# Saproxylic insects in tree hollows:

# drivers of diversity, dispersal and food web structure

## Dissertation

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# Content

## Summary

During the last centuries, intensive forest management has changed the characteristics of forests worldwide. This has caused a worldwide decline of old trees and deadwood structures, leading to a threat for saproxylic species, i.e. those species depending on deadwood at some point in their life cycle. Saproxylic species comprise about 25% of forest biodiversity and are important for various ecosystem functions e.g. wood decomposition and nutrient cycling. A very important key structure for saproxylic species and their diversity are tree hollows, contributing stable and long-lasting habitats for many threatened saproxylic insect species. Tree hollows enable undisrupted development for individuals of species with long developmental times and special habitat preferences. To develop effective management strategies maintaining the diversity of tree hollow associated insect species, evidence-based knowledge on environmental characteristics influencing their diversity, dispersal abilities, and food web structures have to be well understood. For this purpose, I collected all emerging arthropods from hollows with wood mould in beech trees over two consecutive years in a managed forest using emergence traps.

In the first manuscript, I investigated characteristics of tree hollows and the immediate environment influencing the diversity of saproxylic beetles inside. Overall diversity was influenced by the degree of decomposition of the wood mould and increasing hollow entrance area. Additionally, tree hollow volume, height of the hollow above ground, surrounding deadwood structures and surrounding tree hollows, solar irradiation, temperature inside tree hollows and diameter of the tree hollows were influencing the biodiversity of saproxylic beetles, but their importance differed between the two years. Furthermore, tree hollow characteristics influencing the diversity of Red List and non-Red List species were different, as degree of decomposition of the wood mould, height of the hollow above ground and surrounding tree hollows had no influence on Red List species but did have on non-Red List species. This study

showed that the diversity of saproxylic beetles inhabiting tree hollows can be supported by maintaining a high diversity of differently structured and sized tree hollows.

In the second manuscript, I investigated the genetic population structure of three saproxylic insect species (*Anaspis ruficollis,* Coleoptera; *Criorhina floccosa*, Diperta; *Xylomya maculata*, Diptera) inhabiting tree hollows to draw conclusions on their potential dispersal within the study area, using microsatellite analysis. Dispersal is a key trait for species in a changing environment, like managed forests. It allows colonization, gene flow among populations and thus ensures viable populations. These threatened species were chosen based on their relatively high abundance to allow for population genetic analyses. In contrast to the existing assumption, that saproxylic species inhabiting long lasting habitats have limited dispersal, we neither found genetic population substructure nor indications for restricted gene flow in all species investigated indicating dispersal over the whole study area. However, I studied relatively abundant species and our study site may not have been large enough to detect genetic substructure.

The third chapter is based on a book chapter where we reviewed the current knowledge on the dispersal of saproxylic insects. We presented an overview of the studies that have to date tried to measure dispersal distances or dispersal abilities of different saproxylic taxa, methods to measure dispersal, factors influencing dispersal and highlighted open research questions. Dispersal abilities vary a lot between different saproxylic species and long-distance dispersal is not uncommon. We could stress that dispersal is not only a matter of the physical ability of a species but also of habitat quality and availability, feeding strategies, competition and sex-specific dispersal.

In the fourth manuscript I investigated the food web structure of saproxylic beetle communities in tree hollows using stable isotope analysis of nitrogen and carbon isotopes. In this study, the trophic position (feeding guild) of most species is congruent between the classification based on their stable isotope signatures and literature derived classifications. Further, the isotopic

signature of mycetophagous species suggests a highly omnivorous feeding behavior compared to other feeding guilds. Niche redundancy was high in the xylophagous and zoo-xylophagous guilds and niche conservation of saproxylic beetle families was common. Additionally, saproxylic beetle communities followed inverted Eltonian pyramids with zoophagous species contributing the highest biomass. However, considering all saproxylic arthropods in tree hollows and not only saproxylic beetles, no inverted Eltonian pyramids might be present anymore as organisms of lower trophic levels like collembolans comprise a high proportion of total biomass in tree hollow communities. Higher species richness was related to longer trophic food chains, highlighting the importance of high diversity of saproxylic species for ecosystem functioning.

The recommendations based on the results of this thesis can help foresters, political decision makers and conservationists to apply effective management strategies for the conservation of saproxylic diversity.

## Zusammenfassung

Während der letzten Jahrhunderte hat intensive Forstwirtschaft weltweit den Charakter der Wälder geprägt. Die intensive Forstwirtschaft hat zu einer weltweiten Abnahme von großen, alten Bäumen und verschiedenen Totholzstrukturen geführt. Dies hat zur Folge, dass Arten, die auf Totholz angewiesen sind, sogenannte „Saproxyle“, gefährdet sind. Etwa 25% aller Arten im Wald sind abhängig von Totholz. Saproxyle Arten sind bedeutsam für viele ökologische Aufgaben, wie die Zersetzung von Holz und den Nährstoffkreislauf im Wald und tragen maßgeblich zur Artenvielfalt in Wäldern bei. Eine besondere Totholzstruktur und Schlüsselelement für eine hohe Artenvielfalt im Wald sind Mulmhöhlen. Sie stellen ein lang überdauerndes Habitat für viele gefährdete Arten dar, da sie eine ungestörte Entwicklung für Arten mit speziellen Habitatansprüchen ermöglichen. Der Erhalt der Artenvielfalt in Mulmhöhlen erfordert effiziente Managementstrategien. Dafür ist aber Wissen über

Umweltfaktoren, die die Artenvielfalt beeinflussen, Ausbreitung und Nahrungsnetzwerke saproxyler Arten notwendig. Um dies zu untersuchen, habe ich in einem Wirtschaftswald über zwei Jahre hinweg alle Arthropoden aus den Mulmhöhlen in Buchen mit Hilfe von Emergenzfallen abgesammelt.

Im ersten Manuskript habe ich Eigenschaften von Mulmhöhlen und der Umgebung untersucht, die die Artenvielfalt saproxyler Käfer in Mulmhöhlen beeinflussen. Ich konnte zeigen, dass generell die Artenvielfalt durch den Zersetzungsgrad des Mulms und die Größe des Höhleneingangs beeinflusst wird. Weiterhin haben der Zersetzungsgrad des Mulms, die Höhe der Höhle zum Boden, die umgebenden Totholzstrukturen und Baumhöhlen, Sonneneinstrahlung, Temperatur innerhalb der Höhle und der Durchmesser der Mulmhöhle Einfluss auf die Artenvielfalt saproxyler Käfer. Jedoch unterscheiden sich diese Parameter in ihrer Bedeutsamkeit zwischen beiden Jahren. Des Weiteren unterschieden sich auch die Parameter, die die Artenvielfalt von Rote Liste Arten und nicht Rote Liste Arten beeinflussen. Die Artenvielfalt von Rote Liste Arten wurde im Gegensatz zu nicht Rote Liste Arten, weder durch den Zersetzungsgrad des Mulms, die Höhe der Höhle über dem Boden oder die umgebenden Baumhöhlen beeinflusst. Diese Studie zeigte, dass die Artenvielfalt saproxyler Käfer am besten durch unterschiedlich gestaltete Mulmhöhlen gefördert wird.

Im zweiten Manuskript habe ich die genetischen Populationsstruktur von drei Insektenarten (*Anaspis ruficollis,* Coleoptera; *Criorhina floccosa*, Diperta; *Xylomya maculata*, Diptera) aus Mulmhöhlen mit Hilfe von Mikrosatellitenanalyse untersucht um Rückschlüsse über die potentielle Ausbreitung im Untersuchungsgebiet zu ziehen. Ausbreitung ist eine Schlüsseleigenschaft für Arten, die mit einer sich ändernden Umwelt, zum Beispiel Wirtschaftswälder, konfrontiert sind. Ausbreitung ermöglicht die Besiedlung neuer Habitate, Genfluss zwischen Populationen und sichert somit zukunftsfähige Populationen. Diese gefährdeten Arten wurden ausgewählt da sie häufig gefunden wurden und somit eine populationsgenetische Analyse möglich ist. Im Gegensatz zu der gängigen Meinung, dass Arten in Mulmhöhlen sich schlecht ausbreiten können, fanden wir keine Subtrukturierung oder eingeschränkten Genfluss im Untersuchungsgebiet, was auf eine Ausbreitung über das ganze Untersuchungsgebiet hindeutet. Dies kann jedoch auch durch die geringe Größe des Untersuchungsgebietes und die hohe Abundanz der untersuchten Arten bedingt sein.

Das dritte Manuskript ist ein Buchkapitel, in welchem wir eine Übersicht über den jetzigen Wissenstand zur Ausbreitung saproxyler Insekten geben. Das Kapitel zeigt einen Überblick über Studien zu Ausbreitungsdistanzen und Ausbreitungsfähiglkeiten verschiedener saproxyler Arten, den Methoden, die zur Messung von Ausbreitung verwendet werden können und den Faktoren die Ausbreitung beeinflussen. Außerdem konnten wir zeigen, dass lange Ausbreitungsdistanzen durchaus auch bei saproxylen Insekten vorkommen, es jedoch sehr von den untersuchten Arten abhängig ist. Wir konnten herausstellen, dass Ausbreitung oftmals nicht nur von der physischen Ausbreitungsfähigkeit abhängt, sondern auch durch die Menge potentieller Habitate, Habitatqualität, Ernährungsstrategien, Konkurrenz und Geschlecht beeinflusst ist.

Im vierten Manuskript habe ich die Nahrungsnetzwerke saproxyler Käfergemeinschaften in Mulmhöhlen mit Hilfe von stabilen Stickstoff- und Kohlenstoffisotopen untersucht. Ich konnte zeigen, dass die trophische Position der einzelnen Arten (Nahrungsgilde), die ich aus der Untersuchung der stabilen Isotope erhalten habe, sich fast mit den Angaben zur trophischen Position aus der Literatur decken. Die Isotopensignatur von mycetophagen Arten deutet auf eine starke omnivore Ernährungsweise im Vergleich zu anderen Nahrungsgilden hin. Die xylophage und zoo-xylophage Nahrungsgilde zeigte hohe Redundanz innerhalb ihrer Nische und generell gab es eine hohe Nischenkonservierung innerhalb der Käferfamilien. Weiterhin hatten zoophage Arten die höchste Biomasse innerhalb der Mulmhöhlen, was umgekehrten eltonischen Pyramiden entspricht. Betrachtet man jedoch alle saproxylen Arthropoden innerhalb einer Mulmhöhle und nicht nur saproxyle Käfer, findet man wahrscheinlich keine umgekehrten eltonischen Pyramiden, da Arten aus niedrigeren trophischen Ebenen, wie zum

Beispiel Springschwänze, einen großen Anteil zur Gesamtbiomasse in Mulmhöhlengemeinschaften beitragen. Die Länge der Nahrungsketten war in dieser Studie abhängig von Artenvielfalt innerhalb der Höhle, was die Bedeutung einer hohen Artenvielfalt für die Funktionalität des Ökosystems hervorhebt.

Die Empfehlungen aus dieser Doktorarbeit können Förstern, politischen Entscheidungsträgern und Naturschützern helfen durch effizientes Management von Mulmhöhlen einen Beitrag zum Erhalt saproxyler Arten in Wäldern zu leisten.

## Structure of the thesis

Tree hollows in beech trees are keystone structures for forest biodiversity and provide long lasting habitats for saproxylic insects (i.e. dependent on deadwood). However, to maintain saproxylic species diversity in managed forests it is important to understand the crucial processes and interactions leading to the existing patterns of species diversity in tree hollow communities. My thesis covers four aspects that are connected to the species diversity of tree hollows (Fig. 1): tree hollow characteristics driving saproxylic species diversity, dispersal of tree hollow inhabiting species, food web structures in tree hollows and the role of forest management for saproxylic diversity.

Habitat characteristics are not the only factors shaping the community composition in tree hollows. Dispersal is also a crucial mechanism structuring the community composition, as dispersal ability can determine which species are able to colonize suitable habitats away from the natal habitat. Further, species diversity might also influence the food web complexity, as potential trophic interactions increase with an increasing number of different species within a community. Finally, forest management is an important factor in shaping the diversity of tree hollow communities, as forest management influences the abundance of tree hollows, their characteristics, and their spatial and temporal distribution.

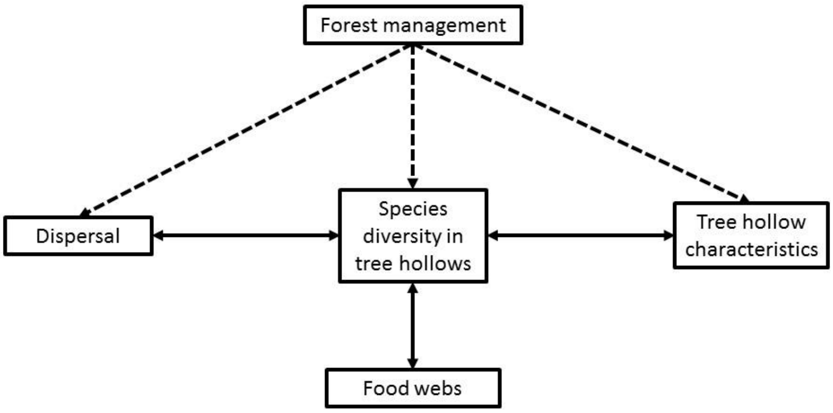

**Fig. 1:** Conceptual framework of the thesis on tree hollow biodiversity and the linkage between the main fields of interest.

My thesis starts with an introduction of deadwood and especially tree hollows as an important habitat and the importance for forest ecosystems and the associated saproxylic organisms. In a next step, I will point out the influence of forest management on deadwood biodiversity and resulting problems for saproxylic insects in general. Afterwards, I will switch to the three main aspects I investigated: environmental factors influencing the biodiversity of beetle communities in tree hollows (Manuscript 1), dispersal of saproxylic insects in general and especially for species associated with tree hollows (Manuscript 2 & 3) and food webs in tree hollows (Manuscript 4). Concluding I want to discuss possible future directions and finally, I give recommendations based on our result for maintaining tree hollows in managed forests and thus preserving biodiversity.

# Introduction

In the past decades the awareness of the importance of deadwood and deadwood structures like tree hollows, and their associated biodiversity arose (Grove, 2002a). However, the early research on saproxylic species started due to economic reasons, as some saproxylic species were considered as pest species (e.g. some bark beetle species), being a risk for forest health and lowering the quality of timber products (Ulyshen and Šobotník, 2018). Despite that, already Elton (1966) recognized the importance of dying and deadwood structures for the diversity of forest ecosystems. He concluded that deadwood represents one of the most important resources in forests for animal species worldwide, and removal of deadwood could lead to a drastic impoverishment of its fauna. At the end of the twentieth century, the conservation of saproxylic species became a major goal in large parts of the world, as a drastic reduction of saproxylic species due to intensive forest management was recognized (Ulyshen and Šobotník, 2018).

## Deadwood – creation of a key resource

Deadwood in natural forest ecosystems is created by tree mortality or partial death of mostly senescent trees. In natural forests the main causes for tree mortality are natural disturbances, like fire, wind, drought or insects and pathogens (Kuuluvainen, 1994; Lindenmayer et al., 2012a; Müller et al., 2014), affecting single to multiple trees or even whole stands (White and Pickett, 1985). The natural creation of deadwood in a forest system is unpredictable as all aforementioned natural disturbances are spatially and temporally random. Besides that, the amount and quality of deadwood differ considerably between different forest types (Fridman and Ståhl, 2001; Lachat and Müller, 2018). The variation of deadwood amount is caused by the volume of living trees, deadwood input and wood decomposition (Seibold and Thorn, 2018). High amounts of deadwood can occur in forests with slow decomposition and high productivity (Harmon et al., 1986; Lindenmayer et al., 1999) or a high input of deadwood, for example after an infestation of bark beetles (Müller et al., 2010). At the other end of the scale, the amount of deadwood in tropical forests is often low. Despite a high productivity, the decomposition rate of wood is fast, leading to reduced amounts of deadwood (Delaney et al., 1998; Grove, 2001). The origin of deadwood is also responsible for a variation in deadwood diversity and quality. Natural disturbances often create uniform deadwood structures. For example, wind throws create uprooted trees leading to sun-exposed branches whereas wildfires mostly create upstanding snags and dead trees. Thus, natural disturbances often lead to a reduced diversity of deadwood structures (Franklin et al., 2000; Seibold and Thorn, 2018; Swanson et al., 2011). Consequently, the intensity, severity, and frequency of natural disturbances are responsible for the amount and quality of deadwood (Lachat and Müller, 2018). In contrast, natural senescence of trees leads to a high diversity of standing and lying deadwood structures, ranging from small twigs to large diameter logs and dead trees. These old and veteran trees are the focus of the so-called mature timber habitat (Grove, 2002a), describing structures which are economically less valuable but at the highest peak of their ecological importance (Speight, 1989). Additionally, a wide range of different microhabitats can occur in these deadwood structures, like water filled rot holes, tree hollows with and without wood mould, fungal consoles and many more (Kraus et al., 2016; Larrieu et al., 2014; Siitonen, 2012a). Thus Speight (1989) compared old veteran trees with different microhabitats as “megalopolis”, highlighting the variety of habitats such a veteran tree can offer.

### “Saproxylic” – a term for wood-inhabiting species

Species associated with decaying wood were given a specific term the first time by Sylvestri (1913), who called a new species of Zoraptera “saproxylophiles”. Later on, Dajoz (1966) continued using the term saproxylic for insects living in deadwood. However, the first and most common definition was given by Speight (1989). He coined the term „saproxylic“ for invertebrate species dependent on dead or dying wood of fallen or standing moribund or dying trees as a resource in at least one stage of their life cycle, either directly by feeding on bark, phloem or wood or indirectly via wood-decomposing fungi or other saproxylic insects. However, using the strict definition of Speight (1989), species living in tree hollows would be excluded, as trees with hollows are mostly healthy and not moribund. This issue was highlighted by Alexander (2008), who suggested a less restrictive definition also including healthy and living trees. Another term worth to mention coined by Schmidl & Bussler (2004), is xylobiont, which is commonly used in the German language, and is similar to the definition of saproxylic by Speight (1989), but also includes healthy trees. However, for species living in late decay stages of wood with contact to the forest floor, the classification of being saproxylic or not might be vague, as they will also use the forest soil as habitat (Ferro et al., 2012). In this thesis, we use the term saproxylic, for all species associated with deadwood, including deadwood structures in healthy trees like tree hollows.

### Deadwood- a hot spot for diversity in forests

Deadwood in forests is a core element for biodiversity. It offers habitat space, with various microhabitats, high amounts of nutritional sources and thus energy for a wide range of species (Stokland et al., 2012). Thus the high heterogeneity of deadwood allows the coexistence, persistence, and diversification of saproxylic species (Seibold et al., 2016). Saproxylic species are taxonomically and functionally very divers, account for a large proportion of forest diversity and are responsible for many forest ecosystem services, like nutrient cycling and decomposition (Bouget et al., 2014; Gouix et al., 2015; Grove, 2002a; Langor et al., 2008; Siitonen, 2001).

In deadwood systems, the majority of saproxylic taxa are arthropods and wood-decaying fungi (Basidiomycota) (Speight, 1989; Stokland et al., 2012). Nonetheless, also vertebrate species like birds, bats, amphibians, reptiles, and other small mammals find habitat and nesting sites in deadwood structures, e.g. tree hollows (Gibbons and Lindenmayer, 2002; Goldingay, 2009; Kosiński, 2006). Even a group of tropical catfish use deadwood for nourishment and several crustaceans and mollusks use downed wood in marine systems (Stokland et al., 2012). Further, deadwood is inhabited by lichens, bryophytes and some tree seedlings can grow on deadwood (Humphrey et al., 2002; Spribille et al., 2008; Stokland, 2012a; Zielonka, 2006). The number of species worldwide is still unknown and thus it is hard to estimate the number of saproxylic organisms, but Siitonen (2001) predicted, that the total amount of saproxylic species might be around 20-25% in boreal forests. Worth to mention are also non-saproxylic species, which benefit from deadwood, for example, insects using deadwood structures as hunting areas, due to the dense prey assemblages or using deadwood structures as shelter or to hibernate (Ulyshen and Šobotník, 2018).

Among the saproxylic insects, beetles (Coleoptera), gnats and flies (Diptera), wasps, bees and ants (Hymenoptera) and in tropical regions termites (Isoptera) are the four dominant orders in decaying and deadwood. However, mites, collembolans, pseudoscorpions, and nematodes might be as abundant and diverse as the before mentioned orders, but their biology and their ecology are less known (Stokland et al., 2012).

Beetles (Coleoptera) is the best-studied order associated with deadwood, especially in Europe (Grove, 2002a; Stokland et al., 2012). Nonetheless, for most species, the biology is still unknown and information on their ecology is scarce. They are very prominent in deadwood e.g. in Central Europe, around 56% of beetle species in forests are associated with deadwood (Köhler, 2000). In tropical forests, the proportion of beetle species being saproxylic is lower (about 30%), but this might be due to a lack of studies on saproxylic insects compared to Central Europe. In total, around 65% of the known beetle families contain saproxylic members (Gimmel and Ferro, 2018). Nonetheless, the number of saproxylic insects worldwide is still unknown (Stokland et al., 2012) but estimates predict that about 25% of forest species are saproxylic (Lachat and Müller, 2018).

## Saproxylic diversity – general theory of diversity patterns

General theory of species richness predicts an increase of species with increasing habitat area (MacArthur and Wilson, 1967), driven by energy availability, habitat heterogeneity, disturbance and population dynamics (Blakely and Didham, 2010; Gaston, 2000; MacArthur and Wilson, 1967; Storch et al., 2005; Williamson, 1988). The influence of energy availability is described by the so-called "more individuals" hypothesis, a variant of the "species energy hypothesis". This hypothesis states that a higher amount of energy is available to all species with increasing area supporting more individuals, ultimately leading to more species within this area (Schuler et al., 2015; Srivastava and Lawton, 1998; Wright, 1983).

Another important mechanism of increased numbers of species with increasing area is the "habitat heterogeneity hypothesis". This hypothesis suggests an increase of different potential habitats with increasing area. Consequently, if species require different habitat characteristics the number of species should also increase with increasing area (MacArthur and MacArthur, 1961; Simpson, 1949; Tews et al., 2004). However, energy availability and habitat heterogeneity are often tightly linked (Whittaker, 1998; Wright, 1983), which is also true for deadwood amount and deadwood diversity (Bouget et al., 2013; Müller and Bütler, 2010; Okland et al., 1996; Similä et al., 2003). Due to this correlation, it is not easy to assess the individual influence of these two mechanisms. Further, the importance of energy availability and habitat heterogeneity might vary across different taxa (Blakely and Didham, 2010; Seibold et al., 2016; Wright, 1983).

Biodiversity patterns in fragmented landscapes can be linked to the theory of metapopulation dynamics (Levins, 1969; Ovaskainen and Hanski, 2004). The persistence of extinction-prone local populations within a metapopulation is driven by the balance of stochastic extinctions and recolonizations (Hanski, 1991; Levins, 1969). The classical view of metapopulations assumes the stability of habitat patches over time, but neglecting the effect of habitat dynamics on metapopulation dynamics (Hanski, 1994). However, the metapopulation dynamics of many species are influenced by habitat dynamics, like formation, successional change and habitat loss (Snäll et al., 2003; Thomas, 1994). According to the theory, colonization and extinctions of populations in patches and thus the number of species within these patches is dependent on the patch size and patch isolation (Hanski, 1994; MacArthur and Wilson, 1967). However, the assumption, that patch size and patch isolation have distinct effects on species richness has been questioned by Fahrig (2003, 2013). Therefore, Fahrig (2013) proposed the "habitat amount hypothesis", where a simpler view on the relation of habitat distribution and species richness provided. She hypothesized, that for most terrestrial ecosystems, the effect of patch size and patch isolation is driven by the sample area effect. This means that a sampling site in a local landscape (the area within an appropriate distance to the sampling site) with a high amount of habitat should have more species than an even sized sampling site from a local landscape with less habitat, regardless of the spatial configuration of the habitat within the local landscape.

Some studies have tested the predictions of these general theories in deadwood systems (Bässler et al., 2010; Bouget et al., 2014; Junninen and Komonen, 2011; Lassauce et al., 2011; Müller and Bütler, 2010; Seibold et al., 2016, 2017). This is not only of general academic interest but the basis for effective deadwood management and conservation strategies. These studies can help to decide about the amount, heterogeneity and spatial distribution of deadwood objects, supporting saproxylic diversity most efficiently.

### Saproxylic insects – sensitive to forest management

The main threats of global biodiversity are deforestation, the degradation of remaining forests and land use intensification (Allan et al., 2015; Lindenmayer et al., 2012a; Siitonen, 2012b). Deforestation and degradation lead to a decline of senescent trees worldwide (Bauhus et al., 2009; Harding and Rose, 1986; Lindenmayer et al., 2012a) and the reduced amounts of deadwood in intensively managed forests are a pronounced threat for saproxylic species (Grove, 2002a; Siitonen, 2012b; Siitonen and Jonsson, 2012a; Winter and Möller, 2008), due to their dependency on deadwood. This makes saproxylic species more sensitive to deforestation compared to non-saproxylic species in the forest ecosystem (Siitonen, 2012b; Siitonen and Martikainen, 1994).

Generally, most saproxylic species are positively related to old forests with long-term habitat continuity (Lachat and Müller, 2018). Due to their sensitivity to natural and anthropogenic disturbances, a change in their trophic and taxonomic diversity can be recognized. Thus, saproxylic communities serve as useful indicators for any habitat changes, natural or caused by management practices, in the forest (Heikkala et al., 2016; Hjältén et al., 2012; Langor et al., 2008; Lee et al., 2015; Siitonen, 2001). Due to intensive forest management coupled with the reduction of deadwood the abundance of many saproxylic species decreased greatly and many of them became threatened or even extinct (Grove, 2002a; Seibold et al., 2015a; Siitonen, 2012b; Speight, 1989). According to the European Red List of saproxylic beetles (Nieto and Alexander, 2010), 11 % of saproxylic beetles are threatened and 13% are considered near threatened in all of Europe. Moreover, there is a data deficiency of scientific information on 28% of the species, making an evaluation of their risk of extinction not possible. 14% of the species assessed have declining populations, 27% are stable and only 2% are increasing. For population growth estimation there is an even higher data deficiency of 57%. In Germany, even 33% of the assessed saproxylic species are threatened (Schauer et al., 2018a).

### Intensively managed forests – a threat for saproxylic biodiversity

Generally speaking, the main factors threatening saproxylic species are forest loss, intensified land use, biomass harvesting for energy and especially forest management resulting in habitat loss and habitat fragmentation (Siitonen, 2012b). In Europe the forest ecosystems have been affected by humans for more than 5000 years (Grove, 2002a, 2002b), with a peak of minimum forest coverage around 1750 A.D. (Whitehouse, 2006), leading to scattered forest patches only decades or few centuries old in most regions (Speight, 1989). Coupled with the increased anthropogenic pressure on forest ecosystems, deadwood was also reduced to maintain forest hygiene, as dying and dead trees in a forest were considered as messy and a source of potential pest outbreaks (Seibold and Thorn, 2018).

In contrast, old-growth forests contain higher amounts of deadwood and a higher variety of different deadwood objects compared to most managed forests (Siitonen, 2001; Siitonen et al., 2000; Spies et al., 1988; Stenbacka, 2010). Higher amounts of deadwood and a greater variety of deadwood objects have been shown to influence the diversity and abundance of saproxylic species positively (Grove, 2002b; Lachat and Müller, 2018; Martikainen et al., 2000; Okland et al., 1996; Vanderwel et al., 2006). Moreover, in old growth forests old trees with valuable structures like tree hollows can be found more frequently (Ulyshen and Šobotník, 2018).

One reason for forest loss was the conversion of forest to agricultural land due to the needs of the growing human population. Additionally, industrial operations like large-scale clearance, cattle ranching and timber extraction coupled with road expansions and human settlement led to a rapid deforestation worldwide (Achard et al., 2006; Butler and Laurance, 2008; Laurance et al., 2009). The overall estimation of global forest loss was 13 million hectares per year during 1990 and 2005 (FAO, 2006), but there is a smaller net loss due to reforestation and afforestation. However, reforested and afforested areas show plantation character, which differs significantly from primary forests in terms of species composition and structure (Siitonen, 2012b). Additionally, due to the increasing needs of timber, broad-leaved forests in Europe have been replaced by fast-growing coniferous trees, often with plantation characters (Grove, 2002a; Zerbe, 2002). Coniferous monocultures are also lower in natural abundances of important cavity structures (Larrieu and Cabanettes, 2012). Saproxylic species are often unable to cope with the unnatural conditions of plantations, as they have high ecological requirements, like high amounts of qualitative deadwood, large senescent trees and natural forest dynamics (Grove, 2002b; Lachat and Müller, 2018). Only a small proportion of saproxylic species can sustain under plantation conditions (Gossner and Ammer, 2006; Lachat et al., 2007).

Land use intensification and urbanization also led to the reduction of over-mature trees and deadwood, especially in non-forested areas like semi-open grasslands and pasture woodlands. However, the scattered over mature trees offered an important habitat for a lot of different saproxylic species (Siitonen, 2012c, 2012b). Coupled with urbanization a higher demand for energy wood arose. Due to the high demand of bioenergy and the increasing prices, also logging residues and stumps became attractive as a source of biomass for bioenergy (Berndes et al., 2003; Field et al., 2008). This leads to a potential reduction of future deadwood, as also small logging residues like twigs and branches are removed and harvesting actions can accidentally destroy existing deadwood (Rudolphi and Gustafsson, 2005; Siitonen, 2012b). Although small logging residues and stumps are mostly small in diameter and thus only contribute small amounts of deadwood, they are also important for species as step stones if more suitable habitats might not be available. It was also shown that these logging residues host a different saproxylic community depending on the tree species and support a lot of different saproxylic species including many Red List species (Jonsell et al., 2007; Siitonen, 2012b).

Industrial forestry has negative effects on saproxylic communities, as all actions change the within-stand microclimate and most importantly cause reduction of deadwood or an alteration of its composition and characteristics, possibly leading to uniform stand structures (Grove, 2002a; Grove and Stamm, 2011; Lee et al., 2015; Siitonen and Jonsson, 2012a). Considerable loss of deadwood due to management practices can lead to a drastic change of saproxylic communities compared to the loss after natural disturbances (Hammond et al., 2017). Intensive forest management, where timber production depends on a shorter rotation age of trees, often does not give sufficient time for trees to develop suitable deadwood habitats (Larrieu et al., 2012). Timber harvesting leads to a change in the mortality patterns of the forest (Debeljak, 2006), as trees cannot reach natural senescent, where partial or complete die-offs occur and the natural creation of deadwood is stopped (Grove and Stamm, 2011; Lee et al., 2015; Siitonen and Jonsson, 2012a).

These changes are of outmost importance, as different saproxylic assemblages respond negatively, because different saproxylic assemblages are restricted to specific habitat characteristics, like tree species, degree of decomposition, diameter, sun exposure and many more (Gouix et al., 2015; Lindhe et al., 2005; Müller et al., 2015; Schauer et al., 2018a; Sverdrup-Thygeson et al., 2010). For example, after timber harvesting, early stages of decomposed wood are greatly reduced, and late stages often become much drier, leading to unsuitable conditions for species dependent on a specific stage of decomposition. Additionally, depending on the tree species and environmental conditions the decomposition of deadwood can be slow and take longer to develop. This can lead to a reduction of the local populations of saproxylic beetles, for example, dependent on early and late successional stages of deadwood and in the worst case to their extinction (Hammond et al., 2017; Lee et al., 2015).

