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Urban fruit orchards: Biodiversity and management restoration effects in the context of land use

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ABSTRACT

Urban areas have increased greatly in recent decades, which has resulted in habitat loss. However, the promotion of urban green spaces could have a profound effect on biodiversity. Traditional fruit orchards are an important land-use type with the potential to host myriad organisms. Our goal was to determine the most important factors that influence orchard biodiversity in the million city of Prague (the capital of the Czech Republic). We used a multitaxon approach to evaluate the effect of orchard restoration in a landscape context. Restoration had a positive impact on species diversity, specifically, the diversity of orthopterans and butterflies. Moreover, landscape context determined the biodiversity of orthopterans, butterflies, and birds but not that of lichens. Our study underlines the importance of both the internal and external structures of traditional fruit orchards for species richness and composition. The results of our study support the restoration of traditional fruit orchards as a suitable management practice for promoting city biodiversity. Furthermore, orchard restoration can improve the attractiveness of suburban areas. Such areas often lack sufficient urban greening. Thus, restoration in these areas can also increase future recreational value.

1. Introduction

Traditional fruit orchards are an important land-use type for biodiversity (Myczko et al., 2013; Horák, 2014; Kajtoch, 2017). Orchards have the potential to host myriads of organisms, from large vertebrates with high dispersal ability to small, sedentary invertebrates (Horák et al., 2013; Varah et al., 2013; Kajtoch, 2017; Čejka et al., 2018). Orchards have recently become the most abundant type of agroforestry management practice in central Europe (Forejt and Syrbe, 2019). The biodiversity of orchards responds to multiple internal factors, such as the type of management (Steffan-Dewenter and Leschke, 2003; Čejka et al., 2018), habitat area (Steffan-Dewenter, 2003) and canopy openness (Martínez-Sastre et al., 2020). Described by these factors, the internal structure of orchards is comparable to that of forests with open canopies (Horák, 2014) or grasslands with scattered trees (Plieninger et al., 2015). Thus, orchards have the potential to serve as transitional habitats or stepping stones for many species (Steffan-Dewenter, 2003; Horák, 2014).

Nevertheless, traditional fruit orchards represent sporadic landscape habitats (Horák, 2014). Therefore, the surrounding landscape has high importance for many species (Steffan-Dewenter, 2003; Martínez-Sastre et al., 2020). The biodiversity of traditional fruit orchards is promoted by the presence of other orchards and seminatural woody habitats in surrounding areas (Horák et al., 2013; García et al., 2018). Traditional fruit orchards might serve as not only biodiversity reservoirs but also corridors connecting isolated patches of natural or seminatural habitats (Tewksbury et al., 2002; Simon et al., 2011; Horák et al., 2013).

The negative effects of fragmentation are particularly strong in urban areas (Di Giulio et al., 2009). In these areas, fragmentation often limits habitat connectivity (Tewksbury et al., 2002; Di Giulio et al., 2009). Moreover, suburbanization affects large areas due to ongoing city development (Ouředníček, 2003). As a result, biodiversity in these areas has become a topic of research interest and needs more attention (Capotorti et al., 2013; Güneralp and Seto, 2013). This topic is also important in terms of optimal management and landscape planning (Ahern, 2013). Organisms might react to changes in not only urban landscape composition but also the orchards themselves (Horák et al., 2018). Hence, the management of urban greening has become extremely important (Bertoncini et al., 2012).

Urban green areas, such as grasslands, might offer suitable habitats for species-rich plant communities (DeCandido et al., 2007; Bretzel et al., 2016). Hence, the management of urban grasslands is the key

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factor that affects their richness and composition (Bertoncini et al., 2012). Moreover, grasslands with high plant diversity support a higher diversity of fauna than those with low plant diversity (Klaus, 2013). Thus, the restoration of urban green areas might promote species diversity (Klaus, 2013; Fischer et al., 2013). Such a response was observed in a study of traditional fruit orchards (Horák et al., 2018).

The present research took place in the urban landscape area of Prague (Czech Republic), where traditional fruit orchards historically have been an important component of urban greening (Janeček et al., 2019). Historically, orchards were most abundant after World War II and have declined since then (Janeček et al., 2019). Management abandonment during the 1980 s and 1990 s led to their overgrowth by shrubs and forest trees (Horák and Trombik, 2016; Horák et al., 2018). However, since 2010, many orchards have been restored to their original form (Horák et al., 2018).

The main aims of this study were to identify drivers of orchard biodiversity and assess the effects of orchard management restoration. To this end, we used a multitaxon approach. We chose four taxa with different reactions to habitat disturbance, contrasting mobility and contrasting use of resources, which enabled us to assess a range of ecological and functional patterns (Aubin et al., 2013). The first taxon chosen was lichens as sedentary organisms with distinct relationships with woody plants, which are the dominant components of orchards. Lichens are often studied in relation to the surface on which they grow, and they illustrate changes in light conditions (Pezzi et al., 2020). Orthopterans and butterflies are common indicator insects of habitat quality and management and differ in dispersal ability (Marini et al., 2008; Varah et al., 2013). Birds represent organisms with high dispersal ability and are commonly used as indicators of habitat and landscape quality (Myczko et al., 2013).

We predicted that sedentary organisms (i.e., lichens) and insects with lower dispersal ability (i.e., orthopterans) would respond strongly to changes in internal structure (Horák et al., 2018). However, for organisms with higher dispersal probabilities, landscape context becomes more important. Thus, we predicted that organisms with medium and high levels of dispersal, represented by butterflies and birds, respectively, would be affected by landscape context.

2. Methods

2.1. Study area

We studied traditional fruit orchards in Prague, which is the capital city of the Czech Republic. This densely populated area (1.3 million citizens in 100 thousand houses) is located in a topographically diverse landscape with an altitudinal range of 177–399 m a.s.l. and a mean altitude of approximately 235 m a.s.l. The mean annual temperature in Prague is approximately 9 °C, and the mean annual precipitation is approximately 525 mm. The landscape surrounding this city is composed predominantly of agricultural land with nonirrigated fields (Geletic et al., 2017). The landscape mosaic comprises patches of mixed forest, grassland, built-up area and orchard (Geletic et al., 2017; Pazúr et al., 2017).

