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Faculty of Science

**The effect of different management strategies on
the dynamics of saproxylic insect habitats**

Ph.D. Thesis

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■ Annotation

The thesis concerns studies on habitats utilized by insects associated with deadwood. It presents a review of current issues in the conservation of saproxylic biodiversity. The effects of active intervention on temperate lowland woodland habitats, such as pollarding or coppicing, are evaluated in terms of their suitability for saproxylic communities and other groups. Further, the importance of open-grown trees for saproxylic diversity is assessed.

■ Declaration [in Czech]

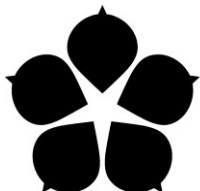
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České Budějovice, 1. 7. 2016

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Pavel Šebek

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■ List of papers and author's contributions

The thesis is based on the following papers (listed chronologically):

- I. **Sebek, P.**, Altman, J., Platek, M. & Cizek, L., 2013. Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. *PLoS One* 8, e60456. (IF = 3.23)
[Pavel Šebek designed the study together with LC, he performed the fieldwork, analyzed the data, and wrote the manuscript with LC and JA.]

- II. **Sebek, P.**, Bace, R., Bartos, M., Benes, J., Chlumska, Z., Dolezal, J., Dvorsky, M., Kovar, J., Machac, O., Mikatova, B., Perlik, M., Platek, M., Polakova, S., Skorpik, M., Stejskal, R., Svoboda, M., Trnka, F., Vlasin, M., Zapletal, M. & Cizek, L., 2015. Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests. *Forest Ecology and Management* 358, 80–89. (IF = 2.66)
[Pavel Šebek performed sampling of several insect groups with JB, MPE, MPI and MZ, he analyzed the data, and wrote the manuscript with LC and JD; the study was designed by LC.]

- III. **Sebek, P.**, Vodka, S., Bogusch, P., Pech, P., Tropek, R., Weiss, M., Zimova, K. & Cizek, L. Open-grown trees as key habitats for arthropods in temperate woodlands: the diversity, composition, and conservation value of associated communities. (Manuscript)
[Pavel Šebek analyzed the data, and wrote the manuscript with LC and RT; the study was designed by LC and SV.]

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Lukáš Čížek, the supervisor of this Ph.D. thesis and co-author of all presented papers, fully acknowledges the major contribution of Pavel Šebek in all presented papers.

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Introduction

Introduction

1. Saproxylic insects in the European landscape

Saproxylic insects depend on dead or dying woody material at some stage of their life cycle (Speight 1989; Dajoz 2000; Alexander 2008a), and constitute a large part of woodland biodiversity (Stokland et al. 2012). They contribute to decomposition as secondary wood decayers and they thus help facilitate the process of nutrient recycling in woodland ecosystems. Members of several insect orders are saproxylic. The three most diverse orders among saproxylics are beetles (Coleoptera), flies (Diptera), represented mostly by crane flies (Tipulidae) and hoverflies (Syrphidae), and bees and wasps (Hymenoptera), represented mostly by the parasitoid families Braconidae and Ichneumonidae, the wood-boring sawfly families Xiphidriidae and Sciricidae, and secondary hole nesting Crabronidae and Vespidae. Moreover, deadwood-dependent species can be found in other insect groups, such as snakeflies (Rhaphidioptera), true bugs (Heteroptera), and moths (Lepidoptera). Saproxylic beetles are considered the most diverse group of saproxylic insects. Around 25% of beetle species are deadwood-dependent; for instance ca. 1400 saproxylic beetle species are found in northern Europe (Stokland et al. 2012), ca. 2200 species occur in France (Bouget et al. 2008), ca. 1600 species in Germany (Möller 2009), and probably around 2000 species in Central Europe. The richness of saproxylic Diptera and Hymenoptera are yet to be quantified, but their richness might even be as high as that of beetles (Stokland et al. 2012). Beetles, due to their great richness and abundance, and well-known taxonomy, are by far the most studied group of saproxylic insects. The relationship between habitat characteristics and the biology or diversity of saproxylics are therefore mostly based on beetles, although the work is carried out also on other insect groups (Hilszczański et al. 2005; Fayt et al. 2006; Ricarte et al. 2009; Quinto et al. 2012; Ramírez-Hernández et al. 2014). Below, I list several environmental factors considered to be the main determinants of saproxylic beetle biodiversity in Europe.

As saproxylic insects are dependent on deadwood as a substrate, the quality and the amount of deadwood seem to be the most important factors driving biodiversity of saproxylic organisms. Several studies have found significant correlations between the richness of saproxylic beetles and the quantity of local available deadwood (Martikainen et al. 2000; Müller et al. 2008; Franc et al. 2007). By contrast, some studies show no relationship between the amount of deadwood and saproxylic beetle diversity (Schiegg 2000; Jukes et al. 2002). A recent meta-analysis by Lassauce et al. (2011) indicated that the species richness of saproxylic organisms is indeed positively correlated with the total amount of available deadwood. However, the correlation was rather weak suggesting that factors other than the amount of deadwood in the local area are helping drive saproxylic insect biodiversity. They also showed that the correlation between the richness of saproxylic organisms and the amount of deadwood was stronger for boreal forests than for temperate forests. This is mostly due to the different environmental characteristics of the two types of forests, but also to a great extent by the history of forest management, since the temperate biome in Europe has been under significant human influence since the Neolithic.