Forest degradation is often the start of forest fragmentation coupled with habitat loss, edge effects and isolation of populations (Fahrig, 2003; Whitmore et al., 1997). Habitat fragmentation is defined as a process leading to the separation of a large habitat by a matrix of habitats unlike the original habitat into smaller patches without connection (Wilcove et al., 1986). Fragmentation has several direct negative effects on biodiversity like decreased species richness (Ranius, 2002a; Schmiegelow and Mönkkönen, 2002; Steffan-Dewenter et al., 2002), genetic diversity (Gibbs, 2001; Knutsen, 2000), population abundance and reduced spatial distribution (Best et al., 2001; Gibbs, 1998; Gibbs and Stanton, 2001; Guthery et al., 2001; Hanski et al., 1996). Additionally, many factors influencing biodiversity are negatively affected by fragmentation, like negative breeding success leading to decreased population growth (Bascompte et al., 2002; Donovan and Flather, 2002; Kurki et al., 2000), reduced trophic chain length (Komonen et al., 2000) and lower effective dispersal (Bélisle et al., 2001; With and Crist, 1995; With and King, 1999). This is also true for saproxylic species as deadwood is an ephemeral habitat and the concept of metapopulations is tightly linked to the population dynamics of saproxylic species especially in fragmented landscapes (Jonsson et al., 2005;

Ranius et al., 2014). Fragmentation of forest habitats often leads to forest patches embedded in a landscape matrix consisting of non-forested areas potentially resulting in dispersal limitation for species (Shepherd and Brantley, 2005). Fragmentation can also take place within forests due to large distances between suitable microsites such as deadwood or tree hollows (Schiegg, 2000). However, deadwood, in general, is a fragmented habitat in space and time, as it is heterogeneously distributed in all forests no matter of the management history or previous natural or anthropogenic disturbances (Amanzadeh et al., 2013; Christensen et al., 2005; Ylisirniö et al., 2009). For deadwood several studies suggested that spatial and temporal continuity is very important for saproxylic species, even more important than the amount or variety of deadwood (Schiegg, 2008; Similä et al., 2003; Sverdrup-Thygeson et al., 2014). Contrastingly, rare species in young forests were positively affected by the amount of deadwood and not by its continuity but common species were affected by both factors (Brin et al., 2016). This indicates that deadwood amount might be more important in ancient forests compared to recent forests (Seibold and Thorn, 2018). Further Seibold et al. (2017) showed that the total amount of deadwood habitat available is the main driver of the diversity of saproxylic beetle species and connectivity might only play a minor role.

Generally speaking, the extraction of wood and thus also the removal of potential deadwood leads to a direct competition of species dependent on deadwood and industrial forestry (Siitonen and Jonsson, 2012a). Concluding, any action leading to reduced amounts of deadwood can impose severe threats to saproxylic organisms.

## Objectives

One of the most fascinating and complex deadwood habitats are tree hollows. They are regarded as keystone structures for the diversity in forest ecosystems (Müller et al., 2014). Tree hollows are a confined space, with unique physical, biotic and abiotic characteristics determining the communities inside (Micó, 2018; Schauer et al., 2018a; Siitonen, 2012a; Speight, 1989). In contrast to other deadwood habitats, like snags and logs, hollows in living trees are long lasting habitats with stable microclimate conditions and food stability as microbes, fungi and animals produce nutrients inside the tree hollow (Micó, 2018; Park et al., 1950; Siitonen, 2012a; Siitonen and Jonsson, 2012b). Tree hollows can last for centuries and over time wood mould accumulates and as consequence the structural complexity increases. Thus, with increasing age and size, tree hollows can offer a lot of different habitat niches for very distinctive communities (Gibbons and Lindenmayer, 2002; Lindenmayer et al., 2012a; Siitonen, 2012a; Speight, 1989). Tree hollows containing wood mould are functionally and taxonomically more diverse than any other deadwood habitat (Müller et al., 2014). The most diverse arthropod taxa found in tree hollows are Coleoptera and Diptera and therefore account for a large proportion of forest diversity and are important for nutrient cycling and ecosystem functioning (Gouix et al., 2015; Grove, 2002a; Köhler, 2000). The species composition of saproxylic beetles in tree hollows with wood mould consists of generalist species utilizing a wide variety of deadwood and wood mould-specialist species. Many of the wood mould specialist species are threatened due to their restriction to that habitat in terms of their dependency on the specific and stable environment tree hollows with would mould can provide (Chiari et al., 2013; Gouix et al., 2015; Micó, 2018; Müller et al., 2014; Nieto and Alexander, 2010; Quinto et al., 2015; Ranius and Jansson, 2000). In Germany, approximately 86% of species associated with tree hollows are threatened (Schmidl et al., 2008).

The high number of endangered species associated with tree hollows might not only be due to their special habitat requirements but also due to potentially limited dispersal. General theory predicts low dispersal propensity of species inhabiting stable and long-lasting habitats like tree hollows (Denno et al., 1996; Nilsson and Baranowski, 1997; Southwood, 1962; Travis and Dytham, 1999). However, dispersal is a key trait of species confronted with a changing environment in terms of habitat loss and fragmentation (Thomas, 2000). Dispersal is required to maintain gene flow between habitat patches, allows the colonization of new habitats, and thus affects population dynamics, extinction risk of populations, and species distributions (Bowler and Benton, 2005; Hanski et al., 1994). Habitat fragmentation can cause the isolation of subpopulations due to dispersal limitation, which may lead to an accelerated loss of genetic variability, due to random genetic drift and a higher risk of inbreeding (Hedrick, 2011; Keller and Largiader, 2003).

Tree hollows are functionally very complex and the deadwood food web comprises several trophic levels above the primary level (Stokland, 2012a). The primary level is wood mould followed by decomposer, e.g. bacteria, fungi and detrivores, the consumers of dead organic matter (Begon et al., 2006), xylophages, organisms feeding on living wood ending in higher trophic levels fungivores, scavengers and predators, as well as parasitoids and hyperparasitoids (Stokland, 2012a). Thus, saproxylic insects are important for ecosystem functioning. Further, according to general theory, the length of trophic chains might also be influenced by species diversity, habitat availability and habitat heterogeneity (Cohen and Newman, 1991; Holt, 1993) A reduction in quality and number of structures, due to intensive management can have severe consequences for the associated species (Lindenmayer et al., 1991; Müller et al., 2014; Ranius and Wilander, 2000; Tews et al., 2004). Thus, it is important to develop effective management strategies and to protect saproxylic insect diversity in managed forests. For this purpose, it is crucial to investigate the microhabitat parameters related to saproxylic beetle diversity, dispersal of saproxylic insects and the food web structure of tree hollow communities.

In this thesis I addressed the following objectives:

I. Identification of the characteristics of tree hollows and their near surrounding influencing the diversity of saproxylic beetle communities (Red List and Non-Red List species) in tree hollows (Manuscript 1).

II. Investigating the population genetic structure of three saproxylic insects (one beetle and two flies) using microsatellite analysis and inferring their dispersal capacity

(Manuscript 2). Additionally, giving an overview of the existing knowledge of dispersal abilities of different saproxylic insects, methods to measure dispersal, factors influencing dispersal, and highlighting open research questions (Manuscript 3)

III. Disentangling trophic relations and dietary information of saproxylic species in tree hollows, using stable isotope analysis (Manuscript 4).

IV. Giving recommendations on tree hollow management, derived from the results gained in all studies and making it accessible to a broad audience of foresters, forestry workers and forest owners (Manuscript 5 & 6, Appendix)

# List of publications

## Publications in peer - reviewed journals:

Schauer, B., J. Bong, C. Popp, E. Obermaier, H. Feldhaar (2018) Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach. *Basic and Applied Ecology*. DOI: doi.org/10.1016/j.baae.2018.01.005 (online early)

Schauer, B., M.J. Steinbauer, L.S. Vailshery, J. Müller, H. Feldhaar, E. Obermaier (2018) Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. *Biodiversity and Conservation* 27: 853-869

## Book chapter (peer - reviewed)

Feldhaar H., Schauer, B. (2018) Dispersal of saproxylic insects. In: Saproxylic insects. Ed. Ulyshen, M. *Zoological Monographs* Vol. 1, Springer, Germany. Pp. 515-546.

## Manuscript in preparation

Schauer, B., Gebauer, G., Obermaier, E., Feldhaar, H.: Trophic structure of saproxylic beetle communities in tree hollows identified by stable isotope analysis.

## Publications in non peer – reviewed journals (see appendix)

*Schauer, B., Feldhaar, H., Obermaier, E. Mulmhöhlen – für die Artenvielfalt im Wald. *Merkblatt 42 der Bayerischen Landesanstalt für Wald und Forstwirtschaft (LWF).*

*Schauer, B., Feldhaar, H., Obermaier, E. Wohnungsnot in deutschen Wäldern. *LWF aktuell 3 2018* (LWF – Bayerische Landesanstalt für Wald und Forstwirtschaft).

*Part of the appendix, as these publications are an important part of this thesis but published in non peer - reviewed journals. These publications inform foresters about the importance of tree hollows for the preservation of arthropod diversity in forests and contain recommendations for tree hollow management.

# Manuscripts and declaration of own contribution

Manuscript 1: Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest.

Authors: Bastian Schauer, Manuel J. Steinbauer, Lionel S. Vailshery, Jörg Müller, Heike Feldhaar, Elisabeth Obermaier

Journal and status: Biodiversity and Conservation (2018) 27: 853-869.

Own contribution: data acquisition: 85%, data analysis and figures: 50%, writing: 75%; concept and discussion: 60%; corresponding author

BS, HF, EO, JM conceived the ideas and designed the methodology. BS, LSV collected the data. BS, LSV and MJS analysed the data. BS, HF, EO, LSV and JM interpreted and discussed results. Figures and tables were created by BS and MJS. BS led the writing of the manuscript.

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ORIGINAL PAPER

# Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest

**Bastian Schauer[1,5] · Manuel J. Steinbauer[2] · Lionel S. Vailshery[1] · Jörg Müller[3,4] · Heike Feldhaar[1] · Elisabeth Obermaier[5]**

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**Abstract** Tree hollows are key structures in forest ecosystems constituting long-lasting habitats and nutritional resources for many saproxylic arthropod species. Due to diverse microhabitat structures and conditions in tree hollows, they can support a broad range of species. However, in the past intensive management practices in parts of Europe reduced the abundance of tree hollows, resulting in a decrease and endangerment of species specialised in this tree habitat. We investigated 40 beech trees with hollows in 2014 and a subset of 23 of these trees in 2015 in a managed forest landscape in Germany. Using

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Heike Feldhaar and Elisabeth Obermaier have contributed equally.

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This article belongs to the Topical Collection: Forest and plantation biodiversity.

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emergence traps we collected 89 beetle species of which 33% were on the Bavarian Red List. We described the tree characteristics, physical hollow characteristics, and their surrounding environment investigating their influence on α-diversity of non-Red List and Red List species. Furthermore, we investigated spatial (between tree hollows) and temporal (same tree hollow but different years) β-diversity, considering the importance of turnover and nestedness components on β-diversity. α-Diversity decreased with increasing decomposition of wood mould and increased with increasing area of hollow entrance in both years. Additional characteristics differed between years and between non-Red List and Red List species. β-Diversity was related to diameter at breast height, number of surrounding tree hollows, area of hollow entrance and a temperature gradient. We found a higher species turnover than nestedness between tree hollows and between years, indicating highly dynamic beetle communities spatially as well as temporally. To support and maintain the diversity of saproxylic beetles inhabiting tree hollows, the heterogeneity of microhabitats is important and should be supported by maintaining the diversity of differently structured and sized tree hollows.

**Keywords** Coleoptera · Conservation · Dead wood · Keystone structure · Threatened species · Wood mould

## Introduction

A decline of large and old trees has been observed in forests all over the world (Lindenmayer et al. 2012). Conservation of biodiversity in forest ecosystems has become a major goal of national forest policies, beside timber production (Brunet et al. 2010). Saproxylic organisms have attracted great interest for conservation due to their vulnerability to timber harvesting and changing habitat quality in terms of habitat loss (Gibbons and Lindenmayer 1996; Ranius 2007). Speight (1989) coined the term “saproxylic” for species dependent on deadwood as a resource in at least one stage of their life cycle, either directly or indirectly (via wood-decomposing fungi or other saproxylic species). In Germany, approximately 34% of all forest arthropod species are saproxylic (Müller et al. 2008). The largest part of saproxylic insect diversity is formed by flies and beetles (Grove 2002). Saproxylic beetles therefore account for a large proportion of forest diversity and are important for nutrient cycling and ecosystem functioning (Gouix et al. 2015; Grove 2002). They have been suggested as indicator species for habitat quality in terms of forest continuity and amount of deadwood, due to their dependency on deadwood and sensitivity to historical and current forest use intensity (Gossner et al. 2013; Nilsson et al. 2001; Siitonen 2001).

Most dead trees, snags or logs undergo a straight succession with strong species turnover over time (Stokland and Siitonen 2012). In contrast, living trees with hollows provide

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long lasting and stable microhabitats to many different species. Therefore, they are regarded as keystone structures maintaining forest biodiversity. A reduction in number and quality of tree hollows can have severe consequences for the associated species (Lindenmayer et al. 1991; Müller et al. 2014; Ranius and Wilander 2000; Tews et al. 2004).

Wood mould in tree hollows consists of fungally decomposed wood, insect frass and excrements of different species, forming a nitrogen-rich habitat (Siitonen 2012b). Tree hollow development often starts with trees being damaged, e.g., by branches breaking off and leaving cracks in the stem. These injuries provide access to sapwood and heartwood, where fungi and invertebrates initiate a combination of decaying processes. Mostly, tree hollows start with small rot holes developing into bigger cavities but the temporal development aspect is still not clear (Siitonen 2012b). On one hand, tree age seems an important determinant for the occurrence of tree hollows. Ranius et al. (2009a) estimated tree hollow occurrence in different age classes in pedunculate oaks (*Quercus robur*) showing higher probability of tree hollows in old age classes (> 200 years). Therefore, intensive forest management, where timber production depends on a shorter rotation age of trees, often does not give sufficient time for trees to develop suitable deadwood habitats (Larrieu et al. 2012). On the other hand, aside from tree age, silvicultural practices can have important influence on tree hollow development. One traditional practice is pollarding, which increases the probability and speed of tree hollow formation (Sebek et al. 2013). Additionally, methods like pruning of branches or damaging the bark to mimic natural injuries can help to speed up tree hollow formation (Carpaneto et al. 2010; Siitonen 2012a).

The species composition of saproxylic beetles in tree hollows with wood mould consists of generalist species which prefer a wide variety of deadwood and wood mould-specialist species such as *Limoniscus violaceus* (violet click beetle, Elateridae), and *Osmoderma eremita* (hermit beetle, Scarabaeidae). Many of the wood mould specialist species are threatened due to their restriction to that habitat in terms of their dependency on the specific and stable environment tree hollows with would mould can provide (Müller et al. 2014; Nieto and Alexander 2010; Quinto et al. 2015; Ranius and Nilsson 1997).

Tree hollows support the high functional diversity and species richness of their insect communities due to their specific and diverse set of micro-environmental features such as their physical (e.g., tree hollow volume, wood mould volume), biotic (e.g., presence of ecosystem engineers) and chemical characteristics (e.g., nitrogen, carbon and phosphorus content of wood mould) (Gouix and Brustel 2012; Jönsson et al. 2004; Micó et al. 2015; Ranius and Nilsson 1997). Due to various combinations of these characteristics each tree hollow can offer a unique deadwood habitat (Micó et al. 2015; Quinto et al. 2014). In general, large tree hollows with a large volume of wood mould support a high invertebrate diversity, as it is assumed that large hollow volumes and a large amount of wood mould can offer highly variable microsites and resources (Quinto et al. 2014; Ranius 2002a, b; Ranius and Jansson 2000). In addition, different stages of decomposed wood provide a wide range of niches for species with different requirements and thus the presence of different stages supports a greater diversity of deadwood associates (Speight 1989).

By identifying the parameters influencing saproxylic diversity and distribution patterns at large scales (landscape) and small scales (microhabitats), a better understanding for the protection of species associated with tree hollows can be gained. Specifically, we address the following questions: (1) Which tree hollow characteristics (micro-environmental and surrounding stand structure characteristics) are explaining $\alpha$-diversity in tree hollows? (2) Is $\alpha$-diversity of Red List saproxylic beetle species related to the same tree hollow characteristics as that of non-Red List species? We expected to find a different set of microhabitat parameters for Red List species based on their specific habitat requirements, such as a large hollow volume. (3) How is β-diversity (spatial and temporal) partitioned into turnover and nestedness components and which tree hollow characteristics relate to β-diversity? We assumed to find a high spatial turnover (between tree hollows) and a lower temporal turnover (same tree hollow but different years) due to the specific microhabitat offered by a focal tree hollow.

As European forests are largely managed, they constitute big areas of potential habitats for saproxylic organisms. Hence it is important to investigate the microhabitat parameters related to saproxylic beetle diversity in managed forest, because these findings can help to protect saproxylic beetle diversity. Furthermore, not much is known about the communities in tree hollows of beech trees (*Fagus sylvatica*), compared to those in oak. Moreover, we focus on the whole community level within tree hollows instead of focusing on only a single species or trophic guild (Quinto et al. 2014).

The knowledge gained can add to the existing studies conducted mostly in oaks and protected areas (Micó et al. 2013, 2015; Ranius 2002a; Sverdrup-Thygeson et al. 2010). Finally, a more complete overview of habitat requirements of saproxylic beetles, will potentially lead to more efficient conservation strategies in the future.

## Materials and methods

### Study site

This study was conducted during the years 2014 and 2015 at the Forest Management District Ebrach in the northern Steigerwald (N 49°50′, E 10°29′). Mean annual temperature of the region is 7−8 °C and a mean annual rainfall of 850 mm (Bässler et al. 2014). The Steigerwald covers an area of approximately 1000 km$^2$ and is described as a temperate, colline to sub-montane, forested landscape. The dominating species in the natural forest is beech with a cover of 43%, followed by sessile oak (*Quercus petraea*, 20% cover). Altogether about 70% of the forest is covered by deciduous trees (Müller et al. 2008). The study area can historically be divided into three different levels of silvicultural management intensities. The northern study area belongs to an intensively managed part of the Steigerwald which was logged intensively over a period of about 70 years until recently. Due to this intensive use these sections of the Steigerwald contained little amounts of deadwood until ~ 2005. The southern part of the study area was treated in a more conservation-orientated direction. There was only slight logging until the 1970s, and afterwards the forest management strategy was to maintain ecologically important structures such as deadwood and damaged trees. The third section of the forest comprises strict forest reserves which are left unmanaged for up to 35 years. These forest reserves are fragmented within the managed forest. The structure of tree age, size and deadwood amount of these reserves is comparable to virgin beech forests (Müller 2004; Müller et al. 2008).

For our study, we chose 40 beeches with hollows in 2014. For the second sampling period in 2015, the number of trees was reduced to a subset of 23 trees. The 17 trees not sampled again contained a low number of saproxylic beetles in the first sampling period (average species per tree 3.53 ± 1.66). Tree hollows were chosen if at least 2 cm of detritus was found on the hollow base as a measure of saproxylic arthropod activity. Tree hollows above 2 m height from ground were not sampled due to safety restrictions and sampling method. The trees with hollows were selected spatially randomly over the whole study site. Eighteen trees in 2014 and 11 trees in 2015 were located in the northern section of the study area. Twenty-two trees in 2014 and 16 trees in 2015 were located in the southern section. Three trees in 2014 and one in 2015 were located in a strict forest reserve (Fig. 1).

## Location and tree hollow parameters

For all hollow trees, we used different ecological variables describing the tree and the hollows themselves (see Table S1):

- Diameter at breast height (DBH) at 130 cm from ground.
- *Tree hollow volume* calculated as standardized cylinder with a circular base with the formula $V = \pi * r^2 * h$ (cm$^3$) whereby r is the radius measured at the entrance and h is the total height of the hollow. Height was measured with a measuring tape from the base to the roof of the hollow.
- *Height above ground* hollow distance to the ground (cm) from the lowest point of the hollow entrance.
- *Hollow entrance* tree hollow opening calculated as an ellipse with the formula area $= \pi * a * b$, where a is half of the height and b half of the width of the ellipse.

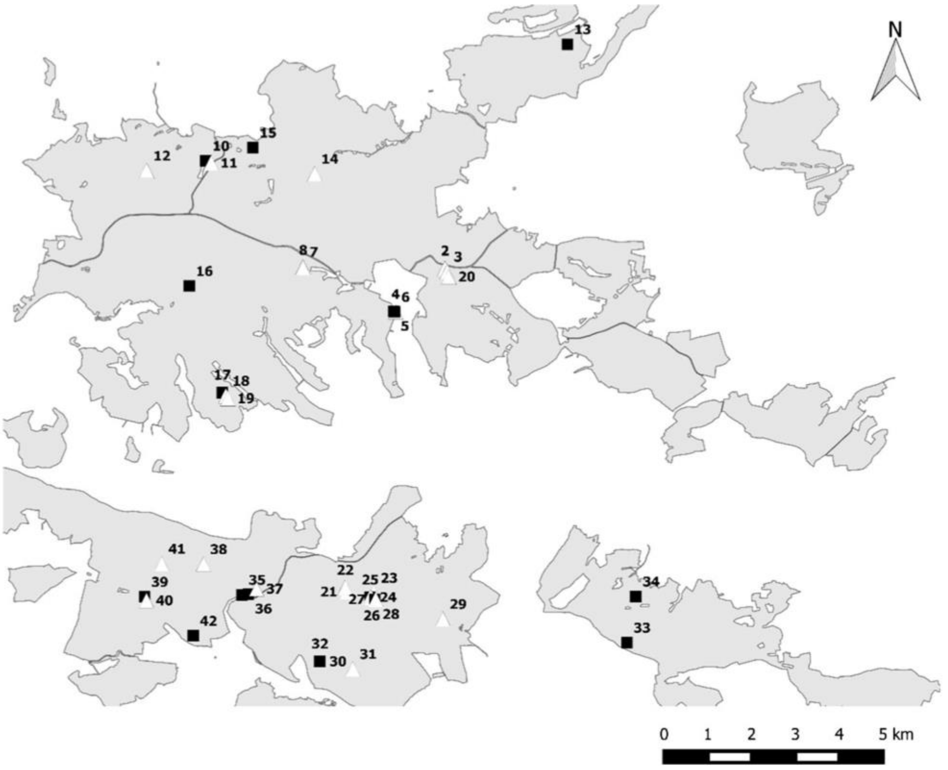

**Fig. 1** Location of all 40 sampled tree hollows in the Forestry Department of Ebrach in the northern Steigerwald. Squares indicate tree hollows only sampled in 2014 (40 hollows), triangles indicate trees sampled in 2014 and 2015 (23 hollows)

- *Lateral surface of the tree hollow* (*area of an object*, *excluding the top and bottom area*) calculated with the formula lateral surface a * b ($cm^2$), where a is the height of the tree hollow and b is the girth of the tree hollow.
- *Proportion lateral surface to hollow entrance* calculated with the formula 100 * a/b, where a is the area of the hollow entrance and b is the lateral surface of the tree hollow.
- *Mean annual solar irradiation* calculated based on surface slope, inclination direction, elevation and coordinates (of tree hollows) using Points Solar Radiation tool as part of the spatial analyst tools for ArcMap 10.3.
- *Degree of decomposition* wood mould was sampled from the base of the hollow. Mould was collected at a depth of 2 cm below the surface of the mould to 7 cm depth. Mould was classified in four stages (1–4 ascending) of decomposition. We used three parameters to determine the stage of decomposition (colour, texture of the detritus and visible woody parts) (Jarzabek 2005).

  *Stage 1* yellow to light brown in colour, visible woody parts of bigger size, low decay.
  *Stage 2* light brown to brown in colour, visible woody parts of smaller size, medium decay.
  *Stage 3* brown to dark brown in colour, almost no visible woody parts, medium to high decay.
  *Stage 4* dark brown to black in colour, no visible woody parts, high decay.

- *Temperature inside the tree hollow* temperature logger measured the temperature inside the tree hollow every hour over the full sampling period.
- *Surrounding tree hollows* the number of all visible tree hollows in a radius of 50 m around each sampled tree hollow.
- *Surrounding structures* all injuries at trees larger than 250 $cm^2$ and woodpecker holes in a radius of 50 m around each sampled tree hollow.

## Sampling method and identification

All selected tree hollows were closed with black acrylic mesh in the period of mid-March to mid-April to prevent the tree hollows from being used as nesting place by vertebrates (Fig. S1). From April to August all tree hollows were closed with black fabric and emergence traps, modified from Gouix and Brustel (2012) (Fig. S1) and were emptied biweekly. The collecting pot contained 99.8% ethanol to preserve trapped emerging insects for further analyses. We chose emergence traps, because it is a very effective method to sample entire saproxylic communities directly after individuals have become mature. Furthermore, the handling and deployment of the traps is easy and the ethanol for trapping does not evaporate at least for 2 weeks. This kind of trap allows efficient sampling and sorting as only species emerging from tree hollows will be trapped compared to window traps where other non-tree hollow related species can also be trapped. However, species not leaving or completing their whole lifecycle inside a tree hollow could not be included with our sampling method. A saproxylic beetle specialist (H. Bußler) identified all saproxylic beetle species associated with tree hollows. Bavarian Red List status (Red List Bavaria, 2005) was used to classify all species and as a proxy for threatened and non-threatened species.

## Data analysis

In order to quantify the effect of microhabitat parameters of tree hollows, for number of species of saproxylic beetles, generalized linear models (GLMs) with Poisson error distribution were implemented. Stepwise model selection based on AIC was used to remove non-relevant variables from the model (R-function step in the stats package). The model was once implemented for the 40 hollows sampled in 2014. It was further repeated for the 23 hollows sampled both in 2014 and 2015 ($2 \times 23 = 46$ observations). In order to quantify potential differences in the relationship between predictor variables and species richness between years, this model tests for interactions between the microhabitat parameters of tree hollows and year of sampling. Analyses were performed for species richness including all species, for non-Red List species as well as for Red List species only. The R-package *visreg* version 2.3 (Breheny and Burchett 2016) was used to visualize results.

Prior to modelling, collinearity among variables was tested using Pearson linear correlation (exclusion criteria $|r| > 0.7$). The variable *lateral surface of the tree hollow* was subsequently excluded from analyses due to correlation with the *tree hollow volume* ($r = 0.95$). All other variables were included. We log-transformed the variables *tree hollow volume*, *lateral hollow surface* and *proportion lateral surface to hollow entrance* after visually inspecting the relationship and residuals of a simple GLM between saproxylic beetles species-richness and each explanatory variable. All models were tested for overdispersion using the dispersion test implemented in R-package *AER* version 1.2-4 (Kleiber and Zeileis 2008).

Spatial and temporal turnover in saproxylic species composition was analysed by comparing similarity in species composition between hollows within 2014 and within 2015 to that of the same respective hollow but between 2014 and 2015. Similarity in species composition was quantified using Sørensen similarity partitioned in its turnover and nestedness component (Baselga 2010, 2012) using the function *beta.pair* in R package *betapart* version 1.3 (Baselga et al. 2013). Significant differences in similarity in species composition between 2014 and 2015 was assessed using Mantel statistics with significance evaluated by permuting rows and columns of the similarity matrix to account for pseudoreplication as implemented in function *mantel* in R-package *vegan* version 2.3-5 (Oksanen et al. 2016). The same approach cannot be used when comparing similarity within years ($n = 253$ non-independent observations per year) to similarity between hollow communities between years ($n = 23$ independent observations). In order to circumvent this problem, the 23 similarity values obtained from the temporal comparison of each hollow between 2014 and 2015 were compared to similarity in species composition between each of the 23 hollows and 1 randomly chosen other hollow sampled in the same year (analyses run separately for 2014 and 2015) using Students *t* test. This approach was repeated 1000 times always randomly choosing alternative other hollows for within year comparisons. The median of the resulting p-values is reported.

Nonmetric multidimensional scaling (NMDS) from R-package *vegan* version 2.4-1 (Oksanen et al. 2016) (two axes, Bray–Curtis distance) was implemented to illustrate similarity in species composition between tree hollows. In order to identify the most important microhabitat parameters of tree hollows for differentiating species composition, these variables were correlated to the resulting ordination axes (function *envfit*). Permutation of variables allowed testing for significance.

A Mantel permutation test as implemented in R-package *vegan* was further used to test for a relationship between similarity in species composition and distance.

## Results

### Saproxylic beetles

We collected 3087 individuals that were all identified to species level (89 species; see Tables S2, S3 for raw data). In 2014, we identified 55 species belonging to 28 families of which 17 species were unique in 2014. In 2015, we identified 72 species in 31 families including 34 species that were unique in 2015. One species was classified as critically endangered, 12 species as endangered, 16 species as vulnerable and 60 species as not endangered (Red List Bavaria, 2005). Thus, 33% of all saproxylic beetles identified were on the Red List.

### Effect of tree hollow characteristics on beetle communities

Across all 40 hollows sampled in 2014 (final model AIC Fig. 2, univariate relationship Fig. S2), total species richness of saproxylic beetles was related to the *degree of*

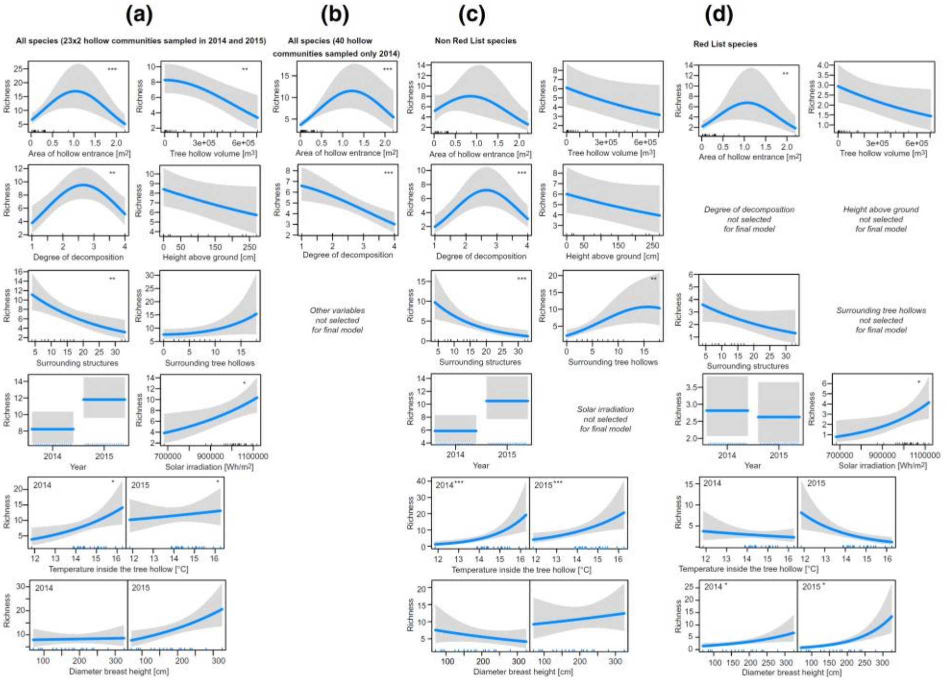

**Fig. 2** Conditional response of explanatory variables explaining species richness for **a** 23 tree hollows sampled both in 2014 and 2015 (23 × 2 = 46 observations), **b** 40 tree hollows sampled in 2014, **c** non-Red List species and **d** Red List species. Modelled individual responses (GLM) are plotted while holding all other variables constant (median for numeric variables, 2014 for year). Confidence band displayed in the plot at an α level (1 − coverage) of 0.05. All models were tested for overdispersion using the dispersion test implemented in R-package AER version 1.2-4 (Kleiber and Zeileis 2008)

*decomposition* (negative relationship, $p < 0.001$) as well as the *area of the hollow entrance* (hump shaped relationship, $p < 0.001$) in the final model after AIC based model evaluation (variables selected in final models and their effects can be inferred from Fig. 2; Table 1).

When analyses were restricted to the 23 hollows sampled in both years ($2 \times 23 = 46$ observations; final model AIC Fig. 2, univariate relationship Fig. S2), species richness was related to *height above ground* (negative relationship, $p < 0.05$), *solar irradiation* (positive relationship, $p < 0.001$), *surrounding tree hollows* (positive relationship, $p < 0.01$), the *degree of decomposition* (hump shaped relationship, $p < 0.001$), *tree hollow volume* (humped shape relation, $p < 0.05$), *area of hollow entrance* (hump shaped being positive if one tree is removed from analyses, $p < 0.01$), *year* (higher number of species in the second year, $p < 0.01$), *temperature inside the tree hollow* (positive relationship, $p < 0.01$) and the interaction between year and temperature, *surrounding structures* (negative relationship, $p < 0.05$) and *DBH* (positive relationship) and the interaction with year (variables selected in final models and their effects can be inferred from Fig. 2; Table 1).

