Active Management of Fruit Orchard Meadows Under The Influence of Suburbanization is Important for Insect Diversity

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Abstract

Fruit orchards under different types of management represent the most common agroforestry practice in central Europe. Traditional fruit orchards with trees usually planted in meadows are at a surplus, providing suitable habitats for many plant and animal species. We examined the influence of different management and biotope types on three insect groups. This study was conducted in thirty orchards across the capital city of the Czech Republic – Prague (496 km²). We investigated the diversities of butterflies, hymenopterans and beetles. Their species richnesses mainly benefitted from orchard management and were partly higher at xerothermic sites than at mesic sites. Red-listed species did not show any clear patterns. Open-landscape specialists were influenced by management, while forest species were influenced by habitat type. Generally, orchard abandonment led to insect biodiversity loss. Therefore, active agricultural management appears to be essential for insect biodiversity conservation in orchards, and different management and biotope types provide suitable conditions for specific species. Mowing and maintaining orchards are two important biodiversity management actions in highly human-populated landscapes.

Introduction

European agroforestry practices have a long history starting with slash-and-burn agriculture and continuing with forest pastures or fruit orchards (King 1987). Traditional fruit orchards are the most abundant type of agroforestry in central Europe. The majority of fruit trees are planted in mowed or pastured grasslands (Herzog 2000; Mosquera-Losada et al. 2009). Agroforestry as such is usually considered to have a positive effect (e.g., Bignal and McCracken 1996; Myczko et al. 2013; Horak 2014a) on biodiversity. However, different types of agroforestry have different impacts (Varah et al. 2013). Schroth et al. (2004) summarized three major positive effects of agroforestry. First, agroforestry provides secondary habitats for species that can tolerate some level of disturbance. Second, it connects natural habitat fragments better than less tree-dominated land use, partly because traditional fruit orchards combine the conditions of forest and grassland habitats in one place (Horak 2014b). Third, in some cases, agroforestry can also reduce the rate of conversion to more intensive practices. This effect may be related to higher biodiversity, which can, for example, successfully control pests without the need for pesticides (Simon et al. 2011).

The habitat area or landscape context of the orchard may be another important factor (Steffan-Dewenter 2003). In this study, we are investigating traditional fruit orchards in the large area of a million-person city that includes more than one hundred freely accessible orchard meadows (Janeček et al. 2019).

Orchard meadow biological diversity depends on many factors (Steffan-Dewenter 2003; Steffan-Dewenter and Leschke 2003; Čejka et al. 2018). Vegetation cover management seems to be very important. However, groups of animals differ in their preferences. While birds or butterflies prefer abandoned or moderately managed orchards (Myczko et al. 2013; Horák et al. 2018), it appears that carabids have the opposite preference for tilled or even herbicide-treated ground cover (Miñarro and

Dapena 2013). In contrast, wasps are indifferent to management practices, according to another study (Steffan-Dewenter and Leschke 2003).

The aims of this paper were to determine whether different types of management, in the context of habitat type, can influence insect biological diversity in traditional fruit orchards and, if so, which management type is the most suitable for current orchards in the city of Prague.

Methods

Study area

We studied traditional fruit orchards in Prague, the capital city of the Czech Republic. The area of Prague is 496 km^2 and is densely populated (1.3 million citizens in 100 thousand houses), but it offers biodiversity hotspots (Kadlec et al. 2008). The topography is diversified, with diverse bedrock, and divided by the Vltava River as well as its river and stream tributaries. This region includes undeveloped areas with habitats ranging from humid (e.g., wetlands close to streams) to very dry (steppes on southern hill slopes) and from seminatural (e.g., natural reserves) to artificial (e.g., brownfields). The mean elevation is 235 m a.s.l. (with a range from 177 to 399 m a.s.l.). The mean annual temperature is approximately 9°C, and the mean annual precipitation is approximately 525 mm.

This area includes more than 100 freely accessible traditional fruit orchards representing artifacts of agroforestry that supplied the city with fruits from its former rural peripheries (Horák and Trombik 2016). We selected 30 of these orchards that were widely distributed throughout the territory of the city for our research (Fig. 1; Table S1).

Sampling methods

The collection of insect diversity data was focused on the three most species-rich insect orders: Lepidoptera, Hymenoptera and Coleoptera. We selected one group for each insect order: day-active butterflies (clade Rhopalocera and family Zygaenidae; hereafter butterflies), Aculeata (hereafter hymenopterans) and click beetles (Elateridae; hereafter beetles).

The taxa studied as biodiversity indicators should meet certain requirements, such as having a well-known taxonomy and natural history and/or being widely geographically distributed with the presence of ecologically specialized species in the study region (Gayubo et al. 2005).

Day-active butterflies are one of the most studied insect groups worldwide, mainly because of their easy identification, well-known niches and ability to colonize new habitats (Thomas 2005). Aculeate hymenopterans are also well studied (Gayubo et al. 2005; de Souza et al. 2010; Heneberg et al. 2013; Heneberg and Bogusch 2020), with a special contribution in the form of social species – mainly bees and ants (de Souza et al. 2010). Elateridae is one of the most diverse beetle families, with a wide range of habitats and economic importance as pests (Traugott et al. 2015). These beetles can also serve as good bioindicator species (Dušánek 2011). All of these reasons led to the selection of these insect groups as our indicator species.