Deadwood diversity (i.e. diversity in type, size and decomposition stage of local deadwood), is often found to be an important factor influencing saproxylic beetle biodiversity (Økland et al. 1996; Jonsell & Weslien 2003; Hjältén et al. 2007; Brin et al. 2009; Djupström et al. 2010; Bouget et al. 2013). Indeed, it is often more important than the total amount of local deadwood because the more diversified the substrate is in physiological conditions, the wider the range of niches that are on offer (Vanderwel et al. 2006; Stokland et al. 2012).

Recently, the scientific community and conservation workers have begun to acknowledge the importance of habitat trees for saproxylic insect biodiversity (Bouget et al. 2013; Bütler et al. 2013; Bouget et al. 2014a; Müller et al. 2014). Habitat trees are defined as standing live or dead trees that provide deadwood microhabitats, such as hollows, patches without bark, large dead branches, cracks, epiphytes, fruiting bodies of fungi, or sap runs (Bütler et al. 2013). They are usually trees of large size or age, and are considered as attributes of old-growthness because they are common in old-growth forest stands (Bauhus et al. 2009) where they increase the value of such forests for biodiversity (Lombardi et al. 2008; Müller et al. 2008; Bouget et al. 2014b). However, habitat trees do

not only occur in old-growth forests, but are also often found in younger forest stands where some trees were retained during logging (Bouget et al. 2014a), in neglected coppice woods, or, often in great abundance, in ancient wood-pastures (Alexander 1998). A few habitat trees (or even one) present in a stand can maintain high saproxylic insect biodiversity, even in forests with low amounts of deadwood on the ground. This can partially explain the low correlation between the amount of deadwood and the richness of saproxylic beetles in temperate woodlands found by Lassauce et al. (2011). Yet some other important factors must also be considered.

One important factor for determining saproxylic beetle biodiversity is stand openness or exposure of deadwood to the sun (Jonsell et al. 1998; Ranius & Jansson 2000; Franc & Götmark 2008; Vodka et al. 2009; Horák & Rébl 2013; Vodka & Cizek 2013; Bouget et al. 2014a; Horak et al. 2014). In general, stands with open-canopy conditions are richer in saproxylics, often even in red-listed species, than shaded, closed-canopy stands. Greater openness to sun offers warmer conditions that are more suitable for larval development (Albert et al. 2012; Siitonen & Ranius 2015), while openness also facilitates the movement of insects through the landscape. Warmer conditions can even compensate for lower amounts of deadwood and sustain a high richness of beetles (Müller et al. 2015a). However, warmer conditions may dry out deadwood (Siitonen & Ranius 2015), which may inhibit the growth of wood-decaying fungi, and therefore potentially limit the occurrence of some mycetophagous species. Indeed, preferences for sun-exposed habitats are less pronounced in southern Mediterranean regions compared to the cooler northern parts of Europe (Chiari et al. 2012).

Another important influence on saproxylic beetle assemblages is tree species composition. Beetle species differ in their host preferences. Primarily, there is a sharp division between communities associated with conifers and those associated with broadleaved species (Stokland et al. 2012). About 60% of European saproxylic beetles prefer broadleaved trees, ~23% prefer coniferous trees, and only ~11% of species are capable of exploiting deadwood of both tree types (combined data from northern Europe and Germany; Köhler 2000; Dahlberg & Stokland 2004). Preferences also differ between individual tree species, although these differences are relatively minor (Milberg et al. 2014; Müller et al. 2015b). Of all European trees, oaks (*Quercus* sp.) host the greatest

number of associated species (Brändle & Brandl 2001; Whitehouse & Smith 2010). Since a majority of saproxylic beetles prefer broadleaved trees, and warmer conditions generally have a positive effect on the biodiversity of saproxylic beetles, it is not surprising that the greatest richness of saproxylic beetles in Europe can be found in lowland deciduous forests (Müller et al. 2015a; Weiss et al. 2016).

To summarize, the local richness and composition of saproxylic insects is dependent on numerous ecological factors that often interact in complex ways. These must be taken into account in conservation biology in order to properly preserve the biodiversity of saproxylic insects. To a great extent, the continual loss of biodiversity in Europe (EEA 2009) is caused by extinctions of forest associated species due to modern forestry practices and insufficient conservation measures. If we want to better understand current conservation issues, in particular why the biodiversity of forests is declining, we must understand the conditions of the habitats in which saproxylic species evolved. A first step should be to examine the history of European woodlands.

2. A brief history of European woodlands

2.1. Early Holocene woodlands

Although some saproxylic species may have persisted in small patches of woodland refugia during the last glacial maximum (around 20 000 years BP), the major expansion of saproxylic insects in Europe is associated with the spread of trees back north to the continent during the latest deglaciation (after ca. 10 500 BP). The main forest zones, the southern sclerophyllous Mediterranean-like forests, the broadleaved deciduous forests of central Europe, and the northern boreal mixed and coniferous forests, were largely established in the Late Atlantic period, around 6500 BP, when the trees, due to the warmer climate, reached their greatest extension (Huntley 1990; Kirby & Watkins 2015).