The Prague region contains more than ninety protected areas that provide a network of biodiversity hotspots (Kadlec et al., 2008). The urban and suburban areas of Prague contain more than one hundred publicly accessible traditional fruit orchards in one small location (Janeček et al., 2019). Orchards represent rural landscape artifacts that have been absorbed by suburbanization and are gradually disappearing due to land use change (Janeček et al., 2019).

We studied thirty of these traditional fruit orchards (Janeček et al., 2019). We chose 15 restored and 15 abandoned traditional fruit orchards distributed evenly across the Prague area (Fig. 1; Table S1).

Selected orchards with restored management were restored from

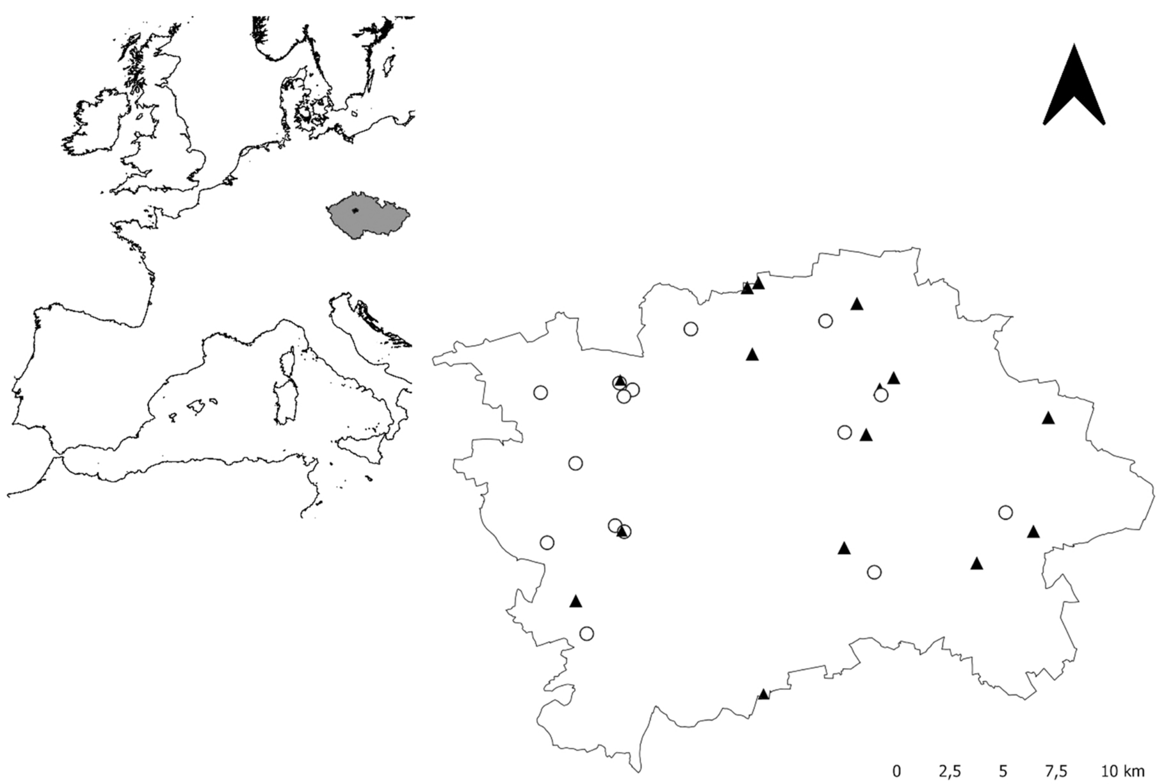

Fig. 1. Distribution of the studied traditional fruit orchards in Prague, Czech Republic. The cadastral area of Prague is shown in black in the context of Europe (white with black continental borders), and the Czech Republic (in gray) on the left side is enlarged on the right side, with the locations of the studied traditional fruit orchards shown. Orchards with restored management are indicated by white points. Abandoned orchards are indicated by black triangles.

2010 to 2018, when shrubs and young forest trees were felled. Fruit tree rows were replanted with new individuals if old trees had decayed and died. Nevertheless, decaying or dead tree trunks are often retained in orchards to support spatial diversity (Horák et al., 2018). Dead branches of fruit trees were cut and removed for public safety reasons. Orchard vegetation cover was partly or completely mowed or partially grazed. Every orchard was mowed at least once during the vegetation season. Mowed grass was removed in the form of hay. No other management practices, such as mulching or the application of chemicals or fertilizer, were used.

The abandoned orchards had not been managed in the last twenty years, and most were overgrown by shrubs or young forests. The majority of the fruit trees had been suppressed by undergrowth, and many were withered.

2.2. Study taxa and sampling

Four different taxa were chosen in our study based on their differing dispersal abilities and ecological requirements (Horák et al., 2018). Sampling was performed independently for each taxon in 2019 using standard sampling methods as described below.

Lichens, as representatives of sedentary organisms with high biodiversity potential, were sampled once at the beginning of August. Lichens that grew on tree bark up to a height of two meters for all trees present were sampled during a time-limited survey walk (15 min per orchard according to an equal stratified sampling method) (Hirzel and Guisan, 2002; Horák et al., 2018). All observed lichens were recorded to the species level based on Smith et al. (2009) and Wirth et al. (2013).

Orthoptera (identified based on Kočárek et al., 2013), representing insects with low dispersal (Horák et al., 2018), were sampled from the beginning of June to the end of August during sunny weather and temperatures between 22 °C and 30 °C to ensure sampling during peaks of both seasonal and daily activity (Weiss et al., 2013). A time-limited method (10 min per orchard) was used. Each orchard was visited once. The survey started in the center of the orchard and was expanded in a spiral, with all individuals and species recorded using visual and audio observations combined with those swept from vegetation. In total, 50 sweeps per orchard were performed with a sweeping net 40 centimeters in diameter.