We used the most suitable sampling method for every group studied during 2017. Butterflies were recorded using a time-limited survey (15 minutes). During the active season (April to August), seven surveys were performed under ideal weather conditions (> 17°C, from sunny to partly cloudy skies, from calm to mild wind). We surveyed all currently available major sources of nectar where more butterfly species were expected in similar habitats of central Europe (e.g., Kadlec et al. 2012).

Hymenopterans were collected using colored Moericke traps (150 x 150 x 45 mm length/width/depth) (e.g., Heneberg and Bogusch 2014; Aranda 2018). We improved the traps by using half-yellow and half-white pan traps. Ten traps were installed in every orchard in May, June, July and August. They were always recollected after 72 hours. A colored stick was placed near every trap to ensure that the traps were installed in similar places during the sampling periods. Traps were installed to cover all major present conditions of orchards; therefore, five of them were placed under the tree canopy, and five were placed between crowns. The traps were filled with saturated saline solution with a small amount of detergent to reduce the surface tension of the liquid. This solution preserves insects.

Beetles were collected using passive window trunk tree traps (i.e., placed on tree trunks) from April until the end of August. Each trap consisted of crossed transparent plastic panes (400 × 500 mm), a dark top cover for protection and a plastic funnel leading down into a container with saturated saline solution and a small amount of detergent. One trap was always placed in every orchard at breast height (approximately 1.3 m above the ground) facing south (Horák et al. 2013a). The traps were recollected every two weeks.

The collected hymenopterans and beetles were then transported in plastic bottles to the laboratory for sorting and identification. Recorded or collected individuals of all studied orders were identified to the species level. The only exception was butterfly species, whose identification was based on DNA sequencing or genital preparation (Friberg and Wiklund 2009). These species were identified as different species sensu lato (e.g., *Leptidea* spp.).

All identified species were divided according to the recent literature (Laibner 2000; Beneš et al. 2002; Macek et al. 2010, 2015) into generalists and species with a preference for forest or open landscapes. This distribution was then adjusted according to our expert knowledge. All identified species were also compared with the Red List of threatened species of the Czech Republic (Hejda et al. 2017). For every orchard, the threatened species index (Harcourt and Parks 2003) was calculated. This index consisted of a threat category number (near threatened (1), vulnerable (2), endangered (3) and critically endangered (4)) multiplied by the number of individuals from every category in the orchard.

Study variables

Three environmental variables were used in this study. The first factor was the intensity of management. The intensity of management often influences biodiversity in different ecosystems (Bengtsson et al.

2000; Rook and Tallowin 2003; Kampmann et al. 2008). Thus, we were interested in whether it has an impact on the biodiversity of traditional fruit orchards. The intensity of management was recorded on an ordinal scale. The first level was abandoned orchard with no management (coded as 1). Management in these orchards usually ended in the early 1990s, and such orchards have since become overgrown with shrubs and young trees (Horák and Trombik 2016; Fig. S1). Moderately managed orchards were those that were mowed a maximum of twice per season, often with unmowed patches left behind (coded as 2), and intensively managed orchards were those that were mowed more than twice per season (coded as 3) but not periodically as an urban lawn. Overall, we studied nine abandoned, 14 moderately managed and seven intensively managed orchards.

The second studied variable was biotope type, which might be essential for the presence of particular species (van Swaay et al. 2006). Biotopes were divided based on the type of vegetation according to Chytrý et al. (2010). Two types of biotopes were recorded: xerothermic and mesic. Xerothermic vegetation consisted of species such as *Festuca* spp., *Stipa* spp., *Dianthus carthusianorum*, *Centaurea stoebe* and *Eryngium campestre*. Mesic vegetation included species such as *Arrhenatherum elatius*, *Poa pratensis*, *Plantago lanceolata* and *Trifolium pratense*. In total, we studied eight orchards with xerothermic biotopes and 22 orchards with mesic biotopes.

The third variable was orchard area (MEAN = 17538.75 (m^2); SE = 4063.25; MIN = 2011.10; MAX = 90512.60). We vectorized all orchards from aerial photographs of Prague from 2015. Then, we adjusted their borders according to a terrain survey and calculated their areas using ArcGIS 10.6.1. Orchard area might influence total biodiversity (Cornelis and Hermy 2004); hence, we used area as one of the predictors to generalize our models.

Statistical analyses

Statistical analyses were performed using R version 3.6.1. Dependent variable normality was tested using the Shapiro-Wilk test, and if necessary and possible, transformation was used to achieve a normal distribution. If the distribution was significantly different from normal or the values were close to significant, 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. If the distribution was significantly different from a Poisson distribution, a negative binomial distribution was used. Theta was calculated for every model using a fitted negative binomial generalized linear model (glm.nb function).

Generalized linear mixed-effect models (GLMMs) were fit using the packages nlme (Pinheiro et al. 2020) and MASS with every dependent variable (glmmPQL function). Intensity of management and type of biotope were included as fixed independent variables. Orchard area was included as a random factor in every model to generalize the results while accounting for the variation in this factor. 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 while accounting for random factors.

The threshold for running dependent variable analysis was set to the presence of at least eight species of a defined category, and cases with only a few observations in interaction with two independent variables were excluded from testing.

Canonical correspondence analyses (CCAs) were performed for every order (Lepidoptera, Hymenoptera and Beetles) using the lattice (Sarkar 2008), permute (Simpson 2019) and vegan (Oksanen et al. 2019) packages to obtain interactions between every single species of the selected orders and independent variables. These analyses revealed the dependency of species composition on independent variables. The results were visualized with the ggplot2 package.