What the forests were like in the early Holocene, before the onset of strong human influence in the Neolithic era, remains a debated topic. Pollen analyses

indicate that early Holocene forests were rather poor in tree-species diversity, being dominated by oak (*Quercus*), hazel (*Corylus*), lime (*Tilia*), and elm (*Ulmus*) (Bakels 1992). Such hypotheses are supported by analyses of charcoal from early-Neolithic human settlements (Jansen & Nelle 2014; Salavert et al. 2014), where ash (*Fraxinus*) was also one of the most important tree species. Great uncertainty, however, still remains about whether the woodland canopy was closed or open (Svenning 2002; Mitchell 2005; Kreuz 2008). The formerly widely-accepted view that Europe was covered by closed-canopy old-growth forests (Iversen 1960; Iversen 1973) has been challenged by the 'open woodland hypothesis' (Bengtsson et al. 2000; Vera 2000). The open woodland hypothesis is principally based on the fact that oak and hazel are light-demanding species that require canopy gaps for regeneration, and thus their dominance in palynological records was conditioned by the prevalence of open woodland canopies in the past. Vera (2000) proposed that grazing by large herbivores, such as aurochs, bison, wild horses, and red deer, was the key factor in maintaining a landscape composed of a mosaic of closed-canopy woodland groves, open parkland, and regenerating scrub. It is important to note that Vera's model is confined to the geographical region lying within the principal temperate zone of Europe north of the Alps.

The importance of large herbivores in driving the dynamics of primeval woodlands has been questioned several times. Firstly, Mitchell (2005) found that there was no significant difference in the relative proportions of oak and hazel in the primeval forests of continental Europe and Ireland, where large herbivores were absent. On the other hand, this might be explained by competition with lime (Birks 2005). Lime was absent from post-glacial Ireland but was abundant over much of lowland temperate Europe, and thus it is likely that oak had a wider realized niche in Ireland than in central Europe. Secondly, the presence of large herbivores in the landscape should be associated with high abundances of dung beetles in the fossil record. Analyses of fossil beetles show high abundances of wood or tree-dependent beetles, including many light-demanding species that favour open canopy conditions (Alexander 2005), and also a high abundance of open ground taxa (Whitehouse & Smith 2004). However, higher abundances of dung beetles only start to appear after around 6000 BP (Whitehouse & Smith 2010), which coincides with the arrival of Neolithic farming communities. Hence, the favoured hypothesis is that the

impact of large herbivores on forests was restricted only to some parts of lowland Europe (Whitehouse & Smith 2010; Salavert et al. 2014), and that other factors, such as windthrows or fires, were largely responsible for natural forest dynamics and the prevalence of open spaces (Bengtsson et al. 2000; Niklasson et al. 2010, Adámek et al. 2015). Lastly, another view is that humans had a local impact on forests earlier than formerly supposed because even Mesolithic hunter-gatherers probably used slash-and-burn practices to create open space for fruit trees, or even to attract herds of large herbivores to regenerating grasslands (Innes & Blackford 2003; Salavert et al. 2014).

2.2. Human impacts on woodland habitats

Since the Neolithic, the human impact on European woodlands has rapidly increased, initially in the lowlands but spreading also to upland regions. The original forest cover has been converted to arable land and pastures, or has been cut for the supply of firewood and construction timber (Haneca et al. 2005). By the Early Middle Ages, areas unaffected by human activity were virtually non-existent in the lowlands (Szabó 2009). Traditional agro-silvicultural land-use systems, particularly wood-pasture and coppicing, had a great impact on the structure and dynamics of wooded habitats (Buckley 1992; Kirby & Watkins 1998; Rackham 2003; Kirby & Watkins 2015), and thus also directly affected saproxylic insect biodiversity.

Wood-pastures are among the oldest land-use types in Europe (Rackham 1998; Rackham 2003; Bergmeier et al. 2010; Hartel et al. 2013; Plieninger et al. 2015). Wood-pasturing offered a valuable combination of keeping livestock for food and providing a supply of wood. The concept of wood-pastures is broad (Rackham 1998; Hartel et al. 2013), but is characterized by open grasslands with more or less scattered trees (sometimes pasture woodland is used for sparser situations). A variety of domestic animals (cattle, sheep, goats, pigs, or horses) were pastured in common woodlands. These livestock also differed in their effect on woody plants (Vera 2000). In the past, pigs were particularly important thanks to their flexible diet (Hooke 2013; Jørgensen 2013). For exchange of a fee (called pannage), swineherds took their pigs to the woods to forage on acorns or beech-mast, which provided a high caloric food source in

the autumn. As acorn production occurs most heavily on branches exposed to light (Johnson et al. 2002), oaks in the common woodlands were often managed in open canopy conditions so that they developed large crowns. The practice of pannage was so common that in many places the size of a forest was measured in the number of pigs it could feed (Dirkx 1998; Hooke 2013; Jørgensen 2013). Furthermore, a growing desire among medieval kings and nobles for hunting led to the establishment of numerous deer-parks, enclosed areas of private woodlands designated to maintain high densities of game (Hooke 2013; Fletcher 2015). The densities of game were usually so high that they prevented trees from regenerating, and deer-parks were thus open, park-like habitats.

