006).

3. Results

We observed 23 species of butterflies (Table S2), 92 species of bees and wasps (TablexS3), 317 vascular plants (Table S4), 33 mosses (Table S5), and 70 lichens (Table S6).

3.1. Response to the plot parameters

Butterflies were significantly positively influenced by the species richness of plants, while other variables did not have a significant effect. Canopy openness had a significant positive effect on bees and wasps, and plants. Other studied variables did not have a significant influence. Plot level variables did not significantly influence mosses. Lichens were significantly positively influenced by canopy openness and spatially autocorrelated – i.e., clustered (Fig. 1).

We found that 40% of herb cover was a significant (Statistic = 33.43; P < 0.001) threshold value for the species richness of butterflies. The mean number of species equal and under this value was 2.1 and above was 4.5. Bees and wasps, plants, and lichens had a significant threshold of canopy openness. Bees and wasps were species richer (mean = 7.4) above 10.79% (Statistic = 23.73; P < 0.001) than under (4.2). Plant species richness was higher (33.4) above 11.37% (Statistic = 12.43; P < 0.01) than under (25.5). The same was for lichens (Statistic = 5.95; P < 0.05), where species richer plots (17.1) were above 9.81% of canopy openness, and a lower number (14.5) was under the threshold.

3.2. Effect of forest permeability

We found that the AIC-based selection resulted in the choice of a lower (i.e., 20 m) radius for the forest environment in most of the taxa. Plants were the only taxa that responded better at 40 m (Table 1). Four of the five taxa revealed a shift of ΔAIC > 2, which indicated that the models received substantial support and were considered when making inferences (Burnham and Anderson, 2002).

Butterflies, bees and wasps, and plants were significantly positively influenced by the increasing percentage of oaks in the tree species composition. The increasing number of tree species positively affected bees and wasps, plants, and lichens. Butterflies and plants were positively influenced by increasing shrub cover. Amount of the large trees had the opposite effect on butterflies. The rest of the variables had an insignificant effect. Mosses did not show any response to forest

Table 1

Results on the forest permeability effect for 20 and 40 m radii on the studied taxa in Prague forests, Czech Republic.

Taxon	Radius (m)	AIC
Butterflies	20	380.1
	40	387.2
Bees and wasps	20	213.9
	40	219.4
Vascular plants	20	83.1
	40	79.5
Mosses	20	904.3
	40	904.4
Lichens	20	1226.6
	40	1233.2
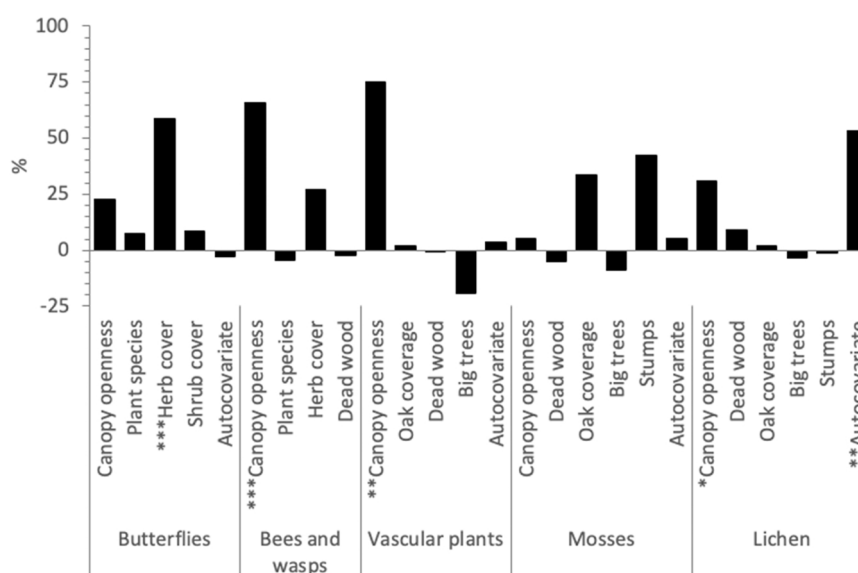
Fig. 1. Response of taxa to the plot parameters in Prague forests, Czech Republic. Significant responses are highlighted by asterisks close to the independent variable name (* for P < 0.05; ** P < 0.01; *** P < 0.001). The values are the percentage of variance explained independently by the variable. Note that estimates are visualized only as positive or negative values.

permeability (Fig. 2).