Results

In total, 50 species of butterflies represented by 2 219 individuals, 165 species of hymenopterans represented by 4 610 individuals and 25 species of beetles represented by 242 individuals were observed and trapped (Table S2).

Species richness

There was a significant positive influence of moderate management ($t = 4.50$; $P < 0.001$) and intensive management ($t = 2.07$; $P < 0.05$; Fig. 2) in fruit orchards on the observed species richness of butterflies in comparison with that in abandoned orchards. There was no significant difference between moderate and intensive management (Table 1). Butterfly species richness was significantly higher in xerothermic than in mesic ($t = 2.84$; $P < 0.01$; Fig. 2) orchards.

Moderate ($t = 2.14$; $P < 0.05$) and intensive management ($t = 2.58$; $P < 0.05$) were significantly preferred by hymenopterans according to species number (Fig. 2). There was no significant difference between moderately and intensively managed orchards. There was no significant difference between the types of biotopes (Fig. 2; Table 1).

Beetle species richness was not significantly influenced by the intensity of management or the type of biotope (Fig. 2; Table 1).

Response of red-listed species

We observed 11 red-listed butterfly species, eight red-listed hymenopterans and two red-listed beetle species.

Red-listed butterfly species were not significantly affected by the intensity of management (Table 1). Significantly more species were recorded in xerothermic biotopes than in mesic biotopes ($t = 2.57$; $P < 0.05$).

There was no significant impact of intensity of management or type of biotope in the case of hymenopteran species (Table 1).

Beetles were not analyzed due to the low number of species.

Open and forest landscape specialists

Open landscape-related butterflies exhibited significantly higher species richness in moderately managed orchards ($t = 3.88$; $P < 0.001$) and intensively managed orchards ($t = 2.12$; $P < 0.05$) than in abandoned orchards. There was no significant difference between moderately and intensively managed orchards (Table 1). No significant difference between types of biotopes was observed (Table 1).

Open landscape-related hymenopteran species richness was significantly higher in moderately ($t = 3.19$; $P < 0.01$) and intensively managed orchards ($t = 3.63$; $P < 0.01$) than in abandoned orchards. There was no significant difference between moderately and intensively managed orchards. There was a significant impact of the type of biotope. There were more species present at xerothermic sites than at mesic sites ($t = 2.44$; $P < 0.05$).

In the case of open landscape-related beetle species richness, there were no observed significant impacts (Table 1).

Forest-related butterfly species richness was not significantly influenced by the intensity of management (Table 1). There were significantly more species in xerothermic biotopes ($t = 3.45$; $P < 0.01$) than in mesic biotopes.

Forest-related hymenopterans were significantly dependent on neither the intensity of management nor the type of biotope (Table 1).

Forest-associated beetles were not significantly dependent on the intensity of management or the type of biotope (Table 1).

Species composition

We did not observe a significant relation between butterfly species composition and intensity of management or type of biotope (Table 2).

Our analysis indicated a significant impact of the environment on hymenopterans (Table 2). Specifically, there were fewer species in abandoned orchards. There were mainly *Andrena carantonica* and *Myrmica rubra*. *Andrena ovatula*, *Andrena strohmella* and *Andrena floricola* had a preference for intensive management of orchards (Fig. 3). *Andrena polita*, *Bombus pascuorum, Formica pratensis* and *Lasioglossum lativentre* preferred moderately managed orchards. *Polistes nimpha*, *Andrena bicolor* and *Andrena dorsata* preferred xerothermic orchards, and *Halictus tumulorum*, *Nomada flavoguttata* and *Andrena varians* were present in mesic biotopes (Fig. 3).

There was a significant influence of orchard management and biotope type on the species composition of beetles (Table 2). *Agriotes ustulatus* preferred abandoned orchards, while *Selatosomus gravidus* occurred in intensively managed orchards. Moderate management was preferred by the species *Ampedus* *glycereus* and *Ampedus pomorum*. *Agriotes pilosellus* and *Melanotus villosus* preferred xerothermic biotopes. Mesic biotopes were preferred by *Agrypnus murinus* (Fig. 3).

Discussion

Our results indicate a mainly positive impact of the management of traditional fruit orchards on the studied insect taxa. We also found that orchards planted in xeric environments tended to have higher species richness.

Traditional fruit orchards might be depicted as grasslands with scattered trees (Plieninger et al. 2015) or forests with very sparse canopies (Horak 2014a). This depends on the density of planted trees and the stamina of the fruit tree species (Janeček et al. 2019). Fruit orchards provide suitable conditions for species associated with open landscapes that were formerly pastured (Mosquera-Losada et al. 2012). The abandonment of pastured grasslands and forests, from a long-term perspective, usually leads to a decline in biological diversity (Benes et al. 2006; Queiroz et al. 2014; Uchida and Ushimaru 2014). Therefore, from this perspective, it is not surprising that any type of orchard management has a positive effect. On the other hand, intensification of mowing regimes is also decreasing biodiversity (Uchida and Ushimaru 2014). Forest management has changed to more intensive approaches using high forests with dense canopies (Benes et al. 2006). Thus, orchards might serve as a habitat for many species that originally lived in traditionally hayed meadows (Cizek et al. 2012) and those associated with open forests (Horak 2014a).