The most remarkable difference between overall richness and the number of Red List species (final model AIC Fig. 2, univariate relationship Fig. S2) was that the latter was negatively related to the temperature inside the hollows ($p < 0.001$). Red List species richness was further related to *solar irradiation* (positive, $p < 0.05$), *DBH* (positive, $p < 0.001$) and *area of hollow entrance* (hump shaped, $p < 0.001$), *tree hollow volume* and the *surrounding structures* in the final model (variables selected in final models and their effects can be inferred from Fig. 2; Table 1).

Richness in non-Red List species largely showed a similar relationship to explanatory variables as the model for overall richness but often with clearer trend. Richness in non-Red List species was related to explanatory variables as follows (final model AIC Fig. 2, univariate relationship Fig. S2): *solar irradiation* (no effect), *height above ground* (negative relationship, $p < 0.05$), *surrounding tree hollows* (positive relationship, $p < 0.001$), *degree of decomposition* (hump shaped relationship, $p < 0.001$), *area of hollow entrance* (hump shaped, $p < 0.01$), *year* (higher richness in second year, $p < 0.01$), *temperature inside the tree hollow* (positive relationship, $p < 0.001$), *surrounding structures* (negative relationship, $p < 0.001$), *DBH* (negative relationship in 2014 and positive in 2015) and *tree hollow volume* (negative relationship) (variables selected in final models and their effects can be inferred from Fig. 2; Table 1). None of the models showed evidence for overdispersion.

## Species turnover

Spatial turnover in species composition between all sites sampled in 2014 had a dissimilarity index of 0.53 ± 0.20 (mean ± SD; $n = 40$) and 0.42 ± 0.21 ($n = 23$) in 2015. In contrast, the nestedness component of species dissimilarity was lower in 2014 (0.15 ± 0.15), when compared to 2015 (0.23 ± 0.19) (Fig. 3). These differences were not significantly different from random variation (Mantel test). A comparison of this spatial change to temporal change within the same hollows from 2014 to 2015 indicated a significantly lower temporal species turnover (0.38 ± 0.18) ($p < 0.05$ for a comparison to 2014, not significant for a comparison to 2015), while the nestedness component of species compositional dissimilarity of the temporal comparison (0.17 ± 0.10) is about equal to that in space (no significant differences).

Similarity in species composition (Bray–Curtis) was significantly declining with spatial distance ($r = 0.09$, Mantel test $p = 0.02$) when analysing all 40 tree hollows from 2014.

**Table 1** Final model structure after stepwise model selection (based on AIC) for 23 tree hollows sampled both in 2014 and 2015 ($23 \times 2 = 46$ observations), 40 tree hollows sampled in 2014, non-Red List species and Red List species

| Dependent | Hollows | Explanatory variables AIC | Est. | Std. Err. | p-values |
|---|---|---|---|---|---|
| All species in tree hollows from 2014 | 40 | Degree of decomposition | −0.05 | 0.02 | *** |
| | | Area hollow entrance | 1.9 | 0.5 | *** |
| All species in 23 hollows sampled 2014 and 2015 | $2 \times 23 = 46$ | Height above ground | $-1.4 \times 10^{-3}$ | $0.8 \times 10^{-3}$ | n.s. |
| | | Solar irradiation | $2.3 \times 10^{-6}$ | $1.0 \times 10^{-6}$ | * |
| | | Time (year 2015) | 3.1 | 2.0 | n.s. |
| | | Surrounding structures | $-4.3 \times 10^{-2}$ | $1.5 \times 10^{-2}$ | ** |
| | | Degree of decomposition | 1.8 | 0.6 | ** |
| | | Diameter at breast height | $3.1 \times 10^{-4}$ | $0.2 \times 10^{-4}$ | n.s. |
| | | Area hollow entrance | 1.9 | 0.5 | *** |
| | | Temperature inside the tree hollow | 0.3 | 0.1 | * |
| | | Tree hollow volume | $-1.8 \times 10^{-12}$ | $0.6 \times 10^{-12}$ | ** |
| | | Time (year 2015): diameter at breast height | $3.6 \times 10^{-3}$ | $1.7 \times 10^{-3}$ | * |
| | | Time (year 2015): temperature inside the tree hollow | 0.2 | 0.1 | n.s. |
| Red List species in 23 hollows sampled 2014 and 2015 | $2 \times 23 = 46$ | Solar irradiation | $3.8 \times 10^{-6}$ | $1.7 \times 10^{-6}$ | * |
| | | Time (year 2015) | 3.8 | 2.7 | n.s. |
| | | Surrounding structures | − 0.03 | 0.02 | n.s. |
| | | Diameter at breast height | $6.1 \times 10^{-3}$ | $2.4 \times 10^{-3}$ | * |
| | | Area hollow entrance | 2.2 | 0.8 | ** |
| | | Temperature inside the tree hollow | − 0.1 | 0.2 | n.s. |
| | | Tree hollow volume | $-1.0 \times 10^{-6}$ | $0.5 \times 10^{-6}$ | n.s. |
| | | Time (year 2015): diameter at breast height | $5.2 \times 10^{-3}$ | $3.0 \times 10^{-3}$ | * |
| | | Time (year 2015): temperature inside the tree hollow | − 0.3 | 0.2 | n.s. |

**Table 1** continued

| Dependent | Hollows | Explanatory variables AIC | Est. | Std. Err. | p-values |
|---|---|---|---|---|---|
| Non-Red List species in 23 hollows sampled 2014 and 2015 | $2 \times 23 = 46$ | Height above ground | $-1.5 \times 10^{-3}$ | $1.0 \times 10^{-3}$ | n.s. |
| | | Diameter at breast height | $-2.3 \times 10^{-3}$ | $2.3 \times 10^{-3}$ | n.s. |
| | | Surrounding tree hollows | 0.2 | 0.1 | ** |
| | | Time (year 2015) | 3.9 | 2.7 | n.s. |
| | | Degree of decomposition | 2.5 | 0.6 | *** |
| | | Tree hollow volume | $-9.3 \times 10^{-7}$ | $4.8 \times 10^{-7}$ | n.s. |
| | | Area hollow entrance | 1.1 | 0.1 | n.s. |
| | | Temperature inside the tree hollow | 0.6 | 0.2 | *** |
| | | Surrounding structures | $-0.07$ | 0.02 | *** |
| | | Time (year 2015): diameter at breast height | $3.5 \times 10^{-3}$ | $2.1 \times 10^{-3}$ | n.s. |
| | | Time (year 2015): temperature inside the tree hollow | $-0.3$ | 0.2 | n.s. |

Models were implemented with a Poisson family error (log-link function). All models were tested for overdispersion using the dispersion test implemented in R-package AER *version 1.2-4* (Kleiber and Zeileis 2008)

*Est*. estimate, *Std. Err* standard error

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, *n.s.* $p > 0.05$

However, this pattern is less strong in the subsample of 23 tree hollows of 2014 ($r = 0.008$, Mantel test $p = 0.4$) and 2015 ($r = 0.12$, Mantel test $p = 0.07$).

A post hoc correlation of environmental variables with the two NMDS ordination axes (Fig. 4) revealed that gradients in similarity in species composition were related to *DBH* ($R^2 = 0.47$, $p < 0.001$), the number of *surrounding tree hollows* ($R^2 = 0.36$, $p < 0.001$), and the *area of the hollow entrance* ($R^2 = 0.15$, $p < 0.05$). One major gradient in species turnover follows an axis representing a *temperature* gradient in the hollows ($R^2 = 0.15$, $p < 0.05$)/*richness* ($R^2 = 0.39$, $p < 0.001$) (Fig. 4). The relatively high NMDS stress value (stress 0.29, Fig. 4) indicated that two NMDS axes miss parts of the variability in species composition between sites. However, while rerunning the NMDS with four axes reduces stress to an acceptable value (stress 0.16), it results in very similar conclusions regarding the relationship between explanatory variables and species composition (Fig. S3). The third and fourths axes would further reveal existing gradients in species composition correlated with solar radiation as well as differences between the two sampled years (Fig. S3). We focus on the main gradients and thus the two-dimensional NMDS in the main text.

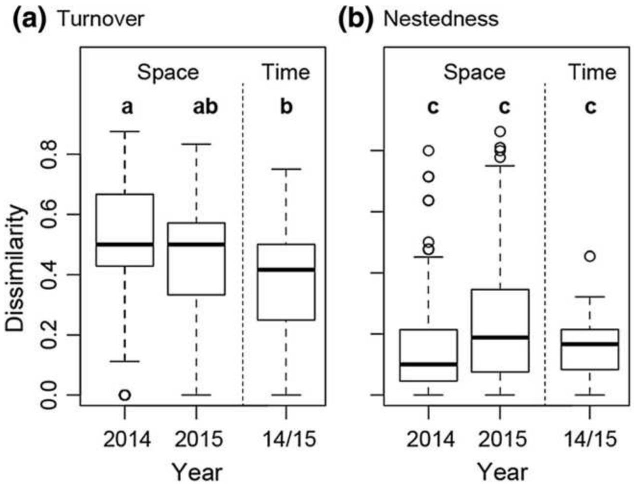

**Fig. 3** **a** Turnover and **b** nestedness component of Sørensen dissimilarity compared among all sites within 2014 (space, n = 253), within 2015 (space, n = 253) and between the same sites but comparing year 2014 and 2015. Bold small letters above the boxes indicate significant differences (see text for details on significance tests)

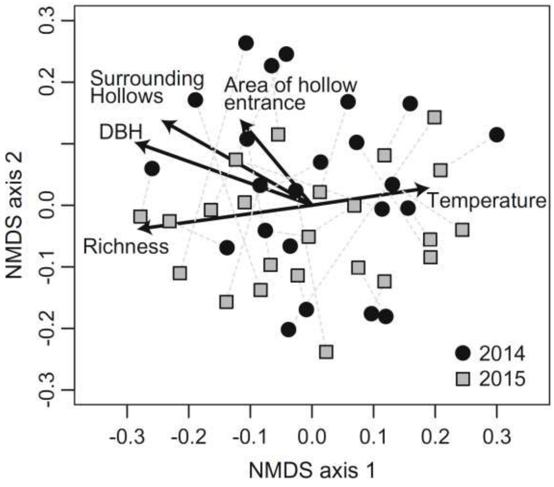

**Fig. 4** Nonmetric multidimensional scaling (NMDS) of similarity in species composition (Bray–Curtis dissimilarity) of all species in the 23 tree hollows sampled in 2014 and 2015. Post hoc correlated environmental variables are indicated by arrows (permutation based $p > 0.05$)

## Discussion

Our results show that the α-diversity of saproxylic beetles in tree hollows is related to different tree hollow characteristics. However, importance of the different tree hollow characteristics varied between years. The degree of decomposition of the wood mould influenced overall α-diversity (Red List and non-Red List species) in both years. At medium stages of decomposition we found the highest number of saproxylic beetles (Fig. 2) which was also shown by Sverdrup-Thygeson et al. (2010). Medium stages of decomposition are thought to be at an optimum in habitat quality, due to increased availability of the important wood mould for most species occurring in tree hollows (Sverdrup-Thygeson et al. 2010). However, the accumulation of wood mould may only benefit a diverse community until a certain stage of decomposition. After that point, wood mould composition may be changing and nutrient availability to a broad community might not be given anymore. At later stages of decay in tree hollows of deciduous trees, the number of species declines (Stokland and Siitonen 2012). Nonetheless, highly decayed tree hollows may support specialised representatives of saproxylic beetle communities and may thus enhance β-diversity. For example, the violet click beetle (*Limoniscus violaceus*), an umbrella species for deadwood species conservation, is a tree hollow specialist preferring advanced stages of decomposed basal tree hollows (Gouix et al. 2015).

We show that medium-sized entrance area is associated with high species numbers in both years. However, when a single tree with a large hollow entry was removed from our analyses, the relationship became positive, indicating that it drove the declining phase of the hump-shaped relationship. One possible explanation for the increasing species richness with increasing hollow entrance may be that many species prefer a less humid microclimate, and an increasing hollow entrance is probably associated with a reduction in humidity inside a tree hollow, leading to drier conditions inside the tree hollow (Ranius 2002a). The preference for a large hollow entrance seems to be species and guild dependent. Ranius (2002a) showed that *Allecula morio* Fabricius (Alleculidae), which was also present in hollows sampled here, prefers larger hollow entries. Quinto et al. (2014) also found a positive effect of large entrances for different guilds, ranging from xylophagous to predatory guilds. Thus, depending on the entrance area, tree hollows can harbour very different species during the decaying process and thus the ageing process (Ranius et al. 2009a, b).

When the subset of 23 tree hollows sampled in both 2014 and 2015 was analysed, α-diversity was related to additional tree hollow parameters, and species numbers were generally higher in 2015 (Fig. 2). We found higher species numbers in tree hollows located close or open to the ground. This agreed with Quinto et al. (2014) who also found higher richness of several saproxylic guilds in tree hollows located close to the ground in Mediterranean sclerophyllous and deciduous oak woodland. There might be a change in wood mould composition, when the hollow is extended towards the ground as the wood mould may contain a higher amount of litter and soil (Taylor and Ranius 2014). Likewise, the presence of generalist predators like carabids and staphylinids is increased in hollows close to the ground (Ranius 2002a). However, Ranius (2002a) showed higher species richness in hollows high above ground in Swedish oaks, which may be due to more optimal microclimatic conditions for the decay of wood. Another reason could be the additional nutrition through the presence of nests in tree hollows, located more frequently in higher hollows (Nilsson 1984; Ranius 2002a).

Tree hollows with a higher solar irradiation contained higher species numbers. Related to higher sun exposure we found higher species numbers in tree hollows with warmer temperatures inside. At our study site, beech, which casts heavy shades, is the dominant tree species. Thus, sun exposure, e.g., due to canopy gaps around the focus tree and openness towards south (Lindhe et al. 2005; Widerberg et al. 2012), can favour the occurrence of species preferring sun exposed habitats (Brunet et al. 2010). Higher species richness in tree hollows facing sunny aspects, and thus with warmer temperatures, has been reported in several other studies (Jonsell et al. 1998; Müller et al. 2015; Ranius 2002b; Ranius and Nilsson 1997).

Another important factor for high species numbers is the number of tree hollows surrounding the focal tree. With an increasing number of tree hollows in the near surroundings (within a 50 m radius) the number of species increased in the focal tree. A higher number of tree hollows in the surroundings potentially leads to greater resource availability and may be a reservoir for populations of potential tree hollow colonizers. Other studies showed that long-term survival of some tree hollow species is difficult without a dense regional network of suitable tree hollows (Ranius and Wilander 2000). The amount of deadwood related structures in general increases species richness of saproxylic beetles (Økland et al. 1996). Surprisingly, the number of surrounding structures in our study is negatively related to species numbers.

We found a positive relationship of tree hollow volume and number of species until a medium sized volume. In tree hollows larger than medium volumes there is a negative relationship. An additional driving factor is the DBH of the hollow tree which was positively related to higher species numbers in our study. In general, larger diameter trees may offer larger hollows, representing larger habitats that can maintain more species in comparison to small trees with smaller habitats. Larger tree hollows may also be associated with a larger amount of wood mould (Sverdrup-Thygeson et al. 2010; Ranius et al. 2009a, b). In addition to hollows with larger volume, large trees may offer a more stable microclimate and thus temporally more stable conditions in tree hollows and wood mould therein, which can positively affect saproxylic species (Ranius and Jansson 2000). Several studies report the association of threatened species with larger tree hollows, such as *Limoniscus violaceus*, and *Osmoderma eremita* (Gouix and Brustel 2012; Ranius and Nilsson 1997).

The relationship of tree hollow characteristics to α-diversity of Red List compared to non-Red List species partly differ. Hollow height above ground, number of surrounding tree hollows and the degree of decomposition of wood mould influence species numbers in non-Red List species but not the majority of Red List species in our study (Fig. 2).

Solar irradiation positively influenced species richness of Red List but not of non-Red List species. In general, sun light exposure is an important factor for Red List but also non-Red List species (Lindhe et al. 2005; Widerberg et al. 2012).

While the number of Red List species decreased with increasing temperature inside the tree hollow, non-Red List species were affected positively. In our study, Red List saproxylic beetle species seem to prefer colder temperatures, which may be caused by the strong natural shading of beech trees. According to the literature, threatened species are often associated with warmer temperatures (Lindhe et al. 2005; Ranius 2002b; Ranius and Nilsson 1997; Widerberg et al. 2012). However, the habitat preference for colder tree hollow temperatures in summer is also reported for the threatened umbrella species *Osmoderma eremita* (Carpaneto et al. 2010). As different temperature preferences were recorded in different climate zones (e.g., in Scandinavia and Italy) it seems that habitat preferences of *Osmoderma eremita* change with the climate, to find an optimal habitat temperature.

The configuration of every tree hollow is considered unique and highly complex, offering different microhabitat characteristics. In accordance with our expectations we found a higher proportion of species turnover than nestedness among all sampled trees (spatial turnover), in both the years investigated (Fig. 3). In contrast, we expected a higher nestedness when comparing communities sampled from the same tree in both years (temporal turnover). However, for the temporal change we again found a higher turnover than nestedness component. This suggests that species replacement also occurs within the same trees between the years. The results underline the complexity of tree hollows as habitat, with a high variability of beetle communities not only spatially but also temporally (Engen et al. 2008).

β-Diversity was related to the DBH of the hollow tree, the number of surrounding tree hollows, the area of hollow entrance and a temperature gradient (Fig. 4). We only found a weak influence of spatial distance on species turnover. This shows that species turnover is not only a matter of time and space, but also dependent on specific tree hollow characteristics and the surrounding forest structure.

Here we could show that different saproxylic beetle communities are supported in tree hollows differing in terms of size, age, exposition and entrance area. The support of formation of new tree hollows should have high priority, as we could show that the degree of decomposition of wood mould within hollows is negatively correlated to species richness. The decay of the wood is a constant process and thus every stage of decay is available only for a limited period of time per tree hollow, consequently leading to a limited availability of a certain stage of decay as habitat for saproxylic beetles. Conservation efforts should focus on preserving existing and potential trees with tree hollows but the formation of new tree hollows should also be supported. Techniques such as pruning branches to mimic naturally occurring fractures and creating injuries at the bark that facilitate the access for decomposing organisms can speed up the formation of tree hollows, promoting a network of tree hollows of different sizes and decay stages (Siitonen 2012a). Thus, ensuring a constant availability of tree hollows in space and time with different characteristics can support a broad set of insect communities with different ecological preferences.

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## Manuscript 2: Dispersal limitation of saproxylic insects in a managed forest? A population genetic approach

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BS, HF, EO conceived the ideas and designed the methodology. BS, JB, CP collected the data. BS, JB, CP analyzed the data. BS, HF and EO interpreted and discussed results. Figures and tables were created by BS. BS led the writing of the manuscript.

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# Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach

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## Abstract

Dispersal is a key trait of species enabling gene flow among populations. For species persistence dispersal may therefore be crucial especially in a patchy or changing environment. Tree hollows are a patchy habitat as their number is locally limited and in addition to that, habitat quality of tree hollows differs. Both factors are important for colonization by saproxylic insects as species may be specialized on a particular age or quality of a tree hollow and may be dispersal-limited. Intensive forest management may further decrease the number of tree hollows and increase distances between them, if trees with hollows are removed. However, not much is known about the dispersal abilities of most saproxylic species, even though such knowledge could improve conservation efforts. To investigate the genetic population structure of saproxylic species, we collected saproxylic organisms with emergence traps from 40 hollows in beech trees in a managed forest in Germany (approximately 14 × 14 km). We focused on three threatened species, one coleopteran and two dipteran (*Anaspis ruficollis*, Scraptiidae; *Criorhina floccosa*, Syrphidae; *Xylomya maculata*, Xylomyidae) emerging from our tree hollows. Microsatellite analysis was used to assess gene flow among tree hollows and population genetic structure. In contrast to other studies reporting limited dispersal in saproxylic insects, we found no indication for restricted gene flow in all three species investigated. However, we studied relatively abundant species and our study site may not have been large enough to detect genetic substructure. This study indicates that the amount and quality of a suitable habitat may at least in some cases be more limiting than the physical ability to disperse.

***Keywords:*** Conservation; Tree hollow; Beech; Coleoptera; Diptera

## Introduction

Dispersal is a key trait of species confronted with a changing environment in terms of habitat loss and fragmentation (Thomas, 2000). It is required to maintain gene flow between habitat patches, allows the colonization of new habitats, and thus affects population dynamics, extinction risk of populations, and species distributions (Hanski, Kuussaari, &

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Nieminen, 1994; Bowler & Benton, 2005). However, habitat fragmentation can cause the isolation of subpopulations due to dispersal limitation, which may lead to an accelerated loss of genetic variability, due to random genetic drift and a higher risk of inbreeding (Keller & Largiader, 2003; Hedrick, 2011, Chap. 4).

Fragmentation of forest habitats often leads to forest patches embedded in a landscape matrix consisting of non-forested areas potentially resulting in dispersal limitation for species (Shepherd & Brantley, 2005). Fragmentation can also take place within forests due to large distances between suitable microsites such as dead wood or tree hollows (Schiegg, 2000). Speight (1989) coined the term "saproxylic" for species dependent on dead wood as a resource in at least one stage of their life cycle, either directly or indirectly (via consumption of wood-decomposing fungi or other saproxylic species). Saproxylic species may be specialized and colonize dead wood only in a certain stage of decay, dimension, exposition, or of a certain tree species (Grove, 2002; Jonsell, Hansson, & Wedmo, 2007; Quinto, Micó, Martìnez-Falcón, Galante, & de los Angeles Marcos-Garcìa, 2014; Gouix, Sebek, Valladares, Brustel, & Brin, 2015). Such specialization may result in a more patchy distribution of habitats as the amount and number of suitable habitat patches becomes more limited. Additionally, due to intensive forest management, the amount of dead wood underwent a strong reduction in forest ecosystems, leading to smaller, fragmented and more isolated habitat patches (Siitonen, 2001; Lindenmayer, Laurance, & Franklin, 2012). Many saproxylic species are therefore assumed to be threatened due to habitat loss and fragmentation (Speight, 1989; Siitonen, 2001; Nieto & Alexander, 2010). In Germany approximately 34% of all forest arthropod species are dependent on dead wood with Diptera and Coleoptera being the most diverse groups of saproxylic insects (Grove, 2002; Müller, Bußler, & Kneib, 2008). Saproxylic beetles are important for nutrient cycling and ecosystem functioning by promoting suitable conditions for other saproxylic organisms (Grove, 2002; Buse, Ranius, & Assmann, 2008; Gouix et al., 2015).

One habitat for saproxylic species are tree hollows, that offer resources and shelter for many different vertebrate and invertebrate species and are the exclusive habitat for some saproxylic specialists. Therefore, they are regarded as keystone structures important for the maintenance of forest biodiversity (Lindenmayer, Cunningham, Tanton, Smith, & Nix, 1991; Müller, Jarzabek-Müller, Bussler, & Gossner, 2014). Tree hollows may persist for many decades (Ranius, Svensson, Berg, Niklasson, & Larsson, 2009), potentially providing a suitable habitat for many generations of saproxylic species (Siitonen, 2012). Species associated with discrete and long lasting habitats such as tree hollows are considered to have limited dispersal ability and low dispersal propensity and the colonization of habitats far from the natal habitat can be difficult for them (Southwood, 1962; Denno et al., 1996; Nilsson & Baranowski, 1997; Travis & Dytham, 1999). On the other hand, the limited number of individuals per species within a tree hollow may select for a high dispersal propensity of at least one sex to avoid inbreeding (Waldbauer & Sternburg, 1979; Perrin & Mazalov, 2000). The naturally patchy distribution of tree hollows may also favor longer dispersal distances as hollows meeting the species-specific requirements need to be searched for.

Dispersal abilities and as a result, population genetic structure of most saproxylic insect species are largely unknown. Nonetheless, knowledge about the dispersal of saproxylic insects is needed to improve conservation strategies and forest management especially in terms of spatial distribution of suitable habitats to enhance species persistence (Brown & Kodric-Brown, 1977; Trakhtenbrot, Nathan, Perry, & Richardson, 2005). Here we investigated the population genetic structure of three saproxylic insect species inhabiting tree hollows to infer their dispersal capacity in a managed beech forest in Southern Germany.

## Materials and methods

### Study site and sampling method

This study was conducted in 2014 and 2015 at the forest management district Ebrach in the northern Steigerwald (N 49°50′; E 10°29′) (see Appendix A.1 for detailed information). For our study we chose 40 beeches with hollows in 2014. For the second sampling period in 2015 the number of trees sampled was reduced to a subset of 23 trees, excluding 17 trees that contained fewer than three individuals of saproxylic organisms in the first sampling period. Tree hollows were only sampled when they contained at least 2 cm of detritus on the hollow ground as a measure of saproxylic arthropod activity. Only tree hollows up to 2 m height from the ground were sampled. The trees with hollows were selected randomly over the whole study area (approximately 14 × 14 km). 18 trees in 2014 (11 in 2015) were in the more intensively managed northern region of the study area. 22 trees in 2014 (12 in 2015) were in the less intensively managed southern region. The regions are separated by an agricultural band. Three trees in 2014 (one in 2015) were situated in a strict forest reserve. Tree hollows were closed with black acrylic mesh from mid-March to mid-April to prevent vertebrates from nesting. In April tree hollows were closed with black fabric and emergence traps were attached to all hollows. The collecting pot contained 99.8% ethanol to preserve emerging insects for genetic analyses.

### Study organisms and distribution

From the 89 species of saproxylic insects sampled from the tree hollows in total (Schauer et al., 2017) we chose three species for the present study based on their relatively high abundance to allow population genetic analyses. Except for bark beetles all other species were less abundant.

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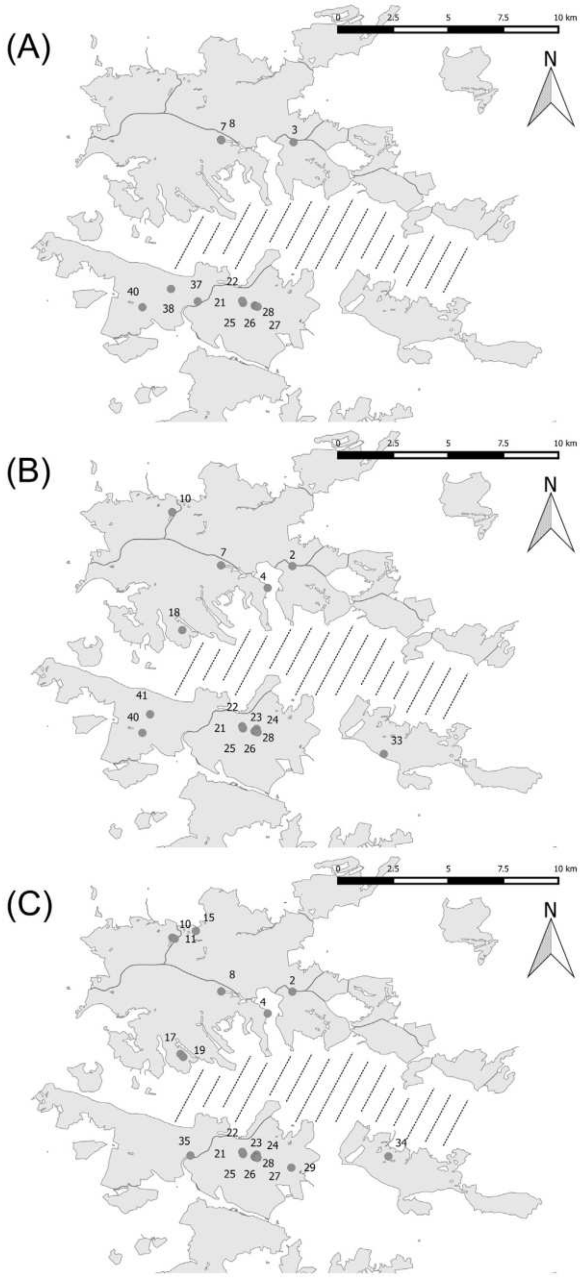

**Fig. 1.** Map of the forest department Ebrach (Northern Steigerwald, Germany) with sampling sites of (A) *Anaspis ruficollis*, (B) *Criorhina floccosa* and (C) *Xylomya maculata* emerging from tree hollows in beech trees. White areas are mostly non-forested areas, dashed lines indicate agricultural area with several roads in between.

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*Anaspis ruficollis* (Scraptiidae; false flower beetles) can be found in Northern and Central Europe. Species of this family are known to occur in grasslands and forests. Adults mostly feed on pollen, whereas larvae are dead wood decomposers (Speight, 1989; Perkovsky & Odnosum, 2009). According to the Red List of Bavaria (Rote Liste Bayern, 2005), *Anaspis ruficollis* is classified as endangered (category 2). In 2014 we collected 77 individuals emerging from 13 (range of individuals per tree hollow: 1 – 23, see Appendix A: Table A1 for detailed information) tree hollows distributed over the whole study area (Fig. 1A). Only a single individual emerged in 2015 but was not included in this study.

*Criorhina floccosa* (Syrphidae; hover flies) has a Palearctic distribution from the Pyrenees to the Caucasus region (Speight 2012). Habitat preferences include deciduous forests, containing mostly *Fagus* and *Quercus* species, with over-mature to senescent trees. Adults of this species can be found visiting various flowers for pollen consumption or around different dead wood structures. Larvae complete their lifecycle in dead wood (Speight 2012). *Criorhina floccosa* is classified as vulnerable (category 3) according to the Red List of Bavaria (Rote Liste Bayern, 2005). We collected 99 individuals (2014: 27 individuals; 2015: 72 individuals, range of individuals per tree hollow: 1 – 36, see Table A1 for detailed information) emerging from 15 tree hollows distributed over the whole study area (Fig. 1B).

*Xylomya maculata* (Xylomyidae; wood soldier flies) is widely distributed in Europe (France, UK, and Italy to the Baltic region and Romania) (Üstüner & Hasbenli, 2011). However, due to its rare occurrence the distributional range is not exactly known. *X. maculata* has been observed in mature forests with high amounts of dead wood (Stubbs & Drake, 2001). Larvae complete their development in dead wood, specifically in tree hollows (Schmidl, 2001; Merkel-Wallner, 2006). Currently, *Xylomya maculata* is not listed in the Red List, but this may be due to data deficiency. According to Schmidl (2001) an endangerment of this species has to be assumed. We collected 159 individuals (2014: 48 individuals; 2015: 111 individuals, range of individuals per tree hollow: 1 – 45, see Appendix A: Table A1 for detailed information) emerging from 19 tree hollows distributed over the whole study area (Fig. 1C).

## Molecular methods

DNA was extracted from three individuals each per species (for getting sufficient amounts of DNA to develop microsatellite enriched libraries) using Puregene DNA Purification Kit (Qiagen) according to the manufacturer's recommendations. Ecogenics (Balgach, Switzerland; http://www.ecogenics.ch) was contracted to develop microsatellite enriched libraries, conduct 454-pyrosequencing and filter for sequences containing microsatellites. 349 sequences in *A. ruficollis*, 113 sequences in *C. floccosa* and 333 sequences in *X. maculata* contained microsatellites. Primer sequences were suggested by Ecogenics. For *A. ruficollis* we optimized 19 polymorphic loci (Table 1), 13 for *C. floccosa* (Table 2), and nine for *X. maculata* respectively (Table 3). A detailed description of PCR conditions is provided in the electronic supplement (see Appendix A.2).

## Data analysis

Hardy-Weinberg Equilibrium (HWE) over all loci, number of alleles (A), expected ($H_E$) and observed ($H_O$) heterozygosity, inbreeding coefficient ($F_{IS}$) for each locus, and linkage disequilibrium between loci (LD) were calculated for each species using GENEPOP v4.0.7 (Raymond & Rousset, 1995). Significance levels for LD were adjusted using Bonferroni correction for multiple testing. We tested the genotype data of all three species for scoring errors, stuttering and the presence of null-alleles using Microchecker (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). We calculated pairwise $F_{ST}$ values (regarding individuals emerging from the same tree hollow as a population) using the R package diveRsity (Keenan, McGinnity, Cross, Crozier, & Prodoehl, 2013). Population differentiation indicated by deviation from zero was investigated by calculating 95% confidence intervals using 999 bootstrap replicates (*A. ruficollis* 9 out of 13 populations, *C. floccosa* 8 of 15 populations and *X. maculata* 10 out of 19 tree hollows). Tree hollows with fewer than three individuals (*A. ruficollis* 4 tree hollows, in total 5 individuals; *C. floccosa* 7 tree hollows, in total 10 individuals and *X. maculata* 9 tree hollows, in total 12 individuals) were removed from the analyses, as this low sample size leads to unprecise confidence intervals in terms of the interval range. To account for small sample size effects, we additionally applied an analysis of spatial genetic structure based on pairwise individual kinship analysis with the program SPAGeDI *v1.5a* (Hardy & Vekemans 2002) (see Appendix A.3 for detailed method and results).