Wood-pastures and medieval deer-parks were mosaics of open grasslands with open-grown solitary trees and groves, which thus represented something quite similar to Vera's conception of primeval forests (Vera 2000). Such structural heterogeneity offered niches for a wide range of organisms, and wood-pastures are therefore biologically rich in plants (Bergmeier et al. 2010), butterflies (Benes et al. 2006), and birds (Hartel et al. 2014). Wood-pastures provide an especially suitable habitat for saproxylic insects. Large, old, open-grown trees with well developed tree crowns act as habitat trees (Bütler et al. 2013; Siitonen & Ranius 2015), offering valuable deadwood microhabitats such as large sun-lit dead branches or tree hollows. Trees in wood-pastures were often managed by pollarding or shredding, a repetitive pruning of branches that provided either firewood or fodder for animals (Rackham 1998; Petit & Watkins 2003; Jørgensen 2013; Plieninger et al. 2015). Pollarding and shredding prolonged the lives of trees, so trees could have persisted for centuries, maintaining temporal continuity in the availability of deadwood (Rackham 1998; Read 2000; Siitonen & Ranius 2015). The fact that in wood-pastures old trees are in close proximity to grasslands is particularly important for saproxylic insects such as jewel beetles (Buprestidae), longhorn beetles (Cerambycidae), bees and wasps (Hymenoptera), and hoverflies (Syrphidae), which require deadwood for larval development or nest sites, but also nectar bearing flowers to feed on in the adult stage (Fayt et al. 2006; Müller et al. 2008; Lachat et al. 2013). In addition, the open canopy conditions and vertical openness of wood-pastures allow for relatively easy movement of species, even for those with low dispersal abilities. Pasture woodlands are thus rich in deadwood-dependent organisms (Alexander 1998; Horak et al. 2014).

Similar conditions to those found in wood-pastures were also found in traditional fruit or chestnut orchards (Alexander 2008b; Bergmeier et al. 2010). Fruit trees need an open canopy for optimal fruiting and flowering, and old fruit trees are usually more productive than newly-planted ones. Thus traditional orchards were typically concentrations of open-grown trees in different stages of growth, with abundant old trees, and a matrix of grasslands (Lush et al. 2005; Alexander 2008b; Plieninger et al. 2015). The open structure of the orchards used to be maintained by extensive grazing by livestock, mostly sheep. Moreover, the trees were often regularly pruned to develop a desirable crown shape, and this resulted in inflicting wounds on bark or branches. The presence of old trees with cavities or bare wood without bark was common and traditional orchards thus offered sun-lit substrates and important microhabitats for deadwood-dependent organisms like saproxylic invertebrates or epiphytic lichens (Lush et al. 2005; Vignon 2006; Dubois et al. 2009; Horak et al. 2013).

In addition to wood-pastures, deer-parks, and orchards, a great number of forests were managed as coppice woods (Rackham 2003; Szabó 2009; Müllerová et al. 2015). Coppice is a forest crop raised from the shoots sprouting from cut stumps (called stools), or from the roots of the previous crop (Evans 1992). Coppice stands usually consisted of several even-aged compartments of ca. 0.5-10 ha (Peterken 1992) where each compartment was harvested on a short rotation cycle (7-30 years) (Szabó 2009; Müllerová et al. 2015). The number of compartments usually corresponded to the length of the rotation cycle, so that every year one compartment could be harvested, providing a regular supply of firewood. Two main types of coppice woods are distinguished; simple coppice, which consists entirely of even-aged coppice compartments, and coppice with standards, in which timber sized trees (called standards) are grown over a coppice crop (Evans 1992). Standards were usually retained for a period of 3-8 coppice cycles. Coppicing became increasingly popular throughout the Bronze Age and during the Roman times. By the Middle Ages it was almost universal, even in large woodland areas (Evans 1992; Peterken 1992; Gulliver 1998; Rackham 2003; Haneca et al. 2005; Müllerová et al. 2015). Coppices were dominated by light demanding species like oak (which was also the commonest standard species) and ash, or by shrub trees such as hazel (Evans 1992; Peterken 1992). Due to the rotation system, coppice woods maintained a mosaic of habitats in different stages of forest succession with an

unnaturally high amount of temporary open space and opportunities for early successional species (Peterken 1992; Thomas 1998; Müllerova et al. 2015). Moreover, the movement of light-demanding species within the stands was often facilitated by the presence of rides, broad roads separating compartments that were used during the harvest and kept open at all times (Peterken 1992; Thomas 1998). The conditions in coppice woods therefore support a high diversity of light-demanding plants and animals (Benes et al. 2006; Dolek et al. 2009; Hédli et al. 2010). For instance, community studies show that the richness of butterflies peaks 2-3 years after a coppice harvest (Warren & Thomas 1992), while bird richness was found to be highest 5-7 years after harvest when shrub vegetation had developed (Fuller & Henderson 1992). The importance of open stages within coppices has also been documented for moths (Bolz 2008) and flies (von der Dunk & Schmidl 2008).

