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Key factors affecting composition and diversity of saproxylic beetle assemblages

Ph.D Thesis

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Annotation

The thesis concerns the community structure of saproxylic insects with a heavy focus on beetles. It presents a review on change of insect assemblages along small-to-large scale gradients and the importance of saproxylic organisms in forest ecosystems. The fine-scale vertical stratification of saproxylic beetles assemblages and their differences between forests habitats of different latitude and altitude are investigated. Further, the importance of open-grown trees for saproxylic diversity is assessed.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Matthias Weiss

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Cover image: *Aesalus scarabaeoides* (Coleoptera: Lucanidae), photo taken by Jiří Procházka

List of Papers and author´s contributions

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

I. **Weiss, M.**, Procházka, J., Schlaghamerský, J. & Cizek, L., 2016. Fine-scale vertical stratification and guild composition of saproxylic beetles in lowland and montane forests: Similar patterns despite low faunal overlap. PloS One 11(3): e0149506 (IF = 3.08)
[*Matthias Weiss analyzed the data and wrote the manuscript together with LC; the study was designed by LC*]

II. **Sebek, P.**, Vodka S., Bogusch, P., Tropek, R., Weiss, M., Zimova, K., & Cizek, L., 2016. Open-grown trees as key habitats for saproxylic insects in temperate woodlands: the diversity, composition, and conservation value of associated communities. Forest Ecology and Management 380, 172-181 (IF = 2.83)
[*Matthias Weiss analyzed part of the data and contributed to the manuscript; the study was designed by LC and SV*]

III. **Weiss, M.**, Didham, R., Basset, Y., Odegaard, F., Tichechkin, A., Schmidl, J., Floren, A., Curletti, G., Aberlenc, H-P., Bail, J., Barrios, H., Leponce, M., Medianero, E., Fagan, L., Corbara, B., Procházka, J., Schlaghamersky, J., Cizek, L. Saproxylic beetles in tropical and temperate forests – a comparison of vertical stratification patterns. (Manuscript)
[*Matthias Weiss analyzed the data and wrote the manuscript together with LC; the study was designed by LC and YB*]

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Matthias Weiss declares that he is the first and corresponding author of one published paper, first author of one manuscript, and co-author of one published paper included in this thesis. The other authors are:

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Co-author agreement

Lukáš Čížek, the supervisor of this Ph.D thesis and co-author of all presented papers, fully acknowledges the major contribution of Matthias Weiss to the papers presented in Chapters I and III.

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Mgr. Lukáš Čížek, Ph.D

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Introduction

Introduction

1. Species distribution patterns on various scales

One of the major challenges in modern ecology is to achieve a better understanding of the patterns of species richness and distribution. These patterns are known to vary on many different scales – from global over regional to single habitats. A considerable portion of the research performed on this topic has centered on arthropods, especially insects. Not only they make up the largest part of all organisms on this planet, they also hold key positions in almost all terestrial ecosystems and thus are of great interest to ecological research.

On the global scale it has long been known that insect species richness, just like that of most plants and animals, generally increases with decreasing latitude (e.g. Kocher & Williams; Lobo & Martín-Piera; Hawkins & DeVries 2009). There are a number of hypotheses to explain the phenomenon (review in Willig et al 2003), among others a greater number of ecological niches and higher rates of speciation in tropical habitats compared to temperate ones due to predation and competition. Patterns along altitudinal gradients, which also display notable differences in climate (Rahbek 1995) and soil conditions (Meng et al. 2013, Geml et al. 2014) along their course, tend to show greater variety: Insect species richness has often been shown to decrease with elevation (e.g. Robertson 2002; Escobar et al. 2007) but may also increase or exhibit a mid-elevation peak (e.g. Davis et al. 1999; Yu et al. 2013).

On the scale of the single habitat an immense amount of research on distribution patterns of insects has been conducted in forests. This is unsurprising, considering that forests are the main terrestrial source of primary production as well as spatially complex habitats (Basset et al. 2003b). Since habitat fragmentation has been deemed on of the major threats to global biodiversity (Haddad et al. 2015) the horizontal patterns of insect distribution, between the edges and the interior of forests, have been intensively investigated during the last decades. It has been discovered that in many cases insect assemblage show higher diversity and abundance on forest edges compared to the interior (e.g. Aaron et al. 2005, Brigić et al. 2014), even though there are also species that only occur in the latter (Peltonen & Heliövaara, 1997). This “edge effect” is hypothesized to be caused, on one hand, by differences in abiotic factors like sun exposure, moisture and wind (Young & Mitchell 1994, Murcia 1995). On the other hand, even biotic factors like parasitism and predation have been shown to differ between edges and interior (e.g. Martinson & Fagan 2014, Kelch et al. 2016).

Despite the high efforts that were put into investigating the distribution of insects in along the horizontal dimension of forest habitats, even more attention may have been paid to the vertical distribution of insects in forests. The question of how insect assemblages are stratified in forests has intrigued entomologists for almost a hundred years, and it will also be a major topic of this thesis. The term “stratification” has been defined as a non-uniform vertical distribution by Moffett (2000). This is also applicable on the different abundance and diversity of organisms between the canopy and the understorey of forests. The idea of a rich biocoenosis in tree canopies – that differs from the ground dwelling fauna – had been existing in the minds of nature researchers since the first half of the last century (Sutton 2001) as a basic concept of ecology (Smith 1973). Besides being obviously the main place of the primary production in forests (Basset et al. 2003a), canopies are affected by different biotic and abiotic factors than the understorey (Parker 1995). Such a vertically definable range is therefore referred to as “stratum” (Moffett 2000). However, it was the poor accessibility of tree crowns had prevented an extensive research on this habitat for a long time. In this context the canopy was also called “the last biotic frontier” (Erwin 1983).

The pioneer work of canopy research started in tropical forests (Lowman & Moffet 1993), because of the obvious complexity of their tree crowns (for a detailed review of the methods see Nadkarni 1994, Lowman & Wittman 1995, Sutton 2001 and Basset et al. 2003a). Over the course of decades canopy research made what Sutton (2001) calls a transition from “the 'wonderland' phase to reality”. This describes a shift from the exploration of an unknown habitat out of sheer scientific curiosity to an extensive investigation of the canopies, which includes habitat traits, bionomics and the impact of anthropogenic influence on the inhabiting organisms. These are important fields of research, considering the key role of tree crowns in ecosystem processes and the dependency of humanity on forests (Basset et al. 2003a). Because of this considerable need for research, this also highlights the importance of long term research projects (Lowman & Wittman 1995, DeVries & Wall 2001, Lewinsohn et al, 2005, Leksono et al. 2005) and the building of scientific networks. Another development against this background is the shift from purely descriptive to manipulative investigations (Sutton 2001, Basset et al. 2003a) which allow more precise investigation for example of effects of predation (Gruner & Taylor 2006) or habitat choice (Vodka et al. 2009, Goßner et al. 2013) of organisms. By now canopy research and the concept of forest stratification has become so well known that it has even widely been featured in popular scientific media (Parker & Brown 2000).

Insects are a group that was heavily focused on in stratification research – at the latest since Terry Erwin´s (1982) startling calculations on global species diversity. Based on his studies on tropical canopy dwelling herbivores he came to the assumption of almost 30 million yet undescribed species. Since then a considerable number of studies showed a stratification of insect assemblages in forests (e.g. Intachat & Holloway 2000, Schulze et al. 2001, Fermon et al. 2005, Bos et al. 2007, Paniagua et al. 2009). Even though Erwin´s conclusions are subject of controversial debate up to date (Stork 1988, Odegaard et al. 2000), the high diversity of arthropods in this stratum and the distinct faunistic turnover to the ground communities in tropical forests is well known today (Basset 2001). This also emphasizes the importance of canopy research to the understanding of conservation and biodiversity (Nadkarni 1994). Furthermore, understanding stratification is a way to understand the mechanisms of species community composition and diversity (Schulze et al. 2001). Sampling of arthropod specimen in tree crowns can be achieved in several ways (with the above mentioned methods of access): By sweeping (e.g: Dowdy 1947) or branch-clipping (e.g: Winchester & Ring 1996, Odegaard et al. 2000, Paniagua et al. 2009) and a wide array of traps like water pan traps (e.g: Leksono et al. 2005), gauze traps (e.g: Fermon et al. 2005), malaise traps (e.g: Birtele & Hardersen 2012, Stireman et al. 2012), light traps (e.g: Intachat & Holloway 2000, Schulze et al. 2001), flight intercept traps (e.g: Ulyshen & Hanula 2007, Gruppe et al. 2008, Ammer et al. 2008) and chemical knockdown fogging (e.g: Erwin 1983, Stork 1988, Ozanne et al. 2000, Lewinsohn et al. 2005, Bos et al. 2007). According to Tanabe (2002), the received information on insect behavior is critically influenced by the type of trap that is used. Winchester & Ring (1996) stress that, because of the complexity of arboreal arthropod communities, a wider array of sampling methods is necessary to sample them representatively.

While the larger part of research projects on stratification and canopy fauna (especially arthropods) has been conducted in tropical habitats, the temperate forests have long been neglected in this matter (Winchester & Ring 1996, Ulyshen & Hanula 2007, Floren & Schmidl 2008). The reason for this is that the number of forest strata is known to decrease with increasing latitude (Smith 1973). This makes temperate and boreal canopies less complex with fewer ecological niches (Lowman et al. 1993) and also seemingly housing a smaller number of canopy specialists (Floren & Schmidl 2008, Ulyshen 2011). Nevertheless the past two decades have shown an increasing number of research works on canopy arthropods (e.g: Dennis et al. 1995, Winchester & Ring 1996, Ozanne et al. 2000, Jukes et al. 2002, Floren & Sprick 2007, Otto & Floren 2007, Asshoff et al. 2008) and the subject of stratification (e.g: Tanabe 2002, Leksono et al. 2005, Gruppe et al. 2008, Birtele & Hardersen 2012, Stireman et al. 2012). Thus also temperate canopies have been recognized as vast and rich habitat (Floren & Schmidl 2008) and the forests as distinctively stratified (Bouget et al. 2011). Vertical distribution of arthropods is influenced by factors like tree species, resources, micro climate and biotic interactions (for a review of stratification factors see: Ulyshen 2011). Recently the enthusiasm about purely descriptive investigations has decreased (Floren & Schmidl 2008). Instead, another aspect of canopy and stratification research has become increasingly interesting: Tree crowns and their inhabitants contribute in a massive way to the diversity and functionality of the forest ecosystem. Understanding these distribution patterns, community dynamics and ecological values of the associated organisms is crucial for the development of nature conservation measures (see e.g: Dennis et al. 1995, Sorensen 2004). This has become an important field of research since destruction and conversion of forest habitats – tropical as well as temperate – have led to an alarming loss of species diversity (Siitonen 2001, Basset et al. 2003a, Jeffries et al. 2006). A great advantage in this matter is the comprehensive faunal knowledge in most temperate regions: As opposed to tropical forest canopies where previously undescribed arthropods are constantly found (Basset et al. 2003a), the autecology of most temperate canopy dwellers is well known (Floren & Schmidl 2008).

All in all this development marks an important change of mind in the field of canopy research: After exploring the “wonderland” the scientists – having arrived in the harsh reality – now look for a way to preserve what they found.

2. The status of saproxylic beetles in forest ecosystems

Saproxylics include all organisms that depend during any part of their life cycle on dead or dying wood of moribund or dead trees (standing or fallen), on wood inhabiting fungi or on the presence of other saproxylics (Speight 1989). Dead wood forms a very variable substrate that can provide hundreds of different microhabitats (Siitonen 2001). This resource can be categorized in several ways: First a difference is made between lying and standing dead wood (Sverdrup-Thygeson & Ims 2002, Hjälten et. Al 2006, Ulyshen 2011). The former includes the objects that have fallen to the ground (logs and branches of different diameters) and the latter still standing parts of dead trees (snags) as well as suspended decaying parts of tree crowns. Furthermore, dead wood objects are classified according to their size as coarse woody debris (CWD) and fine woody debris (FWD) (Siitonen 2001, Nordén et al. 2004, Lassauce et al. 2012). Lastly it is the age of the wood that is of importance: A succession takes place over the process of decay (Bouget & Duelli 2004, Vanderwel et al. 2006) and fresh dead wood objects house distinctively different communities of saproxylics than old ones.

The two most specious saproxylic groups are fungi and beetles (Müller et al. 2008, Lassauce et al. 2011) as 25% of the just European beetle species belong to this group (Schmidl & Bussler 2004). Both provide a substantial contribution to wood decomposition and nutrient cycling in forest systems: The former by directly decomposing the wood matter (Bader et al. 1995) and the beetles by acting as vectors for associated fungi (Yamaoka 1997, Siitonen 2001, Barker 2008) during their colonization of newly dead wood. Of all saproxylic groups the beetles have received by far the most attention of researchers. One reason for this is that they are very well recorded in terms of their taxonomy and autecology (Siitonen 2001, Müller & Goßner 2010) – since beetles have always been an attractive group to entomologists. Certain species like the longhorn beetle *Cerambyx cerdo* have also been identified as ecosystem engineers because of their ability to take major influence on the physical properties and species diversity of the dead wood they inhabit (Buse et al. 2008). Another phenomenon that makes beetles an interesting and important research subject are outbreaks – the mass reproduction events of so called "pest species" (Similä et al. 2003, Floren & Sprick 2007). Several of these species belong to the very diverse (Martikainen et al. 1999) subfamily of bark beeltes (*Curculionidae*: *Scolytinae*). During outbrakes the beetles attack and kill even living trees (Schönherr & Krautwurst 1979, Yamaoka 1997, Hedgren 2003) which can lead to heavy damages in forest stands. That is why understanding these dynamics is also of ecological and economical interest.

Most of the investigations on saproxylic beetles have been performed in the boreal regions of Fennoscandia (Nordén et al. 2004, Müller at al. 2008). On the other hand, the number of studies from tropical habitats is rather low (but see Odegaard 2004). Sampling of the dead wood dwellers is in most instances accomplished by hand (e.g: Jonsell et al. 1999, Siitonen & Saaristo 2000, Abrahamsson & Lindbladh 2006, Schroeder et al. 2007) or by the use of traps: Flight intercept traps (e.g: Martikainen et al. 1999, Similä et al. 2003, Gibb et al. 2006, Cobb et al. 2010, Müller & Goßner 2010, Wu et al. 2013) and stem eclectors (e.g: Hedgren 2003, Hilszczanski et al. 2005) provide a measure of beetle activity (Sverdrup-Thygeson & Ims 2002). Another method is the rearing of saproxylics from collected wood objects in the lab (e.g: Hedgren & Schroeder 2004, Vanderwel et al. 2006, Ulyshen & Hanula 2007, Vodka et al. 2009). Compared to the research of stratification, the studies on saproxylic beetles include a much higher amount of manipulative experiments: Researchers cut and manipulate trees and wood objects to create suitable substrates (e.g: Hedgren 2003, Jonsell et al. 2004, Kappes & Topp 2004, Ulyshen & Hanula 2009) or plant fungi (Jonsell et al. 1999) and dead wood enrichments (Vodka et al. 2009, Bouget et al. 2011, Goßner et al. 2013) as baits. The research of the past decades has revealed that the abundance and community structure of saproxylic beetles is influenced by a wide array of factors: These include tree species (e.g: Kappes & Topp 2004, Jonsell et al. 2004, Jacobs et al. 2007, Goßner et al. 2013), wood size (e.g: Siitonen & Saaristo 2000, Siitonen 2001) and age (e.g: Abrahamsson & Lindbladh 2006, Vanderwel et al. 2006, Laussauce 2012), occurrence of fungi (e.g: Okland et al. 1996, Müller et al. 2008), humidity (e.g: Bouget & Duelli 2004), sun exposure (e.g: Weslien & Schroeder 1999, Franc et al. 2007, Franc & Götmark 2008, Russo et al. 2011, Albert et al. 2012). In forest stands most of these factors are also correlated (Siitonen 2001).

Especially the influence of forest management on the beetle communities has become a subject of interest since they share a massive problem with all the saproxylic groups – the concerning scarcity of their substrate: Over the last centuries the forest habitats in Europe have been diminished or modified, which changed their tree species composition, forest structure, micro climate and ecosystem functions (Reich et al. 2001, Rüther & Walentowski 2008). Todays managed stands contain only 2 – 30 % of the amount of dead wood that can be found in pristine forests (Fridman & Wahlheim 1999). And this small amount of possible substrate is also less diverse than in unmanaged stands (Siitonen et al. 2000). Since many saproxylic beetle species are highly specialized (Schmidl & Bussler 2004) this development has a severely negative effect on them: Today a high proportion of the dead wood associated species in Europe is endangered (see: Jonsell et al. 1998, Fridman & Wahlheim 1999, Siitonen & Saaristo 2000, Floren & Schmidl 2008). The ecological consequences of this loss of saproxylics are hard to estimate (Cobb et al. 2010) Furthermore it has been shown that associated species like predators and parasitoids of saproxylic beetles are more sensitive to habitat disturbance than their prey (Komonen et al. 2000, Siitonen 2001, Hilszczanski et al. 2005). Another problem is that the diminishing diversity of the beetle communities reduces the competition among the remaining species (Löyttyniemi 1975). Together with the predator release and the fact that managed forest stands are very uniform (Jonsell et al. 1998) this condition could favor the above mentioned pest species outbreaks. The reason for the lack of decaying wood in managed forests is that it is thoroughly removed. This is done due to modern forestry practices which are aiming for maximized harvest of biomass (Kappes & Topp 2004). Because of the trend to use wood as CO_2-neutral biofuel this also includes small wood objects (Lassauce et al. 2012). Another reason for the removal is the fear of outbreaks (Jonsell et al. 1998, Bouget et al. 2005a) – even tough Kappes & Topp (2004) stress that continuing dead wood supply could keep both the populations of possible pest species and their antagonists in balance. The removal includes also the wood resulting from natural disturbances like wind throws which are largely responsible for dead wood continuity and the forming of new habitats in natural forests (Bouget & Duelli 2004, Bouget 2005b). Forest fires, another natural disturbance that certain saproxylics depend on – especially in boreal habitats (Buddle et al. 2006, Hjälten 2006) – are generally excluded in managed forests (Toivanen & Kotiaho 2007).

Over the past years many authors have made recommendations for management measures to improve the situation of endangered saproxylic beetles: On one hand the preservation of old growth forests is important because these habitats provide a high amount and long continuity of decaying wood and sustain shade loving beetles as well as species with poor dispersal abilities (Jonsell et al. 1999, Sverdrup-Thygeson & Ims 2002, Schroeder et al 2007). On the other hand it is possible to sustain a high amount of saproxylic beetle diversity in managed forests if a sufficient and continuous amount of dead wood is provided (Martikainen 2001, Schmidl & Bussler 2008). Structural diversity has to be increased and old forest attributes established (Siitonen et al. 2000). A very important point in this is the retention of old standing dead or dying trees (Jonsell & Weslien 2003, Hedin et al. 2008, Ammer et al. 2008, Ulyshen 2011). These contain more diverse communities than younger trees (Buse et al. 2008, Gruppe et al. 2008) because they provide rare habitats like rotholes (Sebek et al. 2013). Another important factor is tree species composition: Mixed forests are generally more favorable for saproxylics than monocultures (Ammer et al. 2008). Special attention should be payed to oak trees because these are substrate for a very diverse assemblage of saproxylic beetles (Schmidl & Bussler 2008, Lassauce et al. 2012) and form a great amount of dead wood already as standing trees (Ammer et al. 2008). A near-to-nature forest management can also include the mimicking or tolerating of natural disturbances like windthrow or fire (Bouget & Duelli 2002, Toivanen & Kotiaho 2007, Liegl & Dolek 2008) to create valuable habitats for specialists. A complete “hands-off” tactic in formerly managed forest can lead to a dense and shaded forests which is a rather negative development (Vodka et al. 2009) since many saproxylic species prefer more open habitats. The reason is not only their need for sun exposed substrate but also the dependence of the adults of flower nectar (Gruppe et al. 2008).

All in all, saproxylic beetles and their feeding- and habitat guilds have become important tools for nature conservation and landscape planning (for a detailed guild classification of the central European saproxylic beetles see: Schmidl & Bussler 2004). Many of them are known to be indicators for valuable habitats (Martikainen et al, 2000, Buddle et al. 2006, Goßner et al. 2013) and some prominent single species – like the above mentioned *Cerambyx cerdo* or *Osmoderma eremita* – have become flag ship species for the whole saproxylic group and the importance of dead wood as a resource (Buse et al 2008).

3. Distribution patterns of saproxylic beetles

Because of the important ecological role of saproxylic beetles it has been of great concern to researches to understand their distribution and community structure in forest habitats. A large number of studies have focused on the horizontal distribution in forests and discovered that the beetle assemblages on forest boundaries or the edges of clearings often show high diversity (e.g. Peltonen et al. 1997, Wermelinger 2007 et al., Vodka et al. 2009, Normann et al. 2016). This is mostly attributed to the warm and sunny microclimate at these localities, which is favorable to many saproxylic beetle species (Jonsell et al. 1998, Lindhe & Lindelöw 2004). On the other hand, there are also species that can only be found in the inner parts of a forest (Peltonen & Heliövaara, 1997). Furthermore it has been shown that the beetles communities often display distinct compositions between forest sections that are subjected to different management regimes (e.g: Martikainen et al. 2000, Schmidl & Bussler 2008).

Since the enthusiasm for stratification research has been delayed for temperate and boreal forests, the investigation of saproxylic beetle distribution patterns along the vertical dimension only started in recent years. Yet, the benefit is obvious, considering the different traits of lying and standing dead wood (Ulyshen 2011) and the key role of saproxylic communities in forest ecosystems (Schmidl & Bussler 2004, Bail & Schmidl 2008). It is important for conservation to find out in what way canopy dwelling saproxylic organisms contribute to the diversity and functionality of the whole forest habitat. The amount of dead wood may seem to be small in this stratum – especially in managed forests (Goßner et al. 2013). But in certain habitats like coppices with oak trees the decaying wood in crowns can make up around 50% of this resource in the whole stand (Ammer et al. 2008). Also Vodka & Cizek (2013) show that the quality and position of dead wood have a more important influence on the saproxylic communities than the quantity.

The first tendencies of stratification could be seen when authors compared saproxylic communities in lying and standing dead wood of logs and snags (Sverdrup-Thygeson & Ims 2002, Kappes & Topp 2004, Hjälten et al. 2006 Ulyshen & Hanula 2009). All found differences between the beetle assemblages of the two substrates and Ulyshen & Hanula (2009) recognized the importance of standing dead wood for species conservation. Abrahamsson & Lindbladh (2006) also found a vertical succession along snags during the process of decay. It was not long before experiments were started that concentrated more on the phenomenon of the distribution of saproxylic beetles between the different forest strata (Wermelinger et al 2007, Gruppe et al. 2008, Vodka et al. 2009, Foit 2010, Bouget et al. 2011, Albert et al. 2012, Goßner et al. 2013, Vodka & Cizek 2013). Again the authors have to face the challenge of sampling specimens from the poorly accessible tree crowns. For the majority of experiments they have relied on flight interception traps that monitor the flying behavior of beetles and are rather easily installed in the canopy. If the study focuses on one single species, another alternative is to access the crown with climbing techniques and detect the beetle presence by their exit holes (Albert et al. 2012). Rearing of specimens from collected wood is another method that is used and several manipulative experiments have included the placement of considerable amounts of dead wood in tree crowns (Vodka et al. 2009, Bouget et al. 2011, Goßner et al. 2013).

The results of these experiments showed a distinct stratification of the saproxylic beetle communities between the forest strata: This applies for the composition of species as well as the guilds: Generally, fungi dwellers and feeders are found to be more abundant and diverse in the understorey (Goßner et al. 2013, Floren et al. 2016). This is most likely due to the more shady and moist micro climatic conditions that are favorable for fungal growth. It has also been noted that the vertical stratification shows differences between certain parts of the forest, i.e. the edge and the interior (Wermelinger et al 2007, Vodka & Cizek 2013, Normann et al. 2016). Furthermore certain species have been noticed as “stratum changers” (Schmidl & Bussler 2008, Vodka & Cizek 2013) that do just use the canopy opportunistically because they prefer a more sun exposed substrate.

The overall results of the studies in this new field of research have shown that canopies contribute in an important way to the abundance, diversity and functionality of saproxylic beetle communities in forest habitats. Therefore they should not be ignored in conservation measures and near-to-nature forestry. Yet there is still much need for further research: It is still largely unknown how forest management affects the canopy assemblages (Bail & Schmidl 2008). Canopy specialists of different forest types and tree species have to be identified. Furthermore, several authors (Su & Woods 2001, Basset al. 2003b) have emphasized the need to extensively sample communities along genuine vertical transects using multiple traps to detect any subtle or gradual differences. Yet almost all studies on the stratification of saproxylic beetles only ever compared one stratum in the understorey and canopy (but see Wermelinger et al. 2007). Additionally, there have been practically no studies where the investigation of horizontal and vertical distribution patterns was combined (but see Vodka & Cizek 2013).

4. Aims and scope of this thesis

This thesis aims to further increase our knowledge on the distribution of saproxylic beetles across multiple scales from latitudinal to the vertical dimension of the forest habitat. For this purpose beetles were sampled in the scope of extensive surveys from different forests in Panama and the Czech Republic. The following chapters contain the results of the analyses of this data.

Chapter I contains a study on the fine-scale vertical stratification of saproxylic beetle assemblages in two different temperate forests habitats. A beech-fir mountain forest and a lowland hardwood floodplain forest in the eastern Czech Republic. Both forests are known hot-spots of saproxylic beetle diversity in this country. Unlike in most studies of vertical stratification of saproxylic beetles, our sampling took place along vertical transects which reached from the ground to the upper canopy and consisted of five flight intercept traps. The main aim of this study is to investigate how species and feeding guild composition change along these transects, and if these observed patterns differ between the mountain and lowland forest.

Chapter II focuses on the role of open-grown, solitary trees in supporting communities of arboricolous insects, including saproxylic beetles, and spiders. Numerous studies often mention the importance of open-grown veteran trees for the biodiversity of saproxylic organisms. This 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. It 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. Furthermore, the stratification of these assemblages is compared between the edges and the interior. The conservation value of particular habitats are also assessed, as well es the current conservation issues associated with solitary trees.

Lastly, Chapter III expands the topic of Chapter I to an additional forest habitat. To explore the influence of latitude on the distribution of saproxylic beetles, the assemblages of the lowland floodplain forest and the mountain forest in the eastern Czech Republic were compared with those of a tropical lowland rainforest in Panama. This was made possible by collecting the beetles in the scope of an extensive survey in the rainforest that used the same sampling design along vertical transects as in both temperate forests. The community structure of saproxylic beetles and especially their stratification has only rarely been investigated in the past. Again the main aim was to investigate how species and feeding guild composition change along these transects, and if these patterns differ between the three different forests.