Managed orchard grasslands with xerothermic biotopes can serve as refugia for many species (Čejka et al. 2018; Šantrůčková et al. 2020). The area of xerothermic grasslands is declining due to land abandonment, afforestation, building activities or even conversion due to atmospheric nitrogen input or fertilization (Tscharntke et al. 2005; Janišová et al. 2011). This has negative consequences for their biodiversity (Buscardo et al. 2008; Janišová et al. 2011). In addition, orchards appear to be very similar to dry traditionally managed woodlands (Hédl et al. 2010), where canopy openness is much higher than in managed forests. This is mainly caused by competition among trees and was even multiplied by wooded pasture (Konvicka et al. 2008) or coppicing in the past (Altman et al. 2013). These forests, typically with xerothermic vegetation, have recently declined (Hédl et al. 2010). Traditional fruit orchards might supplement these natural habitats and serve as habitats for species that originally lived in natural and seminatural habitats. This may lead to higher biodiversity in xerothermic orchards. In addition, such orchards can also serve as transitional habitats that facilitate migration between natural habitats (Steffan-Dewenter 2003).

Butterflies

The species richness of butterflies in our study was most promoted by the management of orchards. Furthermore, dry orchards were more species-rich than mesic orchards.

Abandoned orchards are often akin to shrubland or forests having undergone natural succession for some years after clear cutting (Prach 1994; Balmer and Erhardt 2000). The remaining grafted fruit trees are overgrown, and their crowns are withering due to competition (Horák et al. 2018). The majority of day-active butterflies in central Europe prefer open or at least semiopen habitats (Beneš et al. 2002). There are known examples of gradual declines in butterfly fauna with increasing densities of trees and shrubs (Erhardt 1985; Fartmann et al. 2013). Young tree forests are especially species poor (Balmer and Erhardt 2000). This is probably one of the most important reasons for the preference of butterflies for actively managed sites. This was also confirmed by the preferences of open landscape specialists for managed orchards. Succession toward forests was not profitable even for forest-related species. The main reason is that forest-associated species mainly prefer sparse forest canopies (Beneš et al. 2002, 2006).

We predicted that moderate management would offer more heterogeneous biotope conditions, which usually lead to higher species diversity (Noordijk et al. 2009; Cizek et al. 2012). More heterogeneously managed sites should have more nectar sources and provide a more diverse understory of vascular plants (Erhardt 1985; Steffan-Dewenter and Leschke 2003). In addition, research has shown that butterfly species richness mainly declines with intensive understory cultivation (Erhard 1985; Ekroos et al. 2010) and that butterflies prefer rather patchy mowing (Varah et al. 2013). Surprisingly, there was no significant difference in the effects of moderate and intensive management on the number of butterfly species. This nonsignificant difference can be explained by the complex 3D structure of managed orchards. This means that, even after mowing, this habitat type still offers flowers and shelter in tree crowns (Herzog 1998). In addition, some species can also benefit from tree sap, honeydew or rotting fruits (Shreeve 1984; Ômura and Honda 2003). Nevertheless, this observed issue remains relatively unclear – as abandoned orchards also often offer the abovementioned complementary resources. One of the possible reasons could be the temporal emigration of butterflies to neighboring habitats followed by regression when the condition of the intensively mowed orchard improves (Baum et al. 2004; Ouin et al. 2004). The most surprising finding was that red-listed species were not influenced by management. However, we observed one endangered species, two vulnerable species and eight near-threatened species, which illustrated the importance of orchards in a landscape context. These species might have such a strong biotope preference that variation in local management has little effect (Fattorini 2010).

Xeric orchards contained more butterfly species and of red-listed species. Surprisingly, forest specialists also preferred xeric orchards. Xeric biotopes, including orchards, are often less accessible than other biotopes. This is a possible reason why they have stayed relatively untouched by suburbanization (Ouředníček 2007). Therefore, xeric orchards and similar dry habitats can be suitable for many species – even those not specialized for dry habitats (Dostálek and Frantík 2008; Kadlec et al. 2008). This is confirmed by the finding that some urban areas (such as railway verges or brownfields) could mimic natural xeric habitats (Konvicka and Kadlec 2011). These orchards are still rather marginal. However, they can facilitate connectivity or mimic natural xeric steppes. In addition, they might also serve as transitional habitats or stepping stones (Horak 2014a) in fragmented areas of cities (Horák 2016). This is probably the reason why orchards in xerothermic biotopes contained more species of both butterflies and red-listed butterflies.

Forest specialist species richness was higher in xerothermic biotopes than in mesic biotopes. Xerothermic orchards might imitate and substitute natural xeric forests due to their similarly high canopy openness (Chytrý 1997; Hédl et al. 2010). Such openness is needed for forest specialist butterflies to find suitable basking sites, while forest cover serves as an important food source and shelter (Shreeve 1984; Dennis and Sparks 2006). In addition, xerothermic forests are currently less common in central Europe because modern forestry practices shifted them to mesic forests (Hédl et al. 2010). Thus, butterflies originally associated with dry forests had to find supplementary habitats with similar living conditions, and traditional fruit orchards provided such conditions.

Surprisingly, the species composition of butterflies did not differ among management and biotope types. For example, we observed some forest-related species (e.g., *Argynnis paphia* and *Celastrina argiolus*), but they were present in all types of orchards. Nevertheless, these species were not as common as other species in the orchards, suggesting that orchards are simply transitional habitats for these species in the landscape context. On the other hand, transitional habitats might be as ecologically important as natural habitats (Schmitt and Rákosy 2007), underlining the importance of traditional fruit orchards for insect biodiversity.