AMOVA was used to estimate genetic variability within and among populations on the level of tree hollows (regarding individuals emerging from the same tree hollow as a population) and additionally between the northern and southern population (individuals from different tree hollows per region combined) as the agricultural area between the regions may hinder gene flow. AMOVA was conducted using the R package "poppr" v2.4.1 (Kamvar, Brooks, & Grünwald, 2015) with 999 pairwise permutations.

The program STRUCTURE v2.3.4 (Pritchard, Stephens, & Donnelly, 2000) was used to estimate the number of subpopulations ($K$). We chose a two-step approach, investigating the data either with prior population information (tree hollow) or without, to see the influence of population information on the number of calculated clusters. We carried out five independent runs each with the maximum number of possible populations being the total number of tree hollows a species was sampled from (*A. ruficollis* $K = 1 - 13$, *C. floccosa* $K = 1 - 15$, *X. maculata* $K = 1 - 19$). We used the admixture

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**Table 1.** Microsatellite loci and genetic diversity of *Anaspis ruficollis*. $H_E$, expected heterozygosity; $H_O$, observed heterozygosity; $P_{HWE}$, *p*-value calculated against Hardy-Weinberg Equilibrium (HWE), $F_{IS}$, inbreeding coefficient. Bold Loci were not used due to potential presence of null alleles.

| Locus | Number of amplified individiuals | Repeat motif | Forward primer sequence | Reverse primer sequence | Amplicon size [bp] | Number of alleles | $H_E$ | $H_O$ | $P_{HWE}$ | $F_{IS}$ | GeneBank accession number |
|---|---|---|---|---|---|---|---|---|---|---|---|
| AR37067 | 77 | (TG) | AACACCATGTCGAACTTGCC | ATACTAGTGTGCCTTGACGC | 105–129 | 6 | 0.34 | 0.32 | >0.05 | 0.0400 | MG017985 |
| AR38393 | 76 | (GT) | GTTTTACTAGCTTCACCCGGC | GGCGATCAAGAACCCAAATTAC | 194–236 | 19 | 0.91 | 0.86 | >0.05 | 0.0386 | MG017986 |
| AR45363 | 77 | (TG) | GTTCTTCCGATGCCACACAG | ATTTCATAGCTGAACCGCCC | 219–249 | 15 | 0.90 | 0.83 | <0.05 | 0.0621 | MG017987 |
| AR45589 | 77 | (GT) | ACAATTGGACCAGCCGTTTC | CGGACAAACCTTACAGGTCG | 181–241 | 25 | 0.93 | 0.78 | <0.01 | 0.1467 | MG017988 |
| AR60963 | 77 | (CA) | TATTGGCCATTGAGCTTCGG | AGACGGGTTCATAATCGGAGG | 201–257 | 19 | 0.94 | 0.77 | <0.01 | 0.1519 | MG017989 |
| AR61801 | 77 | (GA) | CCCAGGAAACCTCGCTTTTG | CGCCTTATTTTCGTCCAGGG | 228–258 | 12 | 0.79 | 0.71 | <0.05 | 0.1013 | MG017990 |
| AR62683 | 77 | (AG) | GATGCATGTTGCGGTCCTTC | TACAGCTTCAATTGGCTGCG | 194–248 | 26 | 0.93 | 0.77 | <0.01 | 0.1381 | MG017991 |
| AR11307 | 73 | (ATAG) | TGCGGTCGTCAAGAAGAAAC | ACCTATGTACCGAACAAATAAAAGC | 120–158 | 8 | 0.58 | 0.58 | >0.05 | −0.0554 | MG017992 |
| AR11849 | 73 | (AC) | CGTCGTTCTGGGAATCAACTC | GGTAGCCTCTTTCACTTGGC | 199–219 | 11 | 0.79 | 0.69 | <0.01 | 0.1211 | MG017993 |
| AR12185 | 73 | (AC) | TGAATGACGTGCCAAATTACG | AACGGCGCAAGAAAGGTATG | 200–218 | 10 | 0.67 | 0.60 | <0.01 | 0.0986 | MG017994 |
| AR43217 | 73 | (CA) | AGCCGTCAGGGTTTGGAC | ACCGATGCATTTTATTTACTGCC | 162–250 | 29 | 0.90 | 0.86 | >0.05 | 0.0291 | MG017995 |
| AR63159 | 73 | (GA) | GGTAGGACTCGTTAGGACGC | AAGAACTGCGTCTTTCCTGC | 206–254 | 18 | 0.77 | 0.69 | >0.05 | 0.0897 | MG017996 |
| **AR27749** | – | (TC) | AGTCGGTACAAAGTGGATGC | GTCGCCTTTGAATAACCCCTC | – | – | – | – | – | – | MG017997 |
| **AR28735** | – | (GA) | CATGGCCTCTATCGTTGCAG | AGGTTAAAGTTTCCACCCTGTATG | – | – | – | – | – | – | MG017998 |
| **AR40867** | – | (GA) | GTCGCTTTTAAGGCTGGGAG | AACAAGCCTAATTCGCCTGC | – | – | – | – | – | – | MG017999 |
| **AR55853** | – | (CT) | ACAACGCAATTCCGAAGCTC | GCCTACTTCAATTGCCGACC | – | – | – | – | – | – | MG018000 |
| **AR60217** | – | (TC) | TGTACACCAGATTTCCAATGCG | AGTCAGATCTCAAGCACGAAC | – | – | – | – | – | – | MG018001 |
| **AR54779** | – | (GT) | TGCATTTTTCCGACTCGCTG | CCTCGCAACGACGATATTCC | – | – | – | – | – | – | MG018002 |
| **AR51739** | – | (TG) | AAACCGGACAAATCTGGCTC | GCTAGCTTTGAGATCGCACC | – | – | – | – | – | – | MG018003 |

**Table 2.** Microsatellite loci and genetic diversity of *Criorhina floccosa*. $H_E$, expected heterozygosity; $H_O$, observed heterozygosity; $P_{HWE}$, *p*-value calculated against Hardy-Weinberg Equilibrium (HWE), $F_{IS}$, inbreeding coefficient.

| Locus | Number of amplified individiuals | Repeat motif | Forward primer sequence | Reverse primer sequence | Length [bp] | Number of alleles | $H_E$ | $H_O$ | $P_{HWE}$ | $F_{IS}$ | GenBank accession number |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CF10577s | 99 | (AC) | TACATCCTTGATCCCGGCAC | AGTTGGAGCTGGAGCCATAG | 118–126 | 3 | 0.50 | 0.46 | >0.05 | 0.0720 | MG018004 |
| CF11061s | 99 | (GT) | TATTCCTGGGTGTGTGCCAG | ACAGCAGTATCTACGTCCCG | 167–199 | 5 | 0.14 | 0.15 | >0.05 | −0.0385 | MG018005 |
| CF206s | 99 | (CA) | TCCAGCAATAAAAACGGAGCC | TTGCGTGTTCTACAAAGGCG | 204–218 | 7 | 0.66 | 0.66 | >0.05 | 0.0110 | MG018006 |
| CF2525s | 99 | (CA) | TTCGAAACACGGGTAACTGG | ATGGAACTTACTACATCGTTGC | 115–121 | 3 | 0.67 | 0.50 | <0.01 | 0.2648 | MG018007 |
| CF4012 | 99 | (AC) | TTGCTCGATGGTTTTGGGAC | CTCCTTCCGTGGCAGTAGC | 150–156 | 4 | 0.51 | 0.52 | >0.05 | −0.0479 | MG018008 |
| CF5218s | 99 | (TG) | ATAGACACCTGCCTGCTCTG | TTTGTCGCAGCACATTAGCG | 235–249 | 8 | 0.71 | 0.61 | >0.05 | 0.1447 | MG018009 |
| CF7390s | 96 | (AC) | GGCTTGCAATCTTTACGGGG | TGATTATTCAATTGTACTTGCGCTC | 213–239 | 12 | 0.83 | 0.74 | <0.05 | 0.1095 | MG018010 |
| CF7421s | 98 | (TG) | TAGCTCAAAGGAAACCGTGC | CTCTGACATTGTTGGGTCGC | 226–246 | 10 | 0.81 | 0.79 | <0.01 | 0.0324 | MG018011 |
| CF7555s | 99 | (GA) | AAACCTGACATTCCGCACAC | ATATGTGACTGCCAGGACGG | 118–130 | 7 | 0.46 | 0.40 | <0.01 | 0.1376 | MG018012 |
| CF7578s | 98 | (AG) | ACCTGCACGATTGTTCTGTG | CGCCGCTCGTCTAATCACC | 139–157 | 8 | 0.78 | 0.72 | <0.01 | 0.0684 | MG018013 |
| CF840s | 99 | (AC) | CATCGTCACATGCCCGTAAG | CGATCATGTTCCTCAACGAAAAG | 203–219 | 5 | 0.51 | 0.48 | >0.05 | 0.0633 | MG018014 |
| CF9072s | 98 | (CA) | TGCATAAGTGGAGCTAATTCACC | GAATTTGGCACGAGCTCACC | 146–160 | 8 | 0.54 | 0.47 | >0.05 | 0.1409 | MG018015 |
| CF9832s | 96 | (AC) | ATAATGTCTGGGCTACCCGC | TACGCTCTCCTTGAGTGTGC | 192–224 | 10 | 0.64 | 0.68 | >0.05 | −0.0918 | MG018016 |

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**Table 3.** Microsatellite loci and genetic diversity of *Xylomya maculata*. $H_E$, expected heterozygosity; $H_O$, observed heterozygosity; $P_{HWE}$, *p*-value calculated against Hardy-Weinberg Equilibrium (HWE), $F_{IS}$, inbreeding coefficient.

| Locus | Number of amplified individiuals | Repeat motif | Forward primer sequence | Reverse primer sequence | Length [bp] | Number of alleles | $H_E$ | $H_O$ | $P_{HWE}$ | $F_{IS}$ | GenBank accession number |
|---|---|---|---|---|---|---|---|---|---|---|---|
| XM4929 | 159 | (TC) | CACCACGATTTCATGGCAAC | CCAAGACGGAAAAGTCTGGC | 174–218 | 20 | 0.88 | 0.79 | <0.01 | 0.0860 | MG018017 |
| XM4935 | 159 | (AG) | TCCCAATTTTGTAAAGTTATGATCTTC | GTTAGCAGCAGGTGGACAAG | 152–174 | 10 | 0.75 | 0.71 | <0.05 | 0.0494 | MG018018 |
| XM5083 | 159 | (TC) | GTTAGCAGCAGGTGGACAAG | TCCCAATTTTGTAAAGTTATGATCTTC | 153–175 | 7 | 0.80 | 0.67 | <0.01 | 0.1481 | MG018019 |
| XM5097 | 159 | (CA) | GTTGAACAGCAACCTCTCGG | ACGAAAGACCAAAACTACGGC | 128–146 | 8 | 0.51 | 0.53 | >0.05 | −0.0653 | MG018020 |
| XM5165 | 159 | (AG) | GGGAATCAAGCGATCCCTAATC | CAATAGGTCTTCTAGCACGGAC | 152–168 | 6 | 0.41 | 0.26 | <0.01 | 0.3280 | MG018021 |
| XM5185 | 158 | (AG) | TGGAAAGGATTTGTCGACGC | CTGGTGTGATAAGGGCAACG | 133–175 | 9 | 0.56 | 0.45 | <0.01 | 0.1781 | MG018022 |
| XM5233 | 159 | (AG) | AACGGGGAAAATGTTGCGAG | CGAGAGATCACCTCGCTTATG | 167–241 | 10 | 0.41 | 0.19 | <0.01 | 0.5428 | MG018023 |
| XM5241 | 159 | (AG) | TTGTCGATGCCCTATGCTCC | AGCTGACATTCTCCTCCCAC | 112–136 | 7 | 0.55 | 0.56 | >0.05 | 0.0038 | MG018024 |
| XM83929 | 158 | (GT) | CCCGTGTAAAAACAGAATTGCG | TAACGCCAGAGCGAGAATGG | 129–151 | 9 | 0.45 | 0.46 | >0.05 | −0.0449 | MG018025 |

model with $10^6$ Markov chain Monte Carlo (MCMC) iterations, discarding the first $10^5$ iterations as burnin. To estimate the true number of clusters, STRUCTURE HARVESTER v0.6.94 was used (Earl & von Holdt, 2012), that compares log likelihood estimates of independent runs and different numbers of assumed clusters. CLUMPAK (Kopelman, Mayzel, Jakobsson, Rosenberg, & Mayrose, 2015) was used to form a convergence between iterations of all independent runs of each value of *K*. We validated the results by using the Discriminant Analysis on Principal components (DAPC). In contrast to STRUCTURE, this method is not based on assumptions of HWE equilibrium and defined genetic models (Jombart, Devillard, & Balloux, 2010). DAPC was conducted using the R package "adegenet" v.2.0.0 (Jombart & Ahmed, 2011). Prior to DAPC, cross-validation and $\alpha$-score function was used to identify the optimal number of principal components. Individuals sampled from the same tree hollow were assigned to the same genetic cluster. The DAPC then maximizes differences among genetic clusters.

## Results

### Genetic diversity

In *Anaspis ruficollis* seven of 19 loci were excluded due to the potential presence of null alleles (number of successfully amplified individuals per locus see Table 1). The number of alleles per locus ranged from six (AR37067) to 29 (AR43217). The expected heterozygosity ($H_E$) ranged from 0.34 to 0.94 and observed heterozygosity ($H_O$) ranged from 0.32 to 0.86. Seven of twelve loci showed significant departure from HWE ($p < 0.05$) (Table 1). Significant LD ($p < 0.05$) was not found in any of the pairwise tests.

In *Criorhina floccosa* four of 13 loci showed evidence for null alleles. However, as there was no obvious failure in amplifying individuals at those loci and results did not differ by excluding those we used all loci for analysis (Table 2). The number of alleles per locus ranged from three (CF10577s, CF2525s) to 12 (CF7390). $H_E$ ranged from 0.14 to 0.83 and $H_O$ ranged from 0.15 to 0.79. Five of 13 loci showed significant departure from HWE ($p < 0.05$) (Table 2). Significant LD ($p < 0.05$) was found in only one pairwise test (CF4012 and CF7578s).

In *Xylomya maculata* five of nine loci showed evidence for null alleles, but similar to *C. floccosa* all loci were used for further analysis. The number of alleles ranged from six (XM5165) to 20 (XM4929). $H_E$ ranged from 0.41 to 0.88 and $H_O$ ranged from 0.19 to 0.79. Six of nine loci showed significant departure from HWE ($p < 0.05$) (Table 3). Significant LD ($p < 0.05$) was found in only one pairwise test (XM4935 and XM5083). As for *C. floccosa* no systematic linkage of loci pairs was found. Thus, we assumed no linkage between the loci and used all primer for further analysis.

The inbreeding coefficient $F_{IS}$ of, (a) *A. ruficollis* per locus (Table 1) ranged from − 0.0554 (AR11307) to 0.1519

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(AR60963) (over all loci 0.1046) and per population from – 0.0667 (tree hollow 28) to 0.2532 (tree hollow 41) (see Appendix A: Table A.1), (b) *C. floccosa* per locus (Table 2) ranged from – 0.0918 (CF9832s) to 0.2648 (CF2525s) (over all loci 0.0767) and per population from – 0.1494 (tree hollow 24) to 0.1720 (tree hollow 40) (see Appendix A: Table A.1) and (c) *X. maculata* per locus (Table 3) from – 0.0653 (XM5097) to 0.5428 (XM5233) (over all loci 0.1332) and per population from – 0.2 (tree hollow 29) to 0.2527 (tree hollow 26) (see Appendix A: Table A.1). Relatively high inbreeding coefficients may derive from individuals being related within a respective tree hollow and potentially cause deviations from HWE observed in all three species (Wigginton, Cutler, & Abecasis, 2005).

### Genetic structure analysis

The pairwise $F_{\mathrm{ST}}$ of, (a) *A. ruficollis* ranged from −0.0145 to 0.0401 (mean ± SE, 0.0159 ± 0.0019) (see Appendix A: Table A.2), (b) *C. floccosa* ranged from −0.0338 to 0.0327 (mean ± SE, 0.0017 ± 0.0028) (see Appendix A: Table A.2), (c) *X. maculata* ranged from −0.0076 to 0.0217 (mean ± SE, 0.0088 ± 0.0011) (see Appendix A: Table A.2). FST – values deviating significantly from zero were only found in *A. ruficollis* (tree hollow 7 and tree hollow 21 FST = 0.0151, tree hollow 7 and tree hollow 25 FST = 0.0196).

For all three species the AMOVA revealed that – above the level of genetic variation within an individual – genetic variation was highest among individuals sampled from the same tree hollow with 8.03% in *A. ruficollis* ($p < 0.01$), 7.33% in *C. floccosa* ($p < 0.01$) and 12.14% in *X. maculata* ($p < 0.01$) of total genetic variance being explained at this level. In contrast, only a minor portion of total genetic variance was explained by differences among tree hollows with 1.93% in *A. ruficollis* ($p < 0.01$), 0.17% in *C. floccosa* ($p > 0.05$) and 1.39% in *X. maculata* ($p < 0.01$) or between the northern and southern study area with 1.09% in *A. ruficollis* ($p > 0.05$), 0% in *C. floccosa* ($p > 0.05$) and 0.09% in *X. maculata* ($p > 0.05$) (see Appendix A: Table A.3).

The STRUCTURE analysis revealed that a single population ($K = 1$) had the highest likelihood (Ln P(D)) and smallest standard deviation for all three study species, irrespective of whether a priori information on the origin of individuals was used or not. The estimated likelihood curve for $K = 1$ to the maximum number of populations tested never plateaued (see Appendix A: Fig. A2) and visual inspection showed no meaningful patterns when $K > 1$, indicating no population differentiation in any of the three species.

Results obtained by the AMOVA (largest part of genetic variance was explained by differences between individuals sampled from the same tree hollow, but only little genetic variance among tree hollows) and STRUCTURE ($K = 1$) were largely corroborated by the DAPC for all three species. The DAPC scatterplot (Fig. 2) of *A. ruficollis* showed an overlap of almost all genetic clusters (i.e. populations sampled from different tree hollows) in the ordination space. The cluster of populations 7, 8 and 40 was more distant from and only weakly overlapping with the other clusters, which can be regarded as weak sub-structuring. Here, geographic distance seems not to be the driving factor, as those three clusters grouped together but were collected from distant sampling sites (populations 7 and 8 are in the north of the study area, whereas population 40 is in the south) (Fig. 2). The DAPC scatterplots of *C. floccosa* and *X. maculata* showed a strong overlap of all genetic clusters, indicating only weak genetic differentiation (Figs. 3 and 4).

## Discussion

Theory suggests limited dispersal of species inhabiting long lasting habitats in contrast to species living in ephemeral habitats (Southwood, 1962; Shaffer, 1981; Roff, 1994; Denno et al., 1996). Thus, species associated with long lasting tree hollows are assumed to be rather limited in their dispersal ability (Kirby & Drake, 1993; Nilsson & Baranowski, 1997). However, microhabitat features inside a tree hollow are changing over time (Ranius et al., 2009; Siitonen, 2012) and population sizes are usually small within a tree hollow (in this study the most common species, i.e. *Anaspis ruficollis, Criorhina floccosa* and *Xylomya maculata* had a maximum of 23, 31 and 41 individuals, respectively, from a single tree hollow). Thus, in order to avoid inbreeding with close relatives individuals of at least one sex may be selected to disperse (Perrin & Mazalov, 2000).

In our study we could not identify limited gene flow due to restricted dispersal in three saproxylic species with any of the methods of data analysis applied. Pairwise $F_{\mathrm{ST}}$-values for all species only showed twice a small deviation from zero in *A. ruficollis*, and STRUCTURE as well as DAPC analysis indicated no genetic sub-structuring. DAPC also revealed that individuals collected from the same tree hollow are genetically very similar as the clusters they formed only span a small part of the sample space. Additionally the individual-based kinship analyses using SPAGeDi showed that only within each tree hollow the kinship coefficient was significantly more positive than expected in all three species. In all other distance classes genotypes showed random spatial distribution as individuals were related no more or less than by chance.

The assumption of high genetic similarity is also supported by the relatively high $F_{\mathrm{IS}}$ values found for some populations at the tree hollow-level. Modest levels of inbreeding within tree hollows may also explain the deviation from HWE found for a number of loci as the presence of related individuals (such as siblings) in a sample may result in allele frequency biases. In addition, the AMOVA showed that the largest percentage of genetic variation is explained by differences between tree hollows (7–12%) while the separation between the northern and southern study area by a belt of agricultural land explained less than 2% in all three species. Overall, we conclude that *Anaspis ruficollis*, *Criorhina floc-*

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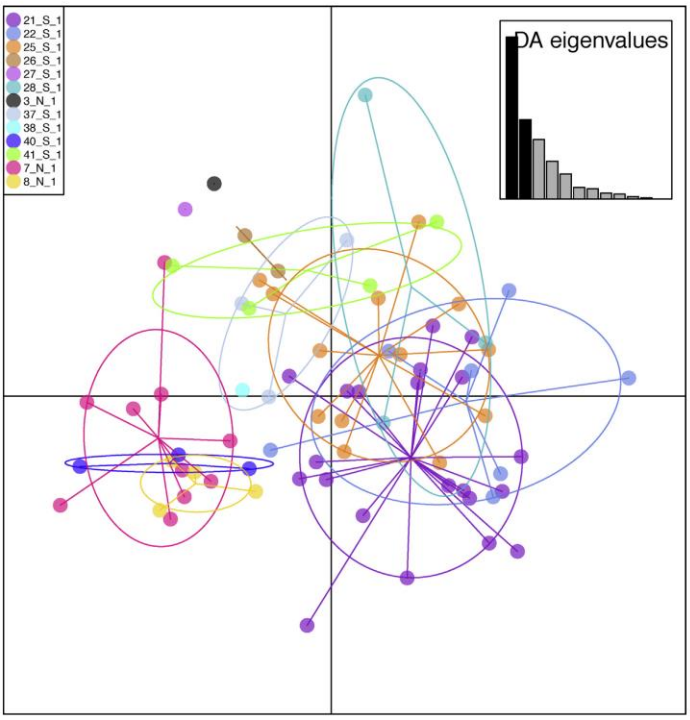

**Fig. 2.** Discriminant analysis of principal components (*DAPC*) of *Anaspis ruficollis*. Individuals sampled from the same tree hollow were assigned to the same genetic cluster. Scatterplot shows the first two principal components of the DAPC. Ellipses show the different populations (tree hollows) and dots represent individuals. Eigenvalues of the principle components are displayed in the inset. N = northern study area, S = southern study area.

*cosa* and *Xylomya maculata* disperse over the whole study area in the managed forests of Ebrach and are not restricted in gene flow within this geographic range. The absence of isolation by distance or population substructuring may not only be due to good dispersal abilities but may have been influenced by the choice of study species. We chose three species occurring with relatively high abundance. As more individuals may disperse in a larger than a smaller population, gene flow may have been enhanced in these species. Furthermore the studied area (approximately 14 × 14 km) might not be large enough to detect genetic substructure. In addition, for the species studied here it is not known how strongly specialized they are toward tree hollows. At least *A. ruficollis* may also occur in lying dead wood (H. Bußler, personal communication), which may serve as stepping stone between tree hollows and may therefore facilitate gene flow.

Colonization of new habitats by saproxylic insects is dependent on two factors. First, habitat quality is important, as colonization can only be successful if the habitat requirements of a species are fulfilled (habitat limitation). Second, the habitat must be located at distances, which can be bridged by the colonizing species (dispersal limitation). This can happen either by being physically able to disperse longer distances between suitable habitats or by having a dense matrix of suitable habitats, where long distance dispersal is not necessary. In our study we cannot distinguish between these two factors as the total number, quality, and density of tree hollows within the study area are unknown.

In the literature there is evidence that saproxylic insects may often be physically able to disperse over long distances. *Osmoderma eremita* may disperse over 700 m to 1.5 km under natural conditions (Dubois & Vignon, 2008; Chiari et al., 2013). Similar dispersal distances were also found for other saproxylic beetles (Rink & Sinsch, 2007; Drag, Hauck, Pokluda, Zimmermann, & Cizek, 2011). Moreover, there is evidence, that even flightless beetles may not be as dispersal limited as formerly assumed, as ancient saproxylic forest relict species were found also in younger forest patches (Janssen et al., 2016). Dispersal distances of up to 5 km were

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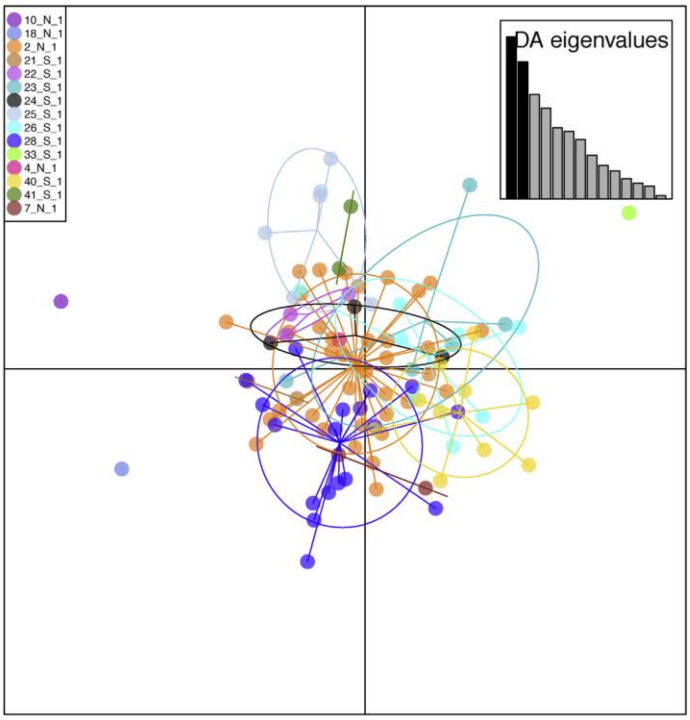

**Fig. 3.** Discriminant analysis of principal components (*DAPC*) of *Criorhina floccosa*. Individuals sampled from the same tree hollow were assigned to the same genetic cluster. Scatterplot shows the first two principal components of the DAPC. Ellipses show the different populations (tree hollows) and dots represent individuals. Eigenvalues of the principle components are displayed in the inset. N = northern study area, S = southern study area.

also shown for the saproxylic hoverfly *Hammerschmidtia ferruginea* (Rotheray, Bussiere, Moore, Bergstrom, & Goulson, 2014). Studies showing low dispersal distances (40–200 m) in *Osmoderma eremita* were conducted in large stands with high densities of suitable hollow oaks (Ranius, 2006; Svensson, Sahlin, Brage, & Larsson, 2011). Despite the high density of tree hollows, *Osmoderma eremita* was only affected positively by connectivity at a scale of around 200 m and thus occurrence patterns suggest that there might be a dispersal limitation (Ranius, Johansson, & Fahrig 2010).

Several population genetic studies conducted with saproxylic beetles on landscape scale also found only little genetic differentiation, suggesting that at least some saproxylic species are rather not dispersal limited. The range without genetic differentiation was between 9 km in *Elater ferrugineus* (Oleksa, Chybicki, Larsson, Svensson, & Gawroński, 2015) to 600 km in *Rosalia alpina* (Drag et al., 2015). Likewise studies on the darkling beetle *Bolitophagus reticulatus* found no substructure in continuous forest habitat over a scale of 100 km (Knutsen, Rukke, Jorde, & Ims, 2000) to 200 km (Jonsson, Johannesen, & Seitz, 2003), while genetic differentiation was three times higher in fragmented habitats (Knutsen et al., 2000) suggesting that decreasing patch connectivity results in lower levels of gene flow. However, other saproxylic beetle species may have more limited dispersal abilities. The two closely related cetoniid beetles *Osmoderma barnabita* and *Protaetia marmorata* collected from old trees along rural roads in Poland showed significant isolation by distance, with the former showing stronger signs of isolation by distance than the latter, which was most likely due to the broader ecological niche of the latter (Oleksa, Chybicki, Gawroński, Svensson, & Burczyk, 2013).

Connectivity has been shown to be an important factor explaining occurrence patterns of saproxylic beetles in tree hollows (Ranius et al., 2010). Recent studies show that habitat patch connectivity within an area seems less important when suitable habitat area is sufficiently large (Fahrig, 2013; Janssen et al., 2016). Janssen et al. (2016) showed that diversity patterns of saproxylic beetles were not driven by dispersal

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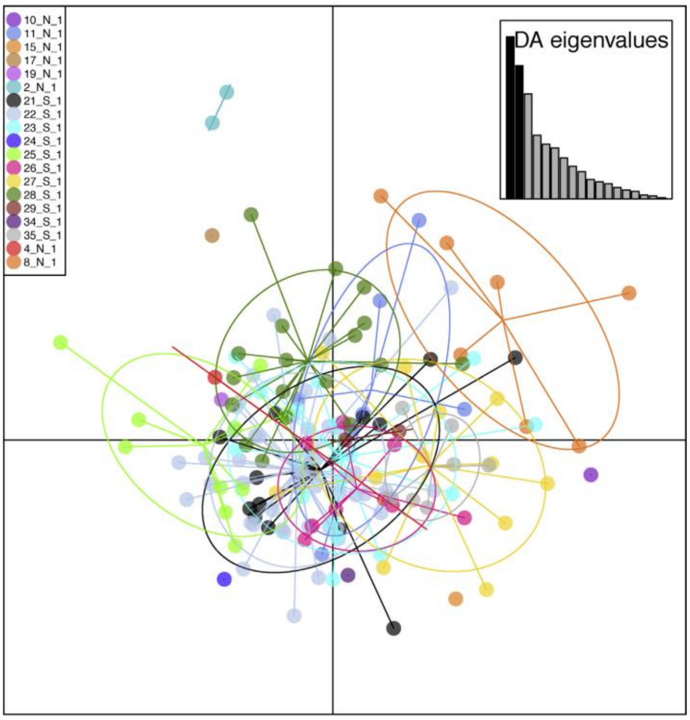

**Fig. 4.** Discriminant analysis of principal components (*DAPC*) of *Xylomya maculata*. Individuals sampled from the same tree hollow were assigned to the same genetic cluster. Scatterplot shows the first two principal components of the DAPC. Ellipses show the different populations (tree hollows) and dots represent individuals. Eigenvalues of the principle components are displayed in the inset. N = northern study area, S = southern study area.

limitation but by habitat availability as even poorly mobile species were able to colonize newly available habitats. Thus, it seems that the physical ability to disperse and the distance per se are not the only limiting factors but habitat boundaries, habitat availability and unsuitable matrix between distant sites are sometimes even more limiting (Müller & Goßner, 2010; Svensson et al., 2011). As our study was conducted in a managed but more or less continuous forest separated only by agricultural land, we assume that the continuous gene flow we found is based on the combination of good dispersal abilities of the species and a sufficient number of tree hollows, serving as suitable habitats. We do not know how population structure will change if habitat fragmentation increases and habitat patches become smaller or are surrounded by unsuitable matrix. However, this may lead to dispersal limitation, as inter-patch distances may increase to an extent which cannot be bridged even by good dispersers.