References

Aaron, M.D., Malcolm, J.R., Smith, S.M., Bellocq, M.I., 2005. Edge effects and the responses of aerial insect assemblages to structural-retention harvesting harvesting Canadian boreal peatland forests. *Forest Ecol. Manag.* 204: 249–266

Abrahamsson, M., Lindbladh, M., 2006. A comparison of saproxylic beetle occurrence between man-made high- and low-stumps of spruce (Picea abies). *Forest Ecol. Manag.* 226: 230–

237

Albert, J., Platek, M., Cizek, L., 2012. Vertical stratification and microhabitat selection by the Great Capricorn Beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae) in open-grown, veteran oaks. *Eur. J. Entomol.* 109: 553–559, 2012

Ammer, U., Goßner, M., Gruppe, A., Simon, U., 2008. Integrating tree crown science with the development of "near to nature" forest management practices: Examples from Bavaria. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nürnberg, Germany, pp. 531–550

Asshoff, R., Keel, SG., Siegwolf, R.T.W., Körner, C., 2008. Tracing arthropod movement in a decidous canpopy using stable stable isotopes. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nürnberg, Germany, pp. 327–338

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-Inhabiting Fungi and Substratum Decline in Selectively Logged Boreal Spruce Forests. *Biol. Conserv.* 72: 355–362

Bail, J., Schmidl, J., 2008. Xylobiontic Beetles (Insecta: Coleoptera) on oak canopies of the central European Danube floodplain: species composition, ecological guilds and the impact of flooding and forestry. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nürnberg, Germany, pp. 327–338

Barker, J.S., 2008. Decomposition of Douglas-fir coarse woody debris in response to differing moisture content and initial heterotrophic colonization. *Forest Ecol. Manag.* 255: 598–604

Basset, Y., 2001. Invertebrates in the canopy of tropical rain forests. How much do we really know? *Plant Ecol.* 153: 87–107

Basset, Y., Hammond, P.M., Barrios, H., Holloway JD, Miller SE., 2003a. Vertical stratification of arthropod assemblages. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (eds.), 2003. Arthropods of Tropical Forests. Cambridge University Press. pp 4–7

Basset, Y., Horlyck, V., Wright, S.J., 2003b. *Studying Forest Canopies from Above: The International Canopy Crane Network*. Smithsonian Tropical Research Institute and UNEP

Basset, Y., 2005. Insects on Plants: Diversity of Herbivore Assemblages Revisited. *Annu. Rev. Ecol. Evol. Syst.* 36: 597–620

Birtele, D., Hardersen, S., 2012. Analysis of vertical stratification of *Syrphidae* (Diptera) in an oak-hornbeam forest in northern Italy. *Ecol. Res.* (2012) 27: 755–763

Bouget, C., 2005a. Short-term effect of windstorm disturbance on saproxylic beetles in broadleaved temperate forests Part I: Do environmental changes induce a gap effect? *Forest Ecol. Manag.* 216: 1–14

Bouget, C., 2005b: Short-term effect of windstorm disturbance on saproxylic beetles in broadleaved temperate forests Part II. Effects of gap size and gap isolation. *Forest Ecol. Manag.* 216: 15–27

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the "last biotic frontier": Are temperate forest canopies special for saproxylic beetles? *Forest Ecol. Manag.* 261: 211– 220

Bouget, C., Duelli, P., 2004. The effects of windthrow on forest insect communities: a literature review. *Biol. Conserv.* 118: 281–299

Bos, M.M., Steffan-Dewenter, I., Tscharntke, T., 2007. The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. *Biodivers. Conserv.* 16: 2429–2444

Brigić, A., Starčević, M., Hrašovec, B., Elek, Z., 2014. Old forest edges may promote the distribution in carabid assemblages (Coleoptera: Carabidae) in Croatian forests. *Eur. J. Entomol.* 111: 715–725

Buddle, C.M., Langor, D.W., Pohl, G.R., Spence, J.R. 2006. Arthropod responses to harvestingand wildfire: Implications for emulation of natural disturbance in forest management. *Biol. Conserv.* 128: 346–357

Buse, J., Ranius, T., Assmann, T., 2008. An Endangered Longhorn Beetle Associated with Old Oaks and Its Possible Role as an Ecosystem Engineer. *Conserv. Biol.* 22: 329–337

Cobb, T.P., Hannam, K.D., Kishchuk, B.E., Langor, D.W., Quideau, S.A., Spence J.R., 2010. Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging. *Agric. For. Entomol.* 12: 9–18

Davis, A.L.V., Scholtz, C.H., Chown, S.L., 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *J. Biogeogr.* 26: 1039–1055. doi: 10.1046/j.1365-2699.1999.00335.x

Dennis, P., Usher, G.B., Watt, A.D., 1995, Lowland woodland structure and pattern and the distribution of arboreal, phytophagous arthropods. *Biodivers. Conserv.* 4: 728–744

DeVries, P.J., Walla, T.R., 2001, Species diversity and community structure in neotropical fruit-feeding butterflies. *Biol. J. Linn. Soc. 74:* 1–15.

Dowdy, W.W., 1947. An Ecological Study of the Arthropoda of an Oak-Hickory Forest with Reference to Stratification. *Ecology.* 28: 418–439

Erwin, T.L., 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopts. Bull.* 36: 74–75

Erwin, T.L., 1983. Tropical Forest Canopies: The Last Biotic Frontier. *Bull. Entomol. Soc. Am.* 29: 14–19.

Escobar, F., Halffter, G., Arellano, L., 2007. From forest to pasture: an elevation of the influence of environment and biogeography on the structure of dung beetle (*Sarabaeinae*) assemblages along three altitudinal gradients in the Neotropical region. *Ecography* 30: 192–208. doi: 10.1111/j.2007.0906-7590.04818.x

Fermon, H., Waltert, M., Vane-Wright, R.I., Mühlenberg, M. 2005. Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodivers. Conserv.* 14: 333–350, 2005.

Floren, A., Schmidl, J., 2008. Introduction: Canopy Arthropod Research in Europe. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high fontier.* Bioform Entomology, Nürnberg, Germany, pp. 13–20

Floren, A., Sprick P., 2007. Arthropod communities of various deciduous trees in the canopy of the Leipzig riparian forest with special reference to phytophageous Coleoptera. In: Unterseher, M., Morawetz, W., Klotz, S., Arndt, E. (eds.), *The Canopy of a Temperate Floodplain Forest – Results from five years of research at the Leipzig Canopy Crane*. University of Leipzig. pp: 127–140

Foit, J., 2010. Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. *Agric. For. Entomol.* 12: 133–141

Franc, N., Götmark, F., Okland, B., Norden, B., Paltto, H., 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biol. Conserv.* 135: 86–98

Franc, N., Götmark, F., 2008. Openness in management: Hands-off vs partial cutting in conservation forests, and the response of beetles. *Biol. Conserv.* 141: 2310–2321

Fridman, J., Wahlheim, D., 1999. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *For. Ecol. Manag.* 131: 23-36

Geml, J., Pastor, N., Fernandez, L., Pacheco, S., Semenova, T.A., Becerra, A.G., Wicaksono, C.Y., Nouhra, E.R. 2014. Large-scale fungal diversity assessment in the Andean Yungas forests reveals strong community turnover along an altitudinal gradient. *Mol Ecol*. 23: 2452–2472. doi: 10.1111/mec.12765

Gibb, H., Pettersson, R.B., Hjälten, J., Hilszczajski, J., Ball, J.P., Johansson, T., Atlegrim, O., Danell, K. 2006. Conservation-oriented forestry and early successional saproxylic beetles: Responses of functional groups to manipulated dead wood substrates. *Biol. Conserv.* 129: 437–450

Gossner, M.M., Floren, A., Weisser, W.W., Linsenmair, K.E., 2013. Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. *For. Ecol. Manag.* 302: 404–413

Gossner, M.M., Lachat, T., Brunet, J., Iscasson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W., Müller, J., 2013. Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests. *Conserv. Biol.* 27: 605–614

Gruppe, A., Goßner, M., Engel, K., Simon, U., 2008. Vertical and horizontal distribution of arthropods in temperate forests. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nürnberg, Germany, pp. 383–406

Gruner, D.S., Taylor, A.D., 2006. Richness and species composition of arboreal arthropods affected by nutrients and predators: a press experiment. *Oecologia* 147: 714–724

Haddad, N.M., Brudvig, L.A., Colbert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins C.N., King, A.J., Laurance W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth´s ecosystem. *Sci. Adv.* 1:e1500052. doi: 10.1126/sciadv.1500052

Hawkins, B.A., DeVries, P.J., 2009. Tropical niche conservatism and the species richness gradient of North American butterflies. *J. Biogeogr.* 36: 1698–1711

Hedin, J., Ranius, T., Nilsson, S.G., Smith, H.G. 2008. Restricted dispersal in a flying beetle assessed by telemetry. *Biodivers. Conserv.* 17: 675–684

Hedgren, P.O., 2003. The bark beetle Pityogenes chalcographus (L.) (*Scolytidae*) in living trees: reproductive success, tree mortality and interaction with Ips typographus. *J. Appl. Ent.* 128: 161–166

Hedgren, P.O., Schroeder, L.M., 2004. Reproductive success of the spruce bark beetle Ips typographus (L.) and occurrence of associated species: a comparison between standing beetle-killed trees and cut trees. *For. Ecol. Manag.* 203: 241–250

Hilszczanski, J., Gibb, H., Hjälten, J., Atlegrim, O., Johansson, T., Pettersson, R.B., Ball, J.P., Danell, K. 2005. Parasitoids (Hymenoptera, Ichneumonoidea) of Saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. *Biol. Conserv.* 126: 456–464

Hjälten, J., Johansson, T., Alivni, O., Danell, K., Ball, J.P., Pettersson, R., Gibb, H., Hilszczanski, J. 2006. The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic Appl. Ecol.* 8: 364—376

Intachat, J., Holloway, J.D., 2000. Is there stratification in diversity or preferred flight height of geometroid moths in Malaysian lowland tropical forest? *Biodivers. Conserv.* 9: 1417–1439

Jacobs, M.J., Spence, J.R., Langor, D.W., 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. *Agric. For. Entomol.* 9: 3–16

Jeffries, J.M., Marquis, R.J., Forkner, R.E., 2006. Forest age influences oak insect herbivore community structure, richness, and density. *Ecol. Appl.* 16: 901–912

Jonsell, M., Weslien, J., Ehnström. B., 1998. Substrate requirements of redlisted saproxylic invertebrates in Sweden. *Biodivers. Conserv.* 7: 749–764

Jonsell, M., Nordlander, G., Jonsson, M., 1999. Colonization patterns of insects breeding in wood-decaying fungi. *J. Insect Conserv.* 3: 145 – 161

Jonsell, M., Weslien, J., 2003. Felled or standing retained wood – it makes a difference for saproxylic beetles. *For. Ecol. Manag.* 175: 425–435

Jonsell, M., Nittérus, K., Sitghäll, K., 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. *Biol. Conserv.* 118: 163–173

Jukes, M.R., Ferris, R., Peace, A.J., 2002. The influence of stand structure and composition on diversity of canopy Coleoptera on coniferous plantations in Britain. *For. Ecol. Manag.* 163: 27–41

Kappes, H., Topp, W., 2004. Emergence of Coleoptera from deadwood in a managed broadleaved forest in central Europe. *Biodivers. Conserv.* 13: 1905–1924

Kelch, N-S., Neves, F.S., Fernandes, G.W., Wirth, R., 2016. Mechanisms driving gelling success in a fragmented landscape: Synergy of habitat and top-down factors along temperate forest edges. *PLoS ONE* 11: e0157448. doi:10.1371/journal.pone.0157448

Kocher, S.D., Williams, E.H., 2000. The diversity and abundance of North American butterflies vary with habitat disturbance and geography. *J. Biogeogr.* 27: 785–794

Komonen, A., Penttilä, R., Lindgren, M., Hanski, I., 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *OIKOS* 90: 119–126

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* 11: 1027–1039

Lassauce, A., Lieutier, F., Bouget, C., 2012. Woodfuel harvesting and biodiversity conservation in temperate forests: Effects of logging residue characteristics on saproxylic beetle assemblages. *Biol. Conserv.* 147: 204–212

Liegl, A., Dolek, M., 2008. Conservation of coppice with standards for canopy arthropods: The Bavarian Conservation Programme for Forests. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high fontier.* Bioform Entomology, Nürnberg, Germany, pp. 551–562

Lindhe, A., Lindelöw, A., 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. *Forest Ecol. Manag.* 203: 1–20

Leksono, A.S., Takada, K., Koji, S., Nakagoshi, N., Anggraeni, T., Nakamura, K., 2005. Vertical and seasonal distribution of flying beetles in asuburban temperate deciduous forest collected by water pan trap. *Insect Sci.* 12: 199–216

Lewinsohn, T.M., Novotny, V., Basset, Y., 2005. Insects on Plants: Diversity of Herbivore Assemblages Revisited. *Annu. Rev. Ecol. Evol. Syst.* 36: 597–620

Lobo, J.M., Martín-Piera, F., 2002. Searching for a predictive model for species richness of Iberian dung beetle based on spatial and environmental variables. *Conserv. Biol.* 16: 158–173

Lowman, M.D., Moffet, M., 1993. The Ecology of Tropical Rain Forest Canopies. TREE 8: 104–106

Lowman, M.D., Taylor, P., Block, N., 1993. Vertical stratification of smallmammals and insects in the canopy of a temperate deciduous forest: a reversal of tropical forest distribution? *Selbyana* 14:25. In: Lewinsohn, T.M., Novotny, V., Lowman, M.D., Wittman, P.K., 1995. The last biological frontier? Advancements in research on forest canopies. *Endeavour.* Volume: 19: 61–165

Löyttyniemi, K., 1975. On the occurence of Ips sexdentatus (Börner) (Col., Scolytidae) in south Finland. *Ann. Ent. Fenn.* 41: 135–136

Martikainen, P., Siitonen, J., Kaila, L., Punttila, P., Rauh, J., 1999. Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *Forest Ecol. Manag.* 116: 233–245

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J., 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests In southern Finland. *Biol. Conserv.* 94: 199–209

Martikainen, P., 2001. Conservation of threatened saproxylic beetles: significance of retained aspen Populus tremula on clearcut areas. *Ecol. Bull.* 49: 205–218.

Martinson, H.M., Fagan, W.F., 2014. Trophic distribution: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecol. Lett.* 17: 1178–1189

Meng, H., Li, K., Nie, M., Wan, J., Quan, Z., Fang, C., Chen, J., Gu, J., Li, B., 2013. Responses of bacterial and fungal communities to an elevation gradient in a subtropical montane forest of China. *Appl Microbiol Biot.* 97: 2219–2230. doi: 10.1007/s00253-012-4063-7

Moffet, M.W., 2000. What´s “Up“? A Critical Look at the Basic Terms of Canopy Biology. *Biotropica* 32: 569–596

Müller, J., Bußler, H., Kneib, T., 2008. Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *J. Insect Conserv.* 12: 107–124

Müller, J., Gossner, M.M., 2010. Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. *Biol. Conserv.* 143: 625–633

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10: 58–62

Nadkarni, N.M., 1994. Diversity of Species and Interactions in the Upper Tree Canopy of Forest Ecosystems. *Am. Zool.* 34:70–78

Nordén, B., Götmark, F., Tönnberg, M., Ryberg, M., 2004. Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. *Forest Ecol. Manag.* 194: 235–248

Normann, C., Tscharntke, T., Scherber, C., 2016. Interacting effects of forest stratum, edge and tree diversity on beetles. *Forest Ecol. Manag.* 361: 421–431

Odegaard, F., Diserud, O.H., Engen, S., Aagaard, K., 2000. The Magnitude of Local Host Specificity for Phytophagous Insects and its Implications for Estimates of Global Species Richness. *Conserv. Biol.* 14: 1182–1186

Odegaard, F., 2004. Species richness of phytophagous beetles in the tropical tree Brosimum utile (Moraceae): the effects of sampling strategy and the problem of tourists. *Ecol. Entomol.* 29: 76–88

Okland, B., Bakke, A., Hagvar, S., Torstein, K., 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodivers. Conserv.* 5: 75–100

Otto, S., Floren, A., 2007. The spider fauna (Araneae) of tree canopies in the Bialowieza Forest. *Fragm. Faun.* 50: 57–70

Ozanne, C.M.P., Speight, M.R., Hambler, C., Evans, H.F., 2000. Isolated trees and forest patches: Patterns in canopy arthropod abundance and diversity in Pinus sylvestris (Scots Pine). *Forest Ecol. Manag.* 137: 53–63

Paniagua, M.R., Medianero, E., Lewis, O.T., 2009. Structure and vertical stratification of plant galler – parasitoid food webs in two tropical forests. *Ecol. Entomol.* 34: 310–320

Parker, G.G., 1995. Structure and microclimate of forest canopies. In: Lowman M.D., Nadkarni N.M.. (eds.), *Forest Canopies*. Academic Press, San Diego. pp. 431–455

Parker, G.G., Brown, M.J., 2000. Forest Canopy Stratification—Is It Useful? *Am. Nat.* 155: 473–484

Peltonen, M., Heliövaara, K., 1997. Incidence of *Xylechinus pilosus* and *Cryphalus saltuarius* (Scolytidae) in forest-clearcut edges. *Forest Ecol. Manag.* 103: 141–147

Peltonen, M., Heliövaara, K., Väisänen, R., 1997. Forest insects and environmental variation in stand edges. *Silva. Fenn.* 31: 129–141

Rahbek, C., 1995. The elevational gradient of species richness: a uniform pattern? *Ecography.* 18: 200-205. doi: 10.1111/j.1600-0587.1995.tb00341.x

Reich, P.B., Bakken, P., Carlson, D., Frelich, L.E., Friedmann, S.K., Grigal, D.F., 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. *Ecology* 82: 2731–2748

Robertson, HG., 2002. Comparison of leaf litter ant communities in woodlands, lowland forests and montane forests of north-eastern Tanzania. *Biodivers. Conserv.* 11: 1637–1652. doi: 10.1023/A:1016883901065

Russo, D., Cistrone, L., Garonna, A.P. 2011. Habitat selection by the highly endangered long-horned beetle Rosalia alpina in Southern Europe: a multiple spatial scale assessment. *J. Insect. Conserv.* 15: 685–693

Rüther, C., Walentowski, H. 2008. Tree species composition and historic changes of the Central European oak/beech region. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high fontier.* Bioform Entomology, Nürnberg, Germany, pp. 61–88

Schmidl, J., Bussler, H. 2004. Ökologische Gilden xylobionter Käfer Deutschlands und ihr Einsatz in der landschaftsökologischen Praxis – ein Bearbeitungsstandard. *Nat.schutz Landsch.pl.* 36: 202–218

Schmidl, J., Bussler, H., 2008. Xylobiontic beetle guild composition and diversity driven by forest canopy structure and management. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high fontier.* Bioform Entomology, Nürnberg, Germany, pp. 299–324

Schönherr, J., Krautwurst, K., 1979. Beobachtungen über den Buchenborkenkäfer Taphroychus bicolor Hbst. (Scolytidae). *Anz. Schädlingskd. Pfl.* 52: 161–163

Schroeder, L.M., Ranius, T., Ekbom, B., Larsson, S., 2007. Spatial Occurrence of a Habitat-Tracking Saproxylic Beetle inhabiting a Managed Forest Landscape. *Ecol. Appl.* 17: 900–909

Schulze, C.H., Linsenmair, K.E., Fiedler, K. 2001. Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. *Plant Ecol.* 153: 133–152

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* e60456

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *For. Ecol. Manage.* 128: 211–225

Siitonen, J., Saaristo, L., 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. *Biol. Conserv.* 94: 212–220

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49: 11–41.

Smith, A.P., 1973. Stratification of Temperate and Tropical Forests. *Am. Nat.* 107: 671–683

Sorensen, L.L., 2004. Composition and diversity of the spider fauna in the canopy of a montane forest in Tanzania. *Biodivers. Conserv.* 13: 437–452

Speight, M., 1989. Saproxylic invertebrates and their conservation. - Council of Europe, Strasbourg. In: Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49: 11–41.

Stireman III, J. O., Cerretti, P.F., Whitmore, D., Hardersen, S., Gianelle, D., 2012. Composition and stratification of a achinid (Diptera: *Tachinidae*) parasitoid community in a European temperate plain forest. *Insect Conserv. Diver.* 5: 346–357

Stork, N.E., 1988. Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc.* 35: 321–337

Su, J.C., Woods, S.A., 2001. Importance of sampling along a vertical gradient to compare theinsect fauna in managed forests. *Environ. Entomol.* 30: 400-408. doi: 10.1603/0046-225X-30.2.400

Sutton, S.L., 2001. Alice grows up: canopy science in transition from Wonderland to Reality.

Plant Ecol. 153: 13–21

Sverdrup-Thygeson, A., Ims, R.A., 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biol. Conserv.* 106: 347–357

Tanabe, S., 2002. Between-forest variation in vertical stratification of drosophilid populations. *Ecol. Entomol.* 27: 720–731

Toivanen, T., Kotiaho, J.S., 2007. Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating deadwood on beetle diversity. *Biodivers. Conserv.* 16: 3193–3211

Ulyshen, M.D., Hanula, J.L., 2007. A Comparison of the Beetle (Coleoptera) Fauna Captured at Two Heights Above the Ground in a North American Temperate Deciduous Forest. *Am. Midl. Nat.* 158: 260–278

Ulyshen, M.D., Hanula J.L., 2009. Habitat associations of saproxylic beetles in the southeastern United States: A comparison of forest types, tree species and wood postures. *Forest Ecol. Manag.* 257*:* 653–664

Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. *Forest Ecol. Manag.* 21: 1479–1489

Vanderwel, M.C., Malcolm, J.R., Smith, S.M., Islam, N., 2006. Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. *Forest Ecol. Manag.* 225: 190–199

Vodka, S., Konvicka, M., Cizek, L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. *J. Insect. Conserv.* 13: 553–562

Vodka, S., Cizek, L., 2013. The effects of edge-interior and understorey canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. *Forest Ecol. Manag. 304*: 33–41

Weslien, J., Schroeder, L.M., 1999. Population of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecol. Manag.* 115: 267–275

Wermelinger, B., Flückinger, P.F., Obrist, M.K., Duelli, P., 2007. Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *J. Appl. Entomol.* 131: 104–114

Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: Pattern, process scale and synthesis. *Annu. Rev. Ecol. Evol. Sys.* 34: 273–309

Winchester, N.N., Ring, R.A., 1996. Northern Temperate Coastal Sitka Spruce Forests with

Special Emphasis on Canopies: Studying Arthropods in an unexplored frontier *Northwest Sci.* 70: 94–103

Wu, J., Pan, H., Yang, S., Niu, X., 2013. Tree species and elevation influence the assemblage composition of saproxylic beetles in subtropical forest of east China. *Forest Ecol. Manag.* 292: 29–38

Yamaoka, Y., Wingfield, M.J., Takahashi, I., Solheim, H., 1997. Ophiostomatoid fungi associated with the spruce bark beetle *Ips typographus* f. *aponicus* in Japan. *Mycol. Res.* 101: 1215–1227

Young, A., Mitchell, N., 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biol. Conserv.* 67: 63–72

Yu, X., Lü, L., Luo, T., Zhou, H., 2013. Elevational gradient in species richness pattern of epigaeic beetles and underlying mechanisms at east slope of Balang mountain in southwestern China. *PLOS ONE* e69177. doi: 10.1371/journal.pone.0069177

Chapter I

Fine-scale vertical stratification of and guild composition of saproxylic beetles in lowland and montane forests: Similar patterns despite low faunal overlap

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Fine-scale vertical stratification and guild composition of saproxylic beetles in lowland and montane forests: Similar patterns despite low faunal overlap

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Abstract

The finer scale patterns of arthropod vertical stratification in forests are rarely studied and poorly understood. Further, there are no studies investigating whether and how altitude affects arthropod vertical stratification in temperate forests. We therefore investigated the fine-scale vertical stratification of diversity and guild structure of saproxylic beetles in temperate lowland and montane forests and compared the resulting patterns between the two habitats.

The beetles were sampled with flight intercept traps arranged into vertical transects (sampling heights 0.4, 1.2, 7, 14, and 21 m). A triplet of such transects was installed in each of the five sites in the lowland and in the mountains; 75 traps were used in each forest type.

381 species were collected in the lowlands and 236 species in the mountains. Only 105 species (21%) were found at both habitats; in the montane forest as well as in the lowlands, the species richness peaked at 1.2 m, and the change in assemblage composition was most rapid near the ground. The assemblages clearly differed between the understorey (0.4 m, 1.2 m) and the canopy (7 m, 14 m, 21 m) and between the two sampling heights within the understorey, but less within the canopy. The stratification was better pronounced in the lowland, where canopy assemblages were richer than those near the forest floor (0.4 m). In the mountains the samples from 14 and 21 m were more species poor than those from the lower heights. The guild structure was similar in both habitats. The main patterns of vertical stratification and guild composition were strikingly similar between the montane and the lowland forest despite the low overlap of their faunas. The assemblages of saproxylic beetles were most stratified near ground.

The comparisons of species richness between canopy and understorey may thus give contrasting results depending on the exact sampling height in the understorey.

Introduction

Understanding the patterns of distribution of organisms on various scales is one of the fundamental questions of current ecology. It is also essential for biodiversity conservation, forestry and agriculture. Altitude is among the most prominent factors influencing the distribution of organisms due to its effect on abiotic factors such as climate (Rahbek 1995) and soil conditions (Meng et al. 2013, Geml et al. 2014). Distinct turnover in community composition thus often occurs along altitudinal gradients (Jung J et al. 2012, Wu et al. 2012, Zou et al. 2014). In arthropod communities, species richness mostly decreases with elevation (Robertson 2002, Escobar et al. 2007); it may, however, also increase or exhibit a mid-elevation peak (Davis et al. 1999, Yu et al. 2013).

Forests are three-dimensional habitats where organisms are also distributed along the vertical gradient between forest floor and tree tops (Basset et al. 2003). Depending on the type of forest and taxa studied, the vertical gradient in stratification of arthropod assemblages might be imperceptible, or it may result in a clear stratification between sampling heights (Tanabe 2002, Leksono et al. 2005, Wermelinger et al. 2007, Maguire et al. 2014, Basset et al. 2015). The stratification patterns also change with latitude as stratification is more pronounced in tropical forests than in temperate ones, probably due to the higher complexity of the vertical structure of tropical forests (Basset et al. 2003). However, the effect of other geographical factors, such as elevation above sea level on the patterns of arthropod vertical stratification, has never been studied.

Insects associated with the wood of dead or live trees (i.e. saproxylic insects), especially beetles, constitute a substantial portion of forest biodiversity. Owing to their ability to weaken or kill trees and start the decomposition process, many beetles are considered essential components of forest dynamics in the natural forest and serious pests in production forests (Wermelinger 2004, Müller et al 2008). The recent decrease in the amount of dead wood and old trees in forests has caused serious decline of numerous species (Siitonen et al. 2000, Floren & Schmidl 2008). Saproxylic beetles are thus intensively studied due to their status as pests or target species of nature conservation (Stokland et al 2004, Stokland et al. 2012, Bouget et al. 2013). They also serve as model organisms for identifying sustainable forest management practices (Siitonen et al. 2000, Martikainen 2001, Grove 2002).

Despite numerous studies on the ecology of saproxylic beetles, very little is known about their response to altitude. One study (Tykarski 2006) reported a decrease in species richness of bark beetles and their associates with altitude, while Procházka et al. (unpublished data) reported shifts in community composition of bark beetles between lowland and montane forests. Patterns of diversity and guild structure between lowland and montane forests thus remain largely unknown for the group.