Diurnal butterflies (clade Rhopalocera and family Zygaenidae, identified based on Macek et al., 2015; hereafter butterflies) were selected to represent organisms with medium dispersal. They were studied throughout the active season from the end of June to the beginning of September. We conducted time-limited surveys (15 min per orchard) during suitable weather conditions (Horák et al., 2021). Six surveys were performed per orchard. All species were recorded based on visual observation, with the exception of those whose identification was based on DNA sequencing or genital preparation (Friberg and Wiklund, 2009). These species were identified as different species sensu lato (i.e., *Leptidea* spp.).

Birds (identified based on Dungel and Hudec, 2001), selected as representatives of organisms with high dispersal, were sampled from the beginning of March to the beginning of June (the most appropriate time for the study region) during the morning hours and favorable weather—calm to mild wind and no rain (Conner and Dickson, 1980). We used a time-limited survey (15 min per orchard), which was repeated twice in each orchard. Birds were counted from the center of the orchard starting 5 min after we entered to allow them to settle. During each survey, both audio and direct observations of species and individuals were recorded, with the exception of birds flying overhead (Zasadil et al., 2020).

2.3. Study variables

Orchard management restoration was the key factor in our study. Thus, it represented our first study variable.

As a second variable, we chose perimeter (mean = 584.57 (meters); SE = 450.94) to describe the extent of the orchard. This measure was chosen instead of orchard area based on studies revealing that in urban areas, it describes plots better than area (e.g., Horák, 2016). Perimeters were calculated in QGIS 3.10.7. after vectorizing each orchard and its surrounding landscape features at a scale of 1:1500 from aerial photographs of Prague. Borders of orchards were adjusted during terrain surveys.

Canopy openness (mean = 51.13 (%); SE = 29.66) was chosen to describe internal orchard structure and was calculated from hemispherical photographs taken at the beginning of July 2019 under full foliage. Three photographs were taken for each orchard using a Cannon EOS 600D camera with a fisheye lens. The photographs were evaluated in Gap Light Analyzer 2.0 (Simon Fraser University and Cary Institute of Ecosystem Studies, 1999) to extract canopy openness. The mean value of canopy openness was used for each orchard.

Land-use variables were calculated in QGIS from the vectorized cadastral area of Prague. The whole area was vectorized at a scale of 1:1500 based on Corine Land Cover classes (Kosztra et al., 2017). Landscape composition was calculated at 15 spatial scales with radii between 100 and 1500 m around the study field (Fig. S1). As habitat requirements may differ among species, we calculated four major measures of landscape composition that might influence orchard biodiversity: (1) the percentage of the landscape consisting of forest, (2) the percentage of the landscape consisting of grassland, (3) the percentage of the landscape consisting of other orchards, and (4) the percentage of the landscape consisting of built-up area (Schmidt et al., 2008; Horák et al., 2013). These measures were chosen because forests, grasslands and orchards represent similar habitats for orchard biodiversity and built-up areas were important as this study took place in a city landscape.

2.4. Statistical analyses

Statistical analyses were performed in R 3.6.3. Our dependent variables were the species richness metrics of the studied taxa (lichens, orthopterans, butterflies and birds). In the first step, we used the Shapiro–Wilk test to test their normality. Lichen and bird species richness had normal distributions. Orthopteran species richness achieved a normal distribution after square root transformation. The distribution of butterfly species richness significantly differed from normality. Thus, we used the packages MASS (Venables and Ripley, 2002) and pscl (Jackman, 2017) to test for adherence to a Poisson distribution using the OdTest function. The distribution was significantly different from a Poisson distribution, and a negative binomial distribution was used to test for possible overdispersion. Theta was calculated using a fitted negative binomial generalized linear model (via the glm.nb function).

Sample completeness was calculated using the package iNEXT (Hsieh et al., 2020). We used the estimateD function and detected sample completeness independently for each studied taxon and management type (abandoned/restored).

The optimal spatial scale of landscape composition was tested separately for each dependent variable (taxon species richness). We used generalized linear models for every radius from 100 m to 1500 m (in increments of 100 m) or until the change in the Akaike information criterion (ΔAIC) exceeded 2 (which in all cases occurred before 1500 m was reached). Then, the radius (and its landscape composition) with the lowest AIC was chosen for the final analyses.

Generalized linear models were fit for each dependent variable and all of the independent variables, which included management (restored/abandoned), perimeter, canopy openness and land-use variables. The variance inflation factor (VIF) was calculated using the packages car (Fox and Weisberg, 2019) and carData (Fox et al., 2018). Canopy openness was excluded from the models based on a VIF> 2 (Graham, 2003). The results were visualized using the packages ggplot2 (Wickham, 2016) and visreg (Breheny and Burchett, 2017), which offer visualization of variable dependency on multiple independent variables.

Canonical correspondence analysis (CCA) was performed for each taxon (lichens, orthopterans, butterflies and birds) using the lattice (Sarkar, 2008), permute (Simpson, 2019) and vegan (Oksanen et al., 2019) packages to obtain interactions between each species of the selected taxa and the independent variables. This type of analysis was performed due to the matrix format of the data, which contained information about species presence/absence, so null values were involved. Hence, CCA was the most appropriate method (e.g., Legendre and Legendre, 1998). The analyses revealed the dependency of species composition on the independent variables. Where species composition was significantly dependent on the independent variables, individual p values were calculated (function anova.cca), and a significance test of each term was performed. The results were visualized with the ggplot2 (Wickham, 2016) and ggrepel (Slowikowski, 2019) packages where significant relationships were found.

In the case that CCA revealed a significant response of species composition to the independent variables, we calculated indicator species for abandoned and restored orchards. We used Dufrene-Legendre indicator species analysis to test for differences in the abundance and frequency distribution of species (Dufrêne and Legendre, 1997). We considered only species with at least 10 individuals in this analysis (Mupepele et al., 2014). Package labdsv was used (Roberts, 2019).