The historical importance of coppice woods for saproxylic insects is questionable, principally due to the presumed lack of deadwood. In medieval times, the coppice was harvested on a fairly short rotation (4-8 years), and the standards were felled when they were 25 to 70 years old (sometimes up to 100 years) (Gulliver 1998). By the 19th century, coppice rotation increased to 30-40 years (Szabó 2010; Müllerova et al. 2015). Standards were also harvested at increased ages, but they were still harvested when relatively young and very few trees reached senescence. Therefore, very large, old trees were usually absent from coppices, or confined to margins (Peterken 1992). Fallen wood was usually removed as a valuable resource, and any deadwood that remained in situ was of small diameter and thus likely to decay quickly if not collected as litter (Kirby 1992). On the other hand, the lack of fallen dead wood might have been mitigated by the presence of coppice stools. These could be centuries old with rotten cores, providing deadwood and basal cavities for saproxylic species. In the past, trees were felled using only axes (crosscut saws, as tools for felling trees, were not introduced until 1880), and the stools were thus usually high enough (up to 0.8 m) to provide sun-lit deadwood. These old stools can even support populations of some veteran tree specialists (such as *Cerambyx cerdo*; L. Čížek, *pers. obs.*). Similarly, some very large trees may have remained untouched because they were too difficult to fell with axes. Despite these circumstances, authors usually claim that traditional coppices were less rich in saproxylic insects than pasture woodlands (Alexander 1998; Lachat et al. 2013).

In summary, European woodlands under the influence of traditional silvicultural practices were mostly mosaics of habitats, with open-canopy conditions that favoured light-demanding species and offered suitable substrates for saproxylic insects, as well as shady habitats like coppices in later stages of forest succession. The situation, however, changed rapidly with the industrial and agricultural revolutions in the second half of the 18th century.

2.3. Modern changes to woodland habitats

The rapid increase in human population in Europe has led to significant social and cultural changes. Changes in forest use were similar over most of Western and Central Europe driven by the industrial revolution that directly affected demands for raw materials (Thomas 1998; Bürgi 1999; Szabó 2013; Savill 2015).

Due to the increase in demand for construction timber, various traditional woodland habitats were abandoned or transformed under different managed systems (Peterken 1992; Gulliver 1998; Bürgi 1999; Müllerova et al. 2015). Since 1800, the value of coppice woods has declined (Gulliver 1998). They were gradually replaced by coppice with standards woods or by high forests. Bürgi (1999) describes the decline in the percentage of coppice and coppice with standards woods in Swiss lowlands over the period 1820-1985. In 1820, each management type constituted about 30% of local woodland habitats. However, simple coppice almost disappeared from the area by 1925, whereas most of the decline of coppice with standards woods occurred after the Second World War. By 1985 more than 85% of all the woodlands in the Swiss lowlands were composed of high forests (Bürgi 1999). The interest in increasing growth stock also had a direct influence on traditional activities, such as pasturing and litter collecting in woodland habitats. Since about 1800, these activities were largely restricted (although usually not completely prohibited), because they were deemed to be damaging to forests. Pasturing had a detrimental effect on tree encroachment and sapling growth, and litter collecting led to the impoverishment of forest soils (Thomas 1998; Bürgi 1999; Szabó 2013).

In the Czech Republic, the transition from traditional forest use to intensive high forest management was enforced by the “Forest Code”, special forest act issued in 1754 by the Habsburg monarchs (Szabó 2013). Its intent was to increase timber production and to secure strategic supplies for the future. This basically marked the beginning of organized forestry in the Czech Republic. The customary rights of forest owners were largely suppressed as the management of forests followed new rules (Szabó 2013). For instance, new plantations were established on formerly non-wooded areas or in woodlands which were until then grazed by livestock.

The demand for high-quality construction timber also led to a gradual shift in species composition towards a greater proportion of conifers, mainly spruce, due to their fast growth and relatively straight-grown trunks (Bürgi 1999; Savill 2015).

Due to the abandonment of coppicing and restricted wood-pasturing, open woodlands began to vanish from the European landscape. This decline was hastened by the simultaneous agricultural revolution. Livestock were fed indoors even during the summer, and the scattered trees of the ancient wood-pastures were often removed in order to increase the productivity of meadows or intensive pastures (Bürgi 1999; Plieninger & Bieling 2013) leading to the disappearance of open-grown, veteran trees. Changes to woodland systems then escalated during the mid 20th century. A steep decline in open woodland habitats occurred after fossil fuels became widely available. Coppicing, until then still practiced as a source of fuelwood or charcoal, lost its importance, and by the end of WW II it was almost completely abandoned (Bürgi 1999; Müllerova et al. 2015). In only a few decades, whole landscapes once covered with open woodlands were transformed into closed-canopy forests (Miklín and Čížek 2014). In the Czech Republic, the situation after WW II became particularly difficult. Due to expropriation and nationalization of land under communist rule, private ownership of forests ceased to exist and all the forest land became state-owned, being managed in an extremely intensive way. The collectivization of agricultural land led to the deliberate removal of open-grown trees that formerly defined field borders between land-owners, and acted as important refuges for some saproxylic insects. Spruce plantations were widely established even in lowland areas.

Eventually, the intensive high forest management practice indeed increased supplies of timber. Forest ecosystems today cover 32% of Europe's land surface (FOREST EUROPE, UNECE & FAO 2011). In the Czech Republic, forests cover 34% (~ 2 665 000 ha) of the area, compared to around 25% in 1780 (ČSÚ 2015).