We found that 15% of shrub cover was a significant (Statistic = 8.32; $P < 0.05$) threshold value for the species richness of butterflies. The mean number of species equal and under this value was 2.4 and above was 3.9.

3.3. Effect of forest parameters

Continuity was a more influential factor than the inner open area. Only bees and wasps were more influenced by open areas than by continuity. Mosses responded significantly to the continuity of the forests (Table S7). We found that their species richness was higher in forests with spatiotemporal continuity. All other taxa were not influenced at the forest level (Fig. 3).

3.4. Landscape effect

Most taxa responded more to the surrounding landscape at the lowest distance. Only lichens responded strongest at a middle distance of 250 m (Table S8).

Bees and wasps, and vascular plants were the most responsive to the scattered tree vegetation in the surrounding landscape. Mosses and lichens were the most affected by the water surfaces in the surrounding landscape, which was also partly important for butterflies. Butterflies were the group most responsive to urban areas. Other forests were marginally important land uses in the surrounding areas (Fig. 4).

Only bees and wasps revealed a statistically significant response to the scattered trees, which was positive. Other variables did not have an effect (Table S9).

4. Discussion

Focusing on the individual taxon response, we found that the cover of herbs at the plot level influenced butterflies. They also profited from oak abundance in the canopy. This result coincides with past studies (Konvicka et al., 2008; Han et al., 2022). Only the profit from the shrub-cover over 15% of the understorey is partly against the published agenda (Berg et al., 2011; Hanula and Horn, 2011). Nevertheless, the maximum shrub cover exceeded only occasionally 50% in our case. Bees and wasps responded positively to the open canopies at over 11%, nearly

similar to plants and lichens, with a threshold close to 10%. All taxa are known to benefit from light penetration to the understorey (Horák et al., 2014; Lanta et al., 2019). Bees and wasps also preferred species-rich oak forests in the nearest surroundings, which is known from other studies (Penado et al., 2022). This knowledge also goes hand in hand with profit from scattered-tree vegetation in the surrounding landscape. The response of bees and wasps was highly similar to vascular plants, which indicates their high community interconnection (Bogusch et al., 2020). Mosses were the only taxa responding to the forest continuity, which confirmed the general information from old-growth forests (e.g., Ohlson et al., 1997). Except for the abovementioned responses, lichens indicated the clustering in their biodiversity and profit from species-rich woodlands (Marini et al., 2011).

The result from the hierarchical perspective was that the openness of the canopy was the most crucial factor at the plot level. The variable indicates that most taxa depend on sufficient light penetrating the forest canopy. The added light led to better microclimatic conditions, mainly in the form of more suitable plot temperatures (Horák et al., 2016). The nearest surrounding forest environment influenced most taxa. The maintenance of tree species-rich and shrub-abundant natural vegetation was essential. This result means that oak-dominated forests with open canopies, a high number of admixed and interspersed trees and shrub density are optimal for forest biodiversity (López-Marcos et al., 2020). As mentioned above, temporal continuity was an important factor for mosses that were not sensitive to other inner forest parameters. This fact indicates that these long-lived organisms are the most sensitive group to forest fragmentation, even in urban environments (Wierzcholska et al., 2020). The response to the surrounding scattered tree vegetation goes hand in hand with the results at the inner forest level, as this indicates that open-canopy tree vegetation is more suitable for urban forest biodiversity (Horák et al., 2014).