Although the distribution of saproxylic beetles along the vertical gradient in temperate forests has received much attention, a number of issues remain to be solved. Saproxylic beetles are generally considered more abundant and diverse in the understorey of temperate forests, they show a clear vertical stratification and the canopy fauna is not a simple subset of the understorey fauna (Jonsell & Weslien 2003, Hjältén et al. 2007,Wermelinger et al 2007, Ulyshen MD & Hanula 2009, Bouget et al. 2011, Floren et al. 2014). Although several authors (Su & Woods 2001, Basset et al. 2003) emphasized the importance of sampling insects along genuine vertical transects, most studies on the vertical distribution of saproxylic beetles have compared two sampling heights only (*cf.* Bouget et al. 2011). Limited numbers, or a lack of replicates, limit the information value of studies investigating stratification on a finer scale (Su & Woods 2001, Leksono et al 2005, Wermelinger et al 2007). One particular study (Basset et al. 2015) used an experimental design that was practically identical to ours (see Method section) but studied the entire arthropod community. As such, we still lack authoritative information on the distribution patterns of saproxylic beetles along genuine vertical gradients in temperate forests.

To address the above issues, we sampled saproxylic beetles along a fine-scale vertical gradient in temperate montane and lowland forests. We investigated patterns of assemblage composition, diversity, and feeding guild distribution along a vertical gradient in lowland and montane forests and compare their patterns between the two habitats. Specifically, we aimed to answer the following questions: (i) Is there a difference in the overall diversity and/or guild structure of the beetle assemblages between montane and lowland forests? (ii) Do the patterns of vertical stratification differ between montane and lowland forests? (iii) Is the change in composition of beetle assemblages between understorey and canopy gradual or rather sudden? (iv) How are the feeding guilds distributed among the sampling heights and are the distribution patterns identical in both forest types?

Methods

Study sites

The sampling was performed in one lowland area and one mountain range in the Czech

Republic. Both forest areas are characterized by diverse and near-to-natural tree species composition with a high volume of dead wood, many veteran trees and a rich, nearly complete saproxylic fauna. The lowland part of the study was conducted in alluvial woodlands along the lower Dyje (Thaya) and Morava (March) rivers in southern Moravia (48°37’- 53’ N, 16°36’- 17°05’ E; 150–153 m a.s.l., mean annual temperature 9 °C, average annual precipitation 524 mm). The terrain was flat, the prevailing trees were pedunculate oak (*Quercus robur*), narrowleaf ash (*Fraxinus angustifolia*), hornbeam (*Carpinus betulus*), field maple (*Acer campestre*), interspersed with limes (*Tilia cordata*, *T. platyphyllos*), European white elm (*Ulmus laevis*), poplars (*Populus alba, P. nigra*), and black alder (*Alnus glutinosa*). Historically, the forests were managed as coppice with standards or pasture woodland. These practices were abandoned 60–150 years ago (Vrška et al 2006). Sampling was conducted in reserves and stands that had escaped the intensification of forestry, but nevertheless turned from oak-dominated sparse woodland to closed-canopy forest dominated by shade-tolerant species (Miklín & Čížek 2014, Vrška et al 2006). Five sites within the four largest remaining fragments of such stands in the area were included in the study (see below & Figure 1). The entire area is a regional biodiversity hotspot and important refuge of saproxylic fauna (Rozkošný & Vaňhara 1996, Schlaghamerský 2000). For an impression of the forest structure at the sampling sites see Figure 1.

The montane part of the study was conducted in the Moravian-Silesian Beskids (Beskydy) – a mountain range belonging to the Western Carpathians, situated in north-eastern Moravia, Czech Republic (49°10’- 39’ N, 17°59’- 18°44’ E, mean annual temperature 7 °C, average annual precipitation 816 mm). The sampling sites had an elevational range of 715–1035 m a.s.l. (mean 814 m). Sampling was performed in reserves, historically partly managed as pasture forests, that have been left unmanaged for several decades (Vrška et al. 2009). The forest stands at the sites were dominated by European beech (*Fagus sylvatica*), interspersed with silver fir (*Abies alba*), Norway spruce (*Picea abies*), sycamore maple (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*) and Scotch elm (*Ulmus glabra*). The reserves are among the most important refuges of montane saproxylic biodiversity in the Czech Republic (Horák et al 2009, Vávra & Stanovský 2013). Five sites within four reserves were selected to match the situation in the lowland area (Figure 2). For an impression of the forest structure at the sampling sites see Figure 1. The research in the lowland sites was conducted under the permit 8375/04-620/1377/04 issued by the Ministry of Environment of the Czech Republic. At the montane sites, the research was conducted under the exemption included in the Resolution of the Government of the Czech Republic No. 302. The research was performed on state owned land.

The above permits grant access to the protected areas involved in the research, and allowed for sampling of insect species explicitly protected under national law.

Figure 1. Photo of the sampling sites Mionší (top) in the montane forest and Ranšpurk in the lowland forest (below)

Sampling design and technique

The sampling design was identical in the lowlands and the mountains. Five sampling sites were selected in each of the two study areas (Figure 2). At each sampling site, three vertical transects were installed. Each vertical transect consisted of five traps exposed at 0.4, 1.2, 7, 14, and 21 meters above the ground (height at the middle of the interception panels). Hereafter the first two of these trap heights will be referred to as “understorey” and the other three as “canopy”. A total of 150 unbaited flight intercept traps were used, with 75 traps in lowland and 75 traps in montane forest. Sampling was carried out in 2007 in the lowland and in 2008 in the mountains. Due to the difference in the length of the vegetation season, traps at the lowland sites were operated from the end of March (after ceasing of inundation) until the end of September, whereas traps at the montane sites were operated from the end of April (ceasing of snow cover) until the end of September. The sampling thus covered virtually the whole period of beetle activity in both sampling areas.

In the lowland, vertical transects were installed at four sites, including Ranšpurk (two triplets, 48°40'42.946"N, 16°56'55.018"E and 48°40'40.446"N, 16°56'47.875"E), Cahnov (48°39'20.132"N, 16°56'26.013"E), Dlúhý hrúd (48°42'44.484"N, 16°54'15.171"E), and Pajdavé Kúty (48°43'4.638"N, 16°53'35.404"E). In the mountains, vertical transects were installed at four sites, including Mionší (two triplets, 49°32'15.947"N, 18°39'34.435"E and 49°32'4.330"N, 18°39'37.149"E), Salajka (49°24'8.243"N, 18°25'6.036"E), Razula (49°21'38.648"N, 18°22'43.441"E), and Smrk (49°29'38.484"N, 18°22'16.705"E).

The distance between the study areas was 150 km. The distances between transects within individual triplets (sites) was between 45 and 314 m (mean 103 m).

The flight intercept traps used were of the cross vane type (the two perpendicular transparent plastic panes were 50 cm high and 25 cm wide) with a roof, and a funnel connected to a collecting bottle with preservative (saturated salt solution with a drop of detergent to eliminate surface tension). The traps were emptied fortnightly. Relative cover of tree crowns (%) above the trap transect was recorded by a camera with fish-eye lens (16 mm focal length) and analysed using the software GapLightAnalyzer (Frazer et al. 1999).

Beetles (Coleoptera) associated with dead wood (i.e. saproxylic and xylophagous ones) were used as the model group in order to avoid contamination of the dataset by species not associated with woodland habitats. All trapped beetle individuals were sorted and identified to family level; saproxylic groups were identified to species level.

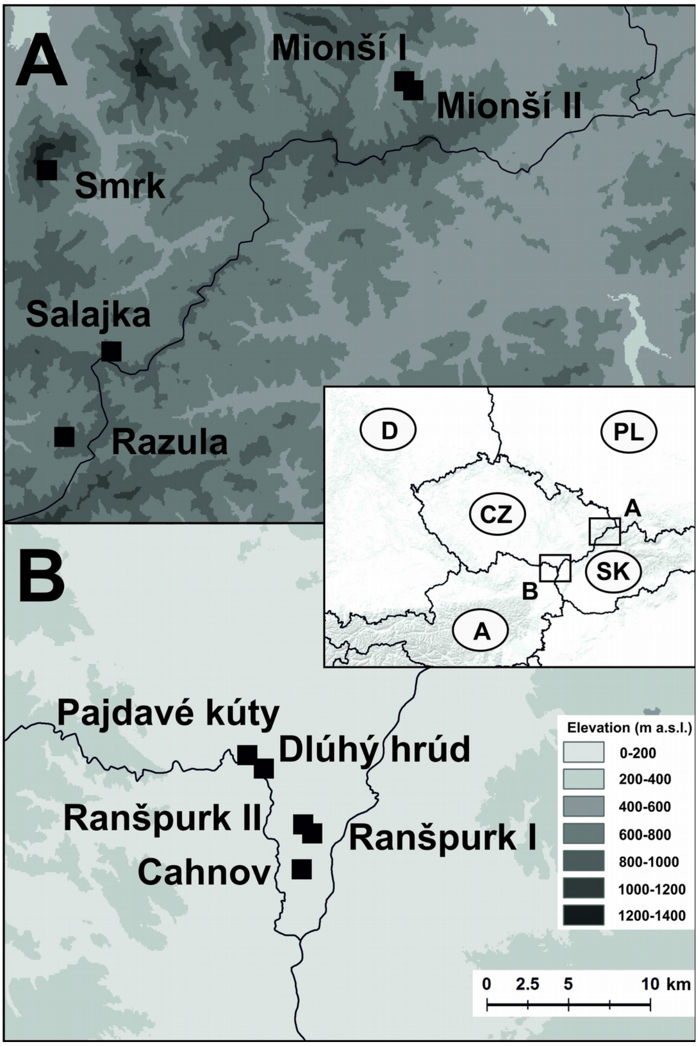

Figure 2. Location of the study areas in Central Europe and positions of sampling sites in the A) mountain forest and the B) lowland floodplain forest.

Species identity was revised by experienced specialists. *Staphylinidae* were omitted from the dataset due to difficulties with their identification. This is a common approach, unlikely to affect our results (Sebek et al. 2012, Parmain et al. 2015). Every saproxylic species was assigned to a feeding guild as either mycetophagous, xylophagous, zoophagous, or saprophagous based on the most authoritative information available (Leschen et al 2010). All species in any way associated with fungi were considered as mycetophagous. Species were classified as threatened according to the Red List of threatened species in the Czech Republic

Invertebrates (Farkač et al 2005). Furthermore, species were classified as “primeval forest” species (stenotopic, and dispersal-limited species with close association to high quality forests habitats) according to (Schmidl & Bussler 2004). The data are deposited in Dryad, a publicly accessible digital repository: http://dx.doi.org/10.5061/dryad.39k32

Data Analysis

Species richness and distribution

For the purpose of the following analyses the data collected fortnightly were pooled per trap across the sampling period. To compare the overall species richness between mountains and lowland as well as among the sampled heights, the expected numbers of species with confidence intervals were computed using sample-based rarefaction using EstimateS 9.1.0 (Colwell 2013). These analyses were conducted with the whole species data set for all samples of the two forest areas (N=75) and for the individual sampling heights (N=15). The total number of species was estimated using the classic Chao1 richness estimator with 100 runs for each of the two sampling areas (Chao 1984). Furthermore, the number of shared species between the pooled samples from each of the two elevations was estimated using the Chao shared species estimator (Chen et al. 1995).

Multivariate analyses

The relations among sample composition and explanatory variables were investigated using Redundancy Analysis (RDA), a linearly constrained ordination method that relates the species composition of samples to external predictors. RDA was chosen as a Detrended Correspondence Analysis conducted in a pre-analysis showed a gradient length of less than 3.0 SD units (Šmilauer &Lepš 2014). Separate ordinations were computed for the lowland and montane datasets. Trap height acted as the explanatory variable while sampling plot and canopy openness (as a surrogate for insolation) acted as covariables. All species with five or more individuals in the respective dataset were included in the analyses. Axes were tested with a Monte Carlo permutation test with 499 permutations. The same ordination was also used to carry out a variation partitioning analysis for the montane and lowland datasets. Sampling plot, trap height, and canopy openness were selected as explanatory variables in this analysis. Ordinations were carried out using Canoco 5 (Ter Braak & Šmilauer 2012). Traps represented samples characterised by captures of beetle species, and explanatory variables. The species abundance data acting as the response variable was log-transformed and centred by species. Trap height acted as a categorical variable. For constructing the ordination diagram scaling was focused on inter-sample distances and species scores were divided by standard deviations.

Dissimilarity patterns

Similarity between assemblages of the five sampling heights in terms of species composition was analysed by computing a Sorensen distance measure on all possible height pairings. For this purpose the data of each sampling height in a given elevation were pooled and then turned into presence-absence-data. Furthermore a measure of partitioning of the dissimilarity between sampling heights into its two components was applied: Dissimilarity reflects two phenomena – species turnover and nestedness. The first stands for replacement of species by others while the latter reflects species loss. Biotas with a smaller number of species that are only subsets of biotas at richer sites are considered nested (Baselga 2010). To quantify the rate of change in assemblage composition along the vertical gradient, the Sorensen dissimilarity was standardised per 1 m of vertical distance between traps by dividing the values of dissimilarity between assemblages from two sampling heights by vertical distance (in m) between them. The Sorensen index (βsor), the Simpson dissimilarity index (βsim) describing spatial turnover and the nestedness-resultant dissimilarity (βnes) were computed with the *betapart* package (Baselga & Orme 2012) in R (R Core Team 2014). Species with less than five individuals were omitted from the analysis.

Feeding guilds

Species indicator values (IndVal) quantify the fidelity and specificity of species to groups of sites (Dufrêne & Legendre 1997). These values were computed for the montane and lowland assemblages to identify beetle species characteristic for the individual trap heights, using the *labdsv* package (Roberts 2012) in R (R Core Team 2014). Only species with five and more individuals were used for computing the IndVal and only those with an IndVal above 0.15 were selected as characteristic. A goodness-of-fit test was performed to test whether the characteristic species were evenly distributed across the heights. This test was applied to each of the four feeding guilds as well as to the sum of all characteristic species. Furthermore, a Chi-Square Test of probabilities was computed for each feeding guild to test if its distribution across the heights was identical with the distribution of all characteristic species, other guilds at the same elevation, or the same guild in the other elevation. The same test was also performed to test if the distribution of feeding guilds was different between the two elevations when all species were taken into account. The p-value was computed using a Monte Carlo simulation with 999 replicates, and Bonferroni correction was applied.

Results

Species richness and distribution

A total of 16,368 individuals of 512 saproxylic beetle species were caught. 7,429 beetle specimens were caught in the lowlands and 8,939 in the mountains. However, with 381 species trapped in the lowland and 236 in the mountains, the assemblage of the former was substantially richer. Only 105 species (21% of total species richness) were collected at both elevations; the number of shared species was estimated to be 169 (30%) using the Chao shared species estimator. The total number of species was estimated to be 463 (95% CI 428–519) in the lowlands and 319 (95% CI 276 – 380) in the mountains using the Chao1 species richness estimator. Of the species trapped in the lowland, 94 (25%) were red-listed and 67 (18%) were classified as “primeval forest” species; whereas of those trapped in the mountains, 32 (14%) were red-listed and 17 (7%) classified as “primeval forest” species.

The number of species collected at a particular height was lower in the mountains for each of the sampled heights, and the difference in species richness was lowest near the ground and highest in the upper sampling heights. In both areas species richness peaked at 1.2 m. In the lowland, the assemblage at 0.4 m was the poorest, and there were no major differences in species richness among the three sampled heights in the canopy (7, 14, and 21 m; Figure 3). In the mountains, the higher canopy heights (14 and 21 m) were the poorest. There were more species collected at 0.4 and 7 m heights than higher in the canopy, but less than at 1.2 m height.

Multivariate analyses

The Redundancy Analysis of the montane dataset revealed a clear difference between the species composition of the two understorey heights (0.4 and 1.2 m), as well as between the understorey and canopy heights, whereas the distinctions between the three canopy heights where minimal (eigenvalue 1st axis = 0.1513, eigenvalue 2nd axis = 0.0478; $F = 15.5$, $p < 0.01$) (Figure 4a). The same analysis of the lowland dataset (eigenvalue 1st axis = 0.2036, eigenvalue 2nd axis = 0.0448; $F = 20.4$, $p < 0.01$) yielded a very similar pattern (Figure 4b).

Variation partitioning showed that trap height accounted for 25.3% of the total variation (73.9% of the variation explained by all combined variables) in the lowland and for 19.6% (55.2% of explained variation) in the mountains, while the study site explained 7.3% (21.4% of explained variation) and 14% (39.5% of explained variation) in the lowland and in the mountains, respectively.

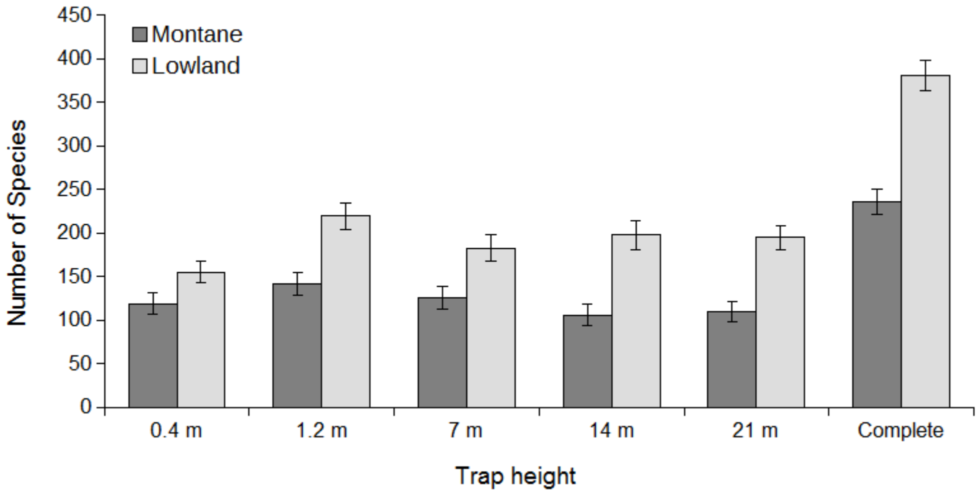

Figure 3. Species richness at the different height levels. Number of species (with 95% CI) of saproxylic beetles along the vertical gradient and overall species richness in the montane and lowland temperate forests as computed by sample-based rarefaction.

Canopy openness explained < 2% of total variation (< 5% of explained variation) in both datasets. The three environmental variables and their combinations altogether explained 34.2% of the total variation in the lowlands and 35.5% in the mountains (Table 1). The permutation test on all ordination axes gave significant results for both montane ($F = 6.1$, $p < 0.01$) and lowland ($F = 5.8$, $p < 0.01$) data.

Species dissimilarity patterns

The Sorensen dissimilarity of beetle assemblages generally increased with the vertical distance between sampling heights in both datasets. It was, however, higher when comparing assemblages between canopy (7–21 m) and understorey (0.4–1.2 m) than within these layers regardless of the vertical distance (Figure 5a). The rate of change in beetle assemblage composition was highest near the ground and rapidly decreased with height in both elevations. The pattern was nearly identical for both elevations. When comparing assemblages of particular heights, the dissimilarity was always higher in the lowland than in the mountains (Figure 5b).

The amount of dissimilarity attributed to nestedness was generally low; it was mostly higher in the mountains than in the lowland. In the latter, the nestedness was highest for the two understorey assemblages, and then mostly decreased with the vertical distance between the respective heights. In the mountains, the nestedness was mostly high among the three canopy heights, while the differences in species composition between the two understorey heights were almost completely attributed to species turnover (Table 1)

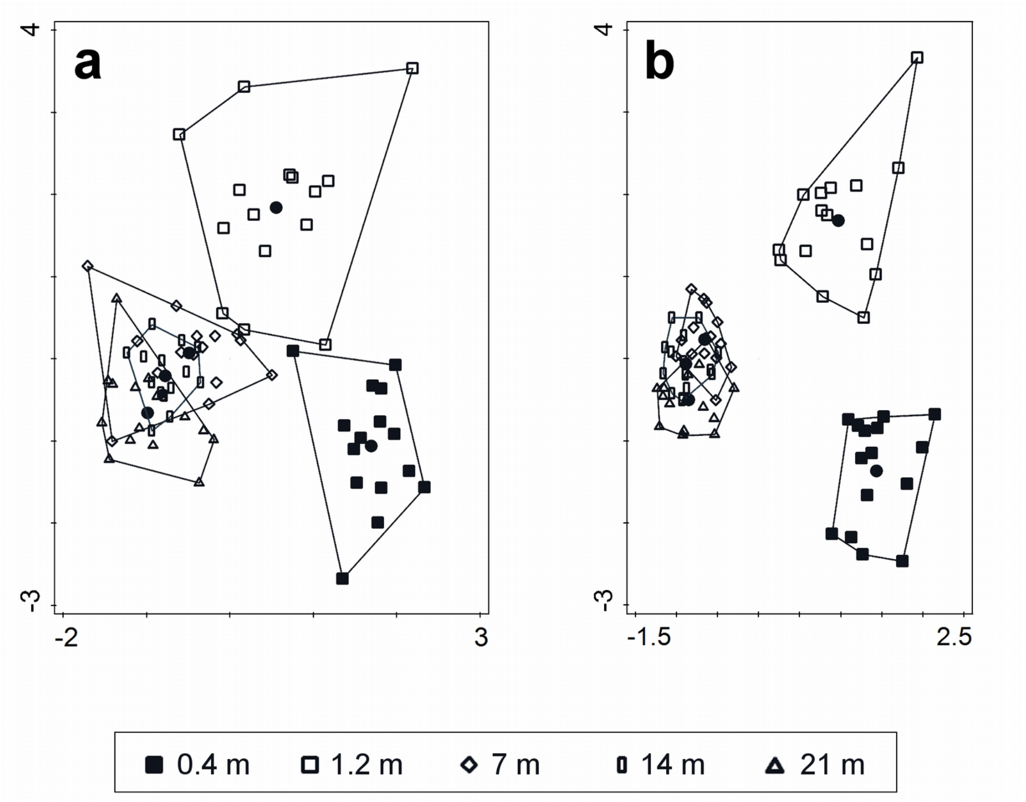

Figure 4. Redundancy Analysis ordination diagram of saproxylic beetle assemblages. The pooled assemblages from individual traps in the montane (a) and lowland (b) forests acted as samples (depicted), trap height acted as the explanatory variable and site and openness acted as covariables. The samples from the understorey (0.4 m, 1.2 m) are clearly separated from the canopy samples (7 m, 14 m, 21 m) along the 1st axis in both the montane (eigenvalue 1st axis = 0.1533) and the lowland datasets (eigenvalue 1st axis = 0.2162). The samples of the two understorey heights are separated along the 2nd axis in the mountains (eigenvalue 2nd axis = 0.0474) and lowlands (eigenvalue 2nd axis = 0.0505

In the lowland the mycetophages were associated with the understorey, but also with the canopy at 21 m. The xylophages peaked at 21 m, followed by 7 m (see Figure 6). The goodness-of-fit test on all the characteristic species showed that in the mountains only the mycetophages were

Table 1. Effect of environmental variables on composition of saproxylic beetle assemblages sampled along a vertical gradient in montane and lowland temperate forests. Computed by variation partitioning of Redundancy Analysis to show the amounts of variation explained by individual variables and their combinations.

	Montane		Lowland	
Environmental Variables	**% of Explained Variation**	**% of Total Variation**	**% of Explained Variation**	**% of Total Variation**
Study Site	39.5	14	21.4	7.3
Trap Height	55.2	19.4	73.9	25.3
% Canopy Openness	4.8	1.7	2	0.7
Study Site + Trap Height	- 4.4	- 1.6	- 3.9	- 1.3
Trap Height + Canopy Openness	- 1.2	- 0.4	0	0
% Canopy Openness + Study Site	6.4	2.3	7.3	2.5
Study Site + Trap Height + % Canopy Openness	- 0.3	- 0.1	- 0.6	- 0.2
	100	**35.5**	**100**	**34.2**

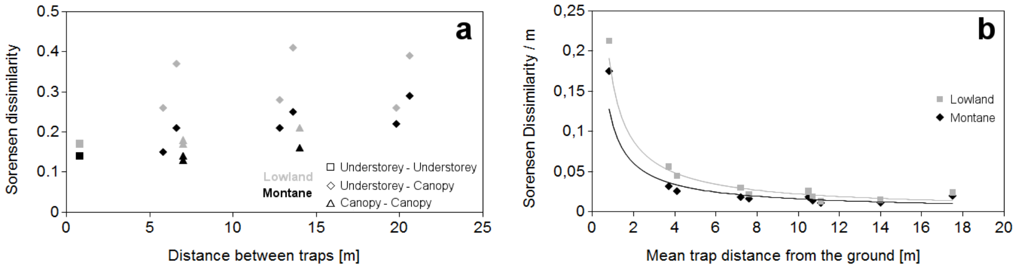

Figure 5. Dissimilarity of saproxylic beetle assemblages along a vertical forest gradient. (a) In both the lowland and montane forests Sorensen dissimilarity within the understorey (0.4 and 1.2 m heights above ground) and within the canopy (7, 14 and 21 m heights), was always lower than between samples from the two forest vertical strata. (b) The rate of change in assemblage composition decreased with distance from the ground along the vertical gradient. To standardize the Sorensen dissimilarity per 1 m of vertical distance between traps, the values of dissimilarity between assemblages from two trap heights were divided by vertical distance (in m) between them. These values are plotted against the mean height of the compared traps.

significantly unevenly distributed among the sampled heights ($\chi^2 = 16.294$, $p < 0.01$), while the result for all characteristic species was marginally insignificant ($\chi^2 = 8.098$, $p = 0.086$). The distribution of the mycetophages also differed from that of the predators ($\chi^2 = 14.162$, $p < 0.01$). In the lowland, neither all the characteristic species ($\chi^2 = 19.25$, $p < 0.001$) nor the mycetophages ($\chi^2 = 18.765$, $p < 0.001$) and saprophages ($\chi^2 = 15.076$, $p < 0.01$) were evenly distributed among the sampled heights. The distribution of the mycetophages differed from that of the xylophages ($\chi^2 = 63.523$, $p < 0.01$) and the predators ($\chi^2 = 47.836$, $p < 0.01$). Likewise, the distribution of the saprophages differed from that of the xylophages ($\chi^2 = 20.482$, $p < 0.01$) and the predators ($\chi^2 = 26.128$, $p < 0.01$). Furthermore, the distributions of the xylophages and predators differed marginally ($\chi^2 = 13.472$, $p < 0.05$).

None of the guilds, however, showed a significantly different distribution between the mountain and lowland forest. The overall distribution of feeding guilds differed only marginally ($\chi^2 = 8.979$, $p < 0.05$) between the two sampling areas. The overall representation of the feeding guilds was rather similar between mountains and lowland: In both areas mycetophages made up the largest share of beetle species. The share of predators was roughly the same in both elevations, while that of xylophages and saprophages was slightly higher in the lowlands.

Table 2. Results of Dissimilarity Partitioning showing what portion of the Sorensen Dissimilarity (β_{SOR}) is accounted for by turnover (β_{SIM}) and nestedness (β_{NES}) for comparison of the beetle assemblages of all strata in montane (**bold**) and lowland (normal) forest. The dissimilarity was generally higher in the lowland and could mostly be attributed to turnover in both areas.