From an ecological point of view, structural changes to woodlands in modern times have had immense consequences for biodiversity in European forests. Species composition has shifted from light-demanding and oligotrophic species towards more generalist, mesic and shade-tolerant species (Hédl et al. 2010; Kopecký et al. 2013; Saniga et al. 2014). Species of open woodlands, once common, have become endangered or even gone extinct in some areas (Bergman 2001; van Swaay et al. 2006; Nieto & Alexander 2010). Under high forest management, very few trees are not harvested, so few reach biological maturity to serve as habitat trees or support rich communities of saproxylic insects. This situation contrasts with the fact that deadwood as a substrate is not that rare. The amount of deadwood lying in forests is very likely to be higher than ever in the past, as a result of declining demand for firewood as well as a decline in litter collecting after WW II (Bürgi 1999; Szabó 2013; Lachat et al. 2013). The paradox exists then, that modern forests are rich in deadwood, but are not favourable to saproxylic biodiversity, because the deadwood lies mostly in shady conditions.

In the next section, I illustrate current attitudes to the conservation of saproxylic insects.

3. Current conservation issues

Currently, there are two contrasting views on the conservation of forest habitats; the minimal intervention approach (sometimes called 'hands-off' management), and the active conservation management approach.

The minimal intervention approach is mainly based on the idea that forests designated for conservation should be left unmanaged in order to protect natural forest dynamics. In most commercial forests, logging systematically eliminates 'defective' trees with low economic value, which is often the case for trees

bearing deadwood microhabitats or those with a high potential to develop them (Bütler et al. 2013). With respect to saproxylic beetles, the general idea of the minimal intervention concept seems promising as deadwood accumulation in unmanaged forests increases with time since last harvest (Vandekerkhove et al. 2009). Similarly, unmanaged stands may develop important attributes of old-growthness (Bauhus et al. 2009; Vandekerkhove et al. 2011). Numerous studies comparing the biodiversity of unmanaged and managed forests have concluded that minimal intervention favours the biodiversity of saproxylic beetles (Martikainen et al. 2000; Müller et al. 2007; Lassaue et al. 2013). However, differences in the richness of saproxylic beetles between unmanaged and managed stands were often rather small (Paillet et al. 2010; Bouget et al. 2014b), indicating either that the studied unmanaged forest stands were relatively young, or that only a small part of the saproxylic beetle community benefited from hands-off management. Thus, in comparison to high forest management, forests set aside for long enough may indeed increase in potential to harbour richer saproxylic insect communities.

In Europe, forest reserves under various protection regimes account for about 10% of the total forest area (Bollman & Braunisch 2013). Currently, about 1.7% of the total forest area are strict forest reserves where human intervention is limited or totally banned (COST Action E4 2000; Parviainen et al. 2000), and a preference of many conservationists is to increase this percentage (Schulze et al. 2014). The concept of strict forest reserves or set-aside forest stands, however, has some limitations. Firstly, questions remain as to the extent that natural dynamics in reserves are able to maintain an open structure of the canopy, which is one of the most important factors for saproxylic insects. It is supposed that natural dynamics can generate or maintain open spaces only if the reserve is sufficiently large (opinions on the minimum size range from 40 km² to 120 km²) (Schulze et al. 2014). However, most strict forest reserves in Europe are too small to allow this (Götmark et al. 2015). Secondly, most forests designated for strict protection are middle-aged, and have typically undergone extensive secondary succession from historically more open habitats (Miklín & Čížek 2014; Götmark et al. 2015). As described above, European forests have largely been influenced by human practices that maintained open structure of the woodlands. Today, primeval forests that have

never been altered by humans account for a maximum of just 0.3% of currently forested areas (FOREST EUROPE, UNECE and FAO 2011).

A growing number of studies in recent years have pointed to the importance of traditional woodland habitats for biodiversity conservation (Benes et al. 2006; Hédli et al. 2010; Bollman & Braunisch 2013; Horák et al. 2013; Ramírez-Hernández et al. 2014; Plieninger et al. 2015), principally because they often harbour rich communities of insects, and also provide refuge for endangered fauna. This is well illustrated by the current distributions of a few emblematic saproxylic species listed in the European Union's 'Habitats Directive' (Council of the European Communities 1992), i. e. species with special conservation consideration. The hermit beetle (*Osmoderma eremita*; Scarabaeidae), the great capricorn beetle (*Cerambyx cerdo*; Cerambycidae), the violet click beetle (*Limoniscus violaceus*; Elateridae), and the stag beetle (*Lucanus cervus*; Lucanidae) occur mainly in habitats that are or used to be managed by traditional silvicultural practices: wood-pastures, traditional orchards, former coppice woods, game reserves, stands of pollard willows, parks and tree alleys along roads or watercourses (Ranius et al. 2005; Vignon 2006; Jonsell 2011; Albert et al. 2012; Gouix et al. 2012). The presence of these species is connected with the availability of open-grown veteran trees (Siitonen & Ranius 2015), which are common in these traditional habitats (Bütler et al. 2013), but rarely found in modern managed forests or in forest stands subjected to minimal intervention. Therefore, the general idea of active conservation management is that in order to effectively conserve communities of saproxylic insects (but also another groups like butterflies, plants, etc.), traditional habitats should be actively restored and maintained.