Knowledge about dispersal is important for developing conservation and management strategies. Long-term survival of species can only be guaranteed, if new habitat patches are situated at distances that allow colonization (Hanski, Pakkala, Kuussaari, & Lei, 1995) and if they fulfill necessary habitat requirements. Thus for conservation efforts a mixed strategy should be considered, because in ecosystems more or less mobile species are likely to coexist: (a) support and preservation of suitable habitats immediately surrounding the habitat of poorly mobile species (Huxel & Hastings, 1999) and (b) maximizing conservation efforts for species with high dispersal ability and colonization over long ranges by supporting even distant sites with high habitat quality, e.g. protecting areas with already existing valuable habitat structures (Ranius & Kindvall, 2006). For our study species connectivity by small patches as step stones seems less important than high numbers of tree hollows at larger distances from each other. However, small habitat patches as step stones may still be important to enhance the persistence of less mobile species. Conservation plans should be based on more than one species and consider a mixed strategy to effectively cover the variation of dispersal abilities of differ-

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ent saproxylic species. This prevents an overestimation of the dispersal ability, which would result in threats for less mobile species.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.01.005.

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## Manuscript 3: Dispersal of saproxylic insects

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HF and BS conceived the ideas. HF and BS interpreted and discussed results. Figures and tables were created by HF and BS. HF led the writing of the manuscript.

# Chapter 15
# Dispersal of Saproxylic Insects

**Heike Feldhaar and Bastian Schauer**

**Abstract** Dispersal is a key trait of species that is required to maintain gene flow between habitat patches. Furthermore, it allows the colonization of new habitats and thus affects population dynamics, extinction risk of populations, and species distributions. Dispersal enables species to persist in a changing environment. Saproxylic insects, depending on deadwood at some stage during their life cycle, must compensate local extinctions resulting from the decay of deadwood with colonizations of new deadwood structures locally and on the landscape scale. Their dispersal strategies are shaped by a suite of driving forces such as spatial and temporal variability of deadwood structures in the environment, feeding strategy, resource competition, kin competition, and inbreeding avoidance. The importance of each factor in selecting for a dispersal strategy will vary among species depending on their life history and interactions with the environment, such as the longevity of the deadwood habitat used. Species using a more transient habitat, such as freshly killed wood, have better dispersal abilities than those in more persistent habitats such as tree hollows that may exist for several decades. Dispersal abilities of only a few saproxylic insect species are known, and these comprise mostly pest species or flagship species of interest to conservation. Dispersal distances vary greatly from a few meters in passalids dispersing by walking to over 100 km in some flying bark beetles. Knowledge of dispersal abilities is of paramount importance though, as it can help to improve conservation strategies and forest management especially in terms of spatial distribution of suitable habitats to enhance species persistence. In this chapter we first review the factors driving dispersal ability and our current knowledge on dispersal distances of saproxylic insects. We provide an overview of different methods used to measure dispersal ability of saproxylic species. We discuss whether saproxylic species are rather dispersal or habitat limited and identify open questions in the study of dispersal of saproxylic insects.

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## 15.1 Introduction

Dispersal is defined as any movement of individuals or propagules with potential consequences for gene flow across space (Ronce 2007). Dispersal is a three-step process where individuals leave their birthplace and then cross a more or less hostile matrix before settling down in a new habitat patch to reproduce (Bonte et al. 2012). Most species live—at least to some degree—in spatially structured populations. Species with such a metapopulation structure are comprised of spatially discrete local populations in patches that are connected by the migration of individuals between local populations. Metapopulations are characterized by frequent extinction of local populations. For long-term persistence of a metapopulation, local extinctions and colonization through local dispersal need to be balanced (Hanski 1998). Dispersal ability (and propensity) is therefore an important life-history trait as it strongly impacts persistence of a species, especially in human-impacted landscapes. Anthropogenic habitat destruction often results in habitat fragmentation, reduced connectivity between suitable habitats, and a reduction in habitat size and quality. These transformations of ecosystems negatively impact many species, potentially driving them toward extinction. Therefore dispersal has received increasing attention by ecologists and conservationists.

As a result of habitat fragmentation, connectivity between suitable habitat patches is often reduced, and species with limited dispersal abilities may not be able to recolonize patches where they have become extinct or reach new habitat patches. In addition, smaller populations often release a smaller number of dispersing individuals, which may reduce not only demographic connectivity but also the genetic exchange between habitat patches even further. Additionally, the smaller the habitat patches, the smaller population sizes will be locally, which renders populations more prone to extinction by stochastic processes (Hanski et al. 1994). The strength of Allee effects (positive density dependence) may also become stronger in smaller populations, and, e.g., finding a mating partner may become more difficult, which may increase dispersal propensity of individuals (Kuussaari et al. 1996). Dispersal has consequences not only for the fitness of the respective individual moving from one habitat patch to another but also for population dynamics and genetic cohesion of species across their range (Bowler and Benton 2005). Spatially structured populations are largely dependent on dispersal for their long-term persistence. Immigrating individuals may rescue small populations by preventing local extinction events due to stochastic processes (Brown and Kodric-Brown 1977; Gotelli 1991) or enhance the fitness in small populations by genetic rescue (Whiteley et al. 2015). Empty habitat patches can only be (re-)colonized by dispersal (Fahrig and Merriam 1994; Hanski et al. 1994), and thus dispersal also determines the ability of populations to track favorable conditions or cope with habitat loss or fragmentation in a changing world (Travis et al. 2013).

Dead and decaying wood represents a spatially and temporally dynamic habitat for insects. Insects depending on deadwood structures at some point of their life cycle have been termed saproxylic insects (Speight 1989). Species depending on wood-decomposing fungi or other saproxylic species are also considered as saproxylic. These saproxylic insects constitute a large part of forest biodiversity and play a major role in nutrient cycling and ecosystem functioning (Stokland 2012; Ulyshen 2016), and diversity is driven by the range of decay stages and types of deadwood structures that provide habitat to different saproxylic insect assemblages (Grove 2002b; Schauer et al. 2018a; Ulyshen 2011; Ulyshen et al. 2004). Habitat patches for saproxylic insects can be as small as an individual deadwood structure, such as a tree, log, or fungal sporocarp, and can host several to many generations of a particular insect species. However, eventually the insect population will become extinct as the resource decomposes. Locally, new habitat patches will become available for colonization with the appearance of new deadwood structures. While forest management or natural disturbances alter patch dynamics and abundance locally, forest fragmentation determines connectivity and ecological continuity on the landscape level (Grove 2002b).

Saproxylic insects are adapted to their spatially and temporally dynamic habitat and have developed a range of dispersal strategies. In general, it is assumed that species inhabiting long-lived (e.g., specialists of tree hollows) or abundant habitat patches are poor dispersers (Nilsson and Baranowski 1997; Ranius and Hedin 2001) in comparison to those relying on more ephemeral or scarce habitat patches (e.g., scolytine beetles on wind- or fire-damaged trees) (Nilssen 1984; Saint-Germain et al. 2008).

Many saproxylic insect species can actively disperse on their wings, while others disperse passively by hitchhiking on dispersing animals (so-called phoresy). Phoresy as dispersal strategy is most often used by small-bodied and/or flightless saproxylic arthropods such as mites or pseudoscorpions (Karpinski et al. 2017; Katlav et al. 2014; Ranius and Douwes 2002; Zeh and Zeh 2013). As dispersal distances of phoretic saproxylic arthropods are determined by the dispersal abilities of the individual they hitchhike on, these often tiny arthropods may be able to disperse over relatively large distances (Ranius and Douwes 2002). Other flightless taxa reach new habitat patches actively by walking and are assumed to be strongly limited in their dispersal range in comparison to flying or phoretic saproxylic arthropods (Buse 2012; Horak et al. 2013; Janssen et al. 2016). A mixture of active and passive dispersal may be used by thrips. Saproxylic species may have rudimentary wings only (Kettunen et al. 2005). However, aside from active dispersal by walking, thrips as tiny insects may potentially sail with the wind and may thus cover larger dispersal distances passively without using energy for flight (Compton 2002).

Many saproxylic insect species are regarded as threatened worldwide due to fragmentation, loss of habitat, or degradation of forests resulting in reduced amounts of deadwood structures (Grove 2002a, b; Seibold et al. 2015; Siitonen 2001; Speight 1989). Aside from the absence of suitable habitat patches (habitat limitation), the entailing lower connectivity between those patches may result in dispersal limitation, i.e. the inability of a species to occupy all suitable patches in the environment or reach suitable habitat patches due to insufficient dispersal abilities. This is often invoked as a reason for the absence of a particular species within a habitat patch (Brin et al. 2016; Brunet and Isacsson 2009; Irmler et al. 2010; Schiegg 2000a, b).

Knowledge on dispersal biology of saproxylic insects is therefore of paramount importance to improve conservation strategies.

This chapter reviews the current knowledge of dispersal abilities of saproxylic insects (also in relation to habitat fragmentation). We first provide an overview of the factors influencing dispersal. As knowledge on dispersal abilities of saproxylic insects is based on different methods we will then compare the direct and indirect methods for measuring dispersal with advantages and drawbacks. We provide an overview of dispersal distances of various taxa. Lastly, we will discuss the role of potential dispersal limitation in population dynamics and colonization of new habitats by saproxylic insects.

## 15.2 Factors Influencing Dispersal Strategies: Why Disperse and How Far?

Dispersal strategies of organisms are shaped by a suite of driving forces such as environmental stochasticity, resource competition, kin competition, and inbreeding avoidance (Benton and Bowler 2012; Bonte et al. 2012; Bowler and Benton 2005; Matthysen 2012). The importance of each factor in selecting for a dispersal strategy will vary among species in accordance to their life-history traits and their interactions with the environment.

### *15.2.1 Longevity and Spatial Distribution of Habitats of Saproxylic Insects*

Theory on dispersal suggests limited dispersal of species inhabiting long-lasting and stable habitats, while those inhabiting ephemeral habitats should have a higher dispersal propensity as suitable habitat is present for a short time only (Southwood 1962; Shaffer 1981; Roff 1994; Denno et al. 1996). The spatial distribution of suitable habitat should also have a strong influence on dispersal abilities. If habitat patches are rare and more isolated, then dispersal ability needs to be greater to colonize new habitat patches. Availability of habitat patches is also dependent on the range of habitats used per species. Habitat specialists potentially have fewer habitat patches available than species being able to use a broader range of habitats.

Habitats of saproxylic insects differ strongly in their persistence and spatial distribution. One habitat type with very short availability only is freshly burned wood. Pyrophilous insects, whose larvae require the nutritional conditions present in the very early decay stages, colonize it immediately after a forest fire (Hanks 1999; Heikkala et al. 2017). These specialists use the freshly burned wood as a habitat for a single to a few generations only before their populations decline again (Hanks 1999; Heikkala et al. 2017). In addition, burn sites are spatially and temporally unpredictable and may occur at relatively great distances from each other. Consequently, spatial separation and transience of the habitat should select for very good dispersal abilities of pyrophilous species. Indeed, pyrophilous species have been shown to colonize freshly burned forest stands quickly, and they do not seem to be dispersal limited if sufficient source populations are available on the landscape scale (Boulanger et al. 2010; Heikkala et al. 2017; Kouki et al. 2012; Ranius et al. 2014; Saint-Germain et al. 2013). Other early decay stages have also been shown to favor good dispersal abilities. For example, bark beetles colonizing stressed or freshly killed trees have excellent dispersal abilities (Forsse and Solbreck 1985).

Standing and downed dead trees or coarse woody debris are deadwood habitats of intermediate longevity. In contrast to early decay stages that are the result of forest fires or other stressors to trees, deadwood at intermediate and late decay stages is a resource that may have become available more gradually and continuously in comparison to the early decay stages (Nilsson and Baranowski 1997). In addition, these habitat types should be the most common within natural forests (Nordén et al. 2004), in contrast to the very early decay stages with limited temporal (and spatial) availability or hollows in living trees with a naturally patchy spatial distribution. Saproxylic insect species utilizing intermediate to late decay stages of deadwood should thus have more limited dispersal abilities in comparison to species utilizing ephemeral early decay stages. However, evidence for limited dispersal abilities of saproxylic species using deadwood structures of intermediate longevity is equivocal. Saint-Germain et al. (2013) did not find an effect of isolation in colonization patterns of burned forest sites by pyrophilous vs. non-pyrophilous beetle species. Other studies suggest that species requiring a more specific habitat may be dispersal limited, which is often the case for threatened species (Gibb et al. 2006; Schiegg 2000a, b; Seibold et al. 2015).

Hollows in living trees are considered an extremely stable habitat as they may persist for many decades (Ranius and Hedin 2001), potentially providing a suitable habitat for many generations of species inhabiting those hollows. Tree hollow specialists are therefore expected to have more limited dispersal abilities and a lower dispersal propensity than species inhabiting more transient deadwood habitats. Direct measurements of dispersal abilities of one specialist, the Hermit beetle *Osmoderma eremita* Scopoli, 1763, suggest more limited dispersal abilities in comparison to other saproxylic insects (Hedin et al. 2008; Ranius 2006). Likewise, Nilsson and Baranowski (1997) found the beetle fauna in hollow trees to be impoverished in previously disturbed stands and argue that this is due to dispersal limitation. On the other hand, the naturally patchy distribution of tree hollows should favor dispersal abilities. In addition, the potentially small population size of a particular species within a tree hollow may select for a high dispersal propensity of at least one sex to avoid inbreeding (Perrin and Mazalov 2000; Waldbauer and Sternburg 1979) and potentially competition among relatives (see below).

### 15.2.2 Influence of Feeding Strategies on Dispersal

Dispersal is defined as the movement from the natal or breeding site to another breeding site. This includes not only the departure from a patch and settlement in the (new) breeding site but also the movement between those patches (Clobert et al. 2009). The movement strategy and potential dispersal distance of saproxylic insects will be strongly influenced by nutritional and habitat requirements of the dispersing life stage—which are usually the adult insects.

While larvae of many saproxylic species are dependent on decomposing wood in some form, adult life stages may rely on very different food sources. At one extreme, adults may not feed at all, which will limit the maximum distance that can be covered during dispersal as only the stored biomass can be utilized for flight or movement and is traded off against reproduction. Nonfeeding species therefore tend to have a more sedentary lifestyle than those feeding as adults (Hanks 1999). A comparison of the life history and dispersal behavior of two cerambycid beetles, the Japanese pine sawyer *Monochamus alternatus* Hope, 1843 and the Sugi bark borer *Semanotus japonicas* Lacordaire, 1869, suggests that dispersal propensity is strongly influenced by adult feeding behavior. While *M. alternatus* Hope, 1843 adults must feed on the bark of twigs of healthy pine trees for maturation and then have to search for weakened or newly killed pine trees to oviposit, *S. japonicus* Lacordaire, 1869 is more sedentary as oviposition may take place on the same tree that larvae developed in and no maturation feeding of the adult is required (Shibata 1986a, b).

Other insects that have to undergo maturation feeding are many saproxylic species of syrphid flies that require protein-rich pollen in order to fully develop their reproductive organs and achieve egg maturation (Speight 2012). Saproxylic syrphid flies therefore require open stands with a rich herb layer within forests (Fayt et al. 2006) and are also frequently found in meadows (Branquart and Hemptinne 2000). In order to meet nutritional demands, they potentially need to cover quite a distance before entering deadwood structures again to reproduce or deposit eggs.

### 15.2.3 Inbreeding Avoidance

Mating between related individuals results in inbreeding. Inbreeding can occur in both large and small populations. In large populations, nonrandom mating of related individuals may occur simply due to geographic proximity of these individuals. In small populations however, the probability of inbreeding is much higher, even with random mating because most individuals within the population will be related.

Local population sizes of saproxylic insects may often be small, which may result in substantial levels of inbreeding if mobility of the species is low. A local population may comprise individuals within the same forest or forest fragment, but may be as small as the group of individuals living in the same habitat patch, which can be a deadwood structure like a tree hollow, a fallen log, or the sporocarp of a bracket fungus. Especially bark and ambrosia beetles show very high levels of inbreeding in some species when mating takes place among kin within the same galleries (Keller et al. 2011; Kirkendall 1983; Kirkendall et al. 2015). Other saproxylic insect species also show considerable levels of relatedness within the same breeding structure such as a particular tree hollow, e.g., the two cetoniine beetles *Osmoderma barnabita* Motschulsky, 1845 and *Protaetia marmorata* Herbst, 1786 (Oleksa et al. 2013) or the beetle *Anaspis ruficollis* Fabricius, 1792, the syrphid fly *Criorhina floccosa* Meigen, 1822, and the wood-soldier fly *Xylomya maculata* Meigen, 1804 (Schauer et al. 2018b).

As inbreeding has been shown to reduce fitness in many insects (Henter 2003), mechanisms to avoid inbreeding are expected to be selected in order to reduce negative fitness effects (Pusey and Wolf 1996). Inbreeding can be avoided either by dispersal (of at least one sex) from natal sites to reduce contact with relatives (Waldbauer and Sternburg 1979) or, when dispersal is not possible, inbreeding may be avoided by mechanisms that prevent breeding with close relatives (Blouin and Blouin 1988).

Sex-biased dispersal has been observed in several species of saproxylic beetles. In *Melandrya barbata* Fabricius, 1792 and *Melanotus villosus* Gmelin, 1789, a larger proportion of males was found to colonize recent forest fragments, suggesting male-biased dispersal (Bouget et al. 2015). In the stag beetle *Lucanus cervus* Linnaeus, 1758, both sexes disperse. However, females fly for shorter distances in comparison to males and then move around on the ground in search for an oviposition site (Rink and Sinsch 2007). Likewise, the sex ratio was more female biased at shorter dispersal distances and unbiased at larger distances in *Ips typographus* Linnaeus, 1758 (Dolezal et al. 2016), which can be explained by males being the pioneer sex. In contrast, tethered flight experiments on *Osmoderma eremita* Scopoli, 1763 suggest that females may have higher flight capacities (Dubois et al. 2010). Several authors point out the observed patterns with potential sex-biased dispersal may be due to differences in the likelihood of catching beetles of one of the sexes (often the males). Thus, recapture rate of male Rosalia longicorn beetles was higher than that of females, but no sex difference in cumulative dispersal distance was found (Drag et al. 2011).

### 15.2.4 Delayed Dispersal, Flightless Males, and Outbreeding Depression in Cooperatively Breeding and Social Saproxylic Insects

A special case of sex-biased dispersal can be found in ambrosia beetles (Scolytinae) where inbreeding polygyny has evolved repeatedly as mating system (Kirkendall 1983). Female ambrosia beetles mate with close kin (brothers) before they disperse (Kirkendall et al. 2015). Adult females often stay within natal galleries where fungus is grown and delay dispersal after mating in order to provide parental care to closely related offspring (Peer and Taborsky 2007). Dispersal of mated females is triggered by a low number of close kin dependent on alloparental care (Biedermann and Taborsky 2011). Males in such species are usually flightless, resulting in highly sex-biased dispersal patterns (Kirkendall et al. 2015). In addition, mating with related individuals may by now be favored in these species as outbreeding has been shown to reduce fitness (Peer and Taborsky 2005).

Likewise in the lower dry-wood feeding termite *Cryptotermes secundus* Walker, 1853, inclusive fitness gains that can be attained by individuals delaying dispersal. Individuals stay as helpers in the natal nest and delay dispersal to found a new colony themselves when the piece of wood they nest in is still large and food abundant. When food becomes scarce, workers develop into winged sexuals more readily and disperse (Korb and Schmidinger 2004).

### *15.2.5 Competition-Colonization Trade-Offs*

Differences in dispersal ability among species may be selected by competitive interactions. Individuals of smaller species are often inferior competitors during scramble or interference competition, i.e., when they have to compete for resources directly and a superior individual can displace an inferior competitor or prevent access to the resource. However, if inferior competitors have better dispersal abilities, coexistence may be enabled. Such a competition-colonization trade-off seems to allow species coexistence of species of spore-feeding beetles on a wood-decaying bracket fungi *Ganoderma* spp. in New Zealand. Here the beetle *Zearagytodes maculifer* Broun, 1880 evades competition with the superior competitor *Holopsis sp.* by dispersing and colonizing distant habitat patches not yet colonized by the latter species (Kadowaki et al. 2011).

## 15.3 Measurement of Dispersal

While dispersal is an important life-history trait influencing the persistence of a species locally and regionally as well as its range, it is notoriously difficult to observe or measure, especially in rare species or those with a mainly cryptic lifestyle such as many saproxylic insect species. Dispersal can be measured either directly or indirectly. Direct measurement of dispersal implies that individuals (or a cohort) are observed during the whole dispersal process from the departure point to the point of settlement. This usually requires that individuals are marked in some way so that they can be identified. Direct measurements of dispersal have the advantage that exact dispersal distances and movement patterns of particular individuals can be measured. Based on the distribution of observed dispersal distances of many individuals, a dispersal kernel, i.e., a probability distribution of the distance traveled by any individual, can be calculated (Etxebeste et al. 2016). In addition to the distance traveled, information on movement behavior can be gained during direct measurements. In contrast, indirect measurement of dispersal is usually based on the interpretation of patterns generated by dispersing individuals. Indirect methods comprise population genetic analyses or patterns of occurrence of saproxylic insects (usually in relation to landscape structure and spatial distribution of potential habitat patches). Direct and indirect measures of dispersal are complementary and not redundant methods (Lowe and Allendorf 2010; Ranius 2006).

### 15.3.1 Direct Measurement of Dispersal: Radio Telemetry

Radio telemetry allows the measurement of exact dispersal distances and movement patterns of particular individuals of saproxylic insects (Chiari et al. 2013; Dubois and Vignon 2008; Hedinand Ranius 2002; Hedin et al. 2008; Moore et al. 2017; Svensson et al. 2011). By closely following movements of single individuals through the habitat, radio telemetry can uncover the use of hitherto unknown or cryptic breeding sites (Moore et al. 2017) or time spent in other habitats (Chiari et al. 2013), which may contribute to increased distances from the natal patch to a breeding site. The most important limiting factor in such studies is the trade-off between the weight of the transmitter that is attached to the insect and the power of the transmitter. Active transmitters used in radio telemetry are powered by batteries and are usually relatively heavy (200–1000 mg), but the signal is transmitted over larger distances of up to 500 m on the ground (Kissling et al. 2014). While a 500 m radius may be enough to monitor movements and short-distance dispersal by telemetry, those individuals that fly beyond the range of the receiver are lost (Moore et al. 2017), and therefore long-distance dispersal events are rarely (if ever) detected with this method. Another problem arises due to the relatively large weight of the transmitter, which precludes their use in studies with smaller saproxylic insects as their normal movement and dispersal behavior may be altered. Consequently, most studies using radio telemetry have been conducted on large beetles such as *Osmoderma eremita* Scopoli, 1763 (Chiari et al. 2013; Dubois and Vignon 2008; Hedin and Ranius 2002; Svensson et al. 2011), the stag beetle *Lucanus cervus* Linnaeus, 1758 (Rink and Sinsch 2007), or rhinoceros beetles (Moore et al. 2017). Passive transmitters (without a power source) such as RFID tags are much lighter than active transmitters (weighing only 0.9 to 100 mg) which would allow the study of small saproxylic insects. However, as the range of the signal is <1 m, landscape-scale studies using transmitters are currently impossible (Kissling et al. 2014).

### 15.3.2 Direct Measurement of Dispersal: Capture-Mark-Recapture

Another method measuring exact dispersal distances is capture-mark-recapture (or mark-release-recapture). This method allows the determination of dispersal distances of particular individuals and dispersal rates of released cohorts (Rossi de Gasperis et al. 2016; Torres-Vila et al. 2017). Recapture efficiency may be increased using odor traps with species-specific semiochemicals if available for the respective species (Meurisse and Pawson 2017; Torres-Vila et al. 2015; Zauli et al. 2014), or traps with fermenting baits (Torres-Vila et al. 2017; Torres-Vila et al. 2012), that are placed at different distances from the release site. Using fermented bait traps to recapture *Cerambyx welensii* Küster, 1846 and *C. cerdo* Linnaeus, 1758, recapture rate ranged from 36% to 66%, which permitted the study of the influence of parameters such as wind speed and direction, air temperature, temporal patterns, and impact of season on dispersal behavior (Torres-Vila et al. 2017). As the study was conducted in two species in parallel, this allowed a direct comparison of dispersal behavior. Nonetheless, capture-mark-recapture studies are often biased toward those individuals that are captured again—often relatively close to the habitat patch they emigrated from. Long-distance dispersal events are rarely observed (Vlasanek et al. 2013), but can be estimated by extrapolation from the dispersal function at shorter distances (Drag et al. 2011; Torres-Vila et al. 2017). Another caveat may be that—depending on the method of marking—the movement abilities and thus movement patterns of insects may be altered (Gall 1984) or make them potentially more conspicuous to predators. In addition, movement behavior may be influenced by the translocation, e.g., if individuals are released in unfamiliar or matrix habitat (Heidinger et al. 2009). Both problems may be overcome by using a passive marking method, where individuals become marked when leaving their breeding site and are then captured after dispersal. Bark beetles have been successfully marked by coating or dusting infested logs with fluorescent dye or powder. As emerging beetles walked on the surface of the logs before flight, they became marked passively as grains of fluorescent powder adhered to cuticular hairs. After recapture, beetles can be inspected for the presence of fluorescent marker using a UV light source (Cronin et al. 1999; Dolezal et al. 2016).

### 15.3.3 Direct Measurement of Dispersal: Assignment Methods Using Genotypic Data of Individuals

Genotypic data (such as multilocus genotypes based on microsatellites) can also be used for direct measurement of dispersal. Such studies may yield comparable results to mark-recapture studies. While the dispersing individual is not directly observed, a particular dispersal event of an individual may be detected and distances measured when offspring can be assigned to their source parents based upon multilocus genotypes unambiguously. This, however, requires some genetic divergence of potential source populations and that these source populations have been sampled (Lowe and Allendorf 2010). This method is best applicable for species where groups of related individuals represent source populations with only a few individuals leaving such a kin group to disperse. Such a scenario can be found in bark beetles with high levels of inbreeding or subsocial beetle colonies as well as in eusocial ants and termites. Genotypes of source populations (or mature colonies) can then be compared with genotypes of individuals that have just dispersed to start new kin groups or colonies (Türke et al. 2010). Winged sexuals of the Formosan subterranean termite *Coptotermes formosanus* Shiraki, 1909 could be assigned unambiguously to their parental colonies based on multilocus genotypes and have been shown to disperse over at least 500 m (Simms and Husseneder 2009).

### 15.3.4 Direct Measurement of Dispersal: Colonization Experiments

Colonization experiments, where empty habitat patches (or odor traps) are provided and distances to potential source populations of colonizing insects are known, can also be utilized to measure dispersal distances. This method has been used to estimate dispersal abilities of beetles associated with bracket fungi (Jonsell et al. 1999; Jonsson and Nordlander 2006) and also for bark beetles and bark weevils on a very large scale (Chase et al. 2017; Nilssen 1984). In the latter study by Nilssen (1984), trap logs of spruce were laid out and colonized by the large pine weevil *Hylobius abietis* Linnaeus, 1758 at a distance of 171 km to the nearest occurrence of spruce forest. Chase et al. (2017), in contrast, used black panel insect traps with α-pinene and ethanol to attract the two bark beetle species *Hylurgus ligniperda* Fabricius, 1787 and *Hylastes ater* Paykull, 1800. Both species were trapped up to approximately 25 km away from the nearest pine stands. Colonization of deadwood structures after a large-scale forest fire can be seen as a natural experiment as abundant resources are generated over a vast area with a clearly visible distinction of burned and unburned parts of the forest. The colonization of large recently burned forest sites by pyrophilous saproxylic beetles as well as non-pyrophilous secondary users suggested that these groups were not negatively affected by up to 8 km distance to the border of the burned area (Saint-Germain et al. 2013).

### 15.3.5 Indirect Measurement of Dispersal: Population Genetic Analyses

Population genetic analyses are frequently used to infer population connectivity, i.e., the degree of gene flow on larger spatial and temporal scales, which is not feasible with direct measurements of dispersal. Population genetic inference is based on the principle that genetic divergence among local populations due to genetic drift (which causes subpopulations to diverge) is counteracted by the cohesive effects of gene flow due to individuals migrating from one population to another (Lowe and Allendorf 2010). The degree of genetic divergence can be used as an indicator of dispersal capacity of a species as it reflects past gene flow and thus dispersal (or absence thereof). When populations are subdivided (e.g., by fragmentation of forest habitats), the number of migrants can be estimated using classical F-statistics approaches. In species distributed continuously over space, limited gene flow (i.e., limited dispersal distances) leads to an increasing genetic differentiation among individuals as geographic distance increases, an effect known as isolation by distance (Allendorf et al. 2013).

Population genetic analyses also allow hierarchical analyses of populations on very different spatial scales within the same analysis. The relatedness and level of inbreeding of a group of individuals collected from a single structure such as a tree hollow can be measured (Schauer et al. 2018b) as well as genetic variation on the local (e.g., same forest patch) to regional scale as described above (Oleksa 2014; Oleksa et al. 2013, 2015; Schauer et al. 2018b). Dispersal distances can be estimated from spatial patterns of relatedness within local populations, where spatial autocorrelation among genotypes at varying distances is estimated. When individuals disperse over short distances, this will result in positive spatial genetic autocorrelation, i.e., the genotypes of individuals that are spatially closer are genetically more similar than at random (Epperson 2005; Oleksa et al. 2015).

Recent studies using population genetic analyses have shown that several saproxylic insects may be able to disperse over much longer distances than expected as no isolation by distance or population substructure was found among populations sampled over a distance of several hundred kilometers. For example, the cerambycid beetle *Rosalia alpina* Linnaeus, 1758 showed only very little genetic substructuring on a range of 600 km and potentially a rapid expansion of one genetic lineage within this area (Drag et al. 2015). Likewise beetles associated with bracket fungi such as *Bolitophagus reticulatus* Linnaeus, 1767 or *Diaperis boleti* Linnaeus, 1758 showed no spatial genetic substructuring over sites up to 200 km apart (Jonsson et al. 2003; Oleksa 2014). When landscape features are included in population genetic analyses, potential barriers to gene flow can be identified (or the lack of dispersal barriers that had been assumed before), which allows some inferences of dispersal behavior (Schauer et al. 2018b). However, this is also a potential drawback of landscape or population genetic analyses as for population substructure to arise gene flow must be lacking or hampered for a number of generation among subpopulations (Epps and Keyghobadi 2015). Furthermore, genetic analyses do not provide information about dispersal rate and exact dispersal distances of single individuals or on dispersal periods and patterns. Another drawback of population or landscape genetic analyses is that they are only feasible when a significant number of individuals per species [>30 to 50 at least, but the more the better (Lowe et al. 2004)] can be analyzed. For very rare species where only a handful of individuals can be analyzed, statistical noise would be too high to produce meaningful results.

### 15.3.6 Indirect Measurement of Dispersal: Analysis of Morphological Traits Impacting Light Performance

Dispersal ability can also be inferred indirectly by measuring traits associated with flight performance such as wing load (body mass divided by wing area) or wing aspect ratio (measure for shape of wings as wing length is divided by wing width) of the insect (Berwaerts et al. 2002). A lower wing load (i.e., less body weight per $mm^2$ of wing) supposedly translates into better flying ability because flight becomes energetically more efficient with decreasing wing load (Angelo and Slansky 1984). Relatively longer wings (higher aspect ratio) are thought to improve efficiency of prolonged flights and increase acceleration capacity or flight speed (Berwaerts et al. 2002; Marden 2000; Wootton 1992). Large body size reduces the mass-specific cost of flight and is thus associated with better dispersal ability (Roff 1991). Dispersal-associated morphological traits have been compared among (Gibb et al. 2006) as well as within (Bouget et al. 2015) species to differentiate between species or sexes with lower or higher dispersal abilities.

### 15.3.7 Indirect Measurement of Dispersal: Tethered Flight Experiments in Flight Mills

Tethered flight experiments are a suitable method to measure the physical dispersal capacity of individuals. As experiments are conducted under laboratory conditions with the surrounding “landscape” being similar for all individuals tested, it is assumed that motivational differences or differences due to environmental factors are reduced. Flight mills are the most common device used for tethered flight experiments, where an insect is attached to a flight arm that rotates due to the forces produced by the insect in flight. Flight time and speed are then used to calculate a maximum flight distance (Forsse and Solbreck 1985; Jactel and Gaillard 1991). Tethered flight experiments are suitable for the estimation of differences in dispersal abilities among species (Jonsson 2003) or within species (Dubois et al. 2010; Forsse and Solbreck 1985; Jactel 1993; Jactel and Gaillard 1991; Taylor et al. 2010). When life-history traits associated with dispersal capacity are compared in parallel among the individuals used for the tethered flight experiments, the proximate mechanisms underlying differences in dispersal ability can be uncovered, e.g., by measuring sex-specific differences or the influence of body condition on flight capacity such as the presence and status of wings and wing muscles (wing load) or fat content

(Akbulut and Linit 1999; David et al. 2014; Dubois et al. 2010; Forsse and Solbreck 1985; Jactel 1993; Jactel and Gaillard 1991; Jonsson 2003; Taylor et al. 2010).