	0.4 m	**1.2 m**	**7 m**	**14 m**	**21 m**
0.4 m		β_{SOR} = 0.17 β_{SIM} = 0.04 (24%) β_{NES} = 0.13 (76%)	β_{SOR} = 0.37 β_{SIM} = 0.31 (84%) β_{NES} = 0.06 (16%)	β_{SOR} = 0.41 β_{SIM} = 0.35 (85%) β_{NES} = 0.06 (15%)	β_{SOR} = 0.39 β_{SIM} = 0.32 (82%) β_{NES} = 0.07 (18%)
1.2 m	**β_{SOR} = 0.14** **β_{SIM} = 0.11 (79%)** **β_{NES} = 0.03 (21%)**		β_{SOR} = 0.26 β_{SIM} = 0.22 (85%) β_{NES} = 0.04 (15%)	β_{SOR} = 0.28 β_{SIM} = 0.24 (86%) β_{NES} = 0.04 (14%)	β_{SOR} = 0.26 β_{SIM} = 0.23 (88%) β_{NES} = 0.03 (12%)
7 m	**β_{SOR} = 0.21** **β_{SIM} = 0.19 (90%)** **β_{NES} = 0.02 (10%)**	**β_{SOR} = 0.15** **β_{SIM} = 0.13 (87%)** **β_{NES} = 0.02 (13%)**		β_{SOR} = 0.18 β_{SIM} = 0.17 (94%) β_{NES} = 0.01 (6%)	β_{SOR} = 0.21 β_{SIM} = 0.20 (95%) β_{NES} = 0.01(5%)
14 m	**β_{SOR} = 0.25** **β_{SIM} = 0.23 (92%)** **β_{NES} = 0.02 (8%)**	**β_{SOR} = 0.21** **β_{SIM} = 0.16 (76%)** **β_{NES} = 0.05 (24%)**	**β_{SOR} = 0.13** **β_{SIM} = 0.09 (69%)** **β_{NES} = 0.04 (31%)**		β_{SOR} = 0.17 β_{SIM} = 0.16 (94%) β_{NES} = 0.01 (6%)
21 m	**β_{SOR} = 0.29** **β_{SIM} = 0.25 (86%)** **β_{NES} = 0.04 (14%)**	**β_{SOR} = 0.22** **β_{SIM} = 0.15 (68%)** **β_{NES} = 0.07 (32%)**	**β_{SOR} = 0.16** **β_{SIM} = 0.10 (60%)** **β_{NES} = 0.06 (40%)**	**β_{SOR} = 0.14** **β_{SIM} = 0.12 (86%)** **β_{NES} = 0.02 (14%)**	

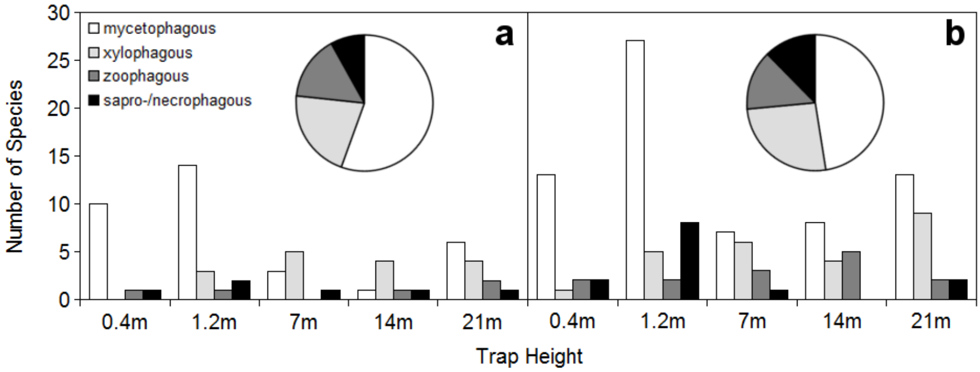

Figure 6. Guild structure of saproxylic beetle assemblages in montane (a) and lowland (b) temperate forests (pie charts), and along a vertical gradient in both forest types (barplots). The overall guild structure includes all recorded species. The barplots depict guild identity of species identified by indicator value analysis as characteristic for the given sampling height.

Discussion

Study outcome and limitations

Our results bring novel information on diversity and guild structure of saproxylic beetle assemblages along fine-scale vertical gradient in temperate lowland and montane forests. Sampling only two forest areas partly limits the validity of our observations. On the other hand, both of the sampling areas are diversity hot-spots of saproxylic fauna and refuges of the last populations of many highly endangered saproxylic species in the wider region (Horák et al. 2009, Vávra & Stanovský 2013, Rozkošný & Vaňhara 1996). Their fauna is thus representative of the habitat. It would be difficult to find other suitable lowland sites due to the high human pressure on lowland forests of Central Europe (Bail & Schmidl 2008); inclusion of impoverished sites would lead rather to underestimation of lowland diversity than to more precise results. Further, the higher amount of variability explained by the sampling site in the mountains (reflecting the distances among and the wider altitudinal range of the sites) shows that the sampling covered higher habitat diversity in the mountains, thus potentially leading rather to overestimation than underestimation of beetle diversity there.

The sampling sites spread over many square kilometres within each sampling area, the sampled areas are representative of habitat types common in Europe and elsewhere, but biologically as diverse as possible. The sampling was intensive and its design followed an identical protocol in both sampling areas. We therefore believe the resulting data are comparable and the results are relevant to the wider region.

Diversity and conservation value of lowland and montane assemblages

The lowland forest accommodated substantially (61%) more species of saproxylic beetles than the montane forest. The turnover of saproxylic beetles between lowland and mountains was substantial, as only about 21% of all sampled species were estimated to occur at both elevations. The lowlands thus hosted a much larger share of species present also in the mountains, than vice versa. Further, the lowland hosted a substantially higher portion of red-listed (Farkač et al. 2005) and "primeval forest" species (Schmidl & Bussler 2004).

Although mountains are an important refuge, our results underline the high importance of lowland forests for conservation of saproxylic biodiversity. Although based on the sampling of only two forest areas (*see above*), our results are fully in line with the findings of other studies (e.g. Seibold et al 2014) and clearly indicate that the conservation of saproxylic beetles in Europe would benefit from focusing more on lowlands. This is, however, not meant to downplay the value of the montane habitats for the preservation of saproxylic beetles since both forests hosted rather distinct communities.

Saproxylic beetle diversity along the vertical gradient

In both study areas the saproxylic beetle fauna displayed clear signs of stratification along the vertical gradient. There were considerable differences in the assemblage composition between the heights sampled in the canopy (7, 14, 21 m) and the understorey (0.4, 1.2 m). This is in accordance with other studies reporting stratification of saproxylic beetles between canopy and understorey of temperate forests (Wermelinger et al. 2007, Ulyshen & Hanula 2009, Bouget et al. 2011, Vodka & Cizek 2013, Floren et al. 2014).

Our results also show differences within both the canopy and the understorey strata. While the differences, as shown by the multivariate analysis, among the three heights sampled in the canopy were rather small, the differences between the two heights sampled in the understorey were substantial at both elevations. The dissimilarity was nearly identical between the two sampling heights in the understorey (0.8 m vertical distance) as among the three sampling heights within the canopy (vertical distance 7 and 14 m). It was also higher when comparing samples between understorey and canopy than within them. In comparison to dissimilarity measures, the multivariate analyses showed even more difference between the two understorey heights. This is, most likely, owing to the fact that the former is based on species presence/absence data, while the latter accounts also for abundances.

We may thus conclude that there is neither a sudden change in assemblage composition along the vertical gradient, nor is there a clear boundary between understorey and canopy in the sampled forests. The rate of change in assemblage composition, however, rapidly decreases with the distance from the ground. The high diversity of dead wood microhabitats and generally high availability of dead wood close to the ground in combination with the rapid change of microclimate near the forest floor are likely the reasons for the observed pattern. Their effects on beetle assemblages are gradually fading somewhere between 1.2 and 7 m above ground in the habitats studied here. This indicates that despite a gradual change, the transition between canopy and understorey occurs somewhere between these two heights in a temperate forest. The high diversity at the 1.2 m height could, perhaps, be partly explained by the overlap between canopy and understorey fauna. Since predation pressure is high on the ground (Šipoš et al. 2013) and herbs and shrubs are concentrated near the ground, the 1.2 m height level might also represent a relatively enemy-free and obstacle-free space frequented even by species exploiting resources found below this height.

Although we found high accordance in vertical stratification of saproxylic beetles between the two elevations, there were also notable differences. Firstly, the multivariate analyses as well as the dissimilarity partitioning indicated that the beetle assemblages were more stratified in the lowland. Secondly, the patterns of species richness along the vertical gradient differed between the two elevations. While the number of species declined with height in the canopy of the montane forest, there was no difference among the three sampled heights in the canopy of lowland forest, and the data even suggested an opposite pattern. All of this might be explained by the more complex vertical structure of the lowland forest, which shows more specific tree layers and therefore a higher variability of habitats (Janik et al. 2013). In the same way, the stronger vertical stratification in tropical forests in comparison temperate forests has been attributed to their more complex vertical structure (Basset et al 2003). Further, the lowest height was the poorest in the lowland, but not in the mountains. The denser undergrowth and the occasional floods at the lowland sites might be responsible for the low beetle numbers at the lowest sampling height.

Many studies concerning vertical stratification are focused on the question of whether the canopy is richer than understorey, or vice versa. Our results from the lowland demonstrate that the outcome of such comparisons may give contrasting results depending on the exact height sampled in the understorey. This, together with the effect of local environmental conditions on vertical stratification of insects (Duelli et al. 2002, Wermelinger et al. 2007, Gossner et al. 2009, Vodka & Cizek 2013) offers another explanation for the inconsistent and often contrasting outcomes of studies dealing with vertical stratification of insects in forests (cf. Vance et al. 2003, Hirao et al. 2009, Müller et al. 2014, Bouget et al. 2011).

We did not sample the upper canopy, thus missing a potentially important part of the stratum. However, the similarity of the assemblages across the three canopy heights sampled in this study, together with the results of Wermelinger et al. (2007), makes it unlikely that the addition of another sampling height in the canopy would have caused a substantial change of the study outcome. The documented within-strata differences are highly similar to the results of a study of comparable design (Basset et al. 2015), that showed a significant decrease of species similarity along their vertical gradient. This illustrates that sampling on a finer scale is indeed crucial for a better understanding of insect vertical distribution in forests (Basset et al 2003). Our results show that the knowledge of vertical stratification would benefit from finer sampling of those parts of the vertical forest gradient where the change of abiotic factors is most pronounced, i.e. near the ground and, possibly, also in the upper canopy.

Distribution of feeding guilds

Despite the differences in species richness and assemblage composition, guild structure was surprisingly similar between lowland and mountains. The largest share of assemblages consisted of the mycetophages, followed by the xylophages and the zoophages. The saprophages constituted the lowest share in both elevations. The main difference was the higher share of xylophages in the lowland compared to the mountains. This is explainable by the fact that lowlands are generally warmer and drier. The climate thus likely favours the xylophages and allows them to exploit a larger share of the available resource (Müller et al. 2014). The cooler and more humid montane climate is likely to favour wood-decaying fungi, as also suggested by the higher diversity of fungal communities found at higher elevations (Gómez-Hernández et al. 2012, Meng et al. 2013, Geml et al. 2014). This is also supported by higher diversity of fungi-associated beetles in moist forests (Hulcr et al. 2008).

The distribution of feeding guilds along the vertical gradient was mostly similar between lowland and mountains. Mycetophages were mostly concentrated in the understorey, probably owing to the fact that higher humidity near the ground provides better conditions for fungi (Ulyshen et al. 2011, Floren et al. 2014). While there were almost no fungi feeders characteristic of the canopy in the montane forest, such species showed a notable presence in the lowland. Predators did not show a clear preference for any specific height or stratum, a finding similar to the results of another study (Floren et al. 2014). The saprophages were concentrated in the understorey in the lowland but not in the montane forest. Despite the above-mentioned differences the patterns of the guild stratification are rather similar in the two forest types. The lack of a clear trend in guilds of lower species richness (predators and saprophages) may reflect an insufficient amount of indicator species rather than reality.

Conclusions

We conclude that temperate lowland forests hosts a substantially more diverse and threatened saproxylic beetle fauna than montane forests. Therefore, while conservation efforts should concern both types of habitats, the attention on lowland forests must be increased to preserve saproxylic species richness in Central Europe. Saproxylic beetles are stratified not only between the understorey and the canopy of temperate forests, but also within the understorey. The rate of change of the beetle community along vertical gradients decreases with distance from the ground. The comparisons of beetle richness between canopy and understorey may thus give contrasting results depending on the exact height sampled in the latter. Despite the fact that species composition differed substantially between montane and lowland forests, most patterns of feeding guild representation and vertical distribution were rather similar in the two forest types.

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References

Bail, J.G., Schmidl, J., 2008. Xylobiontic beetles (Insecta: Coleoptera) on oak canopies of the central European Danube Floodplain: species composition, ecological guilds and the impact of flooding and forestry. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nürnberg, Germany, pp. 327–338

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecol. Biogeogr.* 19: 134-143. doi: 10.1111/j.1466-8238.2009.00490.x

Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. *Methods Ecol. Evol*. 3: 808-812. doi: 10.1111/j.2041-210X.2012.00224.x

Basset, Y., Hammond, P.M., Barrios, H., Holloway JD, Miller SE., 2003. Vertical stratification of arthropod assemblages. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., editors. Arthropods of Tropical Forests. Cambridge University Press, pp. 4-7

Basset, Y., Cizek L., Cuénoud, P., Didham, R.K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A.K., Schmidl, J., Winchester, N.N., Roubik, D.W., Aberlenc, H.P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G., Corbara, B., Curletti, G., da Rocha, W.D., De Bakker, D., Delabie, J.H.C, Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., de Oliveira, E.G., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt J.P., Sørensen, L., Lewinsohn, T.M., Leponce, M., 2015. Arthropod distribution in a tropical rainforest: Tackling a four dimensional puzzle. *PLOS ONE*. doi:10.1371/journal.pone. 0144110

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the “last biotic frontier”: Are temperate forest canopies special for saproxylic beetles? *Forest Ecol. Manag*. 261: 211-220. doi: 10.1016/j.foreco.2010.10.007

Bouget, C., Larrieu, L., Parmain, G., Nusillard, B., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodivers. Conserv.* 22: 2111-2130. doi: 10.1007/s10531-013-0531-3

Chao, A., 1984. Non-parametric estimation of the number of classes in a population. *Scand. J. Stat*. 11: 265-270

Chen, Y.C., Hwang, W.H., Chao, A., Kuo, C.Y., 1995. Estimating the number of common species. Analysis of the number of common bird species in Ke-Yar Stream and Chung-Kang Stream. (In Chinese with English abstract.) *J. Chin. Stat. Assoc*.; 33: 373-393

Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates

Davis, A.L.V., Scholtz, C.H., Chown, S.L., 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *J. Biogeogr.* 26: 1039-1055. doi: 10.1046/j.1365-2699.1999.00335.x

Duelli, P., Obrist, M.K., Fluckinger, P.F., 2002. Forest edges are biodiversity hotspots: also for Neuroptera. *Acta Zool. Acad. Sci. Hung*. 48: 75–87 (Suppl. 2)

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.*; 67: 345-366. doi:

Escobar, F., Halffter, G., Arellano, L., 2007. From forest to pasture: an elevation of the influence of environment and biogeography on the structure of dung beetle (Sarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. *Ecography*. 30: 192-208. doi: 10.1111/j.2007.0906-7590.04818.x

Farkač, J., Král, D., Škorpík, M., 2005. Cervený seznam ohrozených druhu Ceské Republiky Bezobratlí [Red List of threatened species in the Czech Republic Invertebrates]. Praha;

Floren, A., Schmidl, J., 2008. Introduction: Canopy arthropod research in Europe. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nürnberg, Germany, pp. 13-20

Floren, A., Mueller, T., Dittrich, M., Weiss, M., Linsenmair, K.E., 2014. The influence of tree species, stratum and forest management on beetle assemblages responding to dead wood enrichment. *Forest Ecol. Manag*. 323: 57-64. doi:10.1016/j.foreco.2014.03.028

Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true colour fisheye photographs. Users manual and program documentation. Burnaby, Simon Fraser University; Millbrook – New York, Institute of Ecosystem Studies 36. Available at http://www.rem.sfu.ca/forestry/downloads/ Files/GLAV2UsersManual.pdf

Geml, J., Pastor, N., Fernandez, L., Pacheco, S., Semenova, T.A., Becerra, A.G., Wicaksono, C.Y., Nouhra, E.R., 2014. Large-scale fungal diversity assessment in the Andean Yungas forests reveals strong community turnover along an altitudinal gradient. *Mol. Ecol*. 23: 2452-2472. doi: 10.1111/mec.12765

Gómez-Hernández, M., Williams-Linera, G., Guevara, R., Lodge, D.J., 2012. Patterns of macromycete community assemblage along an elevational gradient: options for fungal gradient and metacommunity analyses. *Biodivers. Conserv.* 21: 2247-2268. doi: 10.1007/s10531-011-0180-3

Gossner, M.M., 2009. Light intensity affects spatial distribution of Heteroptera in deciduous forests. *Eur. J. Entomol*. 106: 241-252.

Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. In:

Futuyama DJ editor. *Annu. Rev. Ecol. Syst.* 33, pp. 1-23

Hirao, T., Murakami, M., Kashizaki, A., 2009. Importance of the understory stratum to entomofaunal diversity in temperate deciduous forest. *Eco. Res*. 24: 263–272

Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J.P., Petterson, R., Gibb, H., Hilszczański, J., 2007. The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic. Appl. Ecol*. 8: 364-376. doi: 10.1016/j.baae.2006.08.003

Horák, J., Mertlik, J., Chobot, K., Kubáň, V., 2009. Distribution of a rare saproxylic beetle Cucujus haematodes (Coleoptera: Cucujidae) in the Czech Republic with notes to occurrence in central Europe. *Klapalekiana*. 45: 191-197

Hulcr, J., Beaver, R.A., Puranasakul, W., Dole, S.A., Sonthichai, S., 2008. A Comparison of Bark and Ambrosia Beetle Communities in Two Forest Types in Northern Thailand (Coleoptera: Curculionidae: Scolytinae and Platypodinae) *Environ Entomol*. 37: 461-1470. doi: 10.1603/0046-225X-37.6.1461

Janik, D., Adam, D., Hort, L., Král, K., Šamonil, P., Unar, P., Vrška, T., Horal, D., 2013. Spatiotemporal differences in tree spatial patterns between alluvial hardwood and mountain beech-fir forests: do characteristic patterns exist? *J. Veg. Sci*. 24: 1141-1153. doi: 10.1111/jvs.12018

Jonsell, M., Weslien, J., 2003. Felled or standing retained wood – it makes a difference for saproxylic beetles. *Forest Ecol. Manag*. 175: 425-435. doi:10.1016/S0378-1127(02)00143-3

Jung, J., Kim, S., Lee, S., Park, C., Park, J., Lee, J., 2012. Community structure of ground beetles (Coleoptera: Carabidae) along an altitudinal gradient on Mt. Sobaeksan, Korea. *J. Asia-Pacific Entomol*. 15: 487-494. doi:10.1016/j.aspen.2012.05.007

Leksono, A.S., Takada, K., Shinsaku, K., Nobukazu, N., Anggraeni, T., Nakamura, K., 2005. Vertical and seasonal distribution of flying beetles in a suburban deciduous temperate forest collected by water pan traps. *Insect Sci*. 12: 199-206. doi: 10.1111/j.1744-7917.2005.00025.x

Leschen, R.A.B., Beutel, R.G., Lawrence, J.F., 2010. Coleoptera, Beetles. In: Kristensen, N.P., Beutel, R.G., editors. Handbook of Zoology, Arthropoda: Insecta. De Gruyter, Berlin/New York.

Martikainen, P., 2001. Conservation of threatened saproxylic beetles: significance of retained aspen Populus tremula on clearcut areas. *Ecol. Bull.* 49: 205-218. doi: 10.2307/20113277

Müller, J., Bussler, H., Gossner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle Ips typographus in a national park: from pest to keystone species. *Biodivers. Conserv.* 17: 2979-3001. doi: 10.1007/s10531-008-9409-1

Maguire, D.Y., Robert, K., Brochu, K., Larrivée, M., Buddle, C.M., Wheeler, T.A., 2014. Vertical stratification of beetles (Coleoptera) and flies (Diptera) in temperate forest canopies. *Environ. Entomol.* 43: 9-17. doi: 10.1603/EN13056

Meng, H., Li K., Nie, M., Wan, J., Quan, Z., Fang, C., Chen, J., Gu, J., Li, B., 2013. Responses of bacterial and fungal communities to an elevation gradient in a subtropical montane forest of China. *Appl. Microbiol. Biot.* 97: 2219-2230. doi: 10.1007/s00253-012-4063-7

Miklín, J., Čížek, L., 2014. Erasing a European biodiversity hot-spot: Open woodlands, veteran trees and mature forests succumb to forestry intensification, logging, and succession in a UNESCO Biosphere Reserve. *J. Nat. Conserv.* 22(1): 35-41. doi: 10.1016/j.jnc.2013.08.002

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermeier, E., Heidinger, I.M.M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., Gossner, M.M., 2014. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography.* 37: 1-11. doi: 10.1111/ecog.00908

Parmain, G., Bouget, C., Müller, J., Horak, J., Gossner, M.M., Lachat, T., Isacsson, G., 2015. Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests? *B. Entomol. Res.* 105: 101-109. doi: 10.1017/S0007485314000741

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

Rahbek, C., 1995. The elevational gradient of species richness: a uniform pattern? *Ecography.* 18: 200-205. doi: 10.1111/j.1600-0587.1995.tb00341.x

Roberts, D.W., 2012. labdsv: ordination and multivariate analysis for ecology, R Package Version 1.5-0 edn.

Robertson, H.G., 2002. Comparison of leaf litter ant communities in woodlands, lowland forests and montane forests of north-eastern Tanzania. *Biodivers. Conserv.* 11: 1637-1652. doi: 10.1023/A:1016883901065

Rozkošný, R., Vaňhara, J., 1995- 1996 Terrestrial Invertebrates of the Pálava Biosphere Reserve of UNESCO, I–III. *Folia Fac. Sci. Nat. Un. Biol.* 92: 1–208, 93: 209–408, 94: 409–630.

Schlaghamerský, J., 2000. The saproxylic beetles (Coleoptera) and ants (Formicidae) of central European hardwood floodplain forests. *Folia Fac. Sci. Nat. Un. Biol.* 103: 1-168.

Schmidl, J., Bussler, H., 2004. Ökologische Gilden xylobionter Käfer Deutschlands und ihr Einsatz in der landschaftsökologischen Praxis – ein Bearbeitungsstandard. *Nat.schutz Landsch.plan*. 36: 202–218.

Schroeder, B, Buddle, CM, Saint-Germain, M., 2009. Activity of flying beetles (Coleptera) at two heights in canopy gaps and intact forests in a hardwood forest in Quebec. *Can. Entomol*. 141: 515–520

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2014. Association of extinction risk of saproxylic beetles with ecological degradation in forests of Europe. *Conserv. Biol*. 29: 382-390. doi: 10.1111/cobi.12427

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecol. Manag*. 128: 211–225. doi: 10.1016/S0378-1127(99)00148-6

Šipoš, J., Drozdová, M., Drozd, P., 2013. Assessment of trends in predation pressure on insects across temperate forest microhabitats. *Agr. Forest Entomol*. 15: 255-261. doi: 10.1111/afe.12012

Šmilauer, P., Lepš, J., 2014. Multivariate analysis of ecological data using CANOCO, second edition. Cambridge University Press, Cambridge;

Stokland, J.N., Tomter, S.M., Söderberg, G.U., 2004. Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. In: Marchetti, M. (ed.), Monitoring and indicators of forest biodiversity in Europe – from ideas to operationality. European Forest Institute, EFI Proceedings 51, pp. 207-226.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, 521 pp.

Su, J.C., Woods, S.A., 2001. Importance of sampling along a vertical gradient to compare the insect fauna in managed forests. *Environ. Entomol*. 30: 400-408. doi: 10.1603/0046-225X-30.2.400

Tanabe, S., 2002. Between-forest variation in vertical stratification of drosophilid populations. *Ecol. Entomol*. 27: 720-731. doi: 10.1046/j.1365-2311.2002.00469.x

Ter Braak, C.J.F, Šmilauer, P., 2012. Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power. Ithaca, USA, 496 pp.

Tykarski, P., 2006. Beetles associated with scolytids (Coleopotera, Scolytidae) and the elevational gradient: Diversity and dynamics in the Tatra National Park, Poland. *Forest Ecol. Manag*. 225: 146-159. doi: 10.1016/j.foreco.2005.12.034

Ulyshen, M.D., Hanula, J.L., 2009. Habitat associations of saproxylic beetles in the southeastern United States: A comparison of forest types, tree species and wood postures. *Forest Ecol. Manag*. 257: 653-664. doi:10.1016/j.foreco.2008.09.047

Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation oriented management. *Forest Ecol. Manag*. 261: 1479-1489. doi:10.1016/j.foreco.2011.01.033

Vance, C.C., Kirby, K.R., Malcolm, J.R., Smith, S.M., 2003. Community composition of longhorned beetles (Coleoptera: Cerambycidae) in the canopy and understorey of sugar maple and white pine stands in south-central Ontario. *Environ. Entomol*. 32: 1066–1074

Vávra, J.C., Stanovský, J., Brouci (Coleoptera). 2013 In: Roháček, J., Ševčík, J., Vlk, P. editors. Příroda Slezska. Slezské zemské muzeum. Opava, 480 pp.

Vodka, Š., Cizek, L., 2013. The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. *Forest Ecol. Manag.* 304: 33-41. doi: 10.1016/j.foreco.2013.04.007

Vrška, T., Hort, L., Adam, D., Odehnalová, P., Král, K., Horal, D., 2006. Dynamika vývoje pralesovitých rezervací v České republice II - Lužní lesy – Cahnov-Soutok, Ranšpurk, Jiřina. [Developmental dynamics of virgin forest reserves in the Czech Republic. Volume II, Floodplain forests – Cahnov-Soutok, Ranšpurk, Jiřina] Academia, Praha, 214 pp. (in Czech)

Vrška, T., Adam, D., Hort, L., Kolář, T., Janík, D., 2009. European beech (Fagus sylvatica L.) and silver fir (Abies alba Mill.) rotation in the Carpathians – a developmental cycle or a linear trend induced by man? *Forest Ecol. Manag.* 258: 347–356. doi: 10.1016/j.foreco.2009.03.007

Wermelinger, B., 2004. Ecology and management of the spruce bark beetle Ips typographus – a review of recent research. *Forest Ecol. Manag.* 202: 67-82.

Wermelinger, B., Flückiger, P.F., Obrist, M.K., Duelli, P., 2007. Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *J. Appl. Entomol.*; 131(2): 104–114. doi: 10.1111/j.1439-0418.2006.01128

Wu, J., Pan, H., Yang, S., Niu, X., 2013. Tree species and elevation influence the assemblage composition of saproxylic beetles in subtropical forest of east China. *Forest Ecol. Manag.* 292: 29-38. doi: 10.1016/j.foreco.2012.12.004

Yu, X., Lü, L., Luo, T., Zhou, H., 2013. Elevational gradient in species richness pattern of epigaeic beetles and underlying mechanisms at east slope of Balang mountain in southwestern China. *PLOS ONE.* e69177. doi: 10.1371/journal.pone.0069177

Zou, Y., Sang, W., Zhou, H., Huang, L., Axmacher, J.C., 2014. Altitudinal diversity patterns of ground beetles (Coleoptera: Carabidae) in the forests of Changbai Mountain, Northeast China. *Insect Conserv. Diver.* 7: 161-171. doi: 10.1111/icad.12039

Chapter II

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

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Title: 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 diversity, 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 number of species, 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.