3. Results

In total, we recorded 40 species of lichens, 24 species of orthopterans, 39 species of butterflies and 43 species of birds. (For more details and species abundance data, please see Table S2).

Sample completeness in restored orchards and abandoned orchards was 98.7% and 99.10%, respectively, for lichens and 99.80% and 99.40%, respectively, for orthopterans. The sample completeness of butterflies was 99.60% in restored orchards and 99.50% in abandoned orchards. For birds, sample completeness was 97.10% in restored orchards and 94.70% in abandoned orchards. (For more details, please see Table S3).

3.1. Optimal spatial scale of landscape composition

We used AIC values to identify the most suitable radius for the landscape effect independently for each taxon. The most suitable radius for the landscape effect was 400 m for lichens, orthopterans and birds and 300 m for butterflies (Table S4).

3.2. Species responses to the orchard environment and landscape

Orthopteran species richness was significantly positively influenced by orchard restoration. Lichens, butterflies and birds did not exhibit a significant relationship with management practice (Table 1, Fig. 2).

Lichen species richness did not show a significant relationship with perimeter or any land-use variable (Table 1).

The species richness of orthopterans was negatively affected by the area of built-up surfaces within 400 m (Table 1, Fig. 3). Perimeter and other land-use variables did not have an effect (Table 1).

Butterfly species richness was positively affected by perimeter (Table 1, Fig. 3), which indicated that larger orchards support higher species diversity. Land-use variables had no effect (Table 1).

The species richness of birds was negatively affected by the area of grassland within 400 m (Table 1, Fig. 3). Perimeter and other land-use variables had no effect (Table 1).

3.3. Species composition

CCA did not reveal a significant response of the species composition of lichens (pseudo-F = 1.09; P = 0.251) or birds (pseudo-F = 1.04; P = 0.347) to any of the independent variables.

Orthopteran species composition was significantly influenced (pseudo-F = 1.55; P < 0.01) by aspects of the studied orchard environment, namely, restoration and the percentages of built-up area and grassland within a 400 m radius. The perimeter and areas of forest and orchards within a 400 m radius did not affect the species composition of orthopterans (Table 2).

The cumulative proportion of variation explained by the three axes was 74.63%. (For the proportion explained by each axis, please see Table S5.) Example findings include the following: *Oecanthus pellucens* (O_pel) preferred abandoned orchards, while *Platycleis albopunctata* (P_alb) benefited from restored orchards. *Bicolorana bicolor* (B_bic) was more likely to be present in orchards surrounded by grassland, and *Leptophyes punctatissima* (L_pun) preferred orchards surrounded by built-up area (Fig. 4).

Butterfly species composition significantly depended on the studied variables (pseudo-F = 1.28; P < 0.05). It was influenced significantly by orchard restoration and the area of other orchards within a 300 m radius. Perimeter and the remaining landscape variables (percentages of forest, grassland and built-up area) did not affect butterfly species composition (Table 2).

The cumulative proportion of variation explained by the three axes was 71.69%. (For the proportion explained by each axis, please see Table S5.) Among other findings, we found that *Pararge aegeria* (P_aeg) preferred abandoned orchards, while *Plebejus argus* (P_ar1) preferred orchards with active management, and orchards in the surrounding landscape were preferred by *Pontia daplidicae* (P_dap) (Fig. 5).

Table 1
Responses of the studied taxa to the orchard environment and landscape. Summary of all generalized linear models (GLMs) for the species richness of the selected taxa. Significant p values are in bold.

Dependent variable	Independent variables	Estimate	Std. error	t value	p value
Lichen species richness	Intercept	17.42	3.96	4.39	**< 0.001**
(McFadden's pseudo-R squared = 0.11)	Restoration	1.50	2.34	0.64	0.529
	Perimeter	0.00	0.00	0.73	0.476
	Built-up area	-4.61	6.06	-0.76	0.454
	Forest area	-8.49	6.14	-1.38	0.180
	Orchard area	30.57	49.53	0.62	0.543
	Grassland area	8.64	17.51	0.49	0.626
Orthopteran species richness	Intercept	2.84	0.46	6.15	**< 0.001**
(McFadden's pseudo-R squared = 0.56)	Restoration	0.85	0.27	3.11	**0.005**
	Perimeter	0.00	0.00	0.61	0.550
	Built-up area	-1.55	0.71	-2.19	**0.039**
	Forest area	1.28	0.72	1.79	0.087
	Orchard area	-11.50	5.77	-1.99	0.058
	Grassland area	-1.06	2.04	-0.52	0.608
Butterfly species richness	Intercept	1.92	0.47	4.10	**< 0.001**
(McFadden's pseudo-R squared = 0.39)	Restoration	0.48	0.26	1.84	0.079
	Perimeter	0.00	0.00	2.10	**0.047**
	Built-up area	0.04	0.69	0.05	0.958
	Forest area	1.16	0.62	1.88	0.072
	Orchard area	-3.62	3.62	-1.00	0.329
	Grassland area	-1.33	1.69	-0.79	0.439
Bird species richness	Intercept	8.77	0.98	8.92	**< 0.001**
(McFadden's pseudo-R squared = 0.35)	Restoration	0.76	0.52	1.45	0.159
	Perimeter	0.00	0.00	0.88	0.388
	Built-up area	0.84	1.29	0.65	0.523
	Forest area	1.50	1.60	0.94	0.360
	Orchard area	1.57	13.33	0.12	0.907
	Grassland area	-10.29	4.01	-2.57	**0.017**