With respect to saproxylic insects, conservation management should principally be aimed at ensuring an open canopy structure within woodlands; by for example, substantial thinning, wood pasturing or coppice with standards management. Restoration should primarily be targeted at locations where forest structure was open until recently. Veteran trees in particular, are important for the biodiversity of saproxylic species. The practice of removing these trees from the countryside because they are 'dangerous' or 'defective' should be discouraged (Alexander 1998; Bütler et al. 2013). Their persistence should instead be ensured by arboricultural care, such as crown reduction (Read 2000; Fay 2011). Restoration of pollarding, which tends to prolong a tree's life, has

been tried successfully on old trees even after several decades without cutting (Read et al. 2010). In former pasture woodlands where only very old trees are present, planting young trees will ensure the longterm availability of trees in future. Unfortunately wood-pastures, to date, are still facing the effect of two contrasting land-use changes; abandonment (reduction or exclusion of livestock grazing), and intensification (overgrazing and wood overexploitation) (Bugalho et al. 2011; Hartel et al. 2013; Plieninger et al. 2015). Recently, interest in reintroducing coppicing in order to protect endangered species has been slowly increasing (Leigl & Dolek 2008; Fuller 2013; Vild et al. 2013; Müllerová et al. 2014). However, where coppicing is reintroduced for nature conservation, the retention of at least some of the deadwood accumulated during periods of neglect should be considered to ensure abundant substrates for saproxylic insects (Kirby 1992). Similarly, the revived interest in biofuel energy has led to an appreciation of coppices as a sustainable source of energy (Fuller 2013; Müllerová et al. 2015; Kadavý et al. 2011). Although, unfortunately in practice, coppices for biofuel are often established at new locations, rather than at sites of old abandoned coppices that may still harbour some endangered species.

These are general insights into the current conservation of saproxylic insects. In practice, proper conservation management is largely dependent on the requirements of the focal species, as well as on site-specific characteristics.

4. Aims and scope of this thesis

The aim of this thesis is to contribute to our knowledge about the role of traditional woodland habitats in supporting the biodiversity of saproxylic insects and other associated arthropod groups. The individual chapters cover studies on pollard trees, former coppice forests, solitary trees in former wooded meadows, and their associated saproxylic species. All of the studies presented here were carried out in South Moravia, in the Czech Republic.

Chapter I presents a study of the effect of pollarding on the formation of hollows in trees. Pollarding is a pruning technique in which branches of a tree are regularly cut to provide firewood or fodder for animals. Branches higher than two metres above the ground were usually cut in pollard trees to prevent

livestock from feeding on resprouting shoots. Pollard trees often form hollows where wounds were inflicted by regular pruning. Pollarding together with shredding, a similar pruning technique in which branches are cut even higher up on the tree, used to be widely practiced in ancient wood-pastures, and therefore such trees were a common feature of traditional woodlands. The main aim of the study is to describe to what extent pollarding increases the probability of hollow formation, and how it can serve as a management tool in the conservation of saproxylic species or in restoration ecology.

Chapter II examines the effect of artificial canopy opening on communities of saproxylic and other insects, birds, reptiles and plants. This experimental study was carried out in the oak-dominated forests of Podyjí National Park, which were managed by coppicing and livestock grazing until the 1950s. The abandonment of these traditional practices has led to an increase in canopy closure following secondary succession, and to a disappearance of open forest stands from most of the area. Recently, twelve small experimental clearings were created in the core zone of the park. This study observes plant and animal communities in the clearings in the first season after their creation, and compares them with the assemblages of control habitats, such as closed-canopy forests, forest edges, and remnants of open forests. An emphasis is also placed on the preferences of threatened species of particular groups of organisms, and the effect of connectivity between clearings and open habitats is also discussed.

Finally, Chapter III focuses on the role of open-grown, solitary trees in supporting communities of arboricolous insects, including saproxylic species, and spiders. Numerous studies often mention the importance of open-grown veteran trees for the biodiversity of saproxylic organisms. Our study was carried out in South Moravian floodplain forests that used to be composed of large areas of wood-pastures that still contain some solitary trees in wooded meadows. This study describes communities of insects and spiders on solitary trees and compares these assemblages to those in trees growing at forest edges and in the interior of closed-canopy forests. The conservation value of particular habitats are also assessed, as well as the current conservation issues associated with solitary trees.

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Chapter I

**Is active management the key to the conservation
of saproxylic biodiversity? Pollarding promotes
the formation of tree hollows**

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Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows

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Abstract

Trees with hollows are key features sustaining biodiversity in wooded landscapes. They host rich assemblages of often highly specialised organisms. Hollow trees, however, have become rare and localised in Europe. Many of the associated biota is thus declining or endangered. The challenge of its conservation, therefore, is to safeguard the presence of hollow trees in sufficient numbers. Populations of numerous species associated with tree hollows and dead wood are often found in habitats that were formed by formerly common traditional silvicultural practices such as coppicing, pollarding or pasture. Although it has been occasionally mentioned that such practices increase the formation of hollows and the availability of often sun-exposed dead wood, their effect has never been quantified.

Our study examined the hollow incidence in pollard and non-pollard (unmanaged) willows and the effect of pollarding on incremental growth rate

by tree ring analysis. The probability of hollow occurrence was substantially higher in pollard than in non-pollard trees. Young pollards, especially, form hollows much more often than non-pollards; for instance, in trees of 50 cm DBH, the probability of hollow occurrence was ~0.75 in pollards, but only ~0.3 in non-pollards. No difference in growth rate was found.

Pollarding thus leads to the rapid formation of tree hollows, a habitat usually associated with old trees. It is therefore potentially a very important tool in the restoration of saproxylic habitats and conservation of hollow-dependent fauna. If applied along e.g. roads and watercourses, pollarding could also be used to increase landscape connectivity for saproxylic organisms. In reserves where pollarding was formerly practiced, its restoration would be necessary to prevent loss of saproxylic biodiversity. Our results point to the importance of active management measures for maintaining availability, and spatial and temporal continuity of deadwood microhabitats.