Introduction

Open temperate woodlands host rich communities of plants and animals, including many endangered organisms (Bengtsson et al. 2000; Benes et al. 2006; Spitzer et al. 2008; Bergmeier et al. 2010; Hédl et al. 2010; Bugalho et al. 2011; Horak et al. 2014; Ramírez-Hernández et al. 2014). In Europe, they support a high biodiversity of tree-associated organisms. Evidence that a large proportion of European forests naturally occurred with open canopies for most of the Holocene has substantially increased in recent years (Vera 2000; Whitehouse & Smith 2004; Alexander 2005; Birks 2005). The open structure of these forests was formerly maintained by disturbances caused by fires or windthrows (Niklasson et al. 2010; Adámek et al. 2015; Hultberg et al. 2015), and by the grazing of large herbivores (Bengtsson et al. 2000; Vera 2000). Since the mid-Mesolithic, these natural processes have been supplemented and later substituted by various human activities with a strong impact on woodland habitats. Slash-and-burn practices and later various silvopastoral management practices such as wood-pasturing and coppicing (Rackham 1998; Szabó 2009) have sustained the open structure of many European woodlands.

The situation changed in the 18th century with the industrial and agricultural revolutions. Intensification of forestry management together with abandonment of traditional silvicultural practices led to a substantial increase in canopy closure, and consequently to a transition from open woodlands to closed-canopy mesic forests (Bürgi 1999; Hédl et al. 2010; Kopecký et al. 2013). Today, open woodlands are scarce, fragmented, and still declining (Miklín & Čížek 2014; Varga et al. 2015). Yet these open woodlands still host a rich, specialised community of arboricolous invertebrates (Dolek et al. 2009; Horak et al. 2014; Ramírez-Hernández et al. 2014).

A typical characteristic of open woodlands is the presence of scattered, open-grown, often large and old trees. Such trees are considered keystone ecological features for biodiversity in various temperate and boreal regions (Read 2000; Manning et al. 2006; Fischer et al. 2010; Hall & Bunce 2011; Lindenmayer et al. 2012; Lindenmayer et al. 2014; Siitonen & Ranius 2015).

Although these trees are referred to by various synonyms, such as isolated trees, dispersed trees, pasture trees, paddock trees, remnant trees, etc. (see Manning et al. 2006), here, we call them collectively “solitary trees”, meaning trees with well-developed and separated tree crowns, growing in isolation from closed-canopy forests. Wide-crowned trees can only develop in open woodland conditions, which were formerly common in wood-pastures (Plieninger et al. 2015a; Hartel et al. 2013), traditional fruit or chestnut orchards (Horak et al. 2013; Plieninger et al. 2015b), noblemen’s hunting parks (Fletcher et al. 2015), and in coppice with standards woods (Altman et al. 2013). Today, solitary trees occur in remnants of these habitats (Varga et al. 2015; Plieninger et al. 2015a), as well as in game reserves, parks, and tree alleys (Horak et al. 2014; Jonsell 2011).

Solitary trees in wood-pastures are important breeding sites for birds because they often develop hollows (Hartel et al. 2014). Horak et al. (2014) found solitary trees were particularly attractive for saproxylic beetles since deadwood exposed to the sun is warmer, which enhances larval development. On the other hand, some groups of organisms, such as fungi or lichens, were found to be similarly rich at the edges of closed canopy forests (Horak et al. 2014). Moreover, in temperate forests the richness of arthropods often depends not only on the horizontal openness of the stand, but also on vertical stratification (Floren & Schmidl 2008; Ulyshen 2011), which can result in significant differences in communities between canopy and understorey strata. Therefore, regarding the conservation of woodland biodiversity, the question is to what extent forest edges or forest canopies can substitute for the role of fully open-grown trees. There is a need to explore communities from these habitats separately and then to compare them with solitary trees.

The aim of this study is to examine the ecological role of open-grown, solitary trees in maintaining temperate woodland biodiversity in comparison with closed-canopy forests. We compare the species density, composition, and conservation value of arthropod communities found on solitary trees with the communities found in the canopy and understorey at the forest edge and in the forest interior. We focused on four arthropod groups with a wide range of life-histories: beetles, bees and wasps, ants, and spiders.

Material and Methods

Study area

This study was conducted in alluvial woodlands in South Moravia, Czech Republic (48°45'-48°50'N, 16°45'-16°55'E, alt. 160-170 m a.s.l.), within the floodplain of the lower Dyje (Thaya) river. The flat landscape is composed of managed hardwood forests and meadows with old solitary trees. The prevailing trees are pedunculate oak (*Quercus robur*), narrowleaf ash (*Fraxinus angustifolia*), hornbeam (*Carpinus betulus*), field maple (*Acer campestre*), limes (*Tilia cordata*, *T. platyphyllos*), European white elm (*Ulmus laevis*), poplars (*Populus alba*, *P. nigra*), and black alder (*Alnus glutinosa*). Historically, the local forests were managed as coppice with standards woods or pasture woodlands. These practices were abandoned 60-150 years ago in favour of growing high forest with a 90-150 year rotation (Vrška et al. 2006). These forests are mainly even-aged oak, ash and poplar plantations, wooded meadows with open-grown oaks, and occasional remnants of coppice with standards or pasture woodlands. The forests transitioned from mainly open woodlands to closed canopy stands from the mid 19th to the mid 20th century (Miklín & Čížek 2014). The entire area is rich in saproxylic organisms, forming a hot spot within the Czech Republic and Central Europe (Rozkošný & Vaňhara 1995; Rozkošný & Vaňhara 1996).

Focal groups and sampling design

We sampled four groups of arthropods: beetles (Coleoptera) associated with deadwood and living trees (except for Staphylinidae; see Parmain et al. 2015), bees and wasps (Hymenoptera: Aculeata, except ants) nesting or foraging on trees, ants (Hymenoptera: Formicidae), and spiders (Araneae).

We sampled arthropods on solitary (open-grown) trees in wooded meadows and in a mature, closed-canopy forest that was formerly managed as coppice with standards. Coppicing was abandoned more than 60 years ago, and the stands have gradually transformed into high forests. The standards were already removed from the sampled patches, but the forest grew before the first clear-cut harvest. It thus retained continuity, high tree species richness and structural diversity.

Arthropods were sampled using flight interception traps composed of two crossed transparent polycarbonate sheets (25x50 cm) suspended above a collecting jar containing a saturated salt solution as a preservation liquid. A drop of liquid detergent was used to break the surface tension. Although flight interception traps are not the best method for collecting ants and spiders, we consider our collection of these groups to be adequately representative. Ants and spiders must crawl onto the trap to be caught (winged ant specimens were removed from the data), so their presence in our samples signified the utilization of particular trees.

The traps were installed on solitary trees (6-14 m above ground, mean 9.6 m), and in the canopy (14-26 m above ground, mean 20.3 m) and understorey (2-4 m above ground, mean 3.2 m) of the forest edge and interior. Each sampling site thus consisted of five different habitat types: (i) *solitary tree*, (ii) *edge-canopy*, (iii) *edge-understorey*, (iv) *interior-canopy*, and (v) *interior-understorey*. The DBH of solitary trees ranged from 410-680 cm (mean 513 cm), while trees at the edge ranged between 50-390 cm (mean 192 cm) in DBH, and trees in the forest interior ranged in DBH from 30-320 cm (mean 179 cm).

Sampling in the anopy and understory was undertaken in the same plots. Forest interior plots were established 36-88 m (mean 56.6 m) from the nearest forest edge plots. Solitary trees do not grow to great heights, which meant that we could not suspend traps at similar heights to that in the canopy in our closed forest sites. They also could not be suspended lower as numerous beetle collectors visit the site and often interfere with traps within their reach. However, our trapping design should have little effect on our results since previous work in this system showed very little difference between insect assemblages sampled above seven meters (Weiss et al. 2016).

Eight sampling sites were located 1-8 km apart. Altogether, we had eight replicates for each of the five habitat types, with 40 traps in total. The traps were exposed from 30th April to 2th September 2006 and emptied every two weeks.

Statistical analysis

Number of species and conservation value

We focused on the *species density* (i.e. number of species) (Gotelli & Colwell 2001) and the *conservation value* of arthropod communities found in each habitat type. To compare *species density* among the five habitat types, species accumulation curves with confidence intervals were computed using sample-based rarefaction (Colwell et al. 2012) in EstimateS 9.1.0 (Colwell 2013).

For each group, the *conservation value* (after Tropek et al. 2010) was computed for each trap as the sum of abundances weighted by the individual species' status in the national red lists (the used weights were: regionally extinct (RE) = 5, critically endangered (CR) = 4, endangered (EN) = 3, vulnerable (VU) = 2, near-threatened (NT) = 1; Farkač et al. 2005, Řezáč et al. 2015). For ants, the *conservation values* were computed from the presence of species, since the abundance of ants often reflects the distance from their nest rather than microhabitat suitability (Tropek et al. 2014).

Differences in *conservation values* among habitat types were analysed separately for each group by generalized linear mixed-effect models with quasi-Poisson distributions, with habitat type as a fixed factor, and trap location as a random variable. The models were fitted using the Generalized Estimating Equations algorithm in the *geepack* package (Hojsgaard et al. 2006) in

R 2.14.2 (R Core Team 2012). Post-hoc tests (multiple comparisons with Holm corrections) were carried out to detect differences in conservation values among habitat types.

Species composition and nestedness

Species composition was analyzed first by multivariate ordination analyses, and second by dissimilarity partitioning. Based on the preliminary DCA analyses (gradient lengths of responses of all groups greater than 2.6 SD units), Canonical Correspondence Analysis (CCA) based on the abundances of species in traps (i.e. representing samples) was performed separately for each focal arthropod group. The response data were log-transformed prior to analyses. For flying arthropods (beetles, bees and wasps), only species with more than one individual were included in the analysis to avoid 'tourist' species; for crawling groups (ants and spiders) all species were analysed. Habitat type represented an explanatory factor variable. The significance of ordination axes was tested by Monte Carlo tests with 999 permutations. Ordination analyses were performed in Canoco 5 (ter Braak & Šmilauer 2012).

For the dissimilarity partitioning, Sørensen dissimilarity was computed for all possible pairwise combinations of habitat types. For each group, presence/absence data from all the traps per sampling plot and habitat type were analysed. For beetles and bees and wasps, only species with more than one individual were included in the analysis, while all species of ants and spiders were included in the analysis. Dissimilarity reflects two phenomena – species turnover and nestedness. Species turnover is the replacement of species in different habitats, while nestedness reflects species loss (a particular community is a subset of another). We therefore partitioned between-habitat dissimilarity into these two components according to Baselga (2010). The Sørensen index (β_{sor}) and the Simpson dissimilarity index (β_{sim}), which describe spatial turnover, and the dissimilarity resulting from nestedness (β_{nes}) were computed with the *betapart* package (Baselga et al. 2013) in R 2.14.2 (R Core Team 2012). Dissimilarity partitioning for the sampling situation pairs was computed using the *beta.pair* function.

Results

In total, we sampled and identified 9,492 arthropods. We recorded 349 species of beetles (7,515 individuals), 116 species of bees and wasps (805 individuals), 18 species of ants (839 individuals), and 53 species of spiders (333 individuals); see Table 1 for details on threatened species.

Table 1. Numbers of all species and threatened species. The total number of species identified for each group of studied arthropods, and the number of threatened species according to their status in national red lists.

Group	Total	Regionally extinct	Critically endangered	Endangered	Vulnerable	Near threatened
Beetles	349	-	21	24	29	12
Bees and wasps	116	1	11	5	9	-
Ants	18	-	2	-	1	-
Spiders	53	-	-	2	3	8

Table 2. Variation explained by CCA axes. The effect of habitat types on community composition was tested by CCA for each group of organisms. Numbers in the table show the percentage of variation explained by the first and second constrained axes (displayed in Fig. 3). Pseudo-F statistics and P level were obtained by Monte Carlo tests with 999 permutations.

Group	Axis	Explained variation (%)	Pseudo-F	P
Beetles	1st	8.89	3.4	0.001
	2nd	5.03	2	0.001
Bees and wasps	1st	6.47	2.4	0.001
	2nd	3.76	1.4	0.215
Ants	1st	8.91	2.9	0.01
	2nd	6.87	2.4	0.041
Spiders	1st	5.75	2.1	0.001
	2nd	3.73	1.4	0.081

Of the beetles, 89% of species were obligate or facultative saproxylics, while the remaining 11% were species that occasionally occur on trees. Among the bees and wasps, the ratio was 74% saproxylics to 26% occasional tree visitors. Among ants, 72% of species were obligate or facultative saproxylics. No saproxylic spiders are recognized.

Arthropod diversity

For all focal groups, number of species was higher in sunny habitats (solitary trees, edge) than in the forest interior. For beetles, the number of species decreased from *solitary trees* to the forest interior; the two edge habitat types were intermediate in number of species (Figure 1A). Vertical stratum had no effect on number of beetle species. Bees and wasps exhibited a similar pattern, except that *interior-canopy* was richer than *interior-understorey* (Figure 1B). Number of ant species was highest on *solitary trees*, followed by *edge-understorey,* and lowest in *edge-canopy* and both of the interior habitats (Figure 1C). Number of spider species was highest and nearly identical on solitary trees and in *edge-canopy*, and it was lowest in the interior habitats (Figure 1D).

For beetles, bees and wasps, and ants, significant differences in the conservation value of habitat types were found. For beetles and bees and wasps, pattern in conservation value matched that of species richness, where solitary trees had the highest conservation value, the interior habitats had the lowest, and edge habitat types were intermediate (beetles: $\chi^2_{(4)}=62.6$, $P<0.001$; bees and wasps: $\chi^2_{(4)}=20.2$, $P<0.001$) (Figure 2A and 2B). For ants, all habitat types were equal in their conservation value, except for *interior-canopy* which supported no threatened species ($\chi^2_{(4)}$=9484, P<0.001) (Figure 2C). For spiders, no significant difference in conservation value was found among the habitat types ($\chi^2_{(4)}$=5.2, P=0.28) (Figure 2D).

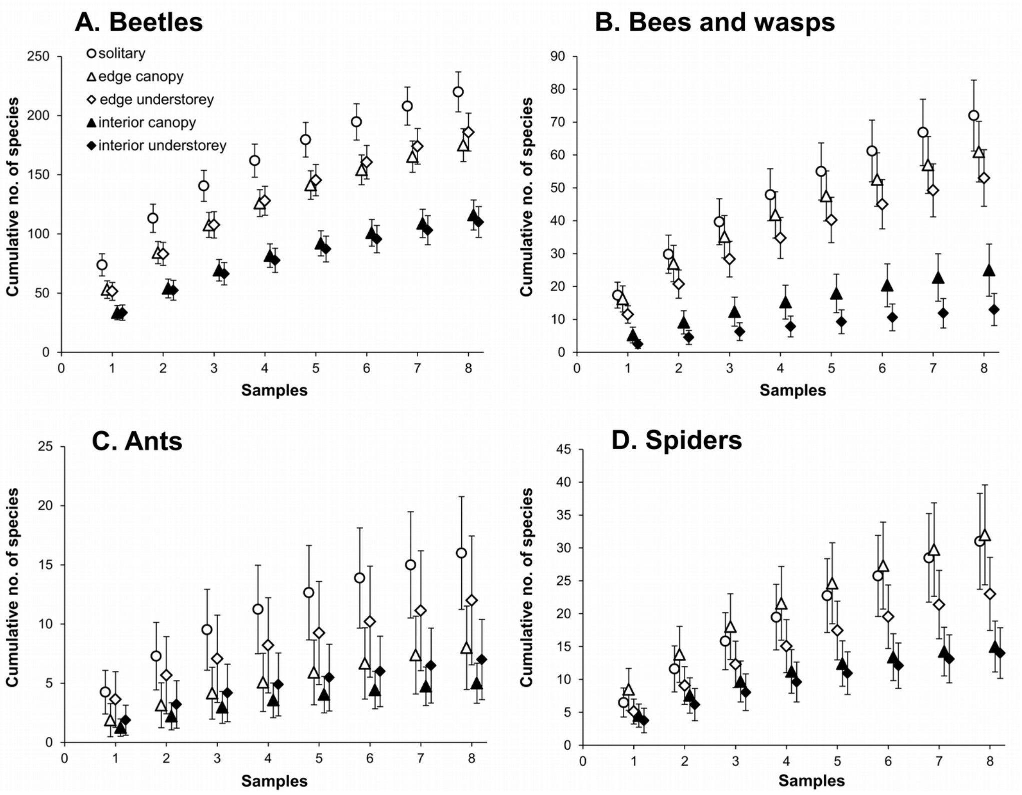

Figure 1. Sample-based rarefaction of species density in each habitat type. The expected number of species in pooled samples for A) beetles B) bees and wasps C) ants and D) spiders

The CCA revealed significant differences in species composition among the habitat types in all four groups of arthropods (Table 2, Figure 3). For beetles and ants, the most unique communities inhabited *solitary trees*. The first axis of the CCA revealed that communities of beetles, ants, and spiders were mostly structured by canopy openness, i.e. a gradient ran from *solitary trees* to the forest interior. For bees and wasps, stratum had a greater effect on community composition. The distribution of threatened species (signified by oval envelopes in Figure 3) showed that open habitats and solitary trees in particular harboured many threatened species.

The general pattern in the dissimilarity analyses was that species composition within *solitary trees* was more similar to that of trees in edge habitat types than to those of the forest interior. Nestedness remained stable or increased from the edge to the forest interior (Table 3).

Assemblages from interior habitat types were thus more nested within assemblages from *solitary trees* than assemblages in edge habitat types within *solitary tree* assemblages. For beetles, the degree of nestedness was low in comparison to the other groups. For ants, *edge-canopy* assemblages were fully nested within those found on *solitary trees*, and assemblages from the *interior-canopy* were fully nested within the *interior-understorey* assemblage.

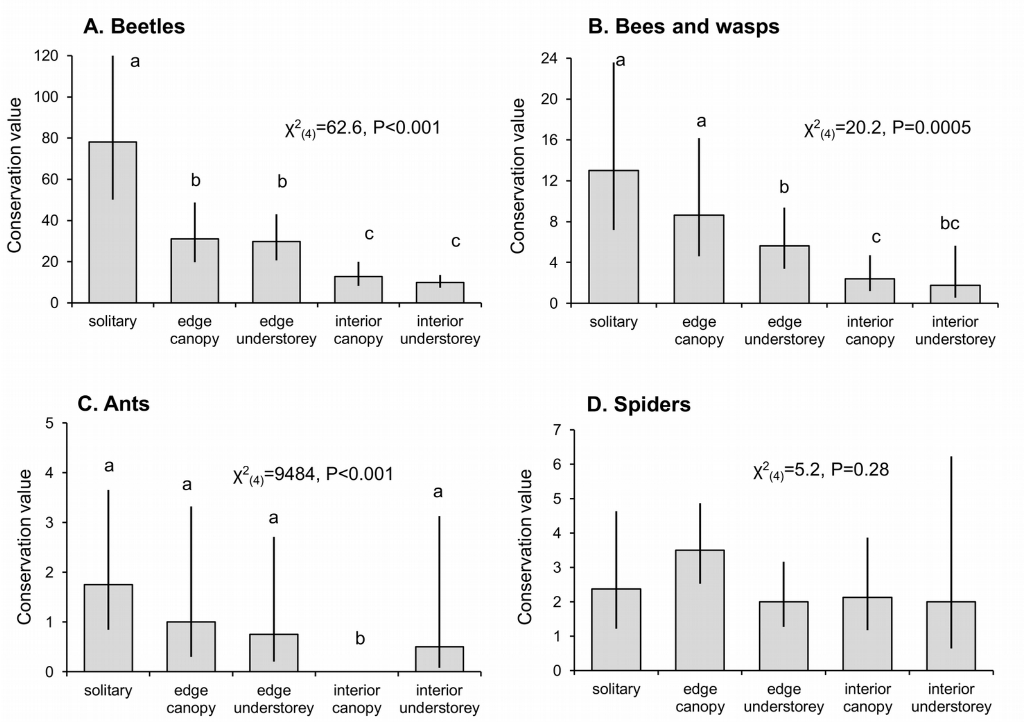

Figure 2. The conservation value of habitat types. Conservation values were estimated by generalized linear mixed-effect models with quasi-Poison distributions for A) beetles, B) bees and wasps, C) ants, and D) spiders. The conservation value was computed for each trap as a sum of abundances (except for ants where presence/absence data were used) weighted by the species' status in national red lists.

For bees and wasps, all habitat types showed a high degree of nestedness. In particular, there was high dissimilarity, but also high nestedness between assemblages sampled from the *interior-understorey* and assemblages sampled from open habitats. Dissimilarity between *solitary trees* and edge habitats in the composition of bee and wasp assemblages was mostly caused by species turnover. Spiders exhibited a similar pattern to bees and wasps.

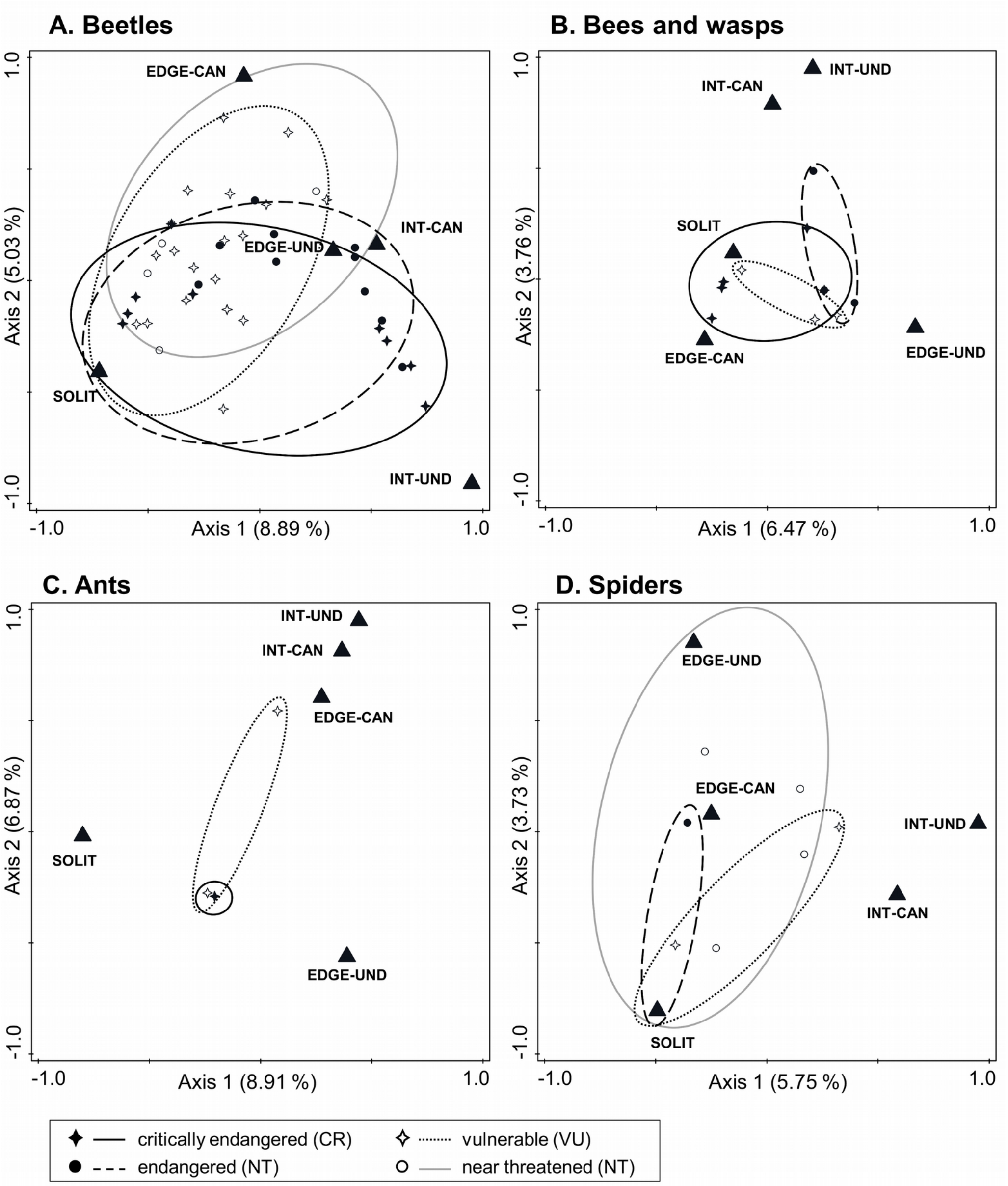

Figure 3. Species composition. Ordination diagrams of Canonical Correspondence Analysis (CCA) for A) beetles, B) bees and wasps, C) ants, and D) spiders. Diagrams are based on all species (singletons excluded for beetles and bees and wasps) but only the threatened species are displayed in the diagrams. (abbreviations in capitals stand for: SOLIT = solitary trees, EDGE-CAN = edge-canopy, EDGE-UND = edge-understorey, INT-CAN = forest interior-canopy, INT-UND = interior-understorey).

Table 3. Dissimilarity index and nestedness of communities. The numbers in the matrices give values of pairwise Sørensen dissimilarity indices (from 0 = species composition is identical in both habitat types, to 1= habitats do not share any species) followed by, in parentheses, the percentage of the value that is accounted to nestedness (100% means that the composition with the lower number of species is fully nested within the composition with the greater number of species). The numbers in parentheses following the habitat labels indicate the number of species subject to analysis (see Material and Methods).

A. Beetles

Edge-canopy (155)	0.39 (28%)			
Edge-understorey (159)	0.32 (16%)	0.33 (3%)		
Interior-canopy (110)	0.46 (39%)	0.39 (31%)	0.37 (38%)	
Interior-understorey (100)	**0.55** (33%)	0.50 (28%)	0.38 (47%)	0.36 (8%)
	Solitary (182)	Edge-canopy (155)	Edge-understorey (159)	Interior-canopy (110)

B. Bees and wasps

Edge-canopy (51)	0.31 (3%)			
Edge-understorey (41)	0.32 (25%)	0.41 (17%)		
Interior-canopy (25)	0.49 (**51%**)	0.47 (**57%**)	0.36 (**66%**)	
Interior-understorey (12)	**0.71** (**65%**)	**0.68** (**75%**)	**0.62** (**73%**)	0.46 (**63%**)
	Solitary (50)	Edge-canopy (51)	Edge-understorey (41)	Interior-canopy (25)

Table 3. Dissimilarity index and nestedness of communities. (*continued*)

C. Ants

	Solitary (16)	Edge-canopy (8)	Edge-understorey (12)	Interior-canopy (5)
Edge-canopy (8)	0.33 (**100%**)			
Edge-understorey (12)	0.29 (42%)	0.40 (37%)		
Interior-canopy (5)	**0.62** (**68%**)	0.38 (48%)	**0.53** (**62%**)	
Interior-understorey (7)	0.48 (**71%**)	0.20 (30%)	0.47 (41%)	0.17 (**100%**)

D. Spiders

	Solitary (31)	Edge-canopy (32)	Edge-understorey (23)	Interior-canopy (15)
Edge-canopy (32)	0.37 (3%)			
Edge-understorey (23)	0.48 (19%)	0.41 (27%)		
Interior-canopy (15)	0.48 (**58%**)	0.44 (**71%**)	**0.63** (16%)	
Interior-understorey (14)	**0.60** (40%)	**0.65** (44%)	**0.57** (25%)	**0.52** (6%)

Differences between *solitary trees* and edge habitats in spider species composition were also mainly due to species turnover. The large difference between the *interior-understorey* and the open habitats among spider assemblages was, however, caused mainly by turnover.
We also performed all of these analyses for beetles and bees and wasps, where we restricted our dataset to include only obligate tree/wood utilizing species.