Hymenopterans

Hymenopterans benefitted from management in orchards, and they were unaffected by the type of biotope. The only exceptions were open-landscape specialists, which preferred xerothermic sites. This might be because ground cover in xerothermic biotopes is often bare soil, which is ideal for nesting in many hymenopteran species (Heneberg et al. 2014; Fortel et al. 2014; Bogusch et al. 2020). In addition, active management such as mowing might multiply this effect since disturbed habitat is often preferred (Fortel et al. 2014). Orchards with old veteran fruit trees also host a high diversity of species that nest in wood cavities, especially smaller ones (Horák et al. 2013b; Bogusch and Horák 2018).

Many hymenopterans prefer habitats in early successional stages (Heneberg et al. 2013; Taki et al. 2013; Heneberg and Bogusch 2020). Such stages could be maintained in orchards by intensive management. A more heterogeneous understory is at a surplus in managed orchards since intermediate disturbance reduces the dominance of competitive species and increases plant species richness (Curry 1994). This offers more available food sources (Steffan-Dewenter and Leschke 2003). In this context, it is not surprising that we observed one critically endangered species (*Andrena similis*), three vulnerable species and four near-threatened species. Their incidence is another indication that traditional fruit orchards could provide suitable habitats for insect biodiversity.

Management practices were clearly preferred, and there were fewer species in abandoned orchards. Nevertheless, some of the species – for example, *Myrmica rubra* and *Andrena carantonica* – preferred abandonment. An explanation in the case of *M. rubra* might be that this species prefers nesting in leaf litter or within woody debris (Groden et al. 2005), which is more common in abandoned orchards. In the case of *A. carantonica*, the only reasonable explanation might be that this species does not require as high a temperature for pollination as the European honeybee (*Apis mellifera*) (Chansigaud 1975) and collects pollen and nectar, usually from tree flowers (Macek et al. 2010; Westrich 2018). Thus, it might use shrub overgrowth as an inhibitor of high temperatures in the understory (Breshears et al. 1998), providing a competition benefit.

Other species found in the abandoned orchards, such as *Temnothorax crassispinus* and *Lasius fuliginosus*, usually occurred in forest biotopes. Therefore, their preference was rather natural (Macek et al. 2010). Moderate management was preferred in the case of species such as *Lasioglossum lativentre* and *Formica pratensis* whose natural biotopes are forest steppes. Thus, moderately managed orchards with patchy mowing and the presence of old-growth trees might serve as artificial supplements. Nevertheless, these orchards were also preferred by habitat generalists such as *Andrena polita* and *Bombus pascuorum* (Macek et al. 2010), which might instead primarily benefit from the continuous presence of nectar (Croxton et al. 2002). Intensively managed orchards were inhabited by species such as *Andrena ovatula*, *A. floricola* and *A. strohmella*, which corresponded to their preference for open biotopes and floral specialization (Macek et al. 2010; Westrich 2018; Bogusch et al. 2020).

Beetles

Click beetles are known to prefer veteran trees exposed to sunlight (Horák and Rébl 2013). Therefore, managed orchards appeared to be ideal habitats. Nevertheless, beetles were indifferent to the management and type of habitat in our study. Species richness was higher in moderately managed orchards than in abandoned orchards, but this difference was not significant. From this trend, we might conclude that moderate management could have a positive impact on beetle diversity.

We trapped species displaying all types of biotope preferences, from a preference for crop fields (*Athous haemorrhoidalis* and *Agrypnus murinus*) to a preference for high forests (*Melanotus villosus* and *Dalopius marginatus*). This leads to the conclusion that traditional fruit orchards can host a very wide range of species that can benefit from meadow, trees or both within one habitat. This was also confirmed by the presence of red-listed species – we trapped one vulnerable (*Brachygonus megerlei*) and one near-threatened species (*Ampedus rufipennis*). Both of these species are saproxylic (Zaharia 2006; Brunet and Isacsson 2009). Thus, old trees present within habitats are essential for them, even in agricultural habitats.

Species composition differed among the studied orchard categories. Abandoned orchards were preferred by *Agriotes ustulatus*. This species is usually found in places with lower vegetation cover (Mertlik 2016), which appears to contradict our findings. However, this species also prefers soil with a higher humus level (Čačija et al. 2018), which is found mostly in abandoned orchards due to decaying plant residuals (Horák et al. 2018). Moderately managed orchards were inhabited by *Ampedus glycereus* and *A. pomorum*, which are mostly known from forests, and they clearly benefitted from the presence of old trees (Laibner 2000). Our studied sites were typical in terms of the presence of old fruit trees, which could mimic the forest environment for these species. Intensive management of orchards was preferred by *Selatosomus gravidus*. This species is usually present in steppe biotopes, and intensively managed orchards are probably also suitable (Laibner 2000), as in the case of some hymenopterans.

Our results were in some cases opposite to the findings of current research regarding species composition between biotopes. In xerothermic biotopes, the species composition included *Agriotes pilosellus*, which is supposed to prefer mesic biotopes, and *Melanotus villosus*, which is usually described as a generalist (Laibner 2000). Nevertheless, in mesic biotopes, we trapped species such as *Selatosomus gravidus*, usually mentioned as having a preference for xerothermic biotopes, and *Agrypnus murinus*, which is thought to be a generalist or even a pest species (Laibner 2000). We can provide context for this information with the finding that *Selatosomus gravidus* could also be found at mesic sites (Bulgakova and Pyatina 2019). Moreover, this species prevailed in intensive orchards, where intensive mowing can cause even mesic biotopes to be drier than in the case of using less intensive practices (Kobayashi et al. 1997). Thus, all of the abovementioned reasons might explain this preference for mesic sites.