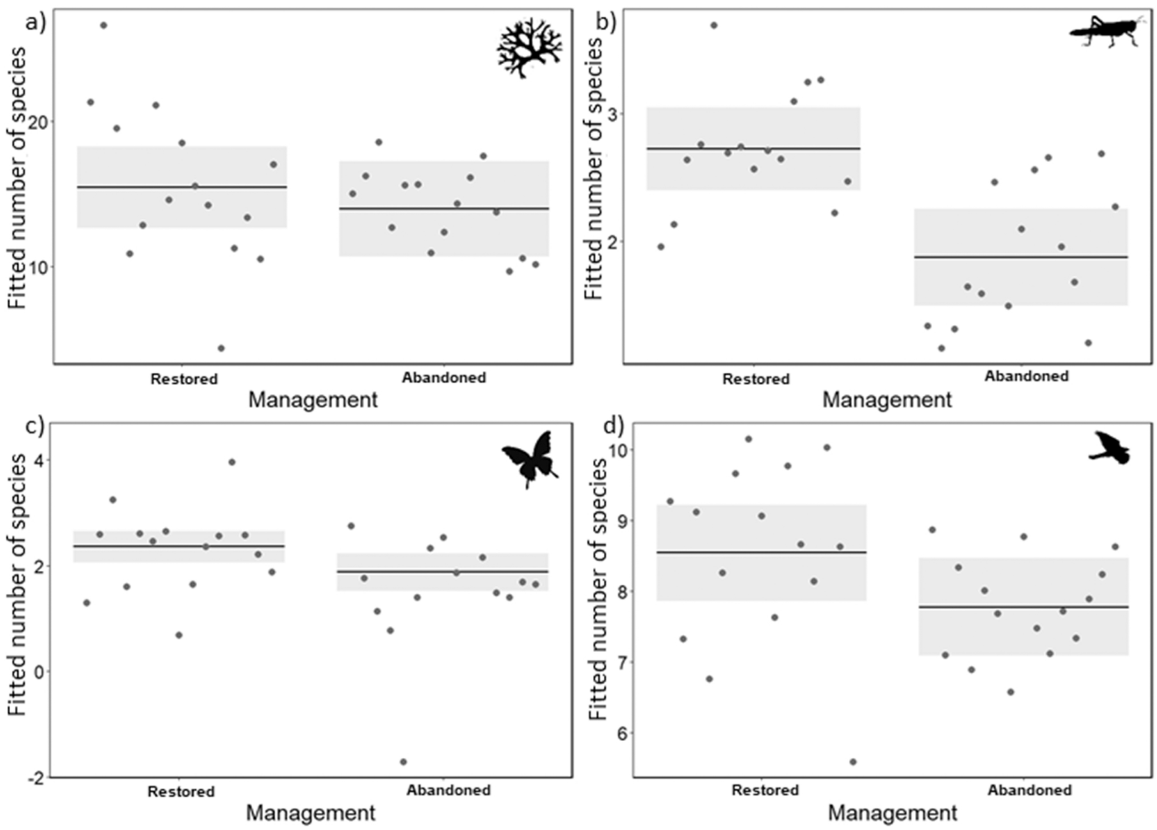

Fig. 2. Responses of the studied taxa to orchard restoration. The upper left panel (a) shows the response of lichens; upper right panel (b), that of orthopterans; lower left panel (c), that of butterflies; and lower right panel (d), that of birds. The black lines show mean values, the dark gray dots represent all observations, and the lightly shaded boxes show 95% confidence intervals.

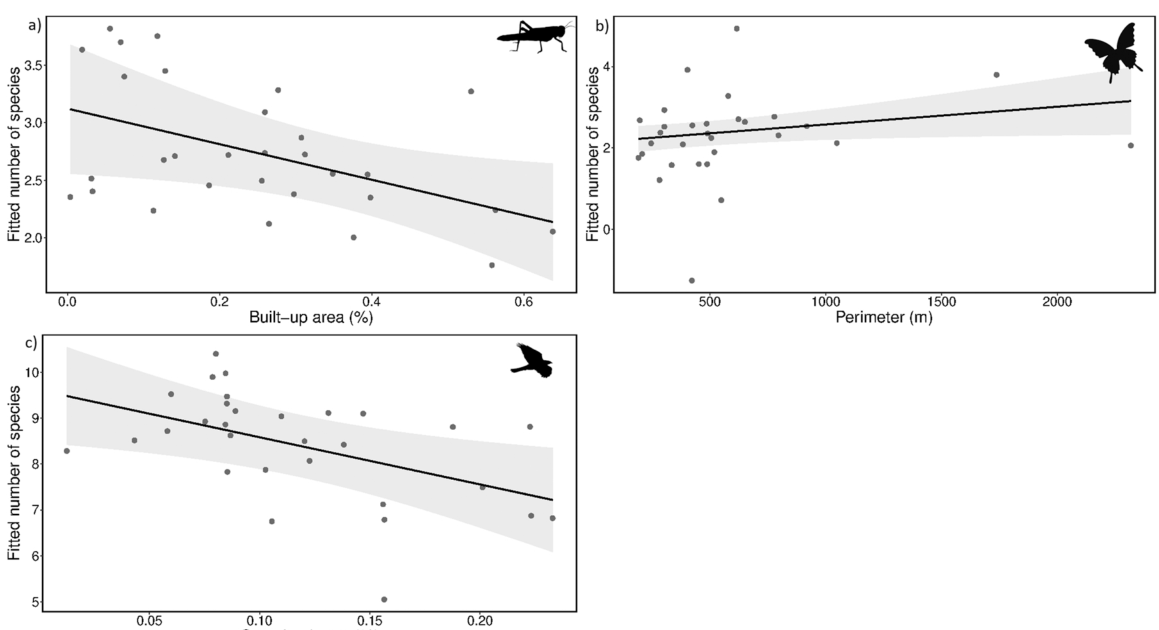

Fig. 3. Visualization of significant responses of the studied taxa to perimeter and land-use variables. The upper left panel (a) shows the response of orthopterans to the percentage of built-up area within 400 m; the upper right panel (b) shows the response of butterflies to perimeter; and the lower left panel (c) shows the response of birds to the percentage of grassland area within 400 m. The black lines show mean values, the dark gray dots represent all observations, and the lightly shaded areas show 95% confidence intervals.

Table 2
Summary of significant canonical correspondence analyses (CCAs). The dependent variable is shown in the left column, and the right columns show independent variables with their pseudo-F value and p value. Significant p values are in bold.