Discussion

Solitary trees, followed by forest edges, were the most important habitats for maintaining a high diversity of tree-associated species in all four focal arthropod groups. Not only did they support the richest assemblages, but also many threatened species. Below, we discuss the relative importance of each of the studied habitats to our focal taxa, and the likely causes of the observed patterns, limitations of our study, and the conservation implications of our findings.

Flight interception traps are activity-based traps, thus more individuals (and species) are caught when species are more active. Higher temperatures in open habitats may result in greater flight activity. However, it is often hard to determine whether there were more individuals or whether they were more active (Lachat et al. 2016). For instance, Müller et al. (2015) found that abundance data on saproxylic beetles obtained from flight traps were comparable with data obtained from emergence traps. We therefore consider our data representative of the particular habitats we sampled.

Stratum vs. openness effects

Among beetles, ants, and spiders, insolation had a greater effect on community composition than vertical stratification, while the opposite was detected for bees and wasps. Regardless of the vertical stratum, communities of each of our focal taxa in the forest interior were generally poorer than those on solitary trees or at the forest edge. Our results thus corroborate findings of numerous other studies from European woodland habitats that have shown that openness is one of the principal factors driving the diversity and structure of arthropod communities (Floren & Schmidl 2008; Spitzer et al. 2008; Dolek et al. 2009; Horak et al. 2014; Müller et al. 2015; Košulič et al. 2016, Seibold et al. 2016).

Vertical stratification in species numbers and composition varied among the studied groups and between the forest edge and forest interior, which corroborates previous studies (Gruppe et al. 2008; Aikens et al. 2013; Maguire et al. 2014). Differences between vertical strata were rather minor, with the exception of ants and spiders at the forest edge. This might be explained by the fact that in temperate forests, ants are most common in the understorey as they often nest near or in the ground, while spiders generally avoid habitats where ants are abundant (Mestre et al. 2013).

A high proportion of tree-associated arthropods are saproxylic (Stokland et al. 2012). In our data, 89% of beetles, 74% of bees and wasps, and 72% of ants were obligate or facultative saproxylics. Although saproxylics are primarily dependent on deadwood as a substrate, patterns in richness and community composition are often influenced by sun exposure (Jonsell et al. 1998; Ranius & Jansson 2000; Franc & Götmark 2008; Horak et al. 2014; Bouget et al. 2014; Seibold et al. 2016), with more open habitats harbouring richer or more specialised communities. Bouget et al. (2011) and Müller & Goßner (2010) found richer communities of saproxylic beetles in the understorey compared to the canopy in various forest types. Both studies also found significant differences in species composition between strata, and ~30% of all of the species they collected preferred the canopy. Vodka et al. (2009), using data on the emergence of two beetle families, Buprestidae and Cerambycidae, from wood bait traps, found that the richness of beetles was also higher in the understorey, but this was largely influenced by sun-exposure. We did not find richer beetle communities in the understorey, but in accordance with Bouget et al. (2011), differences between vertical strata of beetle communities at the forest edge and the forest interior was mostly attributed to species turnover rather than nestedness (see Table 3).

For ants, number of species was rather similar between the two strata, while the community sampled from the canopy in the forest interior was a fully nested subset of that collected from the understory of the forest interior. This is not surprising. Although the forest canopy is an important habitat for some endangered species (Dolek et al. 2009), in temperate forests ants rarely achieve dominance in the canopy (Aikens et al. 2013), and they generally do not build large arboreal nests like many tropical species (Floren et al. 2014). Several species from our sites prefer nesting in deadwood in the canopy (Seifert 2008), although workers can forage also on trunks near the ground. Ants are strongly affected by temperature (Cerdá et al. 1997, Retana & Cerda 2000), and our data support the supposition that ant community structure is mainly driven by horizontal gradients in stand openness (Dolek et al. 2009).

Stand openness has been found to be an important factor also for butterflies (Benes et al. 2006), some families of flies (e.g. Syrphidae; von der Dunk & Schmidl 2008; Fayt et al. 2006). Conversely, although open forests are generally richer in insect species, some groups or species prefer shady conditions or the lower strata of closed forests (Lehnert et al. 2013). For instance, nocturnal species, like moths and some flies, tend to be richer in species in dense forests (Müller et al. 2012; Sebek et al. 2015), although Bolz (2008) found the opposite for moths in

German coppice woods. Regarding saproxylic beetles, Jonsell et al. (1998) found that about 25% of red-listed species preferred sun-exposed conditions, and about 10% showed a preference for shaded conditions. Moreover, the proportion of shade-preferring species increased during the late stages of wood decomposition, while species that preferred sun-exposed conditions decreased. For instance, fungi typically develop best in moist conditions, and therefore organisms dependent on fungi are more likely to be found in shady environments. Many fungi-dependent species can be found among the beetles (e.g. Mycetophagidae, Ciidae, Erotylidae, and some Staphylinidae) and flies (e.g. Mycetophilidae, Platypezidae, Phoridae). Similarly, some organisms may specifically exploit lying deadwood or stumps (Franc 2007; Brin et al. 2013) and therefore could more likely be found in lower strata independent of stand openness. To better explain patterns in community composition and its variation with forest structure and strata, further research on functional traits, like feeding guilds or specific substrate utilization, will be required.

The importance of solitary trees

Our results demonstrate that the biodiversity of temperate woodlands is greatly enhanced by the presence of solitary trees. They harboured rich communities of arthropods, including many endangered species, and these assemblages could not be fully compensated by the assemblages associated with canopy and understorey habitats, either at the forest edge or in the forest interior. Indeed, our observed pattern in assemblage composition, i.e. the increasing dissimilarity but also nestedness among assemblages from solitary trees through forest edges to the interior, indicates that assemblages from the forest interior are only poor subsets of what was found on solitary trees. This suggests that species occurring in the forest interior are mostly generalists that are not affected by openness. Solitary trees by contrast, besides harbouring these generalists, also often provide suitable conditions for light-demanding species that cannot survive in closed-canopy forests. This is supported by the high conservation value of solitary trees, and to a lesser extent, trees on the forest edge. Seibold et al. (2015) have pointed out that specialists to sunny habitats are more likely to be endangered. It is thus the open-grown trees that drive biodiversity patterns in these forests. The importance of open-grown trees for biodiversity can be attributed to the fact that they combine two important factors; insolation and large girth.

Solitary trees are exposed to sunlight and therefore offer suitable conditions for species that require a lighter and/or warmer microclimate. As previously mentioned by other authors, the preference for sun-exposed trees is more pronounced in northern and central Europe, with a decreasing preference in southern Europe and the Mediterranean (Vodka et al. 2009; Chiari et al. 2012; Siitonen & Ranius 2015). However, even in warm southern European conditions, open woodlands are important biodiversity hot-spots (Ramírez-Hernández et al. 2014). Our study forests were composed mainly of oak, ash, hornbeam and maple. The arthropod distribution patterns we found could potentially be applicable to deciduous forests in general, although further research is needed to address this issue.

The proximity of trees to grasslands with abundant flowering plants is also important in structuring insect communities. Some insects need trees or their deadwood for larval development but feed on nectar as adults (Fayt et al. 2006; Müller et al. 2008a; Müller et al. 2008b; Lachat et al. 2013; Siitonen & Ranius 2015). Many such species can be found among beetles (e.g. members of Carambycidae, Buprestidae, Mordellidae, or subfamily Cetoniinae), hoverflies (Syrphidae), or various aculeate hymenopterans (e.g. members of Crabronidae, Megachilidae and Vespidae and their parasitoids of the families Chrysididae and Sapygidae). In our study, the proximity to flowering plants could be responsible for the greater richness of beetles and bees and wasps in solitary trees or at forest edges. On the other hand, for ants and spiders, proximity to nectar sources is of minor importance, and may function only to increase prey abundances.

The solitary trees in our study had much greater DBH than the trees at the forest edge or in the forest interior. This can affect arthropod communities, although this effect could have been at least partly mitigated by the large amount of deadwood in the studied forests, which were former coppice with standards woods that have grown into high forests. Also, in a previous study by Vodka & Cizek (2013) from the same area, the amount of deadwood was shown to be less important than stand openness for saproxylic beetle assemblages (see also similar pattern in Horak et al. 2014). It is evident that light conditions affect tree growth. Greater stand openness usually results in greater incremental growth (Altman et al. 2013). Trees in closed-canopy conditions grow tall and thin, with a lack of lateral branching, which provides limited opportunities for tree-associated organisms. On the other hand, open-grown trees, due to a lack of competition, are usually not as tall as trees growing in closed-canopy forests. They typically develop wide crowns with large lateral branches (Rackham 1998). Open-grown trees thus generally reach larger diameters, and greater wood volume than trees in closed-canopy forests.

Tree microhabitats, such as large dead branches, tree hollows, patches of bark loss, cracks, fruiting bodies of fungi, mistletoe or lichens, are important resources for many arboricolous invertebrates (Winter & Möller 2008; Vuidot et al. 2011; Kraus et al. 2016). Trees growing in open conditions or sparser formations usually support a higher number of microhabitats than otherwise similar trees growing in closed forests (Hall & Bunce 2011; Regnery et al. 2013; Horak et al. 2014; Ouin et al. 2015; Siitonen & Ranius 2015). This is again partly associated with the conditions in which the trees have grown. Microhabitat formation is dependent on the condition of the tree in terms of its health and state of senescence. Trees growing in open conditions without competition live longer even if they are stressed or weakened, and may continue to accumulate microhabitats over time. By contrast, in closed-canopy forests competition for light between trees is high, which increases mortality rates, and prevents the developement and accumulation of deadwood microhabitats. In commercial forests, short rotation times (on average around 100 years) mean that trees are even cut before they reach senescence.

If there are large veteran trees in closed-canopy forests, they are usually the result of past openness of the habitat (Lonsdale 2013). However, with succession, the formerly open-grown trees are often overtopped by younger shade-tolerant trees and subsequently die (Rackham 1998), with flow-on effects to invertebrate communities that relied on such trees. Some saproxylic insects specialize on deadwood in dying trees, and perform poorly in dead trees. For instance, the great capricorn beetle *Cerambyx cerdo*, protected within EU's Habitats Directive (Council of the European Communities 1992), exploits only senescent but still living oaks (Buse et al. 2008; Albert et al. 2012), and females do not lay eggs on dead trees. Therefore, in the forest interior, where large trees may die quickly from overtopping, this beetle cannot establish long-lasting populations. On the other hand, solitary trees, if not cut and removed, can persist for hundreds of years, maintaining temporal continuity of available deadwood. Solitary trees therefore represent an important woodland feature that should be of principal concern in biodiversity conservation.

Implications for conservation

In the modern European landscape, the number of open-grown trees are rapidly declining (Manning et al. 2006; Miklín & Čížek 2014; Varga et al. 2015). The disappearance of these trees represents an actual threat for global biodiversity. Solitary trees are disappearing from commercially managed forests and pastures, either due to deliberate removal (Bugalho et al. 2011) or due to the gradual increase in canopy closure. Moreover, they disappear even from protected woodlands because these are often managed through a minimal intervention approach, which invariably leads to higher canopy closure through succession (Miklín & Čížek 2014). Therefore, in order to protect the biodiversity associated with solitary trees, nature conservation should target two principal objectives. First, to ensure the long-term persistence of extant solitary trees, and second, to promote the recruitment of new cohorts of solitary trees. This can often only be done by active intervention.

Old solitary trees should not be removed from the countryside because they are seen as ‘dangerous’ or ‘defective’ (Alexander 1998; Bütler et al. 2013; Lindenmayer et al. 2014). Detailed guidelines for the special care of veteran trees have already been described (Read 2000; Lonsdale 2013). The long-term persistence of trees can be ensured through proper arboricultural care. For instance, crown reduction reduces the risk of trunk collapse and prolongs the lifespan of trees (Read 2000; Fay 2011). Pollarding or shredding can serve very well in such situations (Rackham 1998; Read 2000; Sebek et al. 2013). Many formerly open-grown veteran trees are overgrown by younger trees, causing shading and jeopardizing their survival. In such cases, it is appropriate to gradually and carefully clear a circle or partial circle around these veteran trees (so-called “haloing”) (Lonsdale 2013) to avoid mortality. The recruitment of a sufficient number of younger solitary trees must take place in order to ensure the temporal availability of trees when existing trees die. In woodlands that are still extensively pastured, young trees can to some extent develop naturally amongst thorn scrub or distasteful plants (Vera 2000), although such recruitment usually takes a very long time. In areas where wood-pasture had been abandoned, or where only very old trees persist and new generations are urgently needed, young trees should be planted. Conservation actions should be primarily targeted at places where the forest structure is still open, or at least was until recently (abandoned wood-pastures or neglected coppices). Wood-pasturing is probably the best management option for the maintenance of sufficient numbers of solitary trees in the long-term. Significant thinning may be employed to ensure the rapid creation of an open woodland structure prior to introducing wood-pasturing, or in places where wood-pasturing is not possible.

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References

Adámek, M., Bobek, P., Hadincová, V., Wild, J., Kopecký, M., 2015. Forest fires within a temperate landscape: A decadal and millennial perspective from a sandstone region in Central Europe. *For. Ecol. Manage*. 336: 81–90. doi:10.1016/j.foreco.2014.10.014

Aikens, K.R., Timms, L.L., Buddle, C.M., 2013. Vertical heterogeneity in predation pressure in a temperate forest canopy. PeerJ 1, e138. doi:10.7717/peerj.138

Albert, J., Platek, M., Cizek, L., 2012. Vertical stratification and microhabitat selection by the Great Capricorn Beetle (Cerambyx cerdo) (Coleoptera: Cerambycidae) in open-grown, veteran oaks. *Eur. J. Entomol.* 109: 553–559.

Alexander, K.N.A., 1998. The links between forest history and biodiversity: the invertebrate fauna of ancient pasture-woodlands in Britain and its conservation. In: Kirby K.J. & Watkins C. (eds.), 1998. The ecological history of European forests. CAB International, Wallingford. pp. 73-81.

Alexander, K.N.A., 2005. Wood decay, insects, palaeoecology, and woodland conservation policy and practice – breaking the halter. *Antenna* 29: 117–178.

Altman, J., Hédl, R., Szabó, P., Mazůrek, P., Riedl, V., et al. 2013. Tree-Rings Mirror Management Legacy: Dramatic Response of Standard Oaks to Past Coppicing in Central Europe. *PLOS ONE* 8(2): e55770. doi:10.1371/journal.pone.0055770

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19: 134–143.

Baselga, A., Orme, D., Villeger, S., 2013. betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.2. http://CRAN.R-project.org/package=betapart

Benes, J., Cizek, O., Dovala, J., Konvicka, M., 2006. Intensive game keeping, coppicing and butterflies: The story of Milovicky Wood, Czech Republic. *For. Ecol. Manage*. 237: 353–365.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manage.* 132: 39–50.

Bergmeier, E., Petermann, J., Schröder, E., 2010. Geobotanical survey of wood-pasture habitats in Europe: Diversity, threats and conservation. *Biodivers. Conserv.* 19: 2995–3014.

Birks, H.J.B., 2005. Mind the gap: How open were European primeval forests? *Trends Ecol. Evol.* 20: 154–156.

Bolz, R., 2008. Diversity of moth communities (Insecta: Lepidoptera) in differently structured oak-hornbeam forests: a comparison of different phases of succession in coppice with standards and forests with high standard trees. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and Applied Studies from the High Frontier.* Bioform Entomology, Nürnberg, Germany, pp. 427–443.

Bouget, C., Brin, A., Brustel, H., 2011. Exploring the "last biotic frontier": Are temperate forest canopies special for saproxylic beetles? *For. Ecol. Manage.* 261: 211–220. doi:10.1016/j.foreco.2010.10.007

Bouget, C., Larrieu, L., Brin, A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecol. Indic.* 36: 656–664.

Brin, A., Bouget, C., Valladares, L., Brustel, H., 2013. Are stumps important for the conservation of saproxylic beetles in managed forests? - Insights from a comparison of assemblages on logs and stumps in oak-dominated forests and pine plantations. *Insect Conserv. Divers.* 6: 255–264. doi:10.1111/j.1752-4598.2012.00209.x

Bugalho, M.N., Caldeira, M.C., Pereira, J.S., Aronson, J., Pausas, J.G., 2011. Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. *Front. Ecol. Environ.* 9: 278–286.

Bürgi, M., 1999. A case study of forest change in the Swiss lowlands. *Landsc. Ecol.* 14: 567–575.

Buse, J., Ranius, T., Assmann, T., 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. *Conserv. Biol.* 22: 329–337. doi:10.1111/j.1523-1739.2007.00880.x

Bütler, R., Lachat, T., Larrieu, L., Paillet, Y., 2013. Habitat trees: key elements for forest biodiversity. In: Kraus D., Krumm F. (eds.), 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. *European Forest Institute.* pp. 84-91.

Cerdá, X., Retana, J., Cros, S., 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. *J. Anim. Ecol.* 66: 363–374. doi:10.2307/5982

Chiari, S., Carpaneto, G.M., Zauli, A., Marini, L., Audisio, P., Ranius, T., 2012. Habitat of an endangered saproxylic beetle, Osmoderma eremita, in Mediterranean woodlands. *Écoscience* 19: 299–307. doi:10.2980/19-4-3505

Colwell, R.K., 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R. K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L., Longino, R.L.,

2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *J. Plant Ecol.* 5: 3–21.

Council of the European Communities (1992) Council Directive 92/43/EEC – on the conservation of natural habitats and of wild fauna and flora. <http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex:31992L0043>

Dolek, M., Freese-Hager, A., Bussler, H., Floren, A., Liegl, A., Schmidl, J., 2009. Ants on oaks: effects of forest structure on species composition. *J. Insect Conserv.* 13: 367–375. doi:10.1007/s10841-008-9181-2

Farkač, J., Král, D., Škorpík, M. 2005. *Červený seznam ohrožených druhů České republiky. Bezobratlí*. AOPK ČR, Praha.

Fay, N., 2011. Conservation Arboriculture – Learning from old trees, artists and dead poets. <http://treeworks.co.uk/press_releases_publications.php>

Fayt, P., Dufrene, M., Branquart, E., Hastir, P., Pontégnie, C., Henin, J.-M., Versteirt, V., 2006. Contrasting responses of saproxylic insects to focal habitat resources: The example of longhorn beetles and hoverflies in Belgian deciduous forests. *J. Insect Conserv.* 10: 129–150.

Fischer, J., Stott, J., Law, B.S., 2010. The disproportionate value of scattered trees. *Biol. Conserv.* 143: 1564–1567. doi:10.1016/j.biocon.2010.03.030

Fletcher J., 2015. The impact of hunting on European woodland from medieval to modern times. In: Kirby K.J & Watkins C. (eds.), 2015. Europe's changing woods and forests: from wildwood to managed landscapes. CAB International, Wallingford, pp. 116-126.

Floren, A., Schmidl, J. (eds.), 2008. *Canopy arthropod research in Europe: Basic and Applied Studies from the High Frontier.* Bioform Entomology, Nürnberg, Germany, 576 pp.

Franc, N., 2007. Standing or downed dead trees-does it matter for saproxylic beetles in temperate oak-rich forests? *Can. J. For. Res.* 37: 2494–2507.

Franc, N., Götmark, F., 2008. Openness in management: Hands-off vs partial cutting in conservation forests, and the response of beetles. *Biol. Conserv.* 141: 2310–2321.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4: 379–391. doi:10.1046/j.1461-0248.2001.00230.x

Gruppe, A., Goßner, M., Engel, K., Simon, U., 2008. Vertical and horizontal distribution of arthropods in temperate forests. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Central Europe: Basic and Applied Studies from the High Frontier.* Bioform Entomology, Nürnberg, Germany, pp. 383–405.

Hall, S.J.G., Bunce, R.G.H., 2011. Mature trees as keystone structures in Holarctic ecosystems – a quantitative species comparison in a northern English park. *Plant Ecol. Divers.* 4: 243–250. doi:10.1080/17550874.2011.586735

Hartel, T., Dorresteijn, I., Klein, C., Máthé, O., Moga, C.I., Öllerer, K., Roellig, M., von Wehrden, H., Fischer, J., 2013. Wood-pastures in a traditional rural region of Eastern Europe: Characteristics, management and status. *Biol. Conserv.* 166: 267–275. doi:10.1016/j.biocon.2013.06.020

Hartel, T., Hanspach, J., Abson, D.J., Máthé, O., Moga, C.I., Fischer, J., 2014. Bird communities in traditional wood-pastures with changing management in Eastern Europe. *Basic Appl. Ecol.* 15: 385-395.

Hédl, R., Kopecký, M., Komárek, J., 2010. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Divers. Distrib.* 16: 267–276. doi:10.1111/j.1472-4642.2010.00637.x

Hojsgaard, S., Halekoh, U., Yan J., 2006. The R Package *geepack* for Generalized Estimating Equations. J. *Stat. Softw.* 15: 1-11.

Horak, J., Peltanova, A., Podavkova, A., Safarova, L., Bogusch, P., Romportl, D., Zasadil, P., 2013. Biodiversity responses to land use in traditional fruit orchards of a rural agricultural landscape. *Agric. Ecosyst. Environ.* 178: 71–77.

Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P., Pech, P., 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. *For. Ecol. Manage.* 315, 80–85. doi:10.1016/j.foreco.2013.12.018

Hultberg, T., Gaillard, M-J., Grundmann, B., Lindbladh, M., 2015. Reconstruction of past landscape openness using the Landscape Reconstruction Algorithm (LRA) applied on three local pollen sites in a southern Swedish biodiversity hotspot. *Veg. Hist. Archaeobot.* 24: 253–266. doi:10.1007/s00334-014-0469-8

Jonsell, M., 2011. Old park trees as habitat for saproxylic beetle species. *Biodivers. Conserv.* 21: 619–642.

Jonsell, M.,Weslien, J., Ehnström, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers. Conserv.* 7: 749–764.

Kopecký, M., Hédl, R., Szabó, P., 2013. Non-random extinctions dominate plant community changes in abandoned coppices. *J. Appl. Ecol.* 50: 79–87. doi:10.1111/1365-2664.12010

Košulič, O., Michalko, R., Hula, V., 2016. Impact of canopy openness on spider communities: implications for conservation management of formerly coppiced oak forests. *PLOS ONE*

11, e0148585.

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A., Winter, S., 2016. Catalogue of tree microhabitats – Reference field list. Integrate+ Technical Paper, 16 pp.

Lachat, T., Bouget, C., Bütler, R., Müller, J., 2013. Deadwood: quantitative and qualitative requirements for the conservation of saproxylic biodiversity. In: Kraus, D., Krumm, F. (eds.), 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, pp 92-103.

Lachat, T., Chumak, M., Chumak, V., Jakoby, O., Müller, J., Tanadini, M., Wermelinger, B., 2016. Influence of canopy gaps on saproxylic beetles in primeval beech forests: a case study from the Uholka-Shyrokyi Luh forest, Ukraine. *Insect Conserv. Divers.* doi:10.1111/icad.12188

Lehnert, L.W., Bässler, C., Brandl, R., Burton, P.J., Müller, J., 2013. Conservation value of forests attacked by bark beetles: Highest number of indicator species is found in early successional stages. *J. Nat. Conserv.* 21: 97–104. doi:10.1016/j.jnc.2012.11.003

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. *Science*, 338: 1305-1306.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A.D., Stein, J.A.R., 2014. New policies for old trees: Averting a global crisis in a keystone ecological structure. *Conserv. Lett.* 7: 61–69. doi:10.1111/conl.12013

Lonsdale, D. (ed.), 2013. Ancient and other veteran trees: further guidance on management. The Tree Council, London, 212 pp.

Maguire, D.Y., Robert, K., Brochu, K., Larrivée, M., Buddle, C.M., Wheeler, T.A., 2014. Vertical stratification of beetles (Coleoptera) and flies (Diptera) in temperate forest canopies. *Environ. Entomol.* 43: 9–17. doi:10.1603/EN13056

Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures - Implications for conservation. *Biol. Conserv.* 132: 311–321. doi:10.1016/j.biocon.2006.04.023

Mestre, L., Piñol, J., Barrientos, J.A., Espadaler, X., 2013. Ant exclusion in citrus over an 8-year period reveals a pervasive yet changing effect of ants on a Mediterranean spider assemblage. *Oecologia* 173: 239–248. doi:10.1007/s00442-013-2594-y

Miklín, J., Čížek, L., 2014. Erasing a European biodiversity hot-spot: Open woodlands, veteran trees and mature forests succumb to forestry intensification, succession, and logging in a

UNESCO Biosphere Reserve. *J. Nat. Conserv.* 22: 35–41. doi:10.1016/j.jnc.2013.08.002

Müller, J., Goßner, M.M., 2010. Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. *Biol. Conserv.* 143: 625–633. doi:10.1016/j.biocon.2009.11.027

Müller J., Bässler H., Kneib T., 2008a. Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *J. Insect Conserv.* 12: 107–124.

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., Duelli, P., 2008b. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. *Biodivers. Conserv.* 17: 2979–3001. doi:10.1007/s10531-008-9409-1

Müller, J., Mehr, M., Bässler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., Klemmt, H.-J., Brandl, R., 2012. Aggregative response in bats: Prey abundance versus habitat. *Oecologia* 169: 673–684. doi:10.1007/s00442-011-2247-y

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I.M.M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., Gossner, M.M., 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography* (Cop.). 38: 499–509. doi:10.1111/ecog.00908

Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojlik, T., 2010. A 350-year tree-ring fire record from Białowieza Primeval Forest, Poland: implications for Central European lowland fire history. *J. Ecol.* 98: 1319–1329.

Ouin, A., Cabanettes, A., Andrieu, E., Deconchat, M., Roume, A., Vigan, M., Larrieu, L., 2015. Comparison of tree microhabitat abundance and diversity in the edges and interior of small temperate woodlands. *For. Ecol. Manage.* 340: 31–39. doi:10.1016/j.foreco.2014.12.009

Parmain, G., Bouget, C., Müller, J., Horak, J., Gossner, M.M., Lachat, T., Isacsson, G., 2014. Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests? *Bull. Entomol. Res.* 105: 1–9. doi:10.1017/S0007485314000741

Plieninger, T., Hartel, T., Martín-López, B., Beaufoy, G., Bergmeier, E., Kirby, K., Montero, M.J., Moreno, G., Oteros-Rozas, E., Van Uytvanck, J., 2015a. Wood-pastures of Europe: Geographic coverage, social–ecological values, conservation management, and policy implications. *Biol. Conserv.* 190, 70–79. doi:10.1016/j.biocon.2015.05.014

Plieninger, T., Levers, C., Mantel, M., Costa, A., Schaich, H., Kuemmerle, T., 2015b. Patterns and drivers of scattered tree loss in agricultural landscapes: Orchard meadows in Germany (1968-2009). *PLOS ONE* 10, e0126178. doi:10.1371/journal.pone.0126178

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Rackham, O., 1998. Savanna in Europe. In: Kirby K.J & Watkins C. (eds.), 1998. The ecological history of European forests. CAB International, Wallingford, pp. 1-24.

Ramírez-Hernández, A., Micó, E., Marcos-García, M.D.L.Á., Brustel, H., Galante, E., 2014. The "dehesa", a key ecosystem in maintaining the diversity of Mediterranean saproxylic insects (Coleoptera and Diptera: Syrphidae). *Biodivers. Conserv.* 23: 2069–2086. doi:10.1007/s10531-014-0705-7

Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* 95: 85–94.