Conclusion

Traditional fruit orchards, as humanmade habitats, appear to be very important for many insect species. Many red-listed species were present in these habitats, which combine the conditions of grassland and forest in one place.

Management of orchards was essential for many species and thus very important for biodiversity. There was a nonsignificant difference in species richness between moderate and intensively managed orchards. Nevertheless, the species composition was different between them. Thus, we can conclude that the presence of both approaches is important in terms of maintaining large-scale and long-term species diversity. Xerothermic biotopes showed, in some cases, higher species diversity, and species composition differed between xerothermic and mesic biotopes. Thus, the presence of orchards with both biotopes is important.

Declarations

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Conflict of interest

All authors declare that they have no conflict of interest.

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Tables

Due to technical limitations, table 1,2 is only available as a download in the Supplemental Files section.

Figures

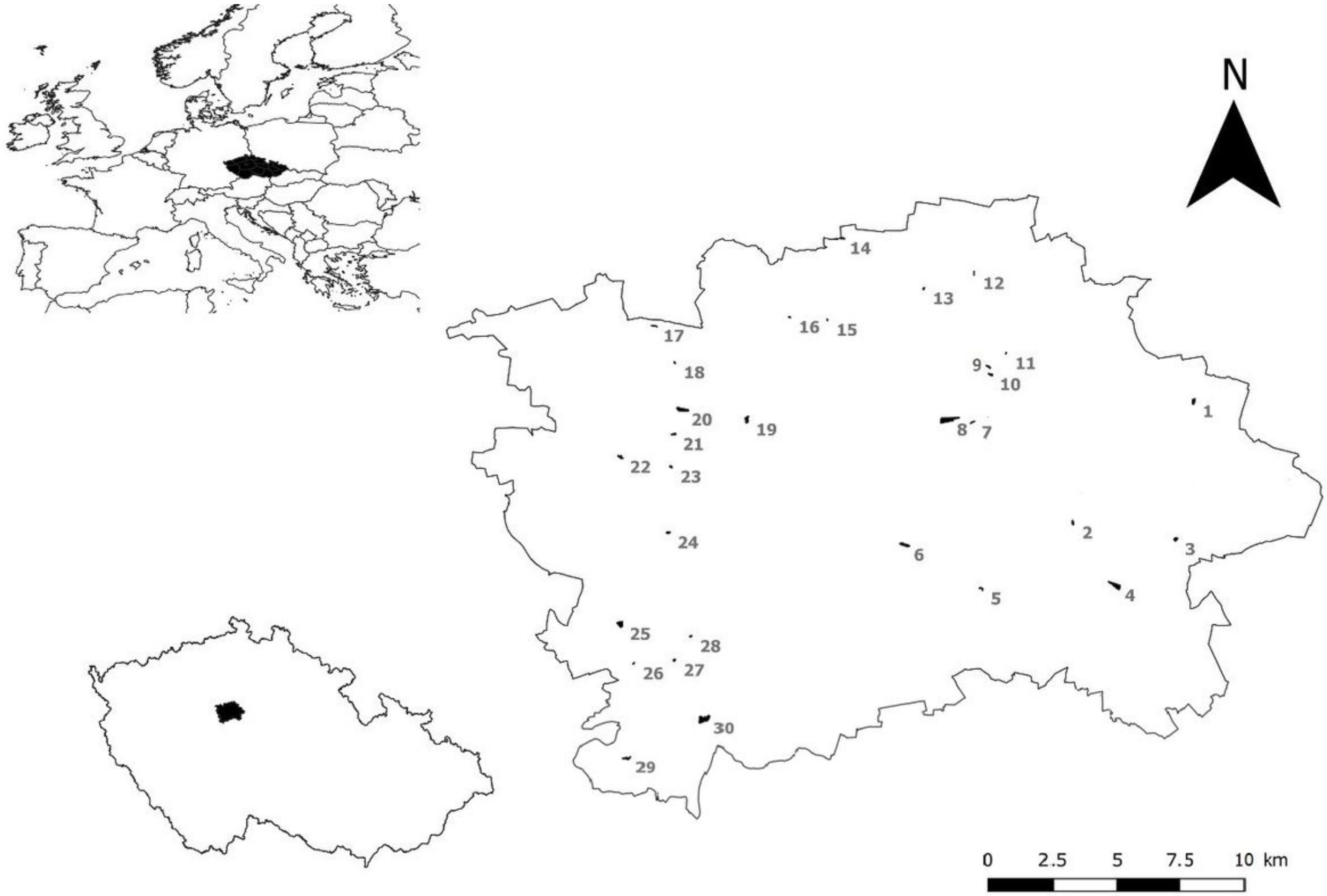

Figure 1

Map of study sites located in the capital city of Prague in the context of the Czech Republic and Europe. The black area in the cadastral map of Prague shows the real orchard area, with the orchard numbers in gray Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