Chapter II

Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests

Forest Ecology and Management 358, 80–89

Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests

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Abstract

Efficient conservation management must be applied in protected areas in order to slow the loss of biodiversity in Europe. Regarding forests, a conservation approach based on minimal intervention prevails in most protected woodlands, thus facilitating the expansion of closed-canopy forests at the expense of open forests. To identify effective conservation strategies for protected forests, the minimal intervention or “hands-off” approach must be compared with active measures to support biodiversity.

We carried out a study in the oak-dominated forests of Podyji National Park (Czech Republic), an historically managed area left for natural succession since 1950. Twelve experimental clearings were created in closed-canopy forests within the core zone of the park; six of these clearings were connected to forest edges and open meadows, the remaining six clearings were isolated from open habitats within closed forest. To assess the importance of minimal intervention and active management measures in protected forests, we compared the richness and composition of insects, reptiles, birds and vascular plants in the clearings and in four reference habitats, including closed forest, forest edge, open forest, and meadow, in the first season following the intervention.

In comparison to closed-canopy forest, the clearings had higher species richness of butterflies, saproxylic and floricolous beetles, reptiles, and vascular plants but lower richness of moths and epigeic beetles, and similar richness of birds. For most groups, the species composition of clearings differed from that of closed forest or even the forest edge, indicating that the latter habitats cannot serve as a sufficient replacements for the conservation of open woodland species. The species richness of isolated clearings was generally lower than that of clearings connected to open habitats, and their communities contained a larger proportion of species associated with closed forest. Most threatened species were associated with clearings or open forest, closed forest and meadow hosted only a few.

The creation of the clearings in closed-canopy forests had a positive effect on overall species richness and supported threatened species in most model groups. It is thus a valuable management tool in the conservation of temperate woodland biodiversity. Our results also point to the importance of connectivity of open habitats in wooded landscapes. Further surveys of the clearings are

needed to ascertain the effect of such interventions to see how communities change throughout succession, or alternatively to what extent hindering succession by repeated cutting may alter communities.

Keywords: coppice; open woodlands; biodiversity conservation; traditional management; forest restoration; active conservation.

Chapter III

Open-grown trees as key habitats for arthropods in temperate woodlands: the diversity, composition, and conservation value of associated communities

Manuscript

Open-grown trees as key habitats for arthropods in temperate woodlands: the diversity, composition, and conservation value of associated communities

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Abstract

Temperate open woodlands are recognized as biodiversity hotspots. They are characterised by the presence of scattered, open-grown, old, large trees (hereafter referred to as “solitary trees”). Such trees are considered keystone ecological features for biodiversity. However, the ecological role of solitary trees and their importance for woodland communities are still not fully understood. Communities of arthropods in temperate forests are often structured not only by the horizontal openness of the stand, but also by vertical stratification. Thus there is a need for comparisons among communities associated with solitary trees and different forest strata. In this study, we analysed the richness, conservation value, and nestedness of four taxonomic groups (beetles (Coleoptera), bees and wasps (non-aculeate Hymenoptera), ants (Formicidae), and spiders (Araneae)) on (i) *solitary trees* in open woodlands, and four habitat types in adjacent closed-canopy forests: (ii) *edge-canopy*, (iii) *edge-understorey*, (iv) *interior-canopy*, and (v) *interior-understorey*.

Across the focal insect groups, solitary trees harboured the greatest species richness, whilst spider communities were also equally rich in forest edge canopies. The conservation value of communities was highest in solitary trees for beetles, and in solitary trees and edge-canopy habitats for bees and wasps. For spiders, the conservation value was similar across all habitat types, but ordination analysis revealed general preferences for solitary trees among threatened species. We also found that communities from the forest interior were mostly only nested subsets of the communities found on solitary trees. Our results show an important and irreplaceable role that open-grown trees have in maintaining temperate woodland biodiversity. Therefore, preservation and maintenance of open-grown trees should be a primary concern in biological conservation.

Keywords: forest ecology; insects; spiders; biodiversity conservation; veteran trees; conservation management

Summary

Summary

The studies presented in this thesis bring new information on the dynamics of saproxylic insect habitats in temperate woodlands, and therefore contribute to the knowledge needed for the designation of proper conservation management strategies in protected areas. The findings confirm that active management is a desirable approach for the conservation of saproxylic insect biodiversity. They also reveal an irreplaceable importance of habitats that have been formed by traditional silvicultural practices. The minimal intervention management, which is widely applied in most protected woodlands in Central Europe, is often not sufficient, and sometimes even detrimental, for maintaining biodiversity of temperate lowland woodlands. Minimal intervention leads to a transition from open woodlands to closed-canopy forests which cannot provide niches for a wide spectrum of saproxylic organisms, in particular those threatened by extinction. In contrast, the creation of mosaics of habitats in different stages of succession, for example by restoring coppicing, pollarding, and wood-pasture, is a favourable way to manage temperate woodlands. The reintroduction of traditional practices may of course pose some administrative or legal difficulties. However, in protected areas, where biodiversity conservation is of primary interest, these issues should never be an excuse for the sole application of minimal intervention strategy.