4.1. Plot level response

Canopy openness was the most influential parameter of the inner forest structure. The open canopies positively influenced three taxa, mainly exceeding 10%. A positive effect reflected microclimatic plot conditions on these taxa, which was indicated in recent studies (Horák et al., 2014; Lanta et al., 2019). Nevertheless, this effect on biodiversity has not been extensively studied in urban forests, as canopy cover is still
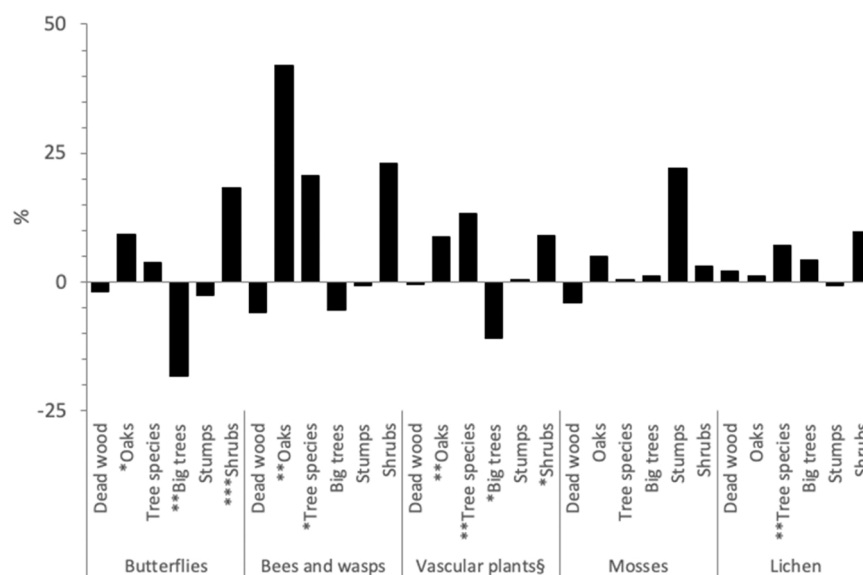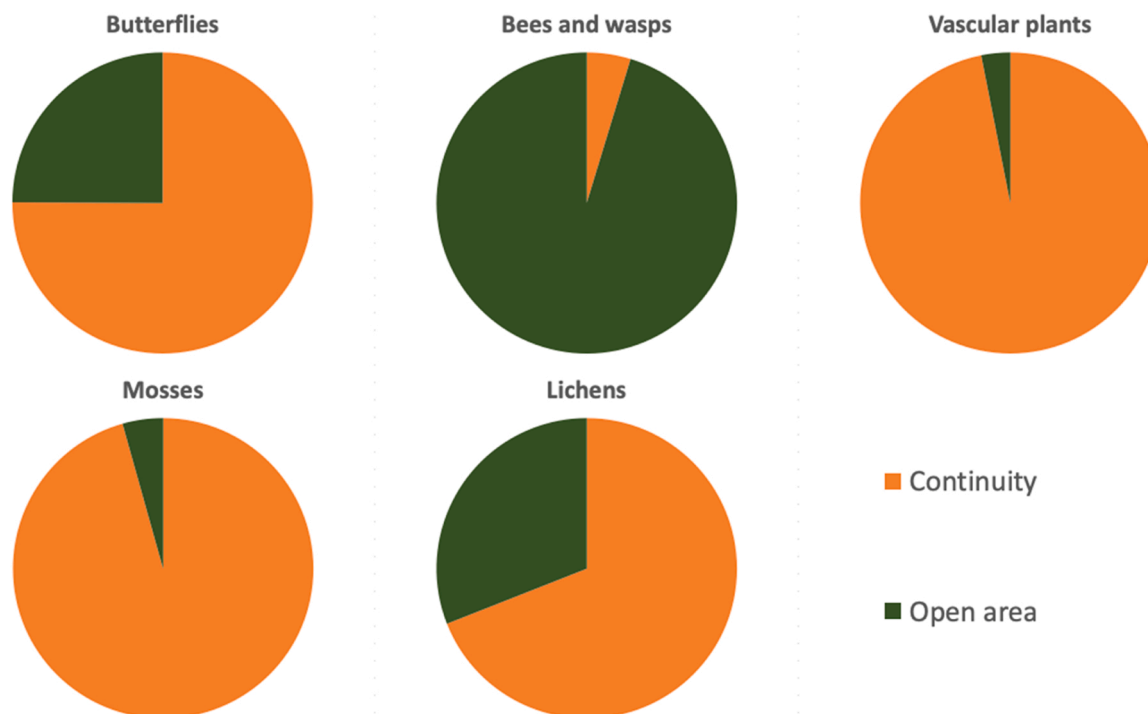

Fig. 2. Response of taxa to the forest permeability surrounding the plots in Prague forests, Czech Republic. Significant responses are highlighted by asterisks close to the independent variable name (* for $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The values are the percentage of variance explained independently by the variable. Note that estimates are visualized as positive or negative values; § vascular plants were analyzed at 40 m.