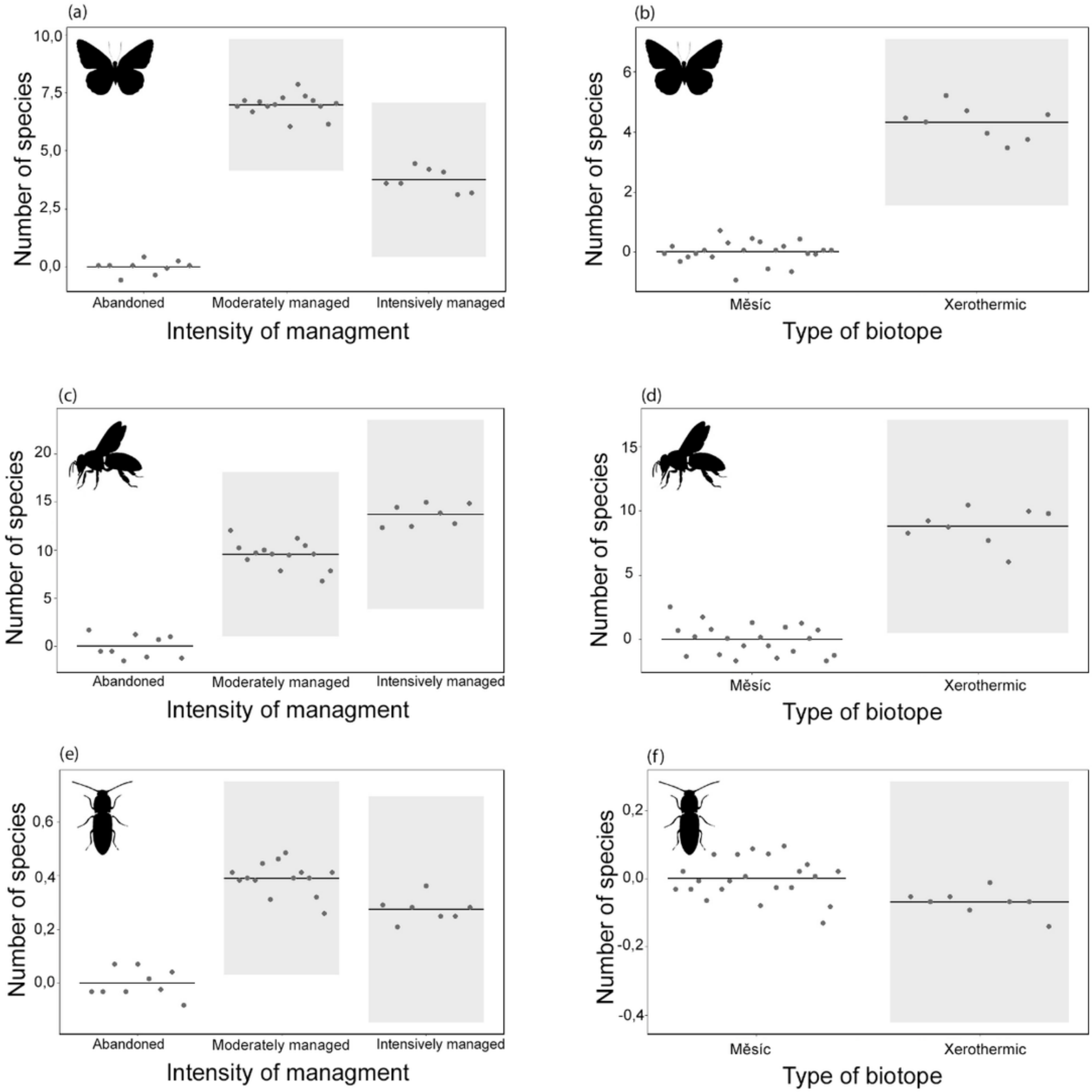

Figure 2

Species richness dependency on the intensity of management for (a) butterflies (Lepidoptera), (c) hymenopterans (Hymenoptera) and (e) beetles (Coleoptera) and the type of biotope for (b) butterflies, (d) hymenopterans and (f) beetles in Prague (Czech Republic) traditional fruit orchards. Note that plots based on GLMMs indicate relative changes in species richness between categories of study treatments, the black line is the mean, shaded boxes represent the 95% confidence intervals, and black dots represent individual observations