A drawback of such experiments may be that flight behavior may be influenced by the insect being tethered. First insects must be handled and fixed to the device. Then, insects must accelerate the flight arm and have to overcome the friction of conventional bearings or the torsional resistance of magnetic mounds. This supposedly results in an underestimation of flight speed of the insects, which makes tethered flight experiments an excellent approach of measuring relative differences in dispersal capabilities but not absolute differences (Taylor et al. 2010).

### 15.3.8 Indirect Measurement of Dispersal: Inferring Dispersal Capabilities from Occurrence Patterns

The analyses of occurrence patterns (presence/absence) can be used to infer colonization abilities of saproxylic insects. Occurrence patterns of species result from their colonization abilities and local extinctions in respective habitat patches. In a number of studies, such occurrence patterns have been used as a proxy for colonization rates of specific habitat types and dispersal ability (Schiegg 2000a, b). However, as present occurrence patterns in habitat patches are confounded not only by current size and quality of the habitat patch itself but also by historical processes (Flensted et al. 2016; Gossner et al. 2008; Hanski and Ovaskainen 2002; Herrault et al. 2016; Janssen et al. 2016; Nordén et al. 2014), the estimation of dispersal abilities from such patterns is often difficult. Presence of a species within a habitat patch with low current connectivity to other habitat patches could either be due to a recent colonization event by a good disperser or the species has persisted locally if the habitat was formerly larger and/or less isolated and is therefore still found in spite of being a poor disperser (Herrault et al. 2016). This problem can be overcome when the same sites are sampled repeatedly, and thus colonization rate (and extinction rate in the metapopulation) can be inferred (Ranius et al. 2014). On the community level, colonization credit, i.e., lower than expected species richness in a habitat patch of a given area and quality, allows an estimation of the proportion of species that may be dispersal limited. After an increase in patch size, the number of species found would then be lower than expected in a habitat of a given size due to a time lag. For example, for hoverflies—a group that is thought to be highly mobile—Herrault et al. (2016) showed that they suffered a colonization credit in isolated woodlands, suggesting dispersal limitation.

In order to determine occurrence patterns, saproxylic insects need to be observed in a particular site or trapped. While direct observation in a particular site (e.g., by searching for individuals on the surface of potential host trees (Ranius et al. 2014) or opening deadwood structures) ensures that the particular insect really uses a site and is not only "passing through," using passive trapping is often preferred as it less labor intensive and captures a larger part of the saproxylic community. Emergence traps or flight interception traps are most often used to this end (Herrault et al. 2016; Irmler et al. 2010; Schiegg 2000a). By comparing the abundance of a particular species in flight interception traps within forest patches to that in traps in matrix habitat (open grassland), dispersal propensity and the potential of a species to cross matrix habitat can be tested, which helps to explain occurrence patterns.

Such an approach was used by Irmler et al. (2010), who showed that most of the 80 beetle species found in traps in the forest, as well as in grassland, were not very mobile, covering only distances of less than 30 m into the open grassland. Abundance of beetle species in forest patches was positively correlated with their mobility (Irmler et al. 2010).

### *15.3.9 Are Results of Different Methods Congruent?*

Results obtained with the different methods described above yield different pictures of dispersal abilities of saproxylic insects (see Table 15.1 and overview of known dispersal distances below). Direct measurements of dispersal distances using telemetry or mark-release-recapture often suggest more limited dispersal abilities as distances measured are usually shorter than distances obtained in flight mill experiments or colonization experiments when conducted with the same species (e.g., several studies on *Bolitophagus reticulatus* Linnaeus, 1767, *Monochamus galloprovincialis* Olivier, 1795, or *Ips typographus* Linnaeus, 1758; for references see Table 15.1). This discrepancy may arise in capture mark-recapture-experiments due to the bias of individuals being recaptured. Recapture rate of those individuals dispersing over shorter distances only is higher than for those dispersing over longer distances. The potential for long-distance dispersal is captured more easily in tethered flight experiments. Likewise, the few population genetic analyses available to date often suggest that dispersal abilities are often better than hitherto thought. Here gene flow enabled by rare long-distance events is captured in absent or low genetic substructure or isolation by distance on larger spatial scales. As population genetic analyses also integrate over longer temporal scales, estimation of dispersal abilities is often not straightforward as genetic connectivity depends on the absolute number of dispersers among populations—and a few are enough to counteract population subdivision. For the persistence of a metapopulation of saproxylic insects, demographic connectivity is important though. Demographic connectivity means the relative contribution to population growth rates of dispersing individuals vs. survival and reproduction of residents (Lowe and Allendorf 2010). The use of a combination of different methods (direct and indirect measurement of dispersal) would therefore be important to gain a deeper understanding of the role of dispersal abilities in shaping community-level occurrence patterns of saproxylic insects locally and regionally.

**Table 15.1** Studies addressing the dispersal abilities of saproxylic insects

| | Dispersal strategy | Method | Distance | Author |
|---|---|---|---|---|
| Coleoptera | | | | |
| *Agrilus planipennis* (Fairmaire 1888) | Flight | Flight mill | 1.13 km | Fahrner et al. (2015) |
| *Agrilus planipennis,* (Fairmaire 1888) | Flight | Flight mill | >50% more than 750 m, 1% > 6 km | Taylor et al. (2010) |
| | | Free flight experiment | >20 km | |
| *Anaspis ruficollis* (Fabricius 1792) | Flight | Genetic studies | No genetic differentiation in a ~10 × 10 km study area | Schauer et al. (2018b) |
| *Anoplophora glabripennis* (Motschulsky 1853) | Flight | Mark-recapture | 2.6 km (98% of individuals recaptured within 920 m) | Smith et al. (2004) |
| *Bolitotherus cornutus*, (Panzer 1794) | Flight | Mark-recapture | 50 m | Starzomski and Bondrup-Nielsen (2002) |
| *Bolitotherus cornutus,* (Panzer 1794) | Flight | Colonization experiment | 365 m | Whitlock (1992) |
| *Bolitophagus reticulatus* (Linnaeus, 1767) | Flight | Field experiment | 55 m | Sverdrup-Thygeson (2010) |
| *Bolitophagus reticulatus* (Linnaeus 1767) | Flight | Flight mill | 29 h 36 min total flight time corresponding to 125 km | Jonsson (2003) |
| *Bolitophagus reticulatus* (Linnaeus 1767) | Flight | Genetic studies | 200 km | Jonsson et al. (2003) |
| *Cerambyx cerdo* (Linnaeus 1758) | Flight | Mark-recapture | 880 m for male, 1700 m for female | Torres-Vila et al. (2017) |
| *Cerambyx welensii* (Küster 1846) | Flight | Mark-recapture | 1100 m for male, 580 m for female | Torres-Vila et al. (2017) |
| *Dendroctonus frontalis* (Zimmermann 1868) | Flight | Mark-recapture | 500 m | Cronin et al. (1999) |
| *Dendroctonus pseudotsugae* (Hopkins 1905) | Flight | Flight mill | 23 h continuous flight | Borden and Bennett (1969) |
| *Diaperis boleti*, (Linnaeus 1758) | Flight | Genetic studies | 150 km | Oleksa (2014) |
| *Elater ferrugineus*, (Linnaeus 1758) | Flight | Mark-recapture | 1.6 km, median 214 m | Zauli et al. (2014) |
| *Elater ferrugineus* (Linnaeus 1758) | Flight | Genetic studies | 100 to ~650 m | Oleksa et al. (2015) |

(continued)

**Table 15.1** (continued)

| | Dispersal strategy | Method | Distance | Author |
|---|---|---|---|---|
| *Hylobius abietis*, (Linnaeus 1758) | Flight | Flight mill | 10–80 km | Solbreck (1980) |
| *Hylastes ater* (Paykull 1800) | Flight | Colonization experiment | 27.6 km | Chase et al. (2017) |
| *Hylurgus ligniperda* (Fabricius 1787) | Flight | Colonization experiment | 26.3 km | Chase et al. (2017) |
| *Hylurgus ligniperda* (Fabricius 1787) | Flight | Mark-recapture | 960 m, model based estimates<br>46% > 1 km,<br>1.6% > 5 km | Meurisse and Pawson (2017) |
| *Ips typographus* (Linnaeus 1758) | Flight | Mark-recapture | 1.1 km | Dolezal et al. (2016) |
| *Ips typographus* (Linnaeus, 1758) | Flight | Field experiment | 8 km | Botterweg (1982) |
| *Ips typographus* (Linnaeus 1758) | Flight | Mark-recapture | 1.2–1.6 km | Forsse and Solbreck (1985) |
| *Ips typographus* (Linnaeus 1758) | Flight | Mark-recapture | 120 m (furthest trapping point) | Zolubas and Byers (1995) |
| *Lucanus cervus* (Linnaeus 1758) | Flight | Telemetry | 2 km | Rink and Sinsch (2007) |
| *Lucanus cervus* (Linnaeus 1758) | Flight | Telemetry | 200 m | Sprecher-Uebersax and Durrer (2001) |
| *Lucanus cervus*, (Linnaeus 1758) | Flight | Telemetry | 2 km | Rink and Sinsch (2007) |
| *Lucanus cervus* (Linnaeus 1758) | Flight | Telemetry | 250 m for males, 144 m for females | Tini et al. (2017) |
| *Monochamus alternatus* (Hope 1843) | Flight | Mark-recapture | 59 m | Shibata (1986b) |
| *Monochamus carolinensis* (Olivier 1792) | Flight | Flight mill | 2200 m ± 1100 m | Akbulut and Linit (1999) |
| *Monochamus galloprovincialis* (Olivier, 1795) | Flight | Mark-recapture | >400 m | Torres-Vila et al. (2015) |
| *Monochamus galloprovincialis* (Olivier 1795) | Flight | Modeling of dispersal kernels in a mark-recapture study | > 4 km | Etxebeste et al. (2016) |
| *Monochamus galloprovincialis* (Olivier 1795) | Flight | Flight mill | 63 km | David et al. (2014) |
| *Monochamus sartor* (Fabricius 1787) | Flight | Flight mill | 3.14 km | Putz et al. (2016) |

(continued)

**Table 15.1** (continued)

| | Dispersal strategy | Method | Distance | Author |
|---|---|---|---|---|
| *Monochamus sutor* (Linnaeus 1758) | Flight | Flight mill | 5.56 km | Putz et al. (2016) |
| *Morimus asper* (Sulzer 1776) | Walking | Mark-recapture | 451 m | Rossi de Gasperis et al. (2016) |
| *Odontotaenius disjunctus* (Illiger 1800) | Flight, walking | Colonization experiment | Ø11.6 m | Jackson et al. (2009) |
| *Oplocephala haemorrhoidalis* (Fabricius 1787) | Flight | Flight mill | 7 h 30 min total flight time corresponding to 29 km | Jonsson (2003) |
| *Oplocephala haemorrhoidalis* (Fabricius 1787) | Flight | Genetic studies | >12 km | Jonsson (2003) |
| *Osmoderma barnabita* (Motschulsky 1845) | Flight | Genetic studies | 200 m | Oleksa et al. (2013) |
| *Osmoderma eremita* (Scopoli 1763) | Flight | Mark-recapture | 190 m | Ranius and Hedin (2001) |
| *Osmoderma eremita* (Scopoli 1763) | Flight | Radio telemetry | 1500 m | Chiari et al. (2013) |
| *Osmoderma eremita* (Scopoli 1763) | Flight | Radio telemetry | 700 m | Dubois and Vignon (2008) |
| *Osmoderma eremita* (Scopoli 1763) | Flight | Flight mill | ~2300 m | Dubois et al. (2010) |
| *Protaetia marmorata* (Herbst 1786) | Flight | Genetic studies | 500 m | Oleksa et al. (2013) |
| *Rhizophagus grandis* (Gyllenhaal 1827) | Flight | Field experiment | 4 km | Fielding et al. (1991) |
| *Rosalia alpina* (Linnaeus 1758) | Flight | Mark-recapture | 1.6 km | Drag et al. (2011) |
| *Rosalia alpina* (Linnaeus 1758) | Flight | Genetic studies | 600 km | Drag et al. (2015) |
| *Spasalus crenatus*, (MacLeay 1819) | Flight, walking | Colonization experiment | 2–6 m | Galindo-Cardona et al. (2007) |
| *Thanasimus dubius* (Fabricius 1777) | Flight | Mark-recapture | 1.25 km, 5% > 5 km, maximum one individual 8 km | Cronin et al. (2000) |
| *Tomicus piniperda* (Linnaeus 1758) | Flight | Field experiment | 95.3% 400 m, 4.7% 780–2000 m | Barak et al. (2000) |
| Diptera | | | | |
| *Criorhina floccosa* (Meigen 1822) | Flight | Genetic studies | No genetic differentiation in a ~10 × 10 km study area | Schauer et al. (2018b) |

(continued)

**Table 15.1** (continued)

| | Dispersal strategy | Method | Distance | Author |
|---|---|---|---|---|
| *Hammerschmidtia ferruginea* (Fallén 1817) | Flight | Mark-recapture | 5 km | Rotheray et al. (2014) |
| *Xylomya maculata* (Meigen 1804) | Flight | Genetic studies | No genetic differentiation in a ~10 × 10 km study area | Schauer et al. (2018b) |
| Hymenoptera | | | | |
| *Tetrastichus planipennisi* (Yang 2006) *(parasitoid of Agrilus planipennis)* | Flight | Flight mill | 1.81 km | Fahrner et al. (2015) |
| Isoptera | | | | |
| *Coptotermes formosanus* (Shiraki 1909) | Flight | Mark-recapture | 890 m | Messenger and Mullins (2005) |
| *Coptotermes formosanus* (Shiraki 1909) | Flight | Mark-recapture | 1.3 km | Mullins et al. (2015) |
| *Coptotermes formosanus* (Shiraki 1909) | Flight | Genetic studies | 510 m | Simms and Husseneder (2009) |
| Pseudoscorpiones | | | | |
| *Allochernes wideri* (C.L. Koch 1837) | Phoresy | Genetic studies | Small but significant genetic substructure at sites up to 900 km apart | Ranius and Douwes (2002) |
| *Larca lata* (Hansen 1884) | Phoresy | Genetic studies | Small but significant genetic substructure at sites up to 900 km apart | Ranius and Douwes (2002) |

If no range or further information is presented in the column "distance" the maximum distance measured or estimated in the study is given

## 15.4 Dispersal Distances: What Is Known for Particular Taxa?

### *15.4.1 Beetles*

The knowledge on dispersal seems to be best for saproxylic beetles compared to other taxa (see Table 15.1). Still there is only knowledge of few species in terms of their dispersal ability.

In the family of Scarabaeidae, *Osmoderma eremita* Scopoli, 1763 is the one species where most direct measurements of dispersal were conducted. Recorded maximum dispersal distances reported in different studies for *O. eremita* Scopoli, 1763 ranged from 190 m (Ranius and Hedin 2001) to 1500 m (Chiari et al. 2013). Physically *O. eremita* Scopoli, 1763 seems to be able to fly over larger distances, as in a tethered flight experiment a distance of ~2300 m was recorded (Dubois et al. 2010). This suggests that dispersal distances are influenced by local landscape and spatial distribution of suitable habitats. Shorter dispersal distances were recorded in the Swedish population with a high local density of suitable habitats surrounded by unsuitable matrix habitat, while in other study areas (Italy, France), larger dispersal distances were found where the beetles inhabit cork oaks in a large woodland area or chestnut trees that are patchily distributed in the landscape (Chiari et al. 2013; Dubois and Vignon 2008). Occurrence patterns on a larger geographic scale strongly suggest that *O. eremita* Scopoli, 1763 is dispersal limited as the presence of the beetle is positively correlated with spatial connectivity of habitat patches (Ranius et al. 2011). In the closely related species *Osmoderma barnabita* Motschulsky, 1845, Oleksa et al. (2013) estimated an average dispersal distance of 200 m and approximately 500 m in *Protaetia marmorata* Herbst, 1786 based on genetic data. Over a sampling range of 100 km, both species showed significant isolation by distance and thus limited gene flow due to the limited dispersal abilities (Oleksa et al. 2013).

In the family Tenebrionidae, the dispersal abilities of several beetle species with a very similar ecological niche have been studied. All species studied to date develop in and feed on the sporocarps of tinder or bracket fungi. Dispersal abilities of *Bolitophagus reticulatus* Linnaeus, 1767 have been measured with several different methods. An observed dispersal distances of 55 m in a field experiment (Sverdrup-Thygeson 2010) suggested that this beetle is likely to be dispersal limited. However, the dispersal abilities of *B. reticulatus* Linnaeus, 1767 should be much higher as the longest total flight time in flight mill-experiments for a single individual was 29 h 36 min which would correspond to an estimated dispersal distance of 125 km and median of ~7 km (Jonsson 2003). These results are corroborated by genetic analyses where no differentiation was found among populations as far apart as 200 km (Jonsson et al. 2003). Dispersal abilities of *B. reticulatus* Linnaeus, 1767 were compared to those of the rarer tenebrionid *Oplocephala haemorrhoidalis* Fabricius, 1787, which also feeds exclusively on tinder fungi. Both, flight mill experiments and genetic analyses suggested that the dispersal abilities were not as good as in *B. reticulatus* Linnaeus, 1767. While the median length of flight was estimated to be >12 km in *O. haemorrhoidalis* Fabricius, 1787, the maximum estimated flight time and distance was shorter (7 h 30 min and 29 km), and dispersal propensity was lower than in *B. reticulatus* (Jonsson 2003). Likewise genetic differentiation was moderate to strong in this species over the same geographic distance where no differentiation was found in *B. reticulatus* Linnaeus, 1767 (Jonsson et al. 2003). Studies on occurrence patterns on the one hand suggest that the beetle has excellent long-distance dispersal capabilities and is not dispersal limited as it occurs wherever the host fungus occurs (Jonsell et al. 2003). In contrast, another study shows habitat fragmentation may lead to a much higher differentiation in a fragmented landscape compared to a continuous area (Knutsen et al. 2000). A lack of spatial genetic substructure was similarly found for the fungus-associated *Diaperis boleti* Linnaeus, 1758 over a spatial scale of 150 km (Oleksa 2014). In the North American species *Bolitotherus cornutus* Panzer, 1794, mark-recapture data suggested a very limited movement radius of around 50 m (like in *B. reticulatus* Linnaeus, 1767, see above) (Starzomski and Bondrup-Nielsen 2002), while dispersal distances of 365 m were found in a colonization experiment (Whitlock 1992).

Dispersal in the family of Curculionidae has been studied for the subfamily Scolytinae, the bark beetles, as major forest pest species of economic interest. Measured dispersal distances in *Ips typographus* Linnaeus, 1758 ranged from 120 m (max. Distance at which traps with lure were placed in this mark-recapture study) (Zolubas and Byers 1995) to a range of 1.1 to 8 km in other studies and field experiments (Botterweg 1982; Dolezal et al. 2016; Weslien and Lindelöw 1990). The percentage of recaptured individuals was still around 2% of all marked individuals at the maximum distance sampled in these latter studies, suggesting that longer dispersal distances may occur under natural conditions. In addition, *I. typographus* Linnaeus, 1758 flies above the tree crowns which may allow the small beetles to be passively dispersed over larger distances by wind (Forsse and Solbreck 1985). Marked individuals of *Dendroctonus frontalis* Zimmermann, 1868 were found between 100 and 500 m from their releasing point (Cronin et al. 1999) and those of the common pine shoot beetle *Tomicus piniperda* Linnaeus, 1758 mostly within 400 m of the releasing point but a few up to 2 km away (Barak et al. 2000). For other Scolytinae, the estimated dispersal distances were much higher, with an estimated 10 to 80 km in a flight mill experiment for *Hylobius abietis* Linnaeus, 1758 (Solbreck 1980) or 23 h continuous flight in *Dendroctonus pseudotsugae* Hopkins, 1905, respectively (Borden and Bennett 1969). In mark-recapture experiment, many individuals were recaptured after a dispersal distance of 920 m, which was the furthest distance of traps from the site of release. Based on diffusion models, the authors estimate that nearly 50% of individuals of *Hylurgus ligniperda* Fabricius, 1787 disperse over at least 1 km and 1.6% further away than 5 km (Meurisse and Pawson 2017). The good dispersal abilities of this as well as another pine bark beetle species, *Hylastes ater* Paykull, 1800, were corroborated by colonization experiments using odor traps. Both species were caught in traps as far away as 26 km from the nearest pine resources (Chase et al. 2017). Based on mark-recapture studies, the dispersal distances of at least 50% of individuals of *Thanasimus dubius* Fabricius, 1777 (Cleridae), a predator of bark beetles in North America, were estimated to disperse at least 1.25 km, but around 5% should disperse over distances >5 km. The maximum dispersal distance of a marked individual was 8 km. Thus, the predator seems to have better or at least similar dispersal ability in comparison to its prey (Cronin et al. 2000).

Dispersal abilities of flightless Curculionidae were indirectly inferred by comparing occurrence patterns of woodlands in Northern Germany. The flightless weevils of the subfamily Cryptorhynchina *Acalles ptinoides* Marsham, 1802, *Trachodes hispidus* Linnaeus, 1758, and *Kyklioacalles navieresi* Boheman, 1837 (belonging to the subfamily Molytinae) were found only in ancient woodlands but not recent ones (Buse 2012), suggesting very strong dispersal limitation.

For Cerambycidae, longhorned beetles, dispersal distances vary considerably in the species that were studied to date, even in related species. The Japanese pine sawyer *Monochamus alternatus* Hope, 1843 seems to be a species with limited dispersal abilities as a dispersal distance of 59 m was observed (Shibata 1986b) using mark-recapture. Flight mill experiments on the congeneric *M. carolinensis* Olivier, 1792 suggest a better dispersal ability of this species, with mean flight distances being 2.2 km for both sexes (Akbulut and Linit 1999). In yet another congeneric, *M. galloprovincialis* Olivier, 1795, marked individuals were found at a distance of >400 m from the release site, while mean dispersal distance was app. 120 m (Torres-Vila et al. 2015). Based on modeling of dispersal kernels in a mark-recapture study, the estimated dispersal distance of *M. galloprovincialis* Olivier, 1795 is still larger though with >4 km (Etxebeste et al. 2016). Flight mill experiments again underscore the good dispersal abilities of *M. galloprovincialis* Olivier, 1795 with a mean estimated potential dispersal distance of 16 km and a maximum of up to 63 km (David et al. 2014). The good dispersal capacity of beetles of this genus was corroborated in a study on another two European species *M. sartor* Fabricius, 1787 and *M. sutor* Linnaeus, 1758 using a flight mill. The maximum distance flown in a single bout by *M. sartor* Fabricius, 1787 was 3.14 km, and the cumulative dispersal distance over the life span of a beetle was 7.5 km. The smaller *M. sutor* Linnaeus, 1758 flew even further, with a maximum flight distance of 5.56 km (Putz et al. 2016). The majority of marked and recaptured Asian longhorned beetles *Anoplophora glabripennis* Motschulsky, 1853 were found to disperse less than 1 km from the release site, while some individuals were caught at distances of 2.6 km from the release site (Smith et al. 2004). Earlier studies of *A. glabripennis* Motschulsky, 1853 showed slightly shorter dispersal distances (Smith et al. 2001).

Dispersal abilities of the threatened Rosalia longicorn *Rosalia alpina* Linnaeus, 1758 were studied using mark-recapture as well as genetic analyses. The maximum distance covered (which included flights over unsuitable matrix habitat) was 1600 m (Drag et al. 2011), suggesting good dispersal abilities. No genetic substructure was found among populations of *R. alpina* Linnaeus, 1758 as far apart as 600 km (Drag et al. 2015), suggesting that the observed dispersal distance translates into high levels of gene flow over large distances, in spite of habitat fragmentation. Dispersal abilities of *Cerambyx welensii* Küster, 1846 and *Cerambyx cerdo* Linnaeus, 1758 were estimated using mark-recapture methods in Spanish populations. Both species showed a pronounced dispersal polymorphism. While some individuals showed a high dispersal propensity and much larger dispersal distances than other individuals (*C. welensii* Küster, 1846, maximum recorded distance of 1100 m for a male and 580 m for a female; *C. cerdo* Linnaeus, 1758, 880 m for a male and 1700 m for a female), many individuals were sedentary and hardly moved away from the site of release (Torres-Vila et al. 2017). This subset of individuals should allow colonization of habitat patches that are further away. In contrast, in the flightless cerambycid *Morimus asper* Sulzer, 1776, only very few individuals left the point where they were released after marking, and the furthest dispersal distance measured was 451 m (Rossi de Gasperis et al. 2016).

Among elaterids, information on dispersal distance is available only for *Elater ferrugineus* Linnaeus, 1758, a facultative predator of *O. eremita* Scopoli, 1763. Here dispersal distances of more than 1.6 km were found using mark-recapture and a median dispersal distance of 214 m, suggesting again similar or better dispersal capacities of the predator in comparison to its prey (see above the clerid *T. dubius* Fabricius, 1777 and its bark beetle prey) (Zauli et al. 2014). Genetic analyses suggest a dispersal distance of 100 to ~650 m as isolation by distance was found at a scale of ~9 km, albeit in a fragmented agricultural landscape where this click beetle can mostly be found in old hollow trees along rural avenues (Oleksa et al. 2015).

In *Lucanus cervus* Linnaeus, 1758 (Lucanidae), telemetry studies revealed dispersal distances between 200 m in a Swiss population (Sprecher-Uebersax and Durrer 2001) and 2 km in a German population (Rink and Sinsch 2007). In another telemetry study conducted in a relict lowland forest in a nature reserve in Italy, the mean dispersal distance of *L. cervus* Linnaeus, 1758 males was 250 m compared to an average of 144 m for females (Tini et al. 2017).

The buprestid *Agrilus planipennis* Fairmaire, 1888 (emerald ash borer) has been shown to fly over distances of up to 1.13 km (Fahrner et al. 2015) to >6 km (Taylor et al. 2010) in flight mill experiments. As insects may show slower flight speed when tethered (see discussion of tethered flight experiments, Sect. 15.3.7), Taylor et al. (2010) measured the speed of flight in free-flying experiments in parallel. Flight distances obtained in the flight mill experiment were then calibrated with flying speed in free-flight and dispersal distances corrected. The median corrected flight distance of females was >3 km and 1% of females flew >20 km.

The passalid beetle *Spasalus crenatus* MacLeay, 1819 was shown to have very limited dispersal abilities. In a colonization experiment, beetles dispersed for 2 to 6 m only from a release point before initiating a colony. The beetles were functionally flightless as their wing muscles were not developed, strong enough to enable flight and thus most likely dispersed by walking (Galindo-Cardona et al. 2007). Similarly, the passalid *Odontotaenius disjunctus* Illiger, 1800 primarily disperses over short distances of on average 11.6 m by walking (Jackson et al. 2009) and has rarely be shown to fly over longer distances (Jackson et al. 2012).

The predator *Rhizophagus grandis* Gyllenhaal, 1827 (Rhizophagidae) was also shown to have good dispersal abilities as individuals were found at their prey 4 km from the release site (Fielding et al. 1991). In the scraptiid beetle *Anaspis ruficollis* Fabricius, 1792, inhabiting tree hollows but also lying deadwood, population genetic analyses did not uncover genetic differentiation in a ~10 × 10 km study area of large forest fragments. However, genetic differentiation was slightly stronger in this beetle species in comparison to the two dipteran species compared in the same study (Schauer et al. 2018b).

### 15.4.2 Other Saproxylic Taxa

For hoverflies and other dipteran species, not much is known about their dispersal abilities. In a mark-recapture study on the syrphid fly *Hammerschmidtia ferruginea*

Fallén, 1817, a dispersal distance of 5 km was shown (Rotheray et al. 2014). Schauer et al. (2018b) could show no genetic differentiation of the syrphid fly *Criorhina floccosa* Meigen, 1822 and the xylomid fly *Xylomya maculata* Meigen, 1804 in a ~10 x 10 km managed forest, suggesting good dispersal abilities of these two species.

The hymenopteran *Tetrastichus planipennisi* Yang, 2006, a parasitoid of the emerald ash borer *Agrilus planipennis* Fairmaire, 1888, has been shown to be able to disperse slightly further than its host. While *A. planipennis* Fairmaire, 1888 flew a maximum distance of 1.13 km, the parasitoid showed a maximum flight distance of 1.81 km under similar conditions in a flight mill experiment (Fahrner et al. 2015).

Winged sexuals of the Formosan subterranean termite *Coptotermes formosanus* Shiraki, 1909 have been shown to disperse over at least 500 m to 1300 m in an urban setting in New Orleans. Dispersing individuals could be assigned unambiguously to their parental colonies either based on multilocus genotypes (Simms and Husseneder 2009) or in mark-recapture experiments (Messenger and Mullins 2005; Mullins et al. 2015). Small flightless arthropods such as pseudoscorpions and mites often hitchhike on larger saproxylic insects for dispersal. Using population genetic analyses, Ranius and Douwes (2002) found very small genetic substructure among populations of *Allochernes wideri* C.L. Koch, 1837 and *Larca lata* Hansen, 1884 as far apart as 900 km, suggesting good passive dispersal through phoresy (Ranius and Douwes 2002). Nonetheless, *L. lata* Hansen, 1884 may still be dispersal limited as its occurrence was positively correlated with spatial connectance on larger spatial scales (Ranius et al. 2011).

## 15.5 Outlook and Conclusion

Researchers and naturalists alike often estimate dispersal abilities of particular taxa—or species—based on their morphology and notion of life-history traits as data on dispersal is often still scarce. To date dispersal distances have been measured mostly either for pest species or threatened species (often "flagship species"). Knowledge of dispersal behavior and its implications for gene flow, population persistence, and colonization of new habitats is still scarce. A better knowledge of dispersal abilities and behavioral aspects of dispersal are needed, especially with respect to the development of management strategies for saproxylic insects in managed forests or fragmented habitats.

Currently, there is ongoing debate in the field whether saproxylic insects are rather dispersal limited or habitat limited. Due to deforestation and ecological degradation of forests, connectivity and habitat availability are both low. Absence of a species in a seemingly suitable habitat patch is often interpreted as dispersal limitation. Local extinction may result from the absence of habitat, poor habitat quality, or unsuitable area around a habitat patch that is not crossed during dispersal (Fahrig 2013; Hanski et al. 1994). The relatively few population genetic analyses available to date suggest that saproxylic insects are often not dispersal limited on a local and regional scale—or at least not as much as assumed. However, this will depend strongly on the species studied as different taxa vary strongly in dispersal distances and dispersal abilities (e.g., passalids dispersing a few meters only in comparison to some flying cerambycids or scolytids that can disperse over several to dozens of kilometers). Studies on occurrence patterns over larger geographic scales have detected dispersal limitation for a broad range of different species. When forest fragments or other habitat structures are more isolated, fewer saproxylic insect species occur (Bergman et al. 2012; Ranius et al. 2011). Likewise, artificial deadwood structures mimicking tree hollows were less often colonized by saproxylic tree hollow specialists when placed further away from sources. As habitat quality was comparable, species have most likely been dispersal limited (Jansson et al. 2009).

Factors influencing different aspects of dispersal behavior, such as the decision to leave a patch, the movement pattern (e.g., what kind of matrix habitats are crossed during dispersal?), and the decision to settle at a particular site are often still unknown. These factors include the sex of an individual, body condition, feeding strategy, breadth of ecological niche, or competition. Even less is known about the interplay of several of these factors. However, such data is needed to assess whether structural connectivity among habitat patches also results in functional connectivity.