Dependent variable	Independent variables	pseudo-F	P value
Orthopteran species composition	Restoration	1.572	**0.044**
	Perimeter	0.555	0.911
	Built-up area	2.506	**0.001**
	Forest area	1.447	0.090
	Orchard area	1.417	0.093
	Grassland area	1.775	**0.014**
Butterfly species composition	Restoration	1.535	**0.027**
	Perimeter	1.168	0.298
	Built-up area	1.036	0.417
	Forest area	1.219	0.196
	Orchard area	1.526	**0.050**
	Grassland area	1.190	0.195

The Dufrene-Legendre indicator species analysis identified four orthopteran indicator species in restored orchards and no orthopteran indicator species in abandoned orchards (Table S6). The analysis also revealed four butterfly indicator species in restored orchards and one butterfly indicator species in abandoned orchards (Table S5).

4. Discussion

Restoration of traditional fruit orchards is an important landscape management practice that can help maintain natural biodiversity (Horák et al., 2018). A wide range of species positively react to traditional orchard management (Myczko et al., 2013; Čejka et al., 2018; Horák et al., 2018). Nevertheless, it is important to test the generality of this pattern in a wider (i.e., landscape) context (Katayama et al., 2014). This appears to be especially important in urban areas (Beninde et al., 2015), where aspects such as habitat fragmentation need to be taken into account.

The results of our study indicated positive effects of restoration on orthopteran species richness. The species compositions of orthopterans and butterflies changed after restoration. Landscape variables influenced the species richness of orthopterans and birds. Moreover, landscape variables influenced the species compositions of orthopterans and butterflies. Lichens were not influenced at any level. Thus, our study emphasizes the importance of both the internal and external structure of traditional fruit orchards for species richness and composition.

4.1. Effects of restoration and orchard structure

The results of our study revealed a positive influence of restoration on the species diversity of orthopterans and butterflies. The strongest response was observed for orthopterans. The increase in their species richness indicated a positive reaction to managed habitats (Alignan et al., 2018). Orthopterans have been known to benefit from moderate management practices implemented after restoration (Marini et al., 2008; Fartmann et al., 2012).

Restored orchards also exhibited different orthopteran species compositions from abandoned orchards. They were preferred by the species *T. subulate*, *C. dorsatus* and *P. albopunctata*. These species benefit from dry grasslands with low and sparse vegetation (Kočárek et al., 2013). In general, restoration caused a shift in orthopteran species composition, with higher species richness observed in the restored orchards than in the abandoned orchards. The same pattern was previously found for this taxon at one site (Horák et al., 2018). Past studies have indicated that short-term abandonment improves orthopteran

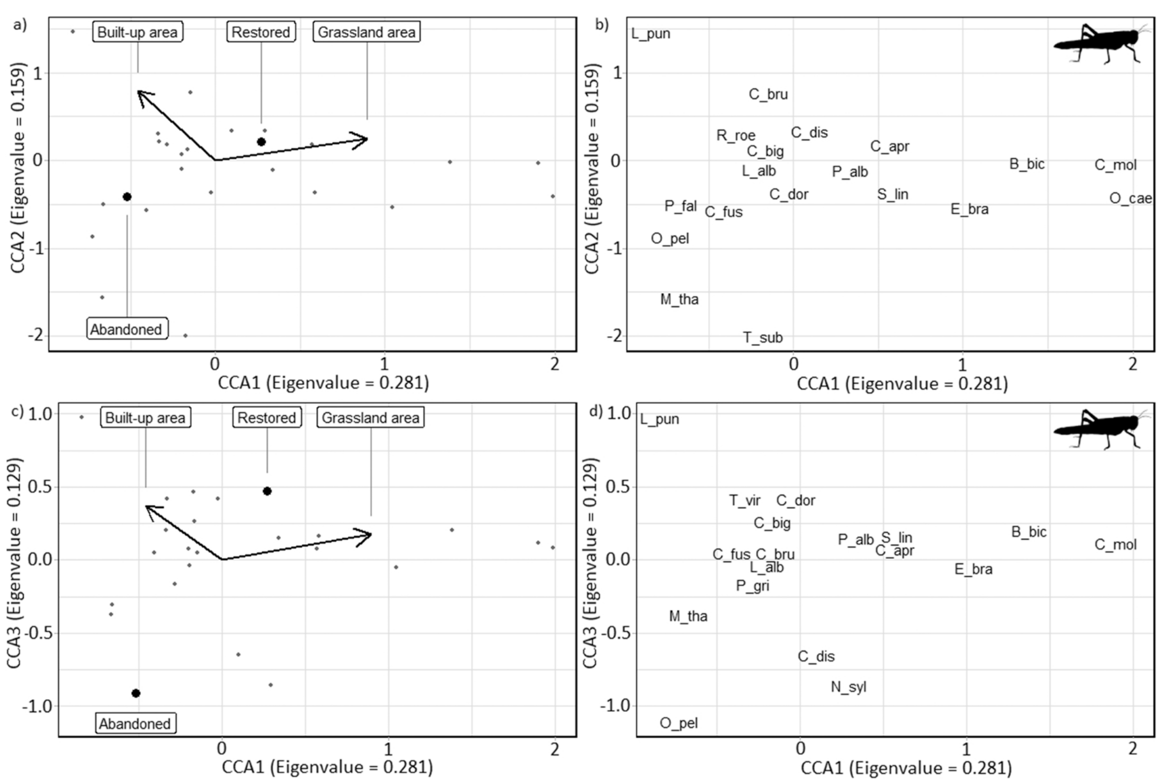

Fig. 4. Species composition relationship of orthopterans with the management of the studied orchard and built-up and grassland areas within a 400 m radius. All plots are based on canonical correspondence analysis (CCA). On the left side, the categorical variable (management) is shown as black points, continuous variables (land-use types) are shown as black arrows, and each species is indicated by a small gray point. The left upper panel (a) shows the relation to axes CCA1 and CCA2, while the left lower panel (c) shows the relation to axes CCA1 and CCA3. On the right side (b, d), gray points of species are replaced by species abbreviations to show their responses. For readability, only selected species abbreviations are shown. Abbreviations are formed from the first letter of the Latin genus name and the first three letters of the species name. For detailed abbreviation of every species, please see Table S2.