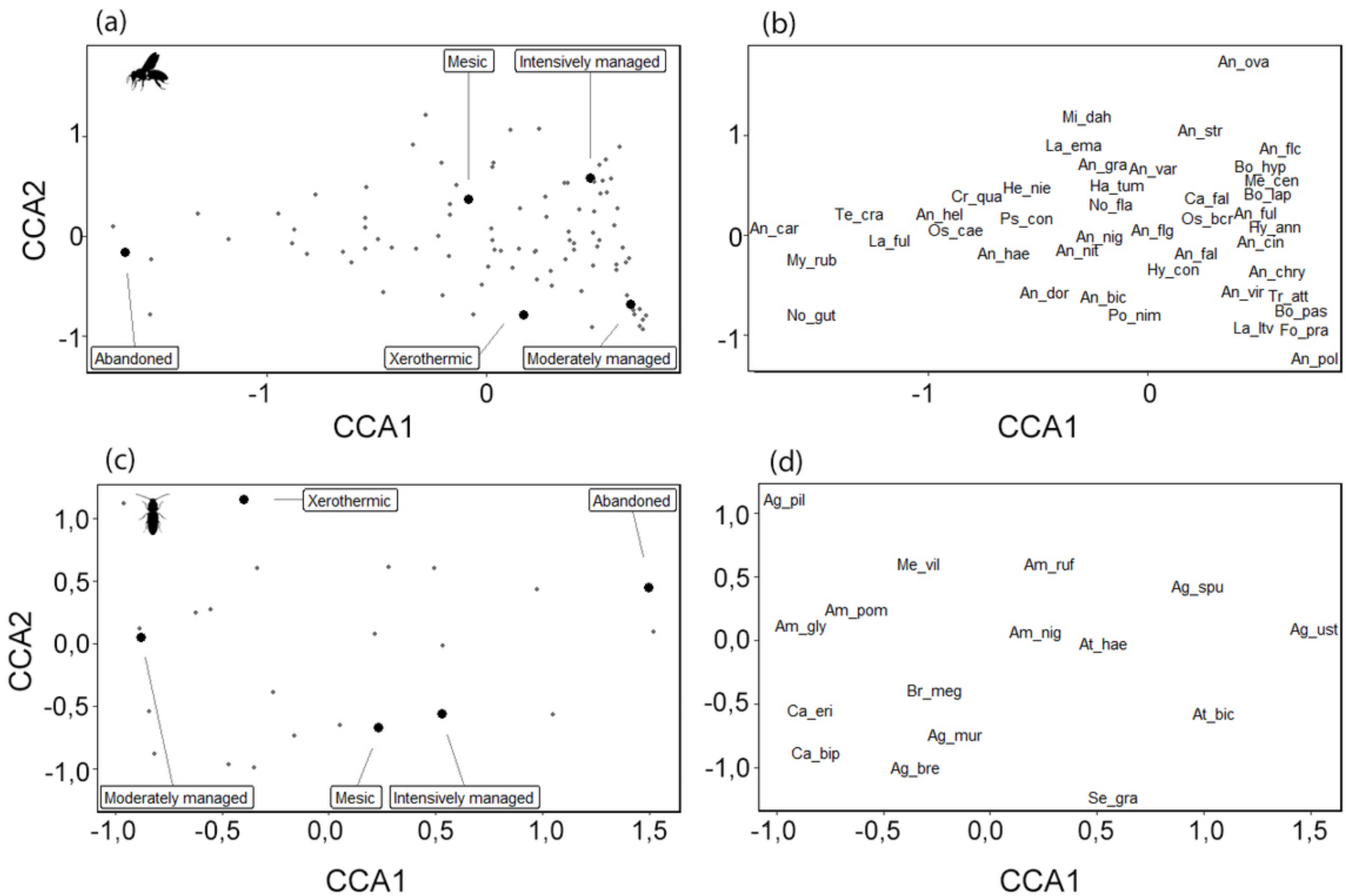

Figure 3

Species composition relationships with the intensity of management and type of biotope for (a, b) hymenopterans (Hymenoptera) and (c, d) beetles (Coleoptera) in Prague (Czech Republic) traditional fruit orchards. Plots based on CCA on the left show individual species distributions (small dots) in relation to the treatment categories (large dots), and species abbreviations (two letters from the Latin genus and three from the species name) are visualized without categories on the right. Abbreviations of species names in alphabetical order are as follows: (b) An_cin = Andrena cineraria; An_dor = Andrena dorsata; An_fal = Andrena falsifica; An_flc = Andrena floricola; An_flg = Andrena florivaga; An_ful = Andrena fulvago; An_gra = Andrena gravida; An_hae = Andrena haemorrhoa; An_hel = Andrena helvola; An_chry = Andrena chrysosceles; An_nig = Andrena nigroaenea; An_nit = Andrena nitida; An_ova = Andrena ovatula; An_pol = Andrena polita; An_str = Andrena strohmella; An_var = Andrena varians; An_vir = Andrena viridescens; Bo_hyp = Bombus hypnorum; Bo_lap = Bombus lapidarius; Bo_pas = Bombus pascuorum; Ca_fal = Camponotus fallax; Cr_qua = Crossocerus quadrimaculatus; Fo_pra = Formica pratensis; Ha_tum = Halictus tumulorum; He_nie = Hedychrum niemelai; Hy_ann = Hylaeus annularis; Hy_con = Hylaeus confusus; La_ema = Lasius emarginatus; La_ful = Lasius fuliginosus; La_ltv = Lasioglossum lativentre; Me_cen = Megachile centuncularis; Mi_dah = Mimumesa dahlbomi; My_rub = Myrmica rubra; No_fla = Nomada flavoguttata; No_gut = Nomada guttulata; Os_bcr = Osmia bicornis; Os_cae = Osmia caerulescens; Po_nim = Polistes nimpha; Ps_con = Psenulus concolor; Te_cra = Temnothorax crassispinus; Tr_att = Trypoxylon attenuatum (d) Ag_bre = Agriotes brevis; Ag_mur = Agrypnus murinus; Ag_pil = Agriotes pilosellus; Ag_spu = Agriotes sputator; Ag_ust = Agriotes ustulatus; Am_gly = Ampedus glycereus; Am_nig = Ampedus nigroflavus; Am_pom = Ampedus pomorum; Am_ruf = Ampedus rufipennis; At_bic = Athous bicolor; At_hae = Athous haemorrhoidalis; Br_meg = Brachygonus megerlei; Ca_bip = Calambus bipustulatus; Ca_eri = Cardiophorus erichsoni; Me_vil = Melanotus villosus; Se_gra = Selatosomus gravidus

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