The use of a combination of methods that integrate several temporal and spatial scales would be desirable to characterize dispersal abilities of species. By combining mark-recapture techniques and population genetic analyses, the dispersal ability of a large proportion of individuals can be tested directly using the former, and the influence of the often small percentage of individuals dispersing over much larger distances on the population structure would be captured with the latter. And how strongly do dispersal distances vary with landscape and are they consistent over time? If such data was available for more species, this would allow for comparative analysis to be conducted, allowing more general conclusions of the dispersal abilities of species with similar ecological niches. For example, the suite of species of tenebrionid beetles feeding on fungal sporocarps seems to have relatively similar dispersal abilities, in spite of belonging to different genera and living on different continents. Does this hold for more groups of species with a similar ecological niche? How strongly is dispersal behavior influenced by spatial and temporal heterogeneity? In the light of climate change and anthropogenic habitat destruction, it is important to assess the plasticity or evolutionary potential of dispersal strategies for different species.

A better knowledge of dispersal of saproxylic insects is required for an understanding of ecological processes but also to inform management decisions for the conservation of threatened species. However, as dispersal is a highly complex phenomenon, more integrative studies would be vital that on the one hand examine physiological and behavioral aspects of dispersal and on the other hand measure dispersal distances using different methods. An increase in availability of data on dispersal collected with different methods will allow drawing more general conclusions and potentially also relatively well-informed predictions of the dispersal abilities of species.

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## Manuscript 4: Trophic structure of saproxylic beetle communities in tree hollows identified by stable isotope analysis

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BS, GG, EO and HF conceived the ideas and designed the methodology, BS, GG collected the data, BS and GG analyzed the data. BS, GG, EO and HF interpreted and discussed results. Figures and tables were created by BS. BS led the writing of the manuscript.

# Trophic structure of saproxylic beetle communities in tree hollows identified by stable isotope analysis

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## Abstract

1. Disentangling trophic relations and dietary information of species with a cryptic lifestyle is difficult. This is the case for saproxylic insects in tree hollows, where information on food resources and trophic relations are still rare.
2. The aim of this study was to characterise the food web of saproxylic beetle communities in tree hollows using stable isotope analysis ($^{15}$N and $^{13}$C).
3. We compared the feeding guild assignment of saproxylic beetle species derived from literature to stable isotope-based analysis. Further, we tested the feasibility of stable isotope analysis to discriminate different feeding guilds. We characterized the isotopic niche represented by the standard ellipse area (SEA) of each feeding guild. Within feeding guilds, we calculated the overlap, to test for functional niche redundancy or complementarity. To test for niche conservation, we tested the SEA overlap within families. Further, we investigated the distribution of biomass of all feeding guilds to test if beetle communities follow Eltonian pyramids. We investigated the influence of habitat heterogeneity and species diversity (ecosystem size hypothesis) on trophic chain length.
4. For most species, the assignment to a guild was congruent between literature and stable isotope analysis. Stable isotope signatures were suitable for distinguishing most feeding guilds except for some guilds with mixed feeding. We found a more omnivorous feeding behaviour of the mycetophagous guild compared to other guilds. Xylophagous and xylo-zoophagous feeding guilds showed a higher functional niche redundancy compared to mycetophagous and zoophagous guilds. Within families niche overlap was high, suggesting niche conservation.

Considering saproxylic beetles only, communities follow inverted Eltonian pyramids, as the highest trophic guilds (zoophagous guilds) constitute the highest biomass. Food chains within tree hollows were longer with a larger number of saproxylic beetle species present in a tree hollow, suggesting ecosystem size determining trophic chain length.

5. Maintaining a high diversity of saproxylic beetles and thus longer trophic chains will support essential ecosystem functions for the forest ecosystem, like controlling pest species due to the high amount of predatory species or nutrient cycling through decomposing species.

## Introduction

Trophic relations are an important factor in structuring communities as organisms compete for food sources or directly prey upon other organisms in the community. According to theory the trophic chain length (number of trophic guilds) is regulated by the productivity of a system (productivity hypothesis) (Pimm, 1982, Briand & Cohen 1987), species diversity, habitat availability and habitat heterogeneity (ecosystem size hypothesis) (Cohen & Newman 1991, Holt 1993), or the combination of both (productive-space hypothesis) (Schoener, 1989).

Dead wood food webs are very complex and consist of several trophic levels above the primary level (Stokland 2012). They comprise the basal trophic levels of decomposer, e.g. bacteria, fungi and detrivores, the consumers of dead organic matter (Bengon et al. 2006), followed by xylophages, organisms feeding on living wood ending in higher trophic levels of fungivores, scavengers and predators, as well as parasitoids and hyperparasitoids (Stokland 2012). The main substrate of tree hollows is wood mould, which collects at the bottom of the tree hollow. The wood mould is an assemblage of fungally decomposed wood, insect frass, carrion and excrements of different vertebrate and invertebrate species (Siitonen 2012). Over time, the tree hollow becomes larger, due to fungal decomposition and insect activity, and larger amounts of wood mould accumulate, and it becomes structurally more complex (Siitonen 2012). The different stages of decomposed wood offer a wide range of niches for different species with different habitat requirements (Speight 1989).

However, for species with a cryptic lifestyle, such as saproxylic beetles, it is often very difficult to obtain dietary information based on direct observations, leading to patchy information about their trophic relations. (Bouget et al. 2008, Bussler and Müller, 2009; Gouix et al., 2012). Speight (1989) coined the term ‘‘saproxylic’’ for species dependent on dead wood as a resource in at least one stage of their life cycle, either directly or indirectly (via consumption of wood-decomposing fungi or other saproxylic species). Saproxylic beetles account for a large proportion of forest diversity and are important for nutrient cycling and ecosystem functioning (Gouix et al. 2015; Grove 2002).

Trophic relations of saproxylic beetle communities are not well understood. This might be related to different facts: they are often very small in body size and difficult to sample (Bouget et al. 2008). Furthermore, many saproxylic beetle species are considered rare, especially in forests with a long management history (Grove 2002). Direct observations are difficult for many species because the access to some forms of dead wood such as tree hollows is difficult. In vivo feeding experiments are not feasible as most saproxylic insects are restricted to specific and stable microhabitats (Gouix et al. 2012, Müller et al. 2014, Quinto et al. 2015). Analysis of gut content may also be problematic as it only shows a snapshot of the food intake prior to sampling. Furthermore, some beetle species switch their diet during their development. For example, larvae of *Elater ferrugineus* (Violet Click Beetle) larvae are considered as predatory (Svensson et al. 2004), omnivorous or carnivorous (Whitehead 2003), or sapro-necrophagous (Iablokoff 1943, Brustel 2004), whereas adults either may not feed at all (Paulian 1988), feed on pollen and nectar (Mendel & Owen 1990) or are xylophagous (Seibold et al. 2014). The example of *E. ferrugineus* clearly shows the problems and uncertainties of describing the trophic niche of saproxylic beetles.

Stable isotope analysis can be used to infer the diet and trophic positions of species in a community (Post 2002) and has been shown to facilitate a precise distinction even of fine-scaled differences in trophic positions in very small arthropods (Maraun et al. 2014). Trophic position can be assessed via stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) ratios, as consumers are enriched in the heavy isotopes $^{15}N$ and $^{13}C$ compared relatively to their diet (DeNiro & Epstein 1981, McCutchan et al. 2003). Furthermore, the isotopic ratios of carbon (C) and nitrogen (N) reflect an integrated measure of diet over time (Hood-Nowotny & Knols 2007).

The aim of this study was to elucidate the trophic relations of saproxylic beetle communities in tree hollows using stable isotope analysis. Specifically, we aim to a) Compare feeding guilds derived from literature with the assignment based on stable isotope analysis, b) Test the feasibility of stable isotope signature to discriminate different feeding guilds, c) Characterize the tropic niche space of species within and among feeding guilds, to test whether species are functionally redundant within guilds and whether niches are conserved on the family level, d) Examine the distribution of biomass over feeding guilds, to see if saproxylic beetle communities are following Eltonian pyramids, where basic feeding guilds should have the highest biomass in a community, e) Investigate if the ecosystem size hypothesis applies for saproxylic beetles by testing the effect of number of beetle species and degree of decomposition of the wood mould, on the trophic chain length.

## Material and Methods

### Sampling of saproxylic beetles

Saproxylic beetles were collected from April to August with emergence traps from 40 tree hollows in beech trees in 2014 and a subset of 23 of these hollows in 2015 in the forest management district Ebrach in the northern Steigerwald (N 49°50´; E 10°29´) (for detailed information see Schauer et al. 2017). Emerging beetles were directly collected and conserved in 99.8 % ethanol in the traps to preserve the insects. All beetles were identified to species level by an expert for saproxylic beetles (H. Bußler).

### Sample preparation

Prior to stable isotope analysis, the body length (measured from the tip of the abdomen to the clypeus) was measured with a Leica M165C dissection microscope and a Leica DFC 298 camera using the Leica Application suite V4 (Leica Biosystems, Nussloch, Germany). Afterwards, the abdomen of all individuals was removed to avoid the bias of results by gut content. Undigested food in the gut may differ from the stable isotope signature from the body biomass and may thus lead to erroneous results, especially in omnivores where current gut content may have a higher or lower stable isotope signature than body tissues of the respective insect. Stable isotope signature of the body tissue integrates food intake over time while gut content is only a snapshot.

### Wood mould preparation

The wood mould of each tree hollow was sampled from the base of the tree hollow at a depth of 2 cm below the surface of the mould to 7 cm depth for subsequent analysis in both years in April. To stop the decomposition processes of the wood mould, it was stored in a freezer at -20°C. The wood mould was assigned to four categories according to its degree of decomposition, ranging from 1 (low decay) to 4 (high decay). With the ongoing decay of the wood mould, it becomes darker in colour (from yellow/light brown to dark brown/black) and the woody parts become finer (from clearly visible woody parts to almost no visible woody parts) (for further details see Schauer et al. 2018). Stable isotope signatures of wood mould were used as a baseline for normalization of data to enable comparisons of beetles collected from different tree hollows (see below). The stable isotope analysis of wood mould was conducted together with the beetle samples after the sampling season.

### Stable isotope analysis

Before stable isotope analysis, all samples (wood mould and beetles) were oven dried overnight at 105 °C. Relative C and N isotope natural abundances were measured in a dual element analysis mode with an elemental analyser (1108; Carlo Erba Instruments, Milano, Italy) coupled to a continuous flow isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany) via a ConFlo III open-split interface (Thermo Fisher Scientific, Bremen, Germany) as described in Bidartondo et al. (2004). Measured relative isotope abundances are denoted as δ values that were calculated according to the following equation: $\delta^{13}C$ or $\delta^{15}N$, $= (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$ (‰), where $R_{\text{sample}}$ and $R_{\text{standard}}$ are the ratios of heavy to light isotope of the samples and the respective standard. Standard gases (Riessner, Lichtenfels, Germany) were calibrated with respect to international standards ($CO_2$ vs. PDB, $N_2$ vs. $N_2$ in air) with the reference substances ANU sucrose and NBS19 for the C isotopes, N1 and N2 for the N isotopes all provided by the IAEA (International Atomic Energy Agency, Vienna, Austria). Reproducibility and accuracy of the C and N isotope abundance measurements were routinely controlled by measuring the laboratory standard acetanilide (Gebauer & Schulze, 1991). In relative C and N isotope natural abundance analyses, acetanilide was routinely analysed with variable sample weight at least six times within each batch of 50 samples. The maximum variation in $\delta^{13}C$ and $\delta^{15}N$ both within and between batches was always below 0.2‰. Total nitrogen concentrations of the samples were calculated from sample weights and peak areas using a six-point calibration curve per sample run based on measurements of the laboratory standard acetanilide with a known nitrogen concentration of 10.36% (Gebauer & Schulze, 1991).

To compare the N and C stable isotope abundances between individuals of different trees we used the isotopic enrichment factor approach to normalize the data (Preiss & Gebauer, 2008) with the stable isotope signatures of wood mould as a reference. The enrichment factors ($\varepsilon$) were calculated as $\varepsilon = \delta_S - \delta_{REF}$, where $\delta_S$ is the single $\delta^{13}C$ and $\delta^{15}N$ value of an individual and $\delta_{REF}$ is the $\delta^{13}C$ and $\delta^{15}N$ of the wood mould of the respective tree hollow the individual emerged from. Most beetle samples were enriched in $^{13}C$ and $^{15}N$ compared to would mould (see Table 1).

### Feeding guild assignment based on the literature

All species were assigned to one of seven feeding guilds, respectively (d = detritivorous, m = mycetophagous, x = xylophagous, xm = xylo-mycetophagous, xs = xylo-saprophagous, xz = xylo-zoophagous, z = zoophagous, and n.a. = species without information) according to the classification of Köhler (2000) and Seibold et al. (2015), where dietary information for most saproxylic beetle species in Germany is provided. The classifications are based on expert knowledge and to a minor part direct observation. The classification of Seibold et al. (2015) is mainly based on the publication of Köhler (2000), but Seibold et al. (2015) do not use mixed feeding guilds (xylo-mycetophagous, xylo-saprophagous, xylo-zoophagous). Further Seibold et al. (2015) introduce the detritivorous feeding guild, which is not present in Köhler (2000). Instead, Köhler (2000) uses the term saprophagous in the mixed guilds but not as a separate guild. Per definition the terms detritivorous and saprophagous are synonyms. They describe species feeding on dead organic matter and the associated microbial and fungal biota (Begon et al., 2006). We decided to keep both terms for two reasons. Firstly, we do not know on which basis Seibold et al. (2015) chose the term detritivorous instead of saprophagous, and secondly, for some species, Köhler (2000) gave no information but Seibold et al. (2015) classified these species as detritivorous.

### Discrimination of feeding guilds (NMDS)

For all statistical analyses and graphical outputs, we used the software environment R (R version 3.4.1, R Development Core Team 2008). We conducted non-metric multidimensional scaling to test if the different feeding guilds can be differentiated based on their isotopic signatures. We used the Bray-Curtis index to calculate the distance matrix between all beetle samples derived from $\delta^{13}C$ and $\delta^{15}N$ values using the function *metaMDS* with 100 permutation and two dimensions in the R-package *vegan* v. 2.4-3 (Oksanen et al. 2017). To test for overall significant differences of the group means we performed a permutational MANOVA with 9999 permutations using the function *adonis* in the R-package *vegan* v. 2.4-3 (Oksanen et al. 2017). To test for pairwise significant differences of the group means, we used the R package *pairwiseAdonis* v0.0.1 (Martinez Arbizu 2017) with Benjamini – Hochberg correction (Benjamini & Hochberg 1995).

Estimation of biomass

To compare the biomass per feeding guild we summed up the dry biomass of each feeding guild per tree hollow and biomass of each feeding guild overall tree hollows. The dry weight biomass per individuals was calculated based on the body size of the beetle with the power function of Rogers et al. (1976).

Characterization of trophic niche

Standard ellipse areas (SEA) reflect the trophic niche width. We calculated the SEA, using the enrichment factors ($\varepsilon^{13}C$ and $\varepsilon^{15}N$), for each species per feeding guild, between guilds and between species in the same family and the overlap of SEA in these groups using the R package *SIBER* (Jackson et al. 2011). To account for small sample sizes and to increase the accuracy of SEA the corrected standard ellipse area (SEAc) was also calculated. The isotopic niche overlap was also calculated using the SEAc, with 100% indicating total overlap. This measure can be used as a proxy for the similarity in the species´ diet (Jackson et al. 2011). For comparison among species within a feeding guild, the 95% confidence interval for the standard ellipse was calculated via bootstrapping (bootstrap = 100000, thinning = 1000). Species with fewer than five individuals were excluded for these calculations as the results would not be statistically meaningful. Detritivorous, xylo-mycetophagous and xylo-saprophagous species were not considered for overlap calculations, as there was only one species per guild and species without information were also excluded. This led to the exclusion of 47 of the 74 species.

Factors influencing the number of feeding guilds per tree hollow

According to ecosystem size hypothesis, the habitat complexity and species diversity might influence the trophic chain length. To test this, we used the degree of decomposition as a proxy for habitat complexity because the complexity of the tree hollows increases with ongoing decomposition (Siitonen 2012). The number of saproxylic beetle species was used to test if species diversity influences trophic chain length. To quantify the effect of the degree of decomposition of the wood mould and the number of saproxylic beetle species on the trophic chain length, two generalized linear models (GLM) with Poisson error distribution were implemented for 2014 and 2015, respectively.

## Results

Species assignment

In total we analysed 74 species of which, based on literature (Köhler 2000, Seibold et al. 2015), two species are classified as detritivorous, 13 species mycetophagous, one species myceto-saprophagous, 18 species xylophagous, 4 species xylo-mycetophagous, two species xylo-saprophagous, 8 species xylo-zoophagous, 25 species zoophagous and one species without information (see Table 1).

Isotopic signature of wood mould

The $\delta^{13}C$ and $\delta^{15}N$ values of the sampled wood mould ranged from -29.43 to -23.11 and -4.49 to 5.81, respectively in 2014 and from -27.98 to -22.92 and -5.18 to 2.61, respectively in 2015 (see Table A1). The $\delta^{13}C$ values were negatively correlated with the degree of decomposition (Pearson's product-moment correlation $\delta^{13}C$, $t = -2.32$, $df = 78$; $p < 0.05$), but not the carbon concentration (Pearson's product-moment correlation $\delta^{13}C$, $t = -1.48$, $df = 78$; $p > 0.05$). In contrast, neither $\delta^{15}N$ values nor the nitrogen content in the wood mould were correlated with the degree of decomposition (Pearson's product-moment correlation $\delta^{15}N$, $t = 1.8$, $df = 78$; $p > 0.05$; nitrogen content, $t = 1.26$, $df = 78$, $p > 0.05$).

Isotopic signatures of saproxylic beetles and feeding guilds

The $\varepsilon^{13}C$ and $\varepsilon^{15}N$ values for all species ranged from -8.15 to 11.23 and -8.57 to 15.71, respectively.

In detail the $\varepsilon^{13}C$ and $\varepsilon^{15}N$ values range for a) detritivorous species from -3.18 to 6.31 and -4.38 to 7.69, b) mycetophagous species from -8.15 to 10.29 and -6.16 to 9.77, c) myceto-saprophagous species from 3.28 to 9.66 and 0.39 to 5.69, d) xylophagous species from -0.11 to 8.68 and -8.57 to 9.21, e) xylo-mycetophagous ranged from -0.94 to 8.95 and -2.96 to 15.71, f) xylo-saprophagous from 0.86 to 4.19 and 0.32 to 5.04, g) xylo-zoophagous from -0.16 to 8.55 and 0.04 to 11.26, h) zoophagous species from -2.1 to 7.64 and -3.12 to 12.05 and e) species without information from 0.63 to 2.22 and 2.86 to 3.01 (see Table 1; Table A2 & Fig 1).

Discrimination of feeding guilds

The NMDS of Bray-Curtis distances based on $\varepsilon^{13}C$ and $\varepsilon^{15}N$ values showed that feeding guilds can be distinguished via stable isotope analysis, with a stress value of 0.08, indicating a good fit. Furthermore, the MANOVA showed significant differences of group centroids ($df = 7$, $R^2 = 0.11$, $p < 0.01$) (Fig A1). The pairwise comparisons of feeding guilds showed significant differences of the group means in 13 out of 28 comparisons (Table 2).

Niche breadth of feeding guilds

The detritivorous, mycetophagous and xylo-mycetophagous show a higher SEAc and thus a more omnivorous feeding behaviour than the other guilds. The niche breadth represented by the SEAc for a) the detritivorous guild was 25.03‰$^2$ b) the mycetophagous guild was 25.34‰$^2$ c) the myceto-saprophagous guild was 7.6‰$^2$ d) the xylophagous guild species guild was 13.09‰$^2$ e) the xylo-mycetophagous guild was 18.41‰$^2$ f) the xylo-saprophagous guild was 4.45‰$^2$ g) the xylo-zoophagous guild was 13.93‰$^2$ and h) the zoophagous guild was 14.83‰$^2$. The average SEAc overlap between the feeding guilds was 39.16% (SD±16.88) with mycetophagous and xylo-saprophagous guilds having the lowest overlap (17.57%) and the zoophagous and the xylo-mycetophagous guild the highest (Fig 2, Table A4).

### Niche breadth and overlap within feeding guilds

To examine if species within the same feeding guild are functionally redundant and potentially competing for food resources (high SEA overlap) or are functionally complementary and specialized in their diet (low SEA overlap), we calculated the SEAc per species within the same feeding guild and their overlap. The xylophagous and xylo-zoophagous guild show a higher functional redundancy compared to the mycetophagous and zoophagous guild, where we found a higher functional complementarity. The mean niche breadth and overlap or niche breath for guilds with only one species was a) 21.95‰$^2$ within the detritivorous guild, b) 15‰$^2$ (SD±9.56) within the mycetophagous guild with an average overlap of 29.23% (SD ± 24.36), c) 11.29‰$^2$ (SD±5.75) within the xylophagous guild with an average overlap of 36.95% (SD ± 13.5%), d) 9.15‰$^2$ within the xylo-mycetophagous guild, e) 4.61‰$^2$within the xylo-saprophagous guild, f) 12.56‰$^2$ (SD±1.77) within the xylo-zoophagous with an average overlap of 46.8% (SD ± 11.78%), g) 9.51‰$^2$ (SD±5.84) within the zoophagous guild with an average overlap of 22.29% (SD ± 12.76%) (Table A4).

### Niche breadth and overlap among species within the same family

Species within the same family should show a high overlap of their trophic niche if they are conserved in their diet. Overall, we found a high overlap within the species of the same family, indicating trophic niche conservation.

Having a look at the families themselves the SEAc overlap of species within a) Anobiidae was 21.48% and, b) 29.7% within zoophagous Elateridae , c) 10.4% within zoophagous Histeridae, d) 66.43% (SD ± 7%) within mycetophagous Scolitidae with the lowest overlap between *Cyclorhipidion bodoanus* and *Xyleborus dispar* (56.84%) and the highest overlap between *Cyclorhipidion bodoanus* and *Xyleborus saxeseni* (78.54%), e) 44.5% (SD ± 15.6%) within xylo zoophagous Scraptiidae with the lowest overlap between *Anaspis thoracia* and *Scraptia fuscula* (30.19%) and the highest overlap between *Anaspis ruficollis* and *Anaspis thoracica* (66.2%), f) 53.2% (SD ± 1.2%) within zoophagous Staphilinidae with the lowest overlap between *Hapalaraea pagmaea* and *Hesperus rufipennis* (51.49%) and with the highest overlap between *Hesperus rufipennis* and *Quedius truncicola* (54.21%). (Table A5).

### Distribution of biomass among feeding guilds

Considering the total biomass over all tree hollows, we found inverted Eltonian pyramids, where zoophagous species (zoophagous and xylozoophagous guild) contribute the highest biomass. In detail the dry biomass per feeding guild divides as follows: detritivorous species have the highest biomass in 1 of 40 tree hollows and 0.75% of total biomass over all tree hollows, mycetophagous species have the highest biomass in 14 of 40 tree hollows and 9.92% of total biomass over all tree hollows, myceto-saprophagous species have the highest biomass in 0 of 40 tree hollows and 0.07% of total biomass over all tree hollows, xylophagous species have the highest biomass in 3 of 40 tree hollows and 22.95% of total biomass over all tree hollows, xylo-mycetophagous have the highest biomass in 3 of 40 tree hollows and 5.54% of total biomass over all tree hollows, xylo-saprophagous species have the highest biomass in 1 of 40 tree hollows and 7.56% of total biomass over all tree hollows, xylo-zoophagous species have the highest biomass in 9 of 40 tree hollows and 27.87% of total biomass over all tree hollows and zoophagous species have the highest biomass in 8 of 40 tree hollows and 23.98% of total biomass over all tree hollows (Table A3).

Effect of wood mould decomposition and species number on trophic chain length

Across the 40 hollows sampled in 2014 the number of beetle species had a significant effect on the number of feeding guilds (positive relationship, estimate 0.08, standard error (SE) 0.02, $p < 0.001$). The degree of decomposition had no significant effect on the number of feeding guilds (hump-shaped relationship, Estimate -0.04, SE 0.11, $p > 0.05$). Across the 23 hollows sampled again in 2015 the biomass of beetles had a significant effect on the number of feeding guilds (positive relationship, Estimate 0.06, SE 0.01, $p < 0.001$). The degree of decomposition had no significant effect on the number of feeding guilds (hump-shaped relationship, Estimate 0.02, SEr 0.16, $p > 0.05$)

## Discussion

All species of our study were assigned to their feeding guild according to a combination of the publications by Seibold et al. (2015) and Köhler (2000). Comparing the literature-based information on the feeding guild and the stable isotope analysis we obtained comparable results for the classification of the trophic niches of saproxylic beetles. The stable isotope signature ($^{15}$N) is always dependent on the resource a species consumes. For example, the zoophagous *Tillus elongatus,* a member of the highest trophic level in our study, feeds on the larvae of the genus *Anobium* (personal communication H. Bußler), members of the xylophagous guild. This relation is also represented well in our study as *Tillus elongatus* shows low $\varepsilon^{15}$N values compared to the other zoophagous species, but it`s potential prey *Anobium nitidum* also has the lowest $\varepsilon^{15}$N values.

In our study *Orchesia micans* and *Arpidiphorus orbiculatus,* both members of the mycetophagous guild, are among the species with the highest $\varepsilon^{15}$N values, even higher than most zoophagous species. However, this seems plausible, as saprotrophic fungi are heterotrophic organisms and can, therefore, show high $\delta^{15}$N values (Henn & Chapela, 2001; Mayor, Schuur and Henkel, 2009). Thus, mycetophagous species feeding on fungi with high $\delta^{15}$N values might show higher enrichment than zoophagous species.

We used the stable isotope signatures to test if feeding guilds can be differentiated in an ordination space (NMDS). The main feeding guilds (zoophagous, mycetophagous and xylophagous) were clearly distinguishable, as the centroids of these groups were significantly different to each other. The detritivorous and myceto-saprophagous guilds, represented by only one and four species respectively, can only be distinguished from the zoophagous and xylo-zoophagous guild and showed the highest overlap to the mycetophagous guild. Species classified as either saprophagous or detritivorous species in the literature did not differ in their isotopic signature, stressing that the two terms describe the same trophic niche. The isotopic niche of the xylo-zoophagous feeding guild was clearly separated from both, the xylo- and the zoophagous guild. The species of the xylo-zoophagous guild showed high $\varepsilon^{15}$N and $\varepsilon^{13}$C values, indicating additional food sources even higher enriched in $\varepsilon^{15}$N and $\varepsilon^{13}$C compared to the other species in the xylophagous and zoophagous guild, respectively. The only two species classified as xylo-saprophagous species were enriched in $\varepsilon^{15}$N compared to the purely xylophagous species. This might be due to a higher $\varepsilon^{15}$N in sap compared to woody material. The other species assigned to mixed guilds (myceto-saprophagous and xylo-mycetophagous) could not be distinguished from the main feeding guilds (myceto- and xylophagous).

Within a community or a trophic level species might compete for a resource or have a similar role in ecosystem functioning (functional niche redundancy) (Lawton, 1994, Rosenfeld, 2002).

The opposite is avoiding competition by specialising in a different kind of diet or having a different functional role (functional niche complementarity). Functional complementarity can promote diversity and has a positive effect on the ecosystem functioning (Levine & HilleRisLambers 2009), but also functional redundancy can help to promote ecosystem stability in case of perturbations (Walker 1995). The xylophagous guild and the xylo-zoophagous guild show higher functional redundancy or interspecific competition as they have the highest average overlap among species within the feeding guild. For the xylophagous feeding guild the species *Alosterna tabacicolor*, *Ischnomera sanguinicollis, Ptilinus pecticornis* and *Rhizophagus bipustulatus* seem to be more specialised in their diet, as they have low SEA. In contrast, *Anobium nitidum* has a larger isotopic niche, potentially due to the small number of individuals tested. However, the trophic niche of *Anobium nitidum* is distinct from that of *Ptilinus pecticornis* suggesting niche complementarity. Within the xylo-zoophagous species, *Scraptia fuscula* seems to be more distinct in comparison to the other species, as the SEA overlap is lower than between all other species in this guild. Considering the high niche redundancy, interspecific competition within the same feeding guild for resources might occur and species showing a lower overlap might try to avoid competition by switching to a different or an additional food source.

The mycetophagous and zoophagous species have a lover overlap among species within the feeding guild, indicating stronger functional complementarity or avoidance of competition. For mycetophagous species the bark beetles show the largest SEA with a high overlap, indicating a similar trophic niche and a low specificity in their diet. In comparison, *Mycetophagus populi* and *Orchesia micans* have very small SEA and show the lowest overlap of species within the mycetophagous feeding guild. This suggests that these species are more specialized and likely feed on different parts of the same fungus or more likely, on completely different fungi. Thus, within the mycetophagous guild, there is a redundancy among bark beetles but complementarity to *Mycetophagus populi* and *Orchesia micans.* Among the zoophagous species, *Hapalaraea pygmaea, Hesperus rufipennis* and *Quedius truncicola* seem to be the most generalized predators with relatively large niche breadth. All other zoophagous species had smaller trophic niches and should thus be more specialized predators, with *Plegaderus dissectus* showing the smallest trophic niche. High SEA overlap among species within the same family suggests that the beetle families in our study are conservative in their trophic niches. Consequently, resource competition between closely related species might be quite high.

According to general theory on the distribution of biomass within an ecosystem, the trophic level of predators is always supposed to have less biomass then its prey or the trophic levels below (Bodenheimer 1938, Elton 1927, Berg & Bengtsson 2007). In the case of the saproxylic beetle communities in this study, we find a high biomass of the zoophagous (purely zoophagous and xylo-zoophagous) guilds, which is often higher than the biomass of all lower feeding guilds and thus showing inverted Eltonian pyramids. However, we have only considered saproxylic beetles and the biomass of other important taxa within saproxylic communities such as collembolans and Diptera was not included in the calculation. Many saproxylic beetle larvae feed on a variety of different prey items present in the tree hollows of which collembolans and dipteran larvae supposedly account for the biggest proportion (Köhler 2000). Thus, we assume if considering all potential prey items in a tree hollow general theory on the distribution of biomass holds and biomass distributions among trophic levels should follow an Eltonian pyramid.

Theory on the predicted length of trophic chains suggests, that either the productivity of a system

(productivity hypothesis) (Pimm, 1982, Briand & Cohen 1987), or species diversity, habitat availability and habitat heterogeneity (ecosystem size hypothesis) (Cohen & Newman 1991, Holt 1993), or the combination of both (productive-space hypothesis) (Schoener, 1989) are the determining factors. Here we assumed that the degree of decomposition might be affecting the food chain length. At medium stages of decomposition, the amount of the important wood mould is increased, nutrient availability is highest and medium stages of decay show the highest habitat complexity (Siitonen 2012), supporting a broad range of species and potentially larger communities (Schauer et al. 2018, Sverdrup-Thygeson et al. 2010). However, we could not find an effect of degree of decomposition of the wood mould on the number of feeding guilds. The number of feeding guilds within tree hollows was positively correlated with the number of saproxylic beetle species in both years. This finding indicates that the ecosystem size hypothesis might hold true for saproxylic beetle communities in tree hollows and thus a functionally diverse community is supported by a high species diversity.

One shortcoming of stable isotope analysis is the inability to assign a species to a certain feeding guild only based on its stable isotope signature. E. g., mycetophagous species feeding on highly $^{15}$N enriched fruiting bodies of fungi could potentially be classified as zoophagous based on stable isotopes only (like the mycetophagous species *Arpidiphorus orbiculatus*, see above). Thus, to achieve a reliable assignment to a certain feeding guild additional knowledge and a combination of methods is needed. To get more insights into the trophic relationship of saproxylic beetles in tree hollows it is important to get detailed knowledge of the basic food sources, especially the components of the wood mould and the associated fungi. Further, the isotopic signature of other taxa, like collembolans and dipterans should also be considered, as they contribute high biomass in tree hollow communities (Köhler 2000) and thus also potential food sources for zoophagous species.

In the present study, we provide insight into the food web of saproxylic beetle communities using stable isotope analysis. We show that the food webs of saproxylic beetles are complex and comprise several feeding guilds and a high degree of omnivory. The trophic structure of saproxylic beetle communities in tree hollows is comparable to brown food webs in soil where with detritus and organic humus as basal food resources. In soil ecosystems, food webs are mostly comprised of two trophic levels, decomposers and predators (Scheu & Falca 2000, Digel et al. 2014). In soil ecosystems, the high degree of omnivory in both trophic levels is due to opportunistic feeding and special foraging strategies (Scheu & Setälä 2002). In tree hollow food webs, we also found high levels of omnivory in the different feeding guilds. Xylophagous and the wood boring species of the mycetophagous guild seem to feed on a large variety of food sources and predatory species may unselectively feed on different prey items.