Fig. 3. Response of taxa to the forest parameters in Prague forests, Czech Republic. The pies are the percentage values of variance explained independently by the variable.
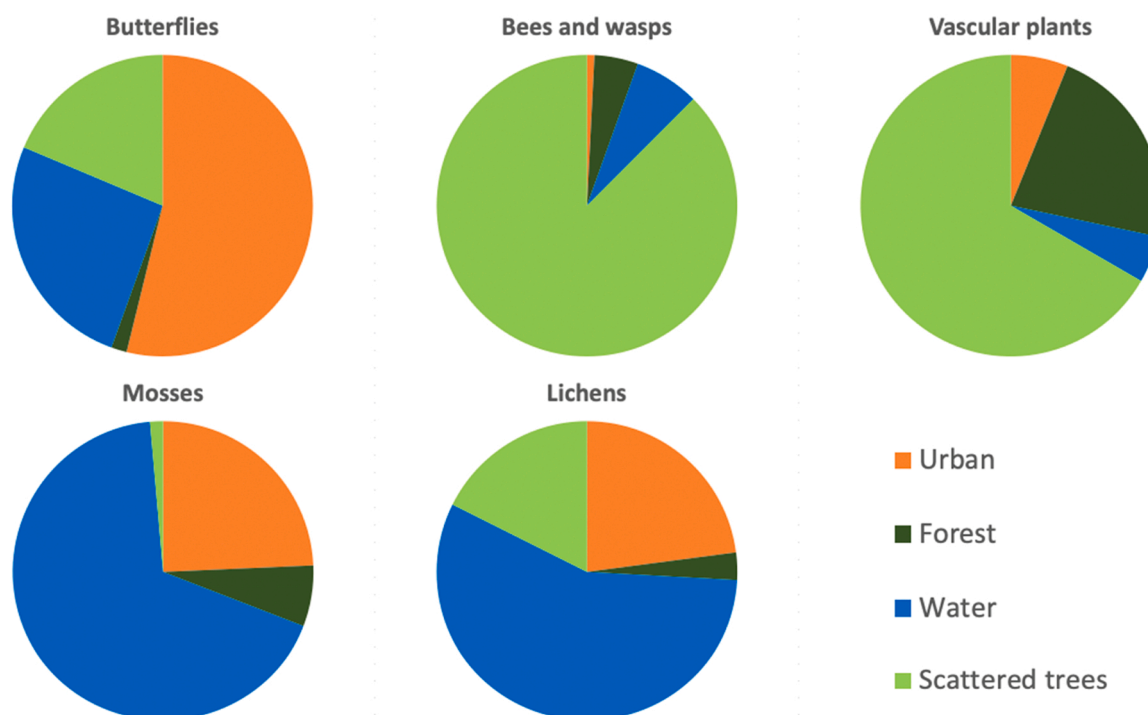
Fig. 4. Response of taxa to the landscape effect in Prague forests, Czech Republic. The pies are the percentage values of variance explained independently by the variable.

used to indicate how well the urban forest is doing (Ordóñez and Duinker, 2012). However, our thresholds indicate that relatively low canopy disturbance could lead to a significant increase in biodiversity. The disturbance in canopies by many abiotic (e.g., drought or wind) and biotic (e.g., insect outbreak or timber harvesting) factors can thus be regarded not only as indicators of poor urban forest conditions (e.g.,

caused by air pollution or pathogens) but also an as important measure for biodiversity. The conclusion of our results in the case of canopy conditions is that the disturbance of the canopy appears to be the most crucial forest management issue in lowland urban forests for promoting biodiversity. Nevertheless, whether it is more critical to protect undisturbed urban forests or promote their biodiversity will always depend on

urban landscape planners.