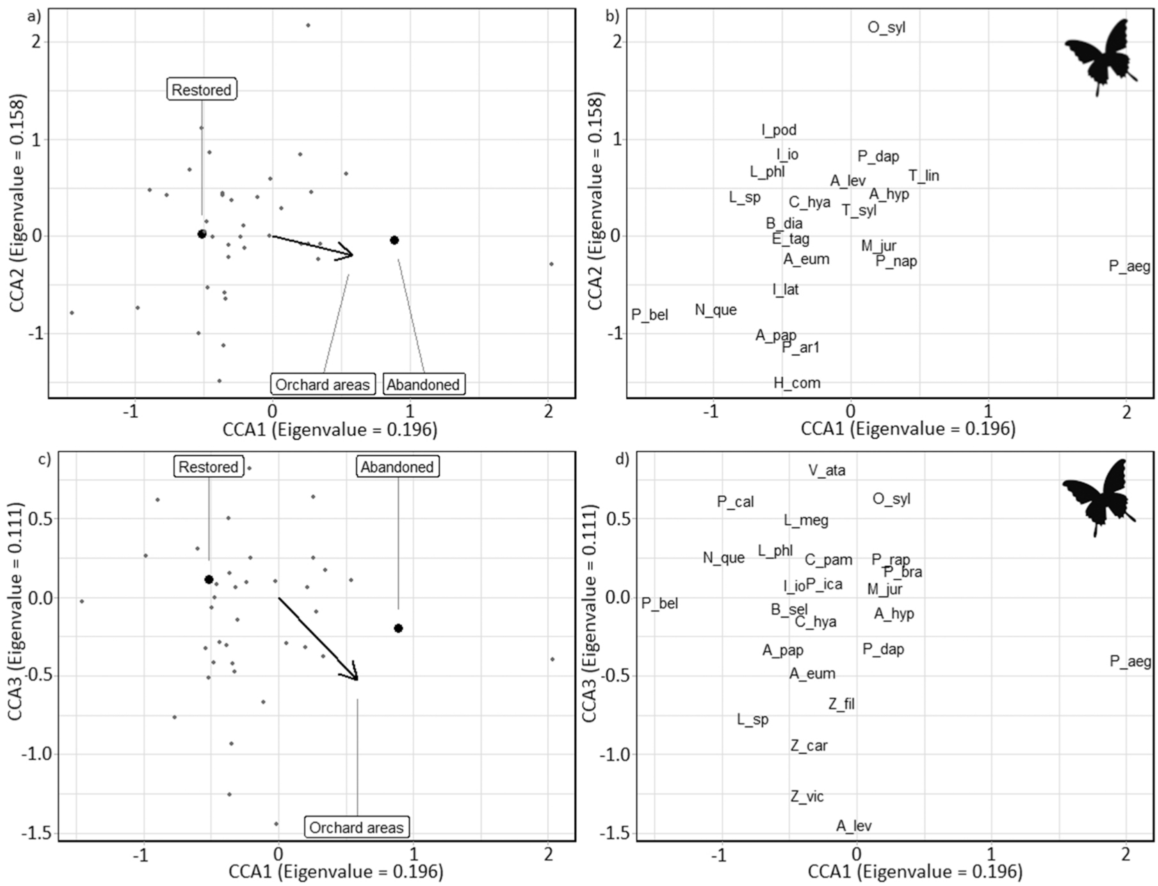

Fig. 5. Species composition relationship of butterflies with the management of the studied orchard and other orchards within a 300 m radius. All plots are based on canonical correspondence analysis (CCA). On the left side, the categorical variable (management) is shown as black points, the continuous variable (other orchards within a 300 m radius) is shown as black arrows, and each species is indicated by a small gray point. The left upper panel (a) shows the relation to axes CCA1 and CCA2, while the left lower panel (c) shows the relation to axes CCA1 and CCA3. On the right side (b, d), gray points of species are replaced by species abbreviations to show their responses. To improve readability, only selected species abbreviations are shown. Abbreviations are formed from the first letter of the Latin genus name and the first three letters of the species name. For detailed abbreviation of every species, please see Table S2.

diversity (Marini et al., 2009; Fartmann et al., 2012). However, long-term abandonment has mainly negative effects (Marini et al., 2009). Orthopterans are a highly diverse group, ranging from species that prefer bare soil to those that live only in forests. Therefore, it was not surprising that some orthopteran species preferred abandoned orchards. These species were common species (*O. pellucens* and *C. dispar*) that prefer high mesophilic grass vegetation (Dvořák et al., 2022). Another example is *N. sylvestris,* a common representative of forest fauna (Kočárek et al., 2013). Its preference for abandoned orchards indicated that such orchards have conditions similar to shady forest conditions (Pezzi et al., 2020).

Butterflies were the second group influenced by orchard management restoration. Their species composition in abandoned orchards was dominated by common species, including those able to survive in forests, such as *P. aegeria* (Macek et al., 2015). The nonsignificant reaction of butterfly species richness to restoration was surprising. Other studies have shown that butterflies prefer managed orchards (Varah et al., 2013; Horák et al., 2018). In addition, abandonment followed by natural succession has been found to lead to lower diversity (Colom et al., 2021). Butterfly richness positively reacted to the extent of orchard area. This was not surprising, as this response has been observed in other insects in similar habitats (Steffan-Dewenter and Tscharntke, 2000; Steffan--Dewenter, 2003). This result indicates that butterflies are more sensitive to external fragmentation than changes in internal structure. They were able to survive in species-rich communities, even in relatively small sunny patches within large, abandoned orchards (our observations). Regarding individual species, our restored orchards hosted species such as *P. argus*, *P. bellargus* and *L. phlaeas*. These species are less common or even protected (Hejda et al., 2017; Macek et al., 2015). They prefer open habitats such as grasslands or rocky areas (Macek et al., 2015). This preference limits their current existence (Thomas et al., 2001) in central European landscapes and illustrates the importance of orchard management restoration.