Read H., 2000. Veteran trees: A guide to good management. *English Nature.*

Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? *For. Ecol. Manage.* 295: 118–125. doi:10.1016/j.foreco.2013.01.009

Retana, J., Cerda, X., 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. *Oecologia* 123: 436–444. doi:10.1007/s004420051031

Řezáč, M., Kůrka, A., Růžička, V., Heneberg, P., 2015. Red List of Czech spiders: 3rd edition, adjusted according to evidence-based national conservation priorities. *Biologia* 70: 645-666.

Rozkošný, R., Vaňhara, J. (1995) Terrestrial Invertebrates of the Pálava Biosphere reserve of UNESCO II. Folia Fac. Sci. Nat. Univ. Masaryk. Brun., Biol., 93. Brno: Masaryk University, 1995. 200 p.

Rozkošný, R., Vaňhara, J. (1996) Terrestrial Invertebrates of the Pálava Biosphere Reserve of UNESCO III. Folia Fac. Sci. Nat. Univ. Masar. Brun., Biol., 94. Brno: Masaryk University, 1996. 224 p.

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.

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. For. Ecol. Manage. 358: 80–89. doi:10.1016/j.foreco.2015.09.008

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv. Biol.* 29: 382–390. doi:10.1111/cobi.12427

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J., 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *J. Appl. Ecol.* 53: 934–943. doi:10.1111/1365-2664.12607

Seifert, B., 2008. The ants of Central European tree canopies (Hymenoptera: Formicidae) – an underestimated population? In: Floren A, Schmidl J (eds.), 2008. *Canopy arthropod research in Europe: Basic and applied studies from the high frontier*. Bioform Entomology, Nürnberg, Germany, pp. 157-172.

Siitonen J. & Ranius T., 2015. The importance of veteran trees for saproxylic insects. In: Kirby K.J. & Watkins C. (eds.), 2015. Europe’s changing woods and forests: from wildwood to managed landscapes. CAB International, Wallingford. pp.140-153.

Spitzer, L., Konvicka, M., Benes, J., Tropek, R., Tuf, I., Tufova, J., 2008. Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. *Biol. Conserv.* 141: 827–837. doi:10.1016/j.biocon.2008.01.005

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in deadwood. Cambridge University Press, Cambridge.

Szabó, P., 2009. Open woodland in Europe in the Mesolithic and in the Middle Ages: Can there be a connection? *For. Ecol. Manage.* 257: 2327–2330. doi:10.1016/j.foreco.2009.03.035

ter Braak, C.J.F., Šmilauer, P., 2012. Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power, Ithaca, USA, 496 pp.

Tropek, R., Cerna, I., Straka, J., Kadlec, T., Pech, P., Tichanek, F., Sebek, P., 2014. Restoration management of fly ash deposits crucially influence their conservation potential for terrestrial arthropods. *Ecol. Eng.* 73: 45–52.

Tropek, R., Kadlec, T., Karesova, P., Spitzer, L., Kocarek, P., Malenovsky, P., Banar, P., Tuf, I.H., Hejda, M., Konvicka, M., 2010. Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. J. Appl. Ecol. 47: 139–147.

Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. *For. Ecol. Manage.* 261: 1479–1489. doi:10.1016/j.foreco.2011.01.033

Varga, A., Ódor, P., Molnár, Z., Bölöni, J., 2015. The history and natural regeneration of a secondary oak-beech woodland on a former wood-pasture in Hungary. *Acta Soc. Bot.* . 84: 215–225. doi:10.5586/asbp.2015.005

Vera, F.W.M., 2000. Grazing Ecology and Forest History. CABI Publishing, Wallingford. 506 pp.

von der Dunk, K., Schmidl, J., 2008. Diptera (Brachycera) in oak forest canopies – management and stand openness gradient determine diversity and community structure. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy arthropod research in Central Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nürnberg, pp. 507-528.

Vodka, S., Konvicka, M., Cizek, L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: Implications for forest history and management. *J. Insect Conserv.* 13: 553–562.

Vodka, Š., Cizek, L., 2013. The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. *For. Ecol. Manage.* 304: 33–41.

Vrška, T., Hort, L., Adam, D., Odehnalova, P., Kral, K., Horal, D., 2006. Developmental dynamics of virgin forest reserves in the Czech Republic II—the lowland floodplain forests (Cahnov-Soutok, Ranspurk, Jirina), Academia, Prague, Czech Republic.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. *Biol. Conserv.* 144: 441–450.

Weiss, M., Procházka, J., Schlaghamerský, J., Cizek, L., 2016. Fine-scale vertical stratification and guild composition of saproxylic beetles in lowland and montane forests: similar patterns despite low faunal overlap. *PLoS One* 11 (3): e0149506. doi:10.1371/journal.pone.0149506

Whitehouse, N.J., Smith, D.N., 2004. "Islands" in Holocene forests: implications for forest openness, landscape clearance and "culture-steppe" species. *Environ. Archaeol.* 9: 203–212.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. *For. Ecol. Manage.* 255: 1251–1261. doi:10.1016 /j.foreco.2007.10.029

Chapter III

Saproxylic beetles in temperate and tropical forests – a comparison of vertical stratification patterns

Manuscript

Saproxylic beetles in tropical and temperate forests – a comparison of vertical stratification patterns

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Abstract

The aim of this study was to compare structural characteristics of saproxylic beetle assemblages between three forest types of different altitude and latitude. Sampling took place in a lowland rainforest in Panama, a hardwood floodplain forest and a beech-fir mountain forest, both in the eastern Czech Republic. The Beetles were sampled by flight intercept traps that were placed along vertical transects (traps were at placed 0, 1.3, 7, 14 and 21 m above ground – additionally 28 m in the tropical forest).

The tropical forest was estimated to host two to three times more species than the temperate lowland and the mountain forest, respectively. Beetle assemblages in all three forest types where clearly vertically stratified, with stratification being most pronounced in the tropical forest. Species richness was similar in the understorey of all three forests; it peaked in the canopy of the tropical forest (at 28 m) but in the understorey (1.3 m) of the temperate ones. Feeding guild composition and stratification exhibited similar patterns in all three forest types as proportions of most feeding guilds along the vertical gradient changed in the same way in the tropical and temperate forests.

The vertical stratification of beetle communities was best pronounced in the structurally most complex tropical forest and least pronounced in the structurally least complex mountain forest. The high richness of saproxylic beetles in the tropical forest was due to the richness of canopy fauna. The similarities in guild composition and stratification suggest that similar factors such as e.g. resource availability govern the structuring of saproxylic beetle assemblages in the three forests in this study and, perhaps, also in most other forests on the Earth.

Introduction

Understanding the patterns of species distribution on a global scale is one of the major challenges in modern ecology. This is especially true in case of terrestrial arthropods which hold key positions in almost all ecosystems around the globe. Arthropod communities are generally showing increasing species richness with decreasing latitude (e.g. Kocher & Williams; Lobo & Martín-Piera; Willig et al. 2003; Hawkins & DeVries 2009). Altitudinal gradients, on the other hand, tend to show a larger variety. Arthropod species richness has been shown to decrease with elevation (Robertson 2002; Escobar et al. 2007) but may also increase or exhibit a mid-elevation peak (Davis et al. 1999; Yu et al. 2013). Research on species distribution patterns on the smaller scale of the respective tropical, temperate, lowland and mountain habitats is also a high priority, since it is essential for biodiversity conservation, forestry and agriculture.

Forests are three-dimensional habitats where organisms are also distributed along the vertical gradient between forest floor and tree tops (Basset et al. 2003a). Depending on the type of forest and taxa studied, the vertical gradient in stratification of arthropod assemblages might be imperceptible, or it may result in a clear stratification between sampling heights (e.g. Tanabe 2002; Leksono et al. 2005; Wermelinger et al. 2007; Maguire et al. 2014; Basset et al. 2015). The stratification patterns also change with latitude as stratification is more pronounced in tropical forests than in temperate ones, probably due to the higher complexity of the vertical structure of tropical forests (Basset et al. 2003a).

Insects associated with the wood of dead or live trees (i.e. saproxylic insects), especially beetles, constitute a substantial portion of forest biodiversity. Owing to their ability to weaken or kill trees and start the decomposition process, many beetles are considered essential components of forest dynamics in the natural forest and serious pests in production forests (Wermelinger 2004; Müller et al. 2008). The recent decrease in the amount of dead wood and old trees in forests has caused serious decline of numerous species (Siitonen et al. 2000; Floren & Schmidl 2008). Saproxylic beetles are thus intensively studied due to their status as pests or target species of nature conservation (Stokland et al. 2004; Stokland et al. 2012; Bouget et al. 2013). They also serve as model organisms for identifying sustainable forest management practices (Siitonen et al. 2000; Martikainen 2001; Grove 2002).

Despite numerous studies on the ecology of saproxylic beetles, little is known about their response on larger ecological scales. Tykarski (2006) reported a decrease in species richness of bark beetles and their associates with altitude, while Procházka et al. (unpublished data) reported shifts in community composition of bark beetles between lowland and montane forests. Another recent study (Weiss et al. 2016) showed very similar patterns in fine-scale vertical stratification and guild composition of the entire saproxylic beetle community of a temperate lowland and mountain forest despite low species overlap. Even less is yet known about the differences of the beetle assemblages between temperate and tropical forests. Despite the fact that the latter host an additional group of arthropod wood decomposers – namely termites – saproxylic beetles still play a crucial role in these forests (Grove & Stork 1999, Ødegaard et al. 2004). Yet there is little knowledge whether and how competition with termites, high tree species diversity, complex vertical structure, feeding pressure on fungi or the higher variation of wood density (Swenson & Enquist 2007) shape communities of saproxylic beetles and if there are differences between tropical and temperate forests. However, directly comparing these communities between habitats of different ecosystems is a problematic task. It requires at the very least a comprehensive sampling of all respective habitats in an identical way. This constitutes a considerable logistical challenge.

In this study we analyze data of saproxylic beetle assemblages that meets the above mentioned requirements. The tropical part was sampled in the scope of the IBISCA project (Basset et al. 2007) in a lowland rainforest in Panama. The temperate part was sampled in a lowland floodplain and mountain forest in the Czech Republic (Weiss et al. 2016). All of these forest types were sampled intensively and with essentially the exact same trapping method along a fine-scale vertical gradient.

Using this data we performed an unprecedented comparison of the saproxlic beetle communities in forests of different altitude and latitude to answer the following questions: (i) How do species richness and guild structure differ between communities of saproxylic beetles in the three forest types? (ii) Do patterns of species distribution along the vertical gradient differ between the three forest types? (iii) Does the distribution of feeding guilds along the vertical forest gradient differ between the three forest types?

Methods

Study sites

The field sampling of the tropical lowland forest took place in the San Lorenzo Protected Area in the Colón Province of the Republic of Panama). The area is located in the middle of the Mesoamerican Biological Corridor “hotspot”, which is known to harbor relatively high levels of biodiversity (Weaver & Bauer, 2004). For a detailed description of this sampling area see Basset et al. (2007).

Sampling of the temperate forests was performed in a lowland floodplain forest and a mountain forest range in the Czech Republic. The lowland part of the study was conducted in the alluvial woodlands along the lower Dyje (Thaya) and Morava (March) rivers in southern Moravia. The entire area is a regional biodiversity hotspot and important refuge of saproxylic fauna (Rozkošný & Vaňhara 1995, Schlaghamerský 2000).

The montane part of tshe study was conducted in the Moravian-Silesian Beskids (Beskydy) – a mountain range belonging to the Western Carpathians, situated in north-eastern Moravia. The area is one of the most important refuges of montane saproxylic biodiversity in the Czech Republic (Horák et a. 2009, Vávra & Stanovský 2013). For a detailed description of these two sampling areas see Chapter I.

Sampling design and technique

Sampling in the tropical lowland forest focused on four sites. Three of those were in the direct reach of the STRI canopy crane while the fourth was situated on a ridge on average 368 meters from the crane sites (see Figure 1e). At each sampling site, three vertical transects were installed. Each vertical transect consisted of six unbaited flight intercept traps exposed at 0, 1.3, 7, 14, 21 and 28 meters above the ground (height at the middle of the interception panels). Hereafter the first two of these trap heights will be referred to as “understorey” and the other three as “canopy”. In sum 120 traps were installed on the sampling sites. Sampling took place from October 2003 until October 2004.

In the temperate lowlands and the mountains five sampling sites were selected in each of the two study areas (see Figure 1c+f). Because of the overall lower tree height in the temperate forests the transects here lacked the uppermost trap at 28 meters. A total of 150 traps were used, with 75 traps in the lowland and 75 traps in the montane forest. Sampling was carried out in 2007 in the lowland and in 2008 in the mountains. Due to the difference in the length of the vegetation season, traps at the lowland sites were operated from the end of March (after ceasing of inundation) until the end of September, whereas traps at the montane sites were operated from the end of April (ceasing of snow cover) until the end of September. The sampling thus covered virtually the whole period of beetle activity in both sampling areas. However, only the samples from half of this period from the tropical forest (October 2003 – May 2004) were used in this studies′ analysis, since the rest of the beetle specimen was not identified.

A list of all sampling sites with all relevant information can be found in the Supplementary Material (Table S1). The flight intercept traps used were of the cross vane type (the two perpendicular transparent plastic panes were 50 cm high and 25 cm wide) with a roof, and a funnel connected to a collecting bottle with preservative (saturated salt solution with a drop of detergent to eliminate surface tension).

The traps were emptied every ten days in tropical lowland forest and every fortnight in the temperate forests. All trapped beetle individuals were sorted and identified to family level; saproxylic groups were identified to species level. Species identity was revised by experienced specialists. *Staphylinidae* were omitted from the dataset due to difficulties with their identification. This is a common approach, unlikely to affect our results (Sebek et al. 2012, Parmain et al. 2015). Every saproxylic species was assigned to a feeding guild as either mycetophagous, xylophagous, zoophagous, or saprophagous based on the most authoritative information available (Leschen et al. 2010). All species in any way associated with fungi were considered as mycetophagous.

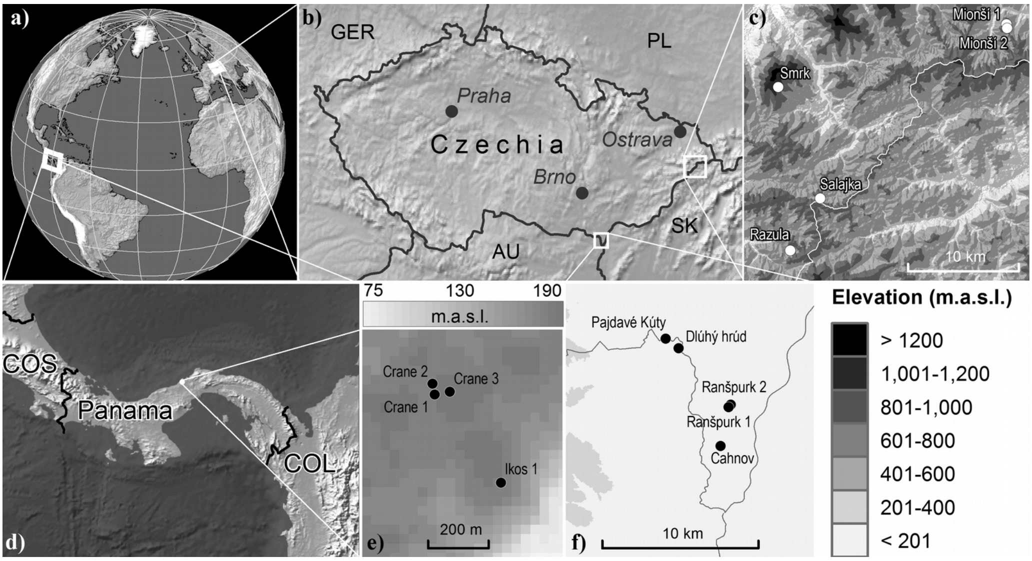

Figure 1. a) Global location of the study areas in b) Czech Republic and d) Panama. Five study sites were selected in c) the Moravian-Silesian Beskid Mountains and f) the alluvial woodlands along the lower Dyje and Morava rivers in southern Moravia, each. Four study sites were selected in e) the San Lorenzo Protected Area in the Colón Province.

Data Analysis

Species richness and distribution

To compare the overall species richness between the three forest types the expected numbers of species with confidence intervals were computed using sample-based rarefaction using EstimateS 9.1.0 (Colwell, 2013). The total number of species was estimated using the classic Chao1 richness estimator with 100 runs for each of the two sampling areas (Chao, 1984). Since sampling covered the entire period of beetle activity in both temperate forest types but only half of it on the tropical forest we also assessed the comparability of the datasets. This was done by calculating the incidence-based sample coverage (Chao & Jost, 2012; Chao et al. 2014) for all forest types. This analysis was carried out with the *iNEXT* package (Hsieh et al. 2016) in R (R Core Team 2014).

Species dissimilarity

To investigate the change of the saproxylic beetle communities along the vertical transects, a species dissimilarity matrix was calculated for the samples of each of the 3 forest types. The Bray-Curtis Index was chosen as a measure of dissimilarity since it has been proven suitable for ecological comparisons (Legendre & de Cáceres, 2013). Following from this, the dissimilarity of each beetle sample (N=72 in the tropical lowland forest, N=75 in the temperate lowlands/mountains) to the forest types´ average ground sample and uppermost canopy sample was calculated. To test the relationship between these dissimilarity values (from now on called $\mathrm{Diss}_{\mathrm{RelGround}}$ for the dissimilarity to the average ground sample) and the sampling height and forest type a linear mixed effects model (LMM) was calculated with log-transformed "height" as a continuous fixed effect and "forest type" as categorical fixed effect. Sampling site and sampling transect were used as hierarchical random effects. The $\mathrm{Diss}_{\mathrm{RelGround}}$ as response variable was logit-transformed. The analysis was conducted with the nlme package (Pinheiro et al. 2016) in R (R Core Team 2014).

Indicator species

To gain further insight into patterns of beetle vertical distribution, we investigated affinities of individual species to the sampled heights. Indicator species for trap heights were by identified for all 3 forest types as described by Dufrêne & Legendre (1997). Only species that were significant ($p < 0.05$) and had an IndVal value > 0.15 were selected for this analysis. Then for each sample the number of indicator species for the samples´ height level were counted.

To explore the relationship between the number of indicator species and the sampling height and forest type a generalized linear mixed effects model (GLMM) with poisson distribution was calculated with "height" as a continuous fixed effect and "forest type" as categorical fixed effect. Sampling site and sampling transect were used as hierarchical random effects. The *labdsv* (Roberts 2016) and *lme4* (Bates et al. 2015) packages was used to conduct the analysis in R (R Core Team 2014).

Feeding guilds

Changes in feeding guild composition along vertical gradient were investigated and compared among the three forests. Each of the four feeding guilds was analyzed separately. The relative guild proportion per sample was log-transformed and from there on the analysis was conducted in the exact same way as with species dissimilarity (see above).

Results

Species richness and distribution

All three forest habitats showed very similar values of incidence-based sample coverage, with 90,5% in the tropical forest, 96,5% in the temperate lowland forest and 96,1% in the temperate mountain forest. In the tropical lowland forest 9,247 beetle species were sampled belonging to 530 species. The total number of species given by the Chao1 species richness estimator was almost twice that number with 947 (95% CI 823 – 1122).

7,429 beetle specimens were caught in the temperate lowlands and 8,939 in the mountains. However, with 381 species trapped in the lowland and 236 in the mountains, the assemblage of the former was substantially richer. Only 105 species (21% of total species richness) were collected at both elevations; the number of shared species was estimated to be 169 (30%) using the Chao shared species estimator. The total number of species was estimated to be 463 (95% CI 429–519) in the lowlands and 312 (95% CI 276 – 380) in the mountains using the Chao1 species richness estimator (see Figure 2b). Overall the estimated species richness suggests that the topical lowland forest was sampled way less exhaustively than both temperate forests.

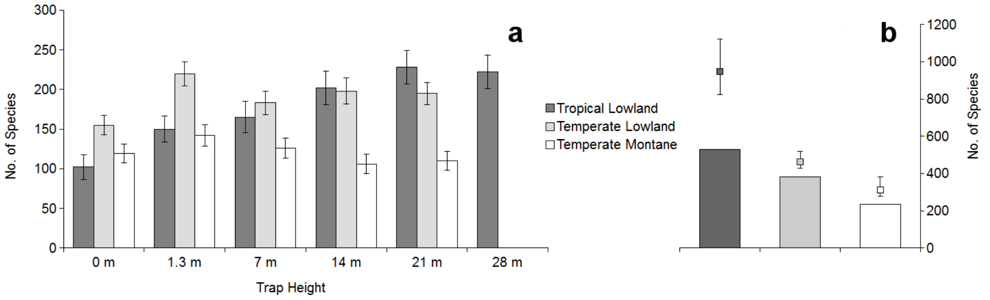

Figure 2. (a) Species richness (including 95% confidence intervals) along the vertical gradient in all three forest types of two temperate and one tropical forest (b) Total species richness of saproxylic beetles (barplots) and estimated total species richness of saproxylic beetles by the Chao1 species richness estimator (dots) in all three forest types of two temperate and one tropical forest (including 95% confidence intervals)

In the tropical lowland forest the number of species collected at each trap height was lowest at 0 m. From there it was continuously rising until it peaked at 21 m with 28 m being slightly poorer in species again.

In the temperate forest forest types the number of species collected at a particular height was lower in the mountains for each of the sampled heights, and the difference in species richness was lowest near the ground and highest in the upper sampling heights. In both areas species richness peaked at 1.3 m. In the lowland, the assemblage at 0 m was the poorest, and there were no major differences in species richness among the three sampled heights in the canopy (7, 14, and 21 m).

In the mountains, the higher canopy heights (14 and 21 m) were the poorest. There were more species collected at 0 and 7 m heights than higher in the canopy, but less than at 1.3 m height. For an overview of the species richness distribution along the vertical transect in all three forest types see Figure 2a.

Species dissimilarity

The results of the LMM show a significant effect of trap height on the species dissimilarity to the average ground sample ($\mathrm{Diss}_{\mathrm{RelGround}}$) as well as a difference between all 3 forest types: The overall $\mathrm{Diss}_{\mathrm{RelGround}}$ was higher in both temperate forests than in the tropical lowland forests even though this difference was more pronounced for the mountain forest. Furthermore the way in which $\mathrm{Diss}_{\mathrm{RelGround}}$ changed with trap height was significantly different between the tropical lowland forest and both temperate forest forest types. The difference in slopes was, again, more significant between in case of the mountain forest. (see Table 1). A plot of the predicted $\mathrm{Diss}_{\mathrm{RelGround}}$ against the log-transformed trap height can be seen in Figure 3.

Table 1. Results of the Linear Mixed Model (LMM) showing the influence of trap height, forest type and the combination of these factors on the species dissimilarity of saproxylic beetles to the average ground sample ($\mathrm{Diss}_{\mathrm{RelGround}}$) (TeL = temperate lowland forest, TeM = temperate mountain forest)

Predictor	Estimate	SE	P-Value
log(Trap Height)	0.72	0.02	< 0.001
Forest Type: TeL	0.45	0.10	< 0.01
Forest Type: TeM	1.43	0.10	< 0.001
Trap Height X Forest Type: TeL	- 0.13	0.03	< 0.01
Trap Height X Forest Type: TeM	- 0.52	0.03	< 0.001

Indicator species

The number of indicator species that were identified for the respective trap heights in all three forest types can be seen in Figure 4. The GLMM showed that all environmental effects and their interactions had a highly significant effect on the number of indicator species (see Table 2). Overall the number of indicator species decreased along the vertical transect in both temperate forests while there was more of a u-shaped pattern in terms of species numbers in the tropical

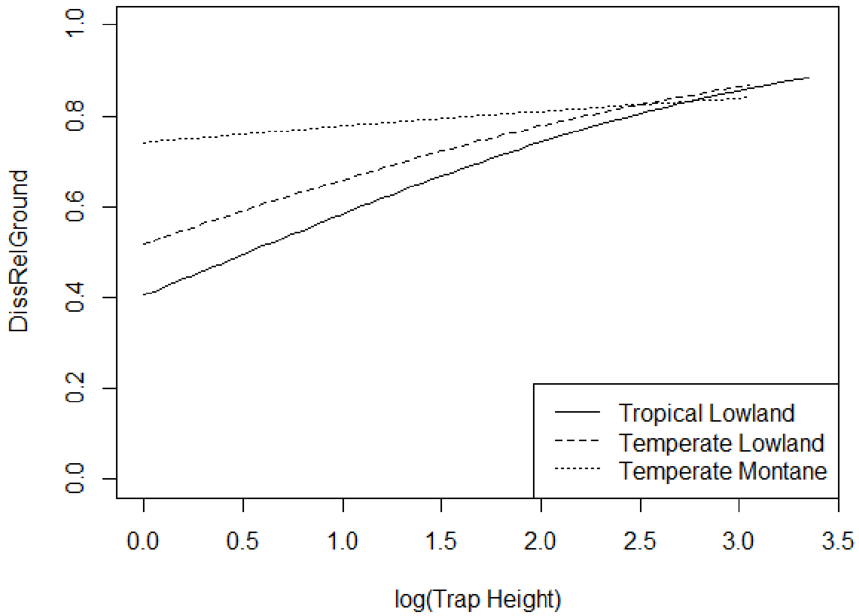

Figure 3. Plot of the Linear-Mixed-Model(LMM)-predicted species dissimilarity of saproxylic beetles to the average ground sample ($\mathrm{Diss}_{\mathrm{RelGround}}$) against log-transformed trap height in all three forest types of two temperate and one tropical forest

forest. Therefore the distribution of indicator species along the transect was different between the tropical and temperate forests. On the other hand, the total number of indicator species was highest in the temperate lowland forest and lowest in the temperate mountain forest (see Figure. 4).

Feeding Guilds

In all studied forests, the proportion of mycetophages decreased with trap height, while that of xylophages, zoophages and marginally also saprophages increased. Mycetophages were less represented in the temperate mountain forest than in the other forests. The proportion of saprophages was higher in the temperate lowland forest than in the other forests, while the proportion of zoophages was higher both temperate forests than in the tropical one. For details see Table 3 and Figure 5.