Other important parameters for biodiversity were herb species richness for butterflies and spatial autocorrelation for lichens. The effect of herb richness is not surprising if we focus on butterflies in general. Their interconnection is well known as herbs are a necessary part of the butterfly's most important habitat type in temperate climates – grasslands (e.g., Franzén and Nilsson, 2008). Therefore, our result would shift the knowledge that the diversity of herbs is also crucial for this herbivorous functional group in urban forests, which was indicated from thermophilic oak forests (Benes et al., 2006).

The response of lichens to autocovariate means that lichens were spatially structured (i.e., autocorrelated) in forest plots. The positive effect reflected that the spatial pattern of lichen species richness was aggregated (de Frutos et al., 2007). Lichen spatial aggregation is well known for individual species (Hedenås et al., 2003) or grasslands (Löbel et al., 2006), but we can see that it also occurs in temperate urban forests. This result, unfortunately, could not be easily explained by the interconnection with some other forest parameters, e.g., clustering of lichen species in light gaps. The reason is that we excluded all collinear variables, and canopy openness was not correlated with the autocovariate of lichen species richness. Therefore, the reason for the clustering of lichen species to particular plots was most likely influenced by other parameters that were more or less studied at higher hierarchical levels, e.g., tree species richness, air humidity, or human intervention.

4.2. Forest permeability and its inner structure

Native oaks, the decisive species in the studied forests, positively affected insects and plants. Oak woodlands were indicated as the dominant potential tree vegetation in our study area (Neuhäuslová et al., 2001). It reflects that the biodiversity of forests highly influenced by humans with maintained native vegetation can host high biodiversity (Horák et al., 2019). This fact is also known for more mobile taxa as woodpecker birds (Vélová et al., 2021). It is even more critical as the research was done in highly urbanized city forests with extremely long temporal human influence on vegetation (e.g., Sklenář, 2005). Therefore, it is questionable whether the high diversity in native vegetation patches was the natural origin or if it resulted from historical human interventions (Whitehouse and Kirleis, 2014).

The dominance of oak is partly in contradiction with the positive influence of the tree species richness in the overstory on bees, plants, and lichens. This result is not surprising from the point of view of the mentioned taxa, as bees (Hausmann et al., 2016) and lichens (Halda et al., 2020) exploit many tree species due to their natural demands (e.g., pollination and epiphytic strategies). Plant species richness is naturally highly interconnected with the diversity of canopy strata. Native oak vegetation is known to be rich in tree species (Mölder et al., 2019). Nevertheless, our multicollinearity test eliminated the apparent contradiction of the species richness of trees with the dominance of oaks. It is, therefore, important to see that tree species richness within a forest patch (smaller for lichens, and bees and wasps or larger for plants) is a supplementary management possibility for native oak vegetation. From the other point of view, more mobile taxa (e.g., birds) can be less responsive to inner forest parameters (Tryjanowski et al., 2017; Zasadil et al., 2020).

Shrub coverage was also important for biodiversity. Shrubs are often more abundant in less intensively managed forests than in plantations. This knowledge goes hand in hand with previous results. Their importance is also known for other taxa, such as birds (Hanberry and Thompson, 2019).

The only observed negative effect was the influence of large trees on butterflies. This effect might be related to the forest successional stages preferred by this taxon (Fartmann et al., 2013). Their positive association with cover of shrubs partly proves this.

Most taxa revealed that their response was better at the smaller permeability level. This result means that forests were much less permeable to butterflies, bees, mosses, and lichens. This was not surprising for lichens and mosses, as they are generally more sedentary taxa than insects. This response was indicated from similar forest habitats for other insects, such as click beetles (Loskotová and Horák, 2016). Nevertheless, the case of butterflies is somewhat unexpected, as their association with strict forests is much lower than in the case of many bees (e.g., Bogusch and Horák, 2018). One of the possible reasons was that the urban environment partly changed the general preferences known from the seminatural and natural habitats (Horák, 2016).