Lichen species richness and composition did not exhibit significant responses to any of the studied internal orchard structure variables. Given the ability of lichen species to indicate long-term changes (Liška and Herben, 2008), the continuity of an orchard might be more important than its current state (Horák et al., 2018).

Bird species richness and composition did not vary depending on internal structure. Nevertheless, the majority of central European bird species have high dispersal abilities and might even benefit from overgrown patches (Horák et al., 2018). Moreover, traditional fruit orchards host both forest dwellers and farmland specialists (Zasadil et al., 2020). Thus, orchards, as a minor habitat type, might reflect only their surrounding landscape (Zasadil et al., 2020).

4.2. Effect of landscape

For the majority of the studied taxa, landscape elements influenced species richness and composition.

Butterfly species composition was influenced by the presence of other orchards in the surrounding landscape. This finding might correspond to the fact that orchard meadows are one of the most species-rich seminatural habitats in Europe (Ernst et al., 2017). The orchards in the present study were inhabited by a mixture of species that prefer meadows and forest edges, such as *A. hyperanthus*, *P. napi* and *P. daplidicae* (Macek et al., 2015). These species have high dispersal abilities and can migrate between suitable habitats (Macek et al., 2015). However, the optimal spatial scale for butterflies was lower than that for the other studied taxa. This unexpected result might be caused by the urban environment, where the landscape is highly fragmented (Horák, 2016).

Orthopteran species richness was negatively influenced by the presence of built-up areas in the surrounding landscape. This finding is consistent with the finding of other studies (e.g., Marini et al., 2008) that an increase in inhospitable habitats decreases orthopteran diversity. In addition, the appearance of such areas leads to dispersal limitations and population fragmentation (Marini et al., 2008). Species such as *E. brachyptera* preferred landscapes with a low percentage of built-up area. These species are found mostly in humid grassland conditions (Kočárek et al., 2013). Built-up areas with concrete or asphalt and mowed urban green areas might serve as barriers for these species, while xeric species (such as *C. brunneus*) might find these areas still suitable for living (Watson et al., 2020). The species composition of orthopterans was affected by the percentage of grassland in the surrounding landscape. Landscapes with grassland were mainly preferred by species of dry grasslands, such as *S. nigromaculus*, *C. mollis* and *B. bicolor* (Kočárek et al., 2013). On the other hand, forest species (such as *M. thalassinus* and *P. griseoaptera*) preferred orchards with little grassland nearby. These forest species prefer to lay eggs in slits in the bark or on organic litter shaded by shrubs, where the hatching temperature is lower (Marini et al., 2009). Hence, meadows might limit their occurrence.

Bird species richness was negatively affected by grasslands in the surrounding landscape. Birds recorded in orchards during our study were mainly forest specialists or urban birds (Hudec and Dungel, 2001). The importance of woody plants for the species richness of urban birds is well known (Sandström et al., 2006; Sattler et al., 2010). Other landscape categories had no significant effects. However, birds are known to prefer heterogeneous landscapes (Söderström and Pärt, 2000; Söderström et al., 2001). Therefore, landscapes belonging to the other studied categories might contribute to the diversity of habitats in urban environments.

5. Conclusion and recommendations for practice

The results of our study support the restoration of traditional fruit orchards as a suitable management practice for promoting city biodiversity. Moreover, orchards have irreplaceable esthetic, social, cultural and historical value (Špulerová et al., 2015). They are the most common agroforestry type in central Europe (Forejt and Syrbe, 2019). Nevertheless, they face many different threats, such as abandonment, intensification, and landscape conversion (Špulerová et al., 2015).

Orchard restoration is one of the hot topics in central Europe as well as in the studied area, where shrubs and young trees are cleared from abandoned orchards. New fruit trees are replanted in gaps, while old, decayed or even dead trees are preserved. Orchard meadows are managed with low-intensity practices such as mosaic mowing and grazing. All these practices help support biodiversity (Varah et al., 2013; Horák, 2014; Kajtoch, 2017).

Restoration of traditional fruit orchards is also currently applied in neighboring countries, such as Poland (Kajtoch, 2017) and Germany (Forejt and Syrbe, 2019). Moreover, agroforestry management practices are a focus of conservationists worldwide (Dosskey et al., 2012; de Oliveira and Carvalhaes, 2016; Hillbrand et al., 2017).

Our results indicate that orchard biodiversity was also influenced by the landscape. The results suggested mainly a negative effect of built-up areas. This finding led us to conclude that restoration, as a factor that promotes biodiversity, would have stronger effects in suburban areas where the built-up area coverage is lower. Thus, these positive factors may be combined. Orchards are also more common in suburban areas than in inner city areas, as they represent artifacts of former rural landscapes absorbed by growing urban development (Janeček et al., 2019). However, suburban areas are often affected by their industrial history (Newton et al., 2012; Liotta et al., 2020). Thus, they lack recreational sites; restored orchards might fill this gap and public need (Liotta et al., 2020). Moreover, we recommend prioritizing restoration in landscapes dominated by forests because doing so leads to higher heterogeneity of the landscape mosaic, which supports the diversity of organisms with higher dispersal rates (Söderström and Pärt, 2000).

CRediT authorship contribution statement

Patrik Rada: Data curation, Formal analysis, Statistical analysis, Funding acquisition, Investigation, Software, Validation, Visualization, Writing – original draft, reviewing, and editing. **Josef P. Halda**: Investigation, reviewing, and editing. **Jaroslav Holuša**: Investigation, reviewing, and editing. **Karolína Maliňáková**: Investigation, reviewing, and editing. **Jakub Horák**: Conceptualization, Formal analysis, Methodology, Project administration, Supervision, Validation, reviewing, and editing. All authors have read and agreed to the published version of the manuscript.

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.

Data availability

Data will be made available on request.

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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.2022.127686.

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