Table 2. Results of the General Linear Mixed Model (GLMM) showing the influence of trap height, forest type and the combination of these factors on the number of indicator species of saproxylic beetles. (TeL = temperate lowland forest, TeM = temperate mountain forest)

Predictor	**Estimate**	**SE**	**P-Value**
log(Trap Height)	- 0.04	0.01	< 0.001
Forest Type: TeL	0.35	0.09	< 0.001
Forest Type: TeM	- 0.43	0.11	< 0.001
Trap Height X Forest Type: TeL	- 0.06	0.01	< 0.001
Trap Height X Forest Type: TeM	- 0.10	0.02	< 0.001

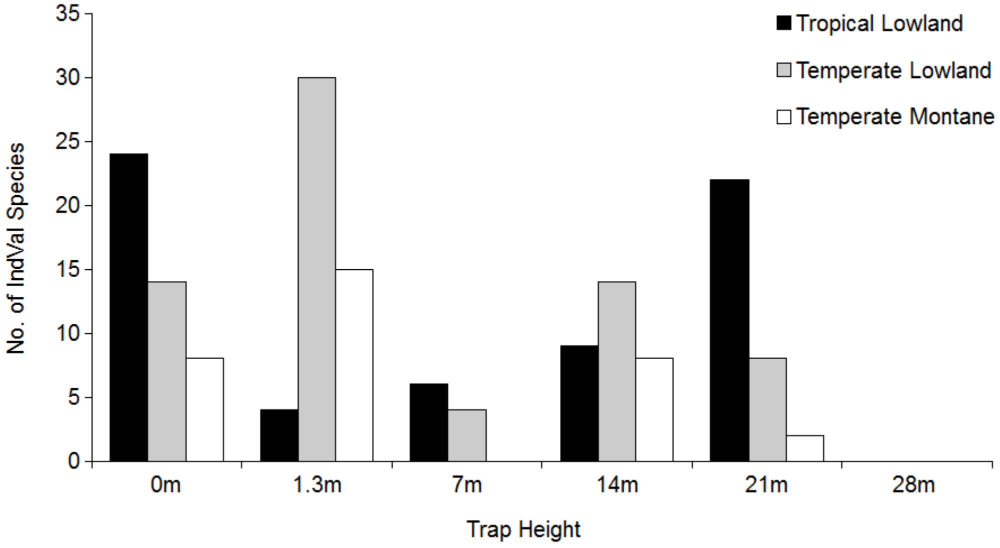

Figure 4. Number of the indicator species (species indicative to a certain habitat) of saproxylic beetles per sampling height in all three forest types of two temperate and one tropical forest

Table 3. Results of the Linear Mixed Model (LMM) showing the influence of trap height, forest type and the combination of these factors on the proportion of the four feeding guilds of saproxylic beetles per sample. (TeL = temperate lowland forest, TeM = temperate mountain forest)

Feeding Guild	**Predictor**	**Estimate**	**SE**	**P-Value**
Mycetophages	log(Trap Height)	- 0.21	0.03	< 0.001
	Forest Type: TeL	- 0.20	0.12	0.131
	Forest Type: TeM	- 0.39	0.12	< 0.01
	Trap Height X Forest Type: TeL	0.02	0.05	0.699
	Trap Height X Forest Type: TeM	- 0.02	0.05	0.643
Saprophages	log(Trap Height)	0.25	0.10	< 0.05
	Forest Type: TeL	1.31	0.33	< 0.01
	Forest Type: TeM	0.56	0.33	0.118
	Trap Height X Forest Type: TeL	- 0.59	0.15	< 0.001
	Trap Height X Forest Type: TeM	- 0.42	0.15	< 0.01
Xylophages	log(Trap Height)	0.15	0.05	< 0.001
	Forest Type: TeL	- 0.97	0.19	< 0.001
	Forest Type: TeM	- 0.06	0.19	0.714
	Trap Height X Forest Type: TeL	0.33	0.06	< 0.001
	Trap Height X Forest Type: TeM	0.16	0.06	< 0.01
Zoophages	log(Trap Height)	0.23	0.08	< 0.01
	Forest Type: TeL	0.98	0.29	< 0.01
	Forest Type: TeM	1.00	0.29	< 0.01
	Trap Height X Forest Type: TeL	- 0.10	0.12	0.376
	Trap Height X Forest Type: TeM	- 0.25	0.12	< 0.05

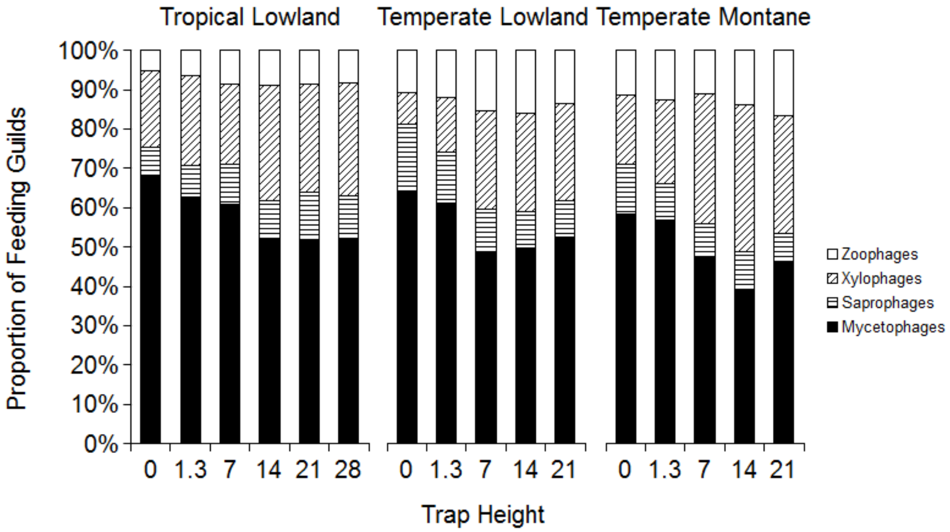

Figure 5. Mean Proportion of the four feeding guilds of saproxylic beetles per flight intercept trap sample along the vertical gradient in three forests types of two temperate and one tropical forest.

Discussion

In this study we present the first comparison of spatial assemblage characteristics of saproxylic beetles between temperate and tropical forests. The fact that we sampled only one among the wide variety of tropical forest habitats partly limits the validity of our observations. Despite this, our results still provide valuable new insight to the altitudinal and latitudinal patterns of species distribution of saproxlic beetles. In all areas the sampling was intensive and followed an identical protocol. We therefore believe that the results are relevant to the wider region.

Another limitation of our study is that we were only able to include about half of the period of beetle activity from the tropical forest. Beetle assemblages in tropical forests, however, display seasonality in terms of diversity and feeding guild composition (e.g. Grimbacher & Stork 2009). Data covering only part of the season in the tropical forest thus present limitation to this study. But since the datasets from the three forests showed very similar values of sample coverage and are therefore statistically comparable (Chao & Jost 2012), we state that the analytic comparisons performed in this study are valid.

Species richness and vertical stratification patterns

The estimated number of beetle species in tropical forest was about two and three times higher than in the temperate lowland and mountain forests, respectively. Yet the vertical distribution of species richness differed highly between the temperate and tropical forests. While the number of species almost constantly increased in the tropical forest and peaked at 21 meters, the species richness peaked in the understorey (1.3 m) of both temperate forests. Interestingly, a temperate forest might seem substantially richer than a tropical rainforest near the forests floor. This is also likely an explanation for the rather low dissimilarity of the near-ground samples in the tropical forest, where the dissimilarity rapidly increases with height. In temperate forests, on the other hand, the dissimilarity is rather high near ground, but its increase with height is slow. The high dissimilarity near the ground in the temperate mountain forest might partly be attributed to the higher variability due to a wider area being sampled and rugged mountain terrain. The most interesting result of the dissimilarity model is that the slopes, indicating the change of dissimilarity with trap height, clearly differ between the forests. In this respect the two lowland forests are more similar to each other than to the mountain forest, where dissimilarity shows the lowest amount of increase along the transect. These patterns of diversity are fully in line with global patterns in distribution of biological diversity (e.g. Prinzing & Woas 2003, Ødegaard et al. 2004, Wermelinger et al. 2007, Basset et al. 2015). They are, nevertheless, the first direct comparison of species richness of saproxylic beetle assemblages between tropical and temperate forest habitats. The high differences in tree species richness at the sampling sites are not mirrored by beetles diversity, suggesting rather low host specificity of saproxylic beetles in tropics. This has also been observed in previous studies (e.g. Beaver 1979, Tavakilian et al. 1997, Ødegaard et al. 2000).

The vertical stratification of beetle communities in the three forest types can best be explained through resource availability and partly also competition. Firstly, the complexity of the vertical forest structure has repeatedly been linked to the stratification of arthropod communities (Basset et al. 2003a). The tropical rainforest has a higher vertical complexity than temperate forests (Smith 1973, Terborgh 1985).The temperate lowland forest has, in turn, more specific tree layers than the mountain forest (Janik et al. 2013). Sun-lit dead wood is an important resource to many saproxylic beetle species (e.g. Franc et al. 2007), but is virtually absent in the tropical forest understorey since almost none of the solar energy reaches the gound (Parker 1995). Close intertwining with lianas ensures a higher occurrence of standing and especially suspended dead wood in the canopy of tropical forests compared to temperate ones (Martius & Bandeira 1998). Furthermore, the concentration of supplementary resources such as flowers and fruits, which a large part of the adult beetles depend on, is much higher in tropical canopies. Another reason for the lower species richness on the forest floor could also be the competition of termites (Ødegaard et al. 2000). They are an equally important part of the saporxylic community in this forest type and are more active on the forest floor than in the canopy (Roisin et al. 2006).

Indicator species along the vertical gradient

The analysis of the indicator species points to further differences in patterns of beetle vertical stratification between tropical and temperate forest. In the former, the indicator species distribution was U-shaped with peaks at the ground level and at the upper canopy (21 m). This suggests that there is a very distinct community of saproxylic beetles near the ground adapted to the dark and humid conditions near the forest floor. These are opposed by communities that prefer the drier, sun exposed canopy, where the number of indicator species rises with trap height. Surprisingly, no species was indicative for 28 meters, the highest and second richest height sampled in the tropical forest. Possibly beetles from bellow frequent this height in search of resources, such as flowers, or use it as flight level in order to avoid navigating in the denser foliage underneath.

In both temperate forests the distribution of the indicator species follows the species richness patterns more closely. In the temperate forest, due to its lower structural complexity, dead wood is more concentrated near ground, sunlight availability gradients are less pronounced and there is less competition for the dead wood from termites and/or fungi. More indicator species thus occur at the heights where most of the wood is accumulated. The lower overall number of indicator species in tropical forest can at least partly attributed to much higher percentage of rare species which is a common phenomenon in tropic forests (Price et al. 1995, Novotný & Basset 2000).

Guild composition

Saproxylic beetles communities are stratified in terms of guild composition, as representation of all four feeding guilds is influenced by trap height in the three forest types studied.

The common patterns in all three forests include the decrease of mycetophages with height, most likely due to the relatively moist conditions near the forest floor that provide better conditions for the fungi that these species rely on (Floren et al. 2014, Ulyshen 2011). The proportion of xylophages generally rises upwards along the vertical gradient. Many xylophages – especially from the families of *Cerambycidae*, *Curculionidae* and *Buprestidae* – prefer dead wood objects in the canopy (e.g. Ødegaard 2003, Kappes & Topp 2004). The proportion of xylophages shows a much stronger increase in the temperate forests than in the tropical one. This, perhaps, is due to the fact that the overall species richness decreases along the vertical gradient in the former, but it rapidly increases in the latter. Therefore increase of the relative proportion of xylophages seems less pronounced compared to the temperate forests. The increasing proportion of zoophages with trap height is also a common phenomenon in all forest types. And important reason for this is most likely that many species of this guild are predatory as larvae as well as adults (Leschen et al. 2010). Therefore the imagines are usually highly mobile and will prefer the upper parts of the forest where vegetation is less dense and insolation is higher – at least in temperate forests. In the tropical forest the preference of predators for the upper end of the transect can best be explained by the higher amount of resources, like leafs flowers and fruits, that attract a higher abundance of prey (Basset et al. 2003b).

Yet, there are also differences in the distribution of feeding guilds between the forest types. For once, the proportion of mycetophages is overall lower in the mountain forest than both lowland forests, even though Weiss et al. (2016) showed that this forest has a high proportion of this guild. The patterns shown here do not necessarily oppose those findings because of the fact that the mountain forest was sampled across a wider area. This can lead to a higher amount of species of a certain guild at forest-level but not necessarily at sample-level. The fact that the overall proportion of xylophages is higher in both the tropical forest and the temperate mountain forest most likely has different reasons in both forests: In the tropical forest it might be the fact that many xylophages are early colonizers, which are usually the most tree species specific group among saproxylic beetles (Stokland et al. 2012). Therefore this might be where the high tree species richness of the tropical forest might have the highest impact on the saproxylic community. In case of the temperate mountain forest the high proportion of xylophages can best be explained that a beech-fir forest is generally a favorable habitat for this guild since many of its members, especially among the *Scolytinae*, are dependent on these tree species **(**Leschen et al. 2010**)**. The saprophage guild shows the most distinct distribution between the tropical and temperate forests: In the temperate forests the proportion is higher at the lower end of the transect, most likely due to the fact that dead organic matter is generally accumulating on the forest floor. In the tropical lowland forest the proportion is rising with trap height. The reason for this might be that the more complex forest structure ensures that dead organic matter is more evenly vertically distributed in the forest (Nadkarni & Longino 1990). Also the beetles might face more competition near the forest floor from less mobile saprophage groups like nematodes and diplopodes.

In conclusion it can be stated that the comparison of the saproxylic beetle communities from three forest areas of different latitude and altitude showed that fine-scale vertical stratification of the saproxylic beetle communities is a clear pattern that all of them share. On the other hand, striking differences in species richness and similarities in feeding guild distribution could be shown between each of them. While at least some of the mechanisms that likely account for these differences have been named here, more research is necessary to provide additional clarity in this regard. This also includes additional investigation on the beetle communities themselves. Even though flight intercept traps provide a good measure of beetle activity, performing rearing experiments and comparing their results with those presented in this work could provide further insight into saproxylic beetle activity. Such data already exist for the tropical lowland forest but have yet to be collected in the temperate forests.

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References

Basset, Y., Hammond, P.M., Barrios, H., Holloway, JD., Miller, S.E., 2003a. Vertical stratification of arthropod assemblages. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., editors. *Arthropods of Tropical Forests*. Cambridge University Press. Pp 4-7

Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., 2003b. Conclusion: arthropods canopies and interpretable patterns. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., editors. *Arthropods of Tropical Forests*. Cambridge University Press. pp 394-405

Basset, Y., Corbara. B., Barrios, H., Cuénoud, P., Leponce, M., Aberlenc, H., Bail, J., Bito, D., Bridle, J.R., Castaño-Meneses, G., Cizek, L., Cornejo, A., Curletti G., Delabie, J.H.C., Dejean, A., Didham, R.K., Dufrêne, M., Fagan, L.L., Floren, A., Frame, D.M., Hallé, F., Hardy, O.J., Hernandez, A., Kitching, R.L., Lewinsohn, T.M., Lewis, O.T., Manumbor, M., Medianeiro, E., Missa, O., Mitchell, A.W., Mogia, M., Novotny, V., Ødegaard, F., de Oliveira, E., Orivel, J., Ozanne, C.M.P., Pascal, O., Pinzón, S., Rapp, M., Ribeiro, S.P., Y., Roslin, T., Roubik, D.W., Samaniego, M., Schmidl, J., Sørensen, L.L, Tishechkin, A., van Osselaer, C., Winchester, N.N., 2007. IBISCA-Panama, a large-scale study of arthropod beta-diverstiy and vertical stratification in a lowland rainforest: rationale, study sites and field protocols. *Bull. Inst. R. Sc. N. B. Entomologie* 77: 39-69

Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A.K., Schmidl, J., Winchester, N.N., Roubik, D.W., Aberlenc, H.P., Bail, J., Barrios, H., Bridle, J.R., Castaño-Meneses, G., Corbara, B., Curletti, G., da Rocha, W.D., De Bakker, D., Delabie, J.H.C., Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., de Oliveira, E.G., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt, J.P., Sørensen, L., Lewinsohn, T.M., Leponce, M. 2015 Arthropod distribution in a tropical rainforest: Tackling a four dimensional puzzle. *PLOS ONE* doi:10.1371/journal.pone.0144110

Bates, D., Maechler M., Bolker B., Walker S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67: 1-48. doi:10.18637/jss.v067.i01.

Beaver, R.A., 1979. Host specificity of temperate and tropical animals. *Nature* 281: 139–141.

Bouget, C., Larrieu, L., Parmain, G., Nusillard, B., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodivers. Conserv.* 22: 2111-2130. doi: 10.1007/s10531-013-0531-3

Chao, A., 1984. Non-parametric estimation of the number of classes in a population. *Scand. J. Stat.* 11: 265-270.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93: 2533-2547.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84: 45-67. doi: 10.1890/13-0133.1

Davis, A.L.V., Scholtz, C.H., Chown, S.L., 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. *J. Biogeogr.* 26: 1039-1055. doi: 10.1046/j.1365-2699.1999.00335.x

Dufrêne, M. & Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67: 345-366

Escobar, F., Halffter, G., Arellano, L., 2007. From forest to pasture: an elevation of the influence of environment and biogeography on the structure of dung beetle (*Sarabaeinae*) assemblages along three altitudinal gradients in the Neotropical region. *Ecography* 30: 192-208. doi: 10.1111/j.2007.0906-7590.04818.x

Floren, A., Schmidl, J. Introduction: Canopy arthropod research in Europe. In: Floren, A., Schmidl, J. (eds.), 2008. *Canopy Arthropod Research in Europe: Basic and applied studies from the high frontier.* Bioform Entomology, Nünberg, Germany, pp 13-20.

Floren A., Mueller T., Dittrich M., Weiss M., Linsenmair K.E., 2014. The influence of tree species, stratum and forest management on beetle assemblages responding to dead wood enrichment. *Forest Ecol. Manag.* 323: 57-64. doi:10.1016/j.foreco.2014.03.028

Franc, N., Götmark, F., Okland, B., Norden, B., Paltto, H., 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biol. Conserv.* 135: 86–98

Grimbacher, P.S., Stork, N.E., 2009. Seasonality of a diverse beetle assemblage inhabiting lowland tropical rainforest in Australia. *Biotropica* 41: 328-337

Grove, S.J., Stork, N.E., 1999. The conservation of saproxlic insects in tropical forests: a research agenda. *J. Insect Conserv.* 3: 67-74

Grove, S.J., Saproxylic insect ecology and the sustainable management of forests. In: Futuyama, D.J., (ed.) 2002. *Annual Review of Ecology, Evolution and Systematics* 33. pp. 1-23

Hawkins, B.A., DeVries, P.J., 2009. Tropical niche conservatism and the species richness gradient of North American butterflies. *J. Biogeogr.* 36: 1698-1711

Horák, J., Mertlik, J., Chobot, K. & Kubáň, V., 2009. Distribution of a rare saproxylic beetle *Cucujus haematodes* (Coleoptera: Cucujidae) in the Czech Republic with notes to occurrence in central Europe. *Klapalekiana*, 45: 191-197.

Hsieh, T. C., Ma, K. H., Chao, A., 2016. iNEXT: Interpolation and Extrapolation for species diversity. R package version 2.0.12 URL: http://chao.stat.nthu.edu.tw/blog/software-download

Janik, D., Adam, D., Hort, L., Král, K., Šamonil, P., Unar, P., Vrška, T., Horal, D., 2013.

Spatiotemporal differences in tree spatial patterns between alluvial hardwood and mountain beech-fir forests: do characteristic patterns exist? *J. Veg. Sci.* 24: 1141-1153. doi: 10.1111/jvs.12018

Kocher, S.D., Williams, E.H., 2000. The diversity and abundance of North American butterflies vary with habitat disturbance and geography. *J. Biogeogr.* 27: 785-794

Legendre, P., & De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol. Lett.* 16: 951-963

Leksono, A.S., Takada, K., Shinsaku, K., Nobukazu, N., Anggraeni, T., Nakamura, K., 2005. Vertical and seasonal distribution of flying beetles in a suburban deciduous temperate forest collected by water pan traps. *Insect Sci.* 12: 199-206. doi: 10.1111/j.1744-7917.2005.00025.x

Leschen R.A.B., Beutel, R.G., Lawrence, J.F., 2010. Coleoptera, Beetles. In: Kristensen NP, Beutel RG, editors. *Handbook of Zoology, Arthropoda: Insecta*. De Gruyter, Berlin/New York.

Lobo, J.M., Martín-Piera, F., 2002. Searching for a predictive model for species richness of Iberian dung beetle based on spatial and environmental variables. *Conserv. Biol.* 16: 158-173

Maguire, D.Y., Robert, K., Brochu, K., Larrivée, M., Buddle, C.M., Wheeler, T.A., 2014 Vertical stratification of beetles (Coleoptera) and flies (Diptera) in temperate forest canopies. *Environ. Entomol.* 43: 9-17. doi: 10.1603/EN13056

Martikainen, P., 2001. Conservation of threatened saproxylic beetles: significance of retained aspen Populus tremula on clearcut areas. *Ecol. Bull.* 49: 205-218. doi: 10.2307/20113277

Martius, C., Bandeira, A.C., 1998. Wood litter stock in tropical moist forests in central Amazonia. *Ecotropica* 4: 115–118.

Müller, J., Bussler, H., Gossner, M., Rettelbach, T., Duelli, P., 2008. The European spruce bark beetle Ips typographus in a national park: from pest to keystone species. *Biodivers. Conserv.* 17: 2979-3001. doi: 10.1007/s10531-008-9409-1

Nadkarni, N.M., Longino, J.T., 1990. Invertebrates in canopy and ground organic matter in a neotropical montane forest, Costa Rica. *Biotropica* 22: 286-289

Novotný, V., Basset, Y., 2000. Rare species in communities of tropical insect herbivores: pondering the mysteries of singletons. *OIKOS* 89: 564-572

Ødegaard, F., 2000. The relative importance of trees versus lianas hosts for phytophagous beetles (Coleoptera) in tropical forests. *J. Biogeogr.* 27: 283–296.

Ødegaard, F., 2003. Taxonomic composition and host specificity of phytophagous beetles in a dry forest in Panama. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L., editors. *Arthropods of Tropical Forests*. Cambridge University Press, pp 220-236

Ødegaard, F., 2004. Species richness of phytophagous beetles in the tropical tree Brosimum utile (Moraceae): the effects of sampling strategy and the problem of tourists. *Ecol. Entomol.* 29: 76-88

Parker, G.G., 1995. Structure and microclimate of forest canopies. In: Lowman, M.D., Nadkarni, N.M., editors. *Forest Canopies*. Academic Press, San Diego, pp. 431-455

Pinheiro J., Bates D., DebRoy S., Sarkar D. & R Core Team (2016). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-128, URL: https://CRAN.R-project.org/package=nlme.

Price, P. W., Diniz, I. R., Morais, H. C., Marques, E. S. A, 1995. The abundance of insect herbivore species in the tropics: the high local richness of rare species. *Biotropica* 27: 468–478.

Prinzing, A., Woas, S., 2003. Habitat use and stratification of Collembola and oribatid mites. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (eds), *Arthropods of Tropical Forests*. Cambridge University Press, pp. 271-281

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Roberts, D. W., 2016. labdsv: Ordination and Multivariate Analysis for Ecology. R package version 1.8-0. https://CRAN.R-project.org/package=labdsv

Robertson, HG., 2002. Comparison of leaf litter ant communities in woodlands, lowland forests and montane forests of north-eastern Tanzania. *Biodivers. Conserv.* 11: 1637-1652. doi: 10.1023/A:1016883901065

Roisin, Y., Dejean, A., Corbara, B., Orivel, J., Samaniego, M., Leponce, M., 2000. Vertical stratification of the termite assemblage in a neotropical rainforest. *Oecologia* 149: 301-311. doi: 10.1007/s00442-006-0449-5

Rozkošný, R. & Vaňhara, J., 1996. Terrestrial Invertebrates of the Pálava Biosphere Reserve of UNESCO, I–III. *Folia Fac. Sci. Nat. Un.* 92, 1–208, 93, 209–408, 94, 409–630

Schlaghamerský, J., 2000. The saproxylic beetles (Coleoptera) and ants (Formicidae) of central European hardwood floodplain forests. *Folia Fac. Sci. Nat. Un.* 103: 1-168

Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrêne, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose, O., Velle, L. & Bouget, C., 2012. A test for assessment of saproxylic beetle biodiversity using subsets of “monitoring species”. *Ecol. Indic.* 20: 304-315

Siitonen, J., Martikainen, P., Punttila, P., Rauh, J., 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecol. Manag.* 128: 211–225. doi: 10.1016/S0378-1127(99)00148-6

Smith, A.P., 1973. Stratification of temperate and tropical forests. *Am. Nat.* 107: 671-683

Stokland, J.N., Tomter, S.M., Söderberg, G.U. Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. In: Marchetti, M. (ed), 2004 *Monitoring and indicators of forest biodiversity in Europe – from ideas to operationality*. European Forest Institute, EFI Proceedings 51, pp. 207-226.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, 521 pp.

Swenson, N.G., Enquist, B.J., 2007. Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and altitude. *Am. J. Bot.* 94: 451-459

Tanabe, S., 2002. Between-forest variation in vertical stratification of drosophilid populations. *Ecol. Entomol.* 27: 720-731. doi: 10.1046/j.1365-2311.2002.00469.x

Tavakilian, G., Berkov, A., Meurer-Grimes, B., Mori, S., 1997. Neotropical tree species and their faunas of xylophagouslongicorns (Coleoptera: Cerambycidae) in French Guiana. *Bot. Rev.* 63: 303–355.

Terborgh, J., 1985. The vertical component of plant species diversity in temperate and tropical forests. *Am. Nat.* 126: 760-776

Tykarski, P., 2006. Beetles associated with scolytids (Coleopotera, Scolytidae) and the elevational gradient: Diversity and dynamics in the Tatra National Park, Poland. *Forest Ecol. Manag.* 225: 146-159. doi: 10.1016/j.foreco.2005.12.034

Ulyshen M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation oriented management. *Forest Ecol. Manag.* 261: 1479-1489. doi:10.1016/j.foreco.2011.01.033

Vávra, J. Ch. & Stanovský, J., 2013. Brouci (Coleoptera), pp. 295-311. *Příroda Slezska. Slezské zemské muzeum* (ed. by J. Roháček, J. Ševčík and P. Vlk). Opava, 480 pp.

Weaver, P.L. & Bauer, G.P., 2004. The San Lorenzo Protected Area: A Summary of Cultural and Natural Resources. International Institute of Tropical Forestry, San Juan, PR.

Weiss, M., Procházka, J., Schlaghamerský J., Cizek, L., 2016. Fine-scale vertical stratification of saproxylic beetles in lowland and montane forests: Similar patterns despite low faunal overlap. *PLOS ONE* 11(3): e0149506.

Wermelinger, B., 2004. Ecology and management of the spruce bark beetle Ips typographus – a review of recent research. *Forest Ecol. Manag.* 202: 67-82.

Wermelinger, B., Flückiger, P.F., Obrist, M.K., Duelli, P., 2007. Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *J. Appl. Entomol.* 131: 104–114. doi: 10.1111/j.1439-0418.2006.01128

Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: Pattern, process scale and synthesis. *Annu. Rev. Ecol. Evol. S.* 34: 273-309

Yu, X., Lü, L., Luo, T., Zhou, H., 2013. Elevational gradient in species richness pattern of epigaeic beetles and underlying mechanisms at east slope of Balang mountain in southwestern China. *PLOS ONE* 8(7), e69177. doi: 10.1371/journal.pone.0069177

Summary

Summary

The studies presented in this thesis provide new insight into the distribution of saproxylic beetles in forest habitats. While further confirming the fact these beetle communities are stratified in tropical and temperate forests, it represents one of the first efforts to analyze this stratification on a finer scale and compare it between different habitats. The results presented here show that, even though the distinction in community composition is largest between understorey and canopy, there are also differences within these strata. The extent of stratification is also clearly connected to the vertical structural complexity of the forest, since it is most pronounced in the tropical forest and least pronounced in the temperate mountain forest. The phenomenon of stratification also extends to the feeding guild composition. These patterns are rather similar in the temperate and tropical forests, while species richness distribution is a major difference between them. On the horizontal forest scale canopy openness greatly influences the distribution of beetles and other saproxylic insect orders. The diversity of their assemblages generally decreases from solitary trees to the forest interior. Yet the difference between the forest edge and interior in the extent of community stratification is very small for beetles compared to other saproxylic groups. Overall, this thesis emphasizes the important contribution of forest canopies and solitary trees to the biodiversity of saproxylic beetles.

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