We found that the response to the temporal continuity and inner spatial discontinuity of biodiversity was relatively low. Only mosses responded to forest continuity. Nevertheless, this appears to be important information regarding the management of forests. Thus, it is essential to maintain forest vegetation cover even in urban areas due to moss species diversity, which is a necessary but neglected part of biodiversity (e.g., Pharo and Blanks, 2000).

4.3. Importance of surrounding land uses

The response of the studied taxa to the surrounding landscape was mainly at the lowest distance from the forest edge. This result was relatively surprising, as insects with potentially higher dispersal had the same response as much less dispersed plants and mosses. The most likely reason was the different response in urban landscapes compared to natural and seminatural habitats (Horák, 2016). Another possibility is that a more robust response to land use might be expected for more mobile taxa such as birds or bats (Jackson and Fahrig, 2012). The insect is also sometimes unwilling to disperse. Their movement is often related to weather factors (e.g., Horák et al., 2021). Lichens were, unexpectedly, the taxon that revealed the response to the higher radius. The possible reason was that they responded to the area of water surfaces and scattered trees that had much less total area than the other land uses. Nevertheless, this is still in contrast with the response of mosses that also preferred moist areas. Therefore, the answer to this unexpected lichens' response might be their relationship with urban areas (Gerdol et al., 2014).

Finally, we found three groups of taxa regarding their response to land uses. As mentioned above, mosses and lichens were the most influenced by the water surfaces, which reflects their known demands for high humidity. Bees and wasps, and vascular plants were the most influenced by scattered tree vegetation. This influence indicated that this type of vegetation, which prevailed in the past in the majority of Europe (Vera, 2000; Whitehouse, 2006) – due to abiotic disturbances (fire or wind) and the activity of large herbivores complemented by insect outbreaks and human interventions (fire and pasture) (Whitehouse and Kirleis, 2014) – is still essential for the temperate biodiversity of plants and wild pollinators. The response of butterflies to urban areas is questionable. Even though it was not statistically significant, its prevailing effect indicates that the fauna of butterflies that can live in forests prefer, for some reason, landscapes that are covered by built-up surfaces. Nevertheless, some cities are known to host species-rich butterfly fauna (Kadlec et al., 2008; Ramírez-Restrepo and MacGregor-Fors, 2017).

4.4. Urban forests and threatened species

The studied forests were habitats of many red-listed species. The presence of some of them was relatively unexpected. If we focus on butterflies, we observed *Hipparchia semele*. This species prefers open areas (Beneš et al., 2002), and its presence in Prague forests was not accidental and highlighted the need for disturbances in canopies.

The fauna of bees and wasps mainly consisted of threatened xeric specialists (Bogusch, 2007). The rare and threatened species that indicated forest-steppe-like habitats were *Allodynerus rossii* and *Ancistrocerus antilope,* and some of them, such as *Andrena mehelyi,* are known only from non-forest habitats. Nevertheless, some species indicated forest

habitats. These species prefer cold climates and dead wood, such as *Ancistrocerus parietinus* and *Bombus norvegicus* (Bogusch and Horák, 2018).

The forest-steppe or non-forest fauna present in Prague forests was also confirmed by flora. We found the species *Filago arvensis* or *Carex michelii* (dependent on the sand and bare soil) or thermophilous *Geranium sanguineum, Asperula tinctoria,* or *Cuscuta lupuliformis*. Historically, the indicators of sparse canopies were also tree and shrub species such as *Sorbus torminalis, Viburnum lantana,* or *Rosa sherardii*. Nevertheless, the urban forest was also a habitat occupied by nonindigenous species such as *Juglans regia, Aesculus hippocastanum, Quercur rubra, Robinia pseudacacia,* or shrub *Symphoricarpos albus*.

The thermophilic stage of the studied forests was partly supported by the absence of threatened mosses, which were sometimes dominated by synanthropic species such as *Amblystegium serpens*. The important species were those that are dead wood dependent, such as *Tetraphis pellucida* or *Aulacomnium androgynum*. This phenomenon of the relatively common presence of dead wood-dependent organisms was also observed across the other taxa studied.

Lichens indicated the same pattern. The mixture of species dependent on open forests and the presence of dead wood specialists was even more conspicuous. We found *Bacidia rubella* and *Flavoparmelia caperata*, which are known from maintained deciduous forests, which is the same for saproxylic *Cladonia parasitica*. Open canopies promoted the presence of the rare *Usnea scabrata*, which appears to prefer a humid mountainous climate.

The conclusion is that most red-listed species in Prague's forests formed an exciting mixture of many species dependent on bare soil, xeric habitats, and open canopies, with others preferring maintained vegetation to some species typical for cold climatic conditions.

4.5. Urban temperate forest management issues

Several management implications were mentioned in the previous sections. In general, improving scattered open structures (i.e., light gaps) within urban forests can be relatively easily solved by actual forest management methods. Based on our results, the gap structure will be more critical than larger non-forest islands within forests. Even if citizens are much more sensitive to active forest management in cities than rural landscapes (Peckham et al., 2013), individual or small-group tree cuttings appear to be proper management. This amendment will improve light conditions within forests, and new regeneration will increase the number of tree species and help oak regeneration.

The application of traditional management methods (Horák et al., 2012a) that would improve the biodiverse forest environment in cities is also possible. Nevertheless, its application is mainly based on sensitive communication with the public and in the conditions of the Czech Republic, also with legislative exceptions from forestry law. This improvement includes the pasture of domestic animals, which can be in some way attractive to citizens. Prague municipality experience is that initiation of pasture at grassland close to forests in the form of a small Zoo and informative panels can help with the future application of forest pasture. Much more problematic will be other management possibilities, such as controlled burning or coppicing. Even if this will be complicated, possibilities such as live fires or offering parts of municipality forests for fuelwood self-production could be used. Nevertheless, such management amendments are essential for urban forest biodiversity.

5. Conclusions

Each taxon responded to a slightly different set of variables, even within different studied hierarchical levels of urban forests. However, our assumption of a differential response was only partially confirmed. In many cases, the response to a particular variable was even identical – for example, the positive relationship of bees and wasps, vascular plants, and lichens to canopy openness. In the case of the hymenopterans and

plants, their response suggested a known link between these taxa. This statement is also consistent with the fact that bees, for example, are essential pollinators of various plant species. Furthermore, the response to each variable was never reversed in the case of significant relationships.

We did not find clear evidence that more sedentary taxa (i.e., mosses or lichens) were more sensitive to the small-scale hierarchical levels than more dispersal (i.e., insects). Our assumption that sedentary organisms are more sensitive to more local factors was not confirmed. Thus, we found that the response of individual taxa either went hand-in-hand or was essentially complementary.

This knowledge is important for forest management. The most characteristic forest stage that can maintain urban biodiversity is an open canopy, tree species-rich, and shrub-abundant temporally continuous native oak vegetation supported by scattered trees in the surrounding landscape. This state is similar to the idea of a landscape mosaic of open temperate deciduous forests that existed before urbanization. We conclude that urban forests have a high potential for native biodiversity and that active forest management is one of the possible ways for their maintenance.

Supplementary data

Supplementary material related to this article can be found at: https://home.czu.cz/horakj/data-repository.

CRediT authorship contribution statement

Michal Andreas: Project administration, Investigation, Data curation, Funding acquisition, Writing – review & editing. **Romana Prausová:** Project administration, Investigation, Data curation, Funding acquisition, Writing – review & editing. **Tereza Brestovanská:** Investigation. **Lucie Hostinská**: Investigation. **Markéta Kalábová:** Investigation, Writing – review & editing. **Petr Bogusch:** Conceptualization, Methodology, Writing – review & editing. **Josef P. Halda**: Investigation, Data curation, Writing – review & editing. **Patrik Rada:** Visualisation, Formal analysis, Writing – review & editing. **Ladislav Štěrba:** Investigation, Data curation, Writing – review & editing. **Martin Čížek:** Conceptualization, Methodology. **Jakub Horák:** Project administration, Conceptualization, Supervision, Methodology, Formal analysis, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2023.127914.

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