Maintaining a high diversity of saproxylic beetles and thus longer trophic chains will support essential ecosystem functions for the forest ecosystem, like controlling pest species due to the high amount of predatory species or nutrient cycling through decomposing species.

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## Figures

Fig 1: Boxplot of ε15N values of saproxylic beetles assigned to their feeding guild according to Seibold et al. (2015) and Köhler (2000). Dashed lines show 3‰ difference in $\varepsilon^{15}N$ values, indicating a trophic level.

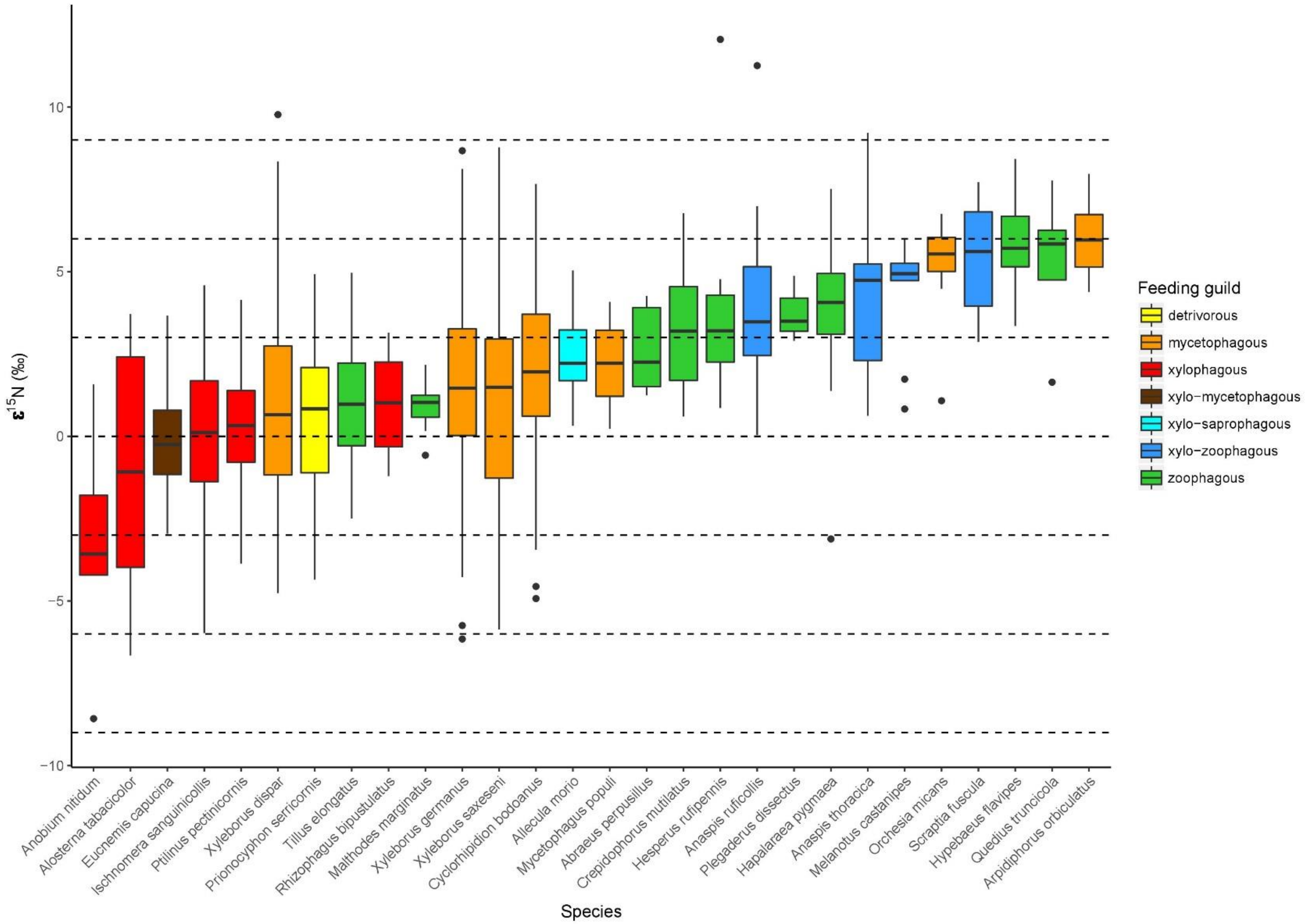
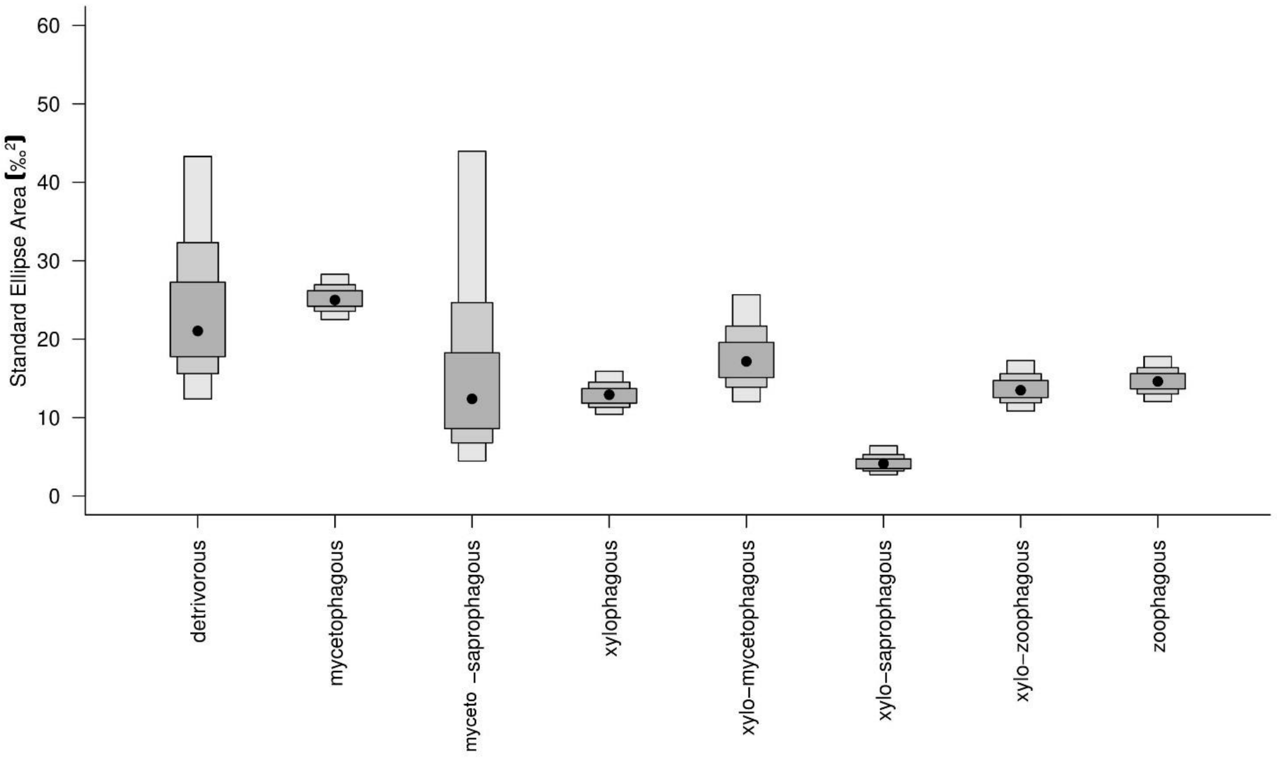


Fig 2: Density plots showing the confidence intervals of the standard ellipse areas (SEAc) for all feeding guilds.



## Tables

Table 1: Information on species; number of tree hollows they emerged from; feeding guild 1 (classification according to Seibold et al. 2015 & Köhler 2000), feeding guild 2 (classification according to Seibold et al. 2015) d = detritivorous, m = mycetophagous, m = myceto-saprophagous, x = xylophagous, xm = xylo-mycetophagous, xs = xylo-saprophagous, xz = xylo-zoophagous, zoo = zoophagous, n.a. = without dietary information; number of individuals; range, mean and standard deviation (SD) of $\delta^{13}C$, $\delta^{15}N$, $\varepsilon^{13}C$ and $\varepsilon^{15}N$; standard ellipse area (SEA) and corrected standard ellipse area for small samples (SEAc) of $\varepsilon^{13}C$ and $\varepsilon^{15}N$. For the calculation of means and SEA/SEAc species with less than five individuals were excluded, as the results would not be statistically meaningful.

| Species | # of tree hollows | Feeding guild 1 | Feeding guild 2 | # individuals | Range δ15N | mean δ15N | SD δ15N | Range δ13C | mean δ13C | SD δ13C | Range ε15N | mean ε15N | SD ε15N | Range ε13C | mean ε13C | SD ε13C | SEA | SEAc |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Abraeus perpusillus* | 4 | z | z | 5 | 0.27 to 2.38 | 1.43 | 0.84 | -23.64 to -22.12 | -22.88 | 0.54 | 1.24 to 4.26 | 2.64 | 1.23 | 1 to 2.68 | 1.93 | 0.56 | 2.70 | 3.60 |
| *Acalles hypocrita* | 2 | n.a | n.a | 2 | 1.18 to 1.75 | - | - | -25.33 to -23.79 | - | - | 2.86 to 3.01 | - | - | 0.63 to 2.22 | - | - | - | - |
| *Aderus populneus* | 1 | xm | x | 1 | 14.6 | - | - | -21.07 | - | - | 15.71 | - | - | 4.94 | - | - | - | - |
| *Allecula morio* | 3 | xs | x | 21 | -2.5 to 3.23 | 0.37 | 1.33 | -25.33 to -22.7 | -23.83 | 0.93 | 0.32 to 5.04 | 2.99 | 1.24 | 0.86 to 4.19 | 2.66 | 1.07 | 4.38 | 4.61 |
| *Alosterna tabacicolor* | 3 | x | x | 12 | -9.48 to 1.91 | -3.19 | 3.50 | -24.43 to -20.7 | -22.44 | 1.01 | -6.66 to 3.72 | -1.03 | 3.38 | 2.28 to 5.59 | 3.62 | 1.01 | 9.42 | 10.36 |
| *Ampedus nigroflavus* | 1 | x | x | 1 | -0.58 | - | - | -22.14 | - | - | 1.32 | - | - | 4.49 | - | - | - | - |
| *Ampedus pomorum* | 1 | x | x | 3 | 1.23 to 2.1 | - | - | -25.39 to -22.59 | - | - | 3.04 to 4.08 | - | - | 0.57 to 2.45 | - | - | - | - |
| *Anaspis frontalis* | 3 | xz | x | 3 | 0.47 to 4.64 | - | - | -22.97 to -20.07 | - | - | 1.87 to 5.7 | - | - | 4.21 to 7.12 | - | - | - | - |
| *Anaspis marginicollis* | 4 | xz | n.a | 4 | -0.68 to 6.03 | - | - | -22.81 to -21.57 | - | - | 1.26 to 7.58 | - | - | 2.63 to 3.6 | - | - | - | - |
| *Anaspis ruficollis* | 12 | xz | x | 25 | -2.05 to 8.93 | 1.65 | 2.28 | -25.15 to -18.94 | -21.98 | 1.34 | 0.04 to 11.26 | 3.93 | 2.29 | 1.48 to 8.55 | 4.66 | 1.54 | 11.29 | 11.79 |
| *Anaspis rufilabris* | 4 | x | x | 4 | 0.7 to 4.34 | - | - | -23.21 to -20.82 | - | - | 4.54 to 6.15 | - | - | 4.34 to 5.19 | - | - | - | - |
| *Anaspis thoracica* | 10 | x | x | 13 | -1.11 to 7.23 | 1.47 | 3.94 | -26.05 to -20.38 | -22.08 | 1.57 | 0.62 to 9.21 | 3.13 | 4.14 | -0.02 to 5.58 | 3.76 | 1.70 | 13.54 | 14.77 |
| *Anisotoma humeralis* | 1 | m | m | 1 | 6.1 | - | - | -21.16 | - | - | 7.55 | - | - | 6.03 | - | - | - | - |
| *Anobium costatum* | 1 | x | x | 1 | 0.46 | - | - | -24.43 | - | - | 1.56 | - | - | 1.57 | - | - | - | - |
| *Anobium nitidum* | 1 | x | x | 5 | -9.68 to 0.48 | -4.42 | 3.31 | -24.59 to -20.91 | -22.95 | 1.62 | -8.57 to 1.58 | -3.31 | 3.31 | 1.42 to 6.2 | 3.50 | 2.16 | 16.74 | 22.32 |
| *Arpidiphorus orbiculatus* | 1 | m | m | 6 | 3.43 to 6.42 | 4.64 | 0.94 | -22.58 to -19.38 | -20.72 | 1.09 | 4.39 to 7397 | 6.02 | 1.20 | 2.88 to 5.91 | 4.74 | 1.21 | 5.15 | 6.44 |
| *Calambus bipustulatus* | 1 | xz | x | 1 | 0.86 | - | - | -24.99 | - | - | 1.96 | - | - | 1.02 | - | - | - | - |
| *Cerophytum elateroides* | 1 | x | x | 1 | -3.3 | - | - | -22.49 | - | - | -1.41 | - | - | 3.24 | - | - | - | - |
| *Choragus sheppardi* | 1 | xm | x | 1 | -3.15 | - | - | -22.69 | - | - | 2.02 | - | - | 5.29 | - | - | - | - |
| *Cis bidentatus* | 1 | m | m | 1 | -1.95 | - | - | -1.95 | - | - | -1.45 | - | - | 5.31 | - | - | - | - |
| *Crepidophorus mutilatus* | 3 | z | z | 6 | -1.36 to 4.22 | 1.47 | 1.82 | -23.1 to -20.23 | 0.73 | 0.96 | 0.6 to 6.78 | 1.79 | 2.08 | 1.94 to 5.79 | 1.14 | 1.33 | 4.21 | 5.27 |
| *Cryptophagus labilis* | 4 | ms | m | 4 | -1.6 to 4.58 | - | - | -21.9 to -17.45 | - | - | 0.39 to 5.69 | - | - | 3.28 to 9.66 | - | - | - | - |
| *Cyclorhipidion bodoanus* | 19 | m | n.a | 30 | -5.75 to 6.56 | -0.04 | 2.47 | -25.67 to -17.34 | -0.04 | 1.72 | -4.93 to 7.67 | 1.87 | 3.04 | 0.01 to 10.29 | 3.57 | 2.46 | 23.44 | 24.27 |
| *Denticollis rubens* | 1 | xz | x | 1 | 1.36 | - | - | -22.47 | - | - | 1.87 | - | - | 2.64 | - | - | - | - |
| *Dissoleucas niveirostris* | 1 | xm | x | 1 | -3.37 | - | - | -22.69 | - | - | -2.27 | - | - | 3.32 | - | - | - | - |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dorcatoma substriata* | 1 | m | m | 1 | 3.2 | - | - | -18.51 | - | - | 4.59 | - | - | 7.48 | - | - | - | - |
| *Epuraea variegata* | 1 | z | z | 1 | 2.19 | - | - | -21.95 | - | - | 4 | - | - | 4.01 | - | - | - | - |
| *Ernoporicus fagi* | 1 | x | x | 1 | -3.73 | - | - | -24.91 | - | - | -4.6 | - | - | -0.11 | - | - | - | - |
| *Eucnemis capucina* | 13 | xm | x | 24 | -3.97 to 1.11 | -2.40 | 1.12 | -26.84 to -20.76 | -23.29 | 1.31 | -2.96 to 3.66 | -0.16 | 1.62 | -0.94 to 5.95 | 2.54 | 1.65 | 8.75 | 9.15 |
| *Hapalaraea pygmaea* | 10 | z | z | 14 | -0.96 to 4.31 | 1.97 | 2.17 | -26.47 to -18.98 | -22.37 | 1.84 | -3.12 to 7.51 | 3.67 | 2.64 | -0.28 to 7.64 | 3.47 | 2.02 | 16.12 | 17.46 |
| *Hesperus rufipennis* | 6 | z | z | 9 | -1.12 to 9.18 | 3.50 | 2.43 | -25.37 to -20.87 | -23.15 | 1.16 | 0.86 to 12.05 | 5.03 | 2.41 | -0.33 to 3.86 | 3.01 | 1.45 | 13.78 | 15.75 |
| *Hylecoetus dermestoides* | 1 | x | x | 1 | 0.79 | - | - | -25.79 | - | - | 2.48 | - | - | 2.29 | - | - | - | - |
| *Hypebaeus flavipes* | 5 | z | z | 16 | 1.54 to 7.03 | 4.38 | 1.32 | -24.59 to -21.88 | -23.35 | 0.63 | 3.35 to 8.42 | 5.90 | 1.30 | 0.05 to 5.02 | 3.49 | 1.22 | 5.12 | 5.49 |
| *Ischnomera caerulea/cyanea* | 1 | x | x | 1 | -1.67 | - | - | -22.47 | - | - | 0.89 | - | - | 4.2 | - | - | - | - |
| *Ischnomera sanguinicollis* | 12 | x | x | 23 | -5.24 to 2.08 | -1.50 | 1.91 | -24.96 to -20.31 | -22.59 | 0.93 | -5.97 to 4.59 | -0.11 | 2.47 | 1.14 to 5.34 | 3.05 | 1.07 | 8.65 | 9.07 |
| *Malachius bipustulatus* | 1 | z | z | 1 | 6.4 | - | - | -22.92 | - | - | 8.21 | - | - | 3.04 | - | - | - | - |
| *Malthinus punctatus* | 1 | z | z | 1 | 0.07 | - | - | -27.61 | - | - | 1.61 | - | - | -1.59 | - | - | - | - |
| *Malthodes marginatus* | 4 | z | z | 7 | -2.63 to 0.06 | 1.02 | 1.89 | -26.79 to -25.51 | -24.14 | 1.72 | -0.58 to 2.17 | 3.18 | 2.17 | -2.1 to 1.3 | 1.98 | 2.30 | 2.94 | 3.53 |
| *Megatoma undata* | 5 | d | d | 1 | 4.89 | - | - | -24.39 | - | - | 7.69 | - | - | 4.81 | - | - | - | - |
| *Melanotus castanipes* | 8 | xz | x | 9 | 0.43 to 3.17 | 2.02 | 1.06 | -24.96 to -22.52 | -22.46 | 1.76 | 0.83 to 5.97 | 3.88 | 1.77 | -0.16 to 6.68 | 3.50 | 1.94 | 11.89 | 13.59 |
| *Melanotus rufipes* | 2 | xz | x | 3 | 1.41 to 4.22 | - | - | -24.5 to -22.25 | - | - | 2.52 to 6.03 | - | - | 1.46 to 3.71 | - | - | - | - |
| *Mycetophagus populi* | 3 | m | m | 7 | 0.53 to 2.09 | 2.16 | 2.24 | -22.4 to -20.5 | -20.75 | 1.65 | 0.23 to 4.08 | 3.36 | 2.63 | 2.79 to 4.97 | 4.90 | 1.66 | 2.63 | 3.16 |
| *Neuraphes carinatus* | 1 | z | z | 1 | 3.11 | - | - | -24.07 | - | - | 4.66 | - | - | 1.96 | - | - | - | - |
| *Orchesia micans* | 5 | m | m | 10 | 1.38 to 5.76 | 2.06 | 2.40 | -22.27 to -18.2 | -20.70 | 1.65 | 1.08 to 6.76 | 3.34 | 2.70 | 5.81 to 7.62 | 4.99 | 1.56 | 2.29 | 2.57 |
| *Orthoperus atomus* | 1 | z | z | 1 | 2.97 | - | - | -23.09 | - | - | 4.44 | - | - | 3.1 | - | - | - | - |
| *Paromalus flavicornis* | 1 | z | z | 1 | 2.93 | - | - | -22.28 | - | - | 4.73 | - | - | 3.68 | - | - | - | - |
| *Phloeonomus punctipennis* | 1 | z | z | 1 | 0.5 | - | - | -20.09 | - | - | 1 | - | - | 5.03 | - | - | - | - |
| *Phloeophagus lignarius* | 2 | x | x | 3 | -4.57 to -0.88 | - | - | -22.61 to -21.67 | - | - | -2.76 to -1.18 | - | - | 2.06 to 3.35 | - | - | - | - |
| *Pityophagus ferrugineus* | 1 | z | z | 1 | -0.81 | - | - | -23.96 | - | - | 0.5 | - | - | 4.22 | - | - | - | - |
| *Platycis cosnardi* | 1 | z | z | 1 | 0.9 | - | - | -21.41 | - | - | 2.71 | - | - | 4.56 | - | - | - | - |
| *Plegaderus dissectus* | 5 | z | z | 7 | 0.06 to 3.32 | 0.14 | 2.45 | -22.28 to -19.7 | -22.89 | 1.97 | 2.9 to 4.87 | 1.83 | 2.44 | 3.58 to 5.66 | 3.15 | 2.15 | 1.49 | 1.78 |
| *Prionocyphon serricornis* | 7 | d | d | 10 | -6.26 to 3.41 | -1.16 | 2.33 | -28.22 to -21.51 | -23.26 | 1.71 | -4.56 to 4.92 | 0.57 | 2.47 | -3.18 to 6.31 | 3.03 | 2.10 | 19.52 | 21.96 |
| *Procraerus tibialis* | 1 | x | x | 1 | 2.26 | - | - | -22.44 | - | - | 3.81 | - | - | 3.58 | - | - | - | - |
| *Pseudocistela ceramboides* | 1 | xs | x | 1 | 1.48 | - | - | -22.48 | - | - | 2.87 | - | - | 3.51 | - | - | - | - |
| *Ptilinus pectinicornis* | 6 | x | x | 25 | -5.32 to 2.33 | -1.75 | 1.50 | -24.35 to -17.47 | -21.72 | 1.37 | -3.87 to 4.14 | 0.30 | 1.68 | 2.57 to 8.68 | 4.47 | 1.63 | 8.88 | 9.27 |
| *Quedius brevicornis* | 1 | z | z | 1 | 2.12 | - | - | -24.32 | - | - | 3.93 | - | - | 1.38 | - | - | - | - |
| *Quedius microps* | 1 | z | z | 1 | 4.19 | - | - | -20.32 | - | - | 8.45 | - | - | 6.99 | - | - | - | - |
| *Quedius truncicola* | 4 | z | z | 6 | 0.42 to 3.81 | 0.80 | 2.02 | -24.54 to -21.52 | -22.76 | 1.64 | 1.64 to 7.77 | 3.00 | 2.41 | -0.27 to 4.51 | 3.20 | 2.13 | 8.10 | 10.79 |
| *Rhagium mordax* | 1 | x | x | 1 | -1.05 | - | - | -21.78 | - | - | 0.50 | - | - | 4.25 | - | - | - | - |
| *Rhizophagus bipustulatus* | 5 | x | x | 6 | -2.94 to 1.6 | 0.96 | 2.38 | -23.95 to -22.17 | -21.88 | 2.15 | -1.21 to 3.15 | 3.26 | 2.56 | 1.24 to 3.54 | 4.32 | 2.49 | 4.36 | 5.45 |
| *Rhizophagus depressus* | 3 | z | z | 3 | -2.77 to 1.91 | - | - | -26.23 to -22.15 | - | - | -1.28 to 4.68 | - | - | 2.06 to 4.66 | - | - | - | - |
| *Rhizophagus dispar* | 1 | z | z | 1 | -0.55 | - | - | -23.82 | - | - | 3.78 | - | - | 5.61 | - | - | - | - |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rhizophagus perforatus* | 3 | z | z | 3 | -1.85 to 2.87 | - | - | -23.65 to -23.3 | - | - | -0.37 to 4.23 | - | - | 1.47 to 2.87 | - | - | - | - |
| *Scraptia fuscula* | 5 | xz | x | 10 | 0.67 to 4.9 | 0.85 | 2.25 | -23.74 to -18.24 | -21.07 | 1.71 | 2.87 to 7.72 | 2.92 | 2.79 | 1.3 to 8.47 | 4.96 | 2.06 | 8.98 | 10.11 |
| *Siagonum quadricorne* | 1 | z | z | 1 | 0.15 | - | - | -19.52 | - | - | 2.58 | - | - | 6.63 | - | - | - | - |
| *Tetropium castaneum* | 1 | x | x | 1 | -3.14 | - | - | -22.51 | - | - | -1.66 | - | - | 3.68 | - | - | - | - |
| *Tillus elongatus* | 6 | z | z | 11 | -2.75 to 1 | -0.37 | 2.36 | -24.57 to -21.48 | -23.62 | 2.27 | -2.5 to 4.97 | 0.86 | 2.62 | 2.62 to 5.05 | 3.16 | 2.07 | 3.95 | 4.39 |
| *Triplax russica* | 1 | m | m | 2 | 1.52 to 2.58 | - | - | -20.3 to -19.41 | - | - | 2.91 to 3.97 | - | - | 5.69 to 6.59 | - | - | - | - |
| *Velleius dilatatus* | 2 | z | z | 1 | 5.04 | - | - | -24.97 | - | - | 6.14 | - | - | 1.034 | - | - | - | - |
| *Xyleborus dispar* | 22 | m | m | 40 | -5.36 to 6.29 | -1.08 | 2.64 | -29.38 to -21.67 | -25.43 | 1.60 | -4.76 to 9.77 | 0.87 | 3.23 | -2.77 to 6.91 | 1.68 | 2.28 | 21.90 | 22.48 |
| *Xyleborus germanus* | 39 | m | n.a | 129 | -5.12 to 6.82 | -0.01 | 2.00 | -34.86 to -16.45 | -24.24 | 2.00 | -6.16 to 8.67 | 1.59 | 2.76 | -8.15 to 10.18 | 1.98 | 2.56 | 22.39 | 22.57 |
| *Xyleborus monographus* | 2 | m | m | 2 | -3.34 to -1.21 | - | - | -22.69 to -21.27 | - | - | -2.84 to 0.34. | - | - | 3.34 to 3.85 | - | - | - | - |
| *Xyleborus saxeseni* | 27 | m | m | 60 | -4.29 to 6.77 | -0.57 | 2.05 | -25.03 to -16.27 | -22.46 | 1.73 | -5.87 to 8.78 | 1.07 | 3.01 | 0.12 to 11.23 | 3.89 | 2.48 | 23.10 | 23.50 |
| *Xyloterus signatus* | 3 | m | m | 2 | -3.35 to 1.46 | - | - | -25.35 to -22.04 | - | - | -0.3 to 2.34 | - | - | -0.77 to 7.16 | - | - | - | - |

Table 2: Pairwise comparisons of the group means between all feeding guilds. P-values were adjusted with Benjamini-Hochberg correction. * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, n.s. = not significant, df = degrees of freedom

| | detritivorous | mycetophagous | myceto-saprophagous | xylophagous | xylo-mycetophagous | xylo-saprophagous | xylo-zoophagous | zoophagous |
|---|---|---|---|---|---|---|---|---|
| detritivorous | - | | | | | | df = 83, $R^2 = 0.16$ | df = 111, $R^2 = 0.06$ |
| mycetophagous | n.s. | - | | df = 376, $R^2 = 0.04$ | | | df = 364, $R^2 = 0.07$ | df = 392, $R^2 = 0.03$ |
| myceto-saprophagous | n.s. | n.s. | - | | | | | |
| xylophagous | n.s. | *** | n.s. | - | | df = 106, $R^2 = 0.1$ | df = 157, $R^2 = 0.29$ | df = 185, $R^2 = 0.2$ |
| xylo-mycetophagous | n.s. | n.s. | n.s. | n.s. | - | df = 49, $R^2 = 0.12$ | df = 100, $R^2 = 0.27$ | df = 128, $R^2 = 0.13$ |
| xylo-saprophagous | n.s. | n.s. | n.s. | *** | ** | - | df = 94, $R^2 = 0.13$ | |
| xylo-zoophagous | ** | *** | n.s. | *** | *** | *** | - | df = 173, $R^2 = 0.04$ |
| zoophagous | * | *** | n.s. | *** | *** | n.s. | * | - |

# Discussion

## Characteristics influencing the biodiversity of saproxylic insects

Habitat heterogeneity of deadwood objects (veteran trees, fruiting bodies of different fungi, snags, logs, dead tree crowns and many more) influence the diversity of saproxylic organisms at the forest level (Bouget et al., 2014; Seibold et al., 2016). This is also true for tree hollow heterogeneity at a local level. Differently shaped tree hollows, varying in their physical characteristics define the diversity and the composition of tree hollow communities. As all tree hollows are unique in their characteristics, there is a high temporal and spatial turnover of species inhabiting tree hollows (Gouix et al., 2015; Quinto et al., 2014; Ranius, 2002a; Schauer et al., 2018a; Schmidl et al., 2008). Several studies could show that a wide variety of different parameters are influencing saproxylic species diversity (see Table 1 for a detailed information), irrespective of the deadwood type. Parameters structuring the communities within a tree hollow are numerous and complex and thus there is no general predictor of high saproxylic diversity. The importance of parameters influencing the diversity within a tree hollow is changing between different species groups, environments, landscapes, and climate zones. For example, the degree of decomposition, height above the ground and the amount of surrounding tree hollows positively influence the number of non-threatened beetle species but not the majority of threatened ones (Schauer et al., 2018a). However, the habitat preference of some saproxylic beetles is also dependent on the climate zone. In warmer climate zones, colder habitats are preferred and vice versa in colder climate zones habitats with higher temperatures are preferred (Carpaneto et al., 2010; Müller et al., 2015; Schauer et al., 2018a). Not only physical characteristics of tree hollows are important in shaping the communities inside but species interactions. Fungi are responsible for the creation of tree hollows and the nutrient basis for mycetophagous species. Fungi are important for the nutrient composition and quality of the wood mould during the successional changes of the tree hollow. Therefore the fungal community will determine to a certain degree the future species assemblages as they modify the characteristics of the tree hollow (Boddy, 2001; Micó, 2018; Siitonen, 2012a; Stokland, 2012b). Insects can help to spread the decaying fungi on or in their body and also facilitate the vectoring of the fungi in boring tunnels through the whole tree (Ulyshen, 2016). Further, the interspecific interactions of insects like facilitation in a tree hollow might be an important factor shaping the assemblage. Through the presence of larvae of ecosystem engineering genera like *Cerambyx* or *Cetonia* the diversity in tree hollows is increased (Micó et al., 2015). Moreover, the faeces of the larvae of these genera positively influence the growth rate of syrphid larvae (Sánchez-Galván et al., 2014, 2018). In the interactions between scirtid beetles and mosquito larvae, faeces of the beetle positively influence the survival rate and emergence to higher instar levels (Daugherty and Juliano, 2003). However, the species interactions and their influence on the community structure of tree hollow arthropods are not well understood until today.

General theory predicts that larger habitats offer more available energy and increased habitat heterogeneity, with both factors leading to higher species richness (MacArthur and MacArthur, 1961; Schuler et al., 2015; Simpson, 1949; Srivastava and Lawton, 1998; Tews et al., 2004; Wright, 1983). The predicitions that larger habitats and increased habitat heterogeneity are leading to increased species richness can also be applied to deadwood systems. The amount of deadwood is the determining factor for the amount of available resources and chemical energy. Further, also the deadwood surface area will increase leading to more different deadwood habitats (Bässler et al., 2010; Boecklen, 1986). According to the "more individuals" hypothesis increased deadwood amounts should lead to more available resources consequently leading to increased numbers of species. This prediction holds true for most deadwood systems and was shown in several studies considering different saproxylic taxa (Grove, 2002a; Junninen and Komonen, 2011; Lassauce et al., 2011; Müller and Bütler, 2010; Riffell et al., 2011).

Table 1: Parameters positively influencing saproxylic species diversity in deadwood. For many studies, no specific definition for the investigated deadwood types was given. Thus, all different deadwood objects (coarse woody debris, logs, snags, veteran trees with dead parts) were summed up as deadwood.

| **Parameter** | **Deadwood object** | **Positive Relation** | **Country** | **Tree species** | **References** |
|---|---|---|---|---|---|
| Decomposition | Deadwood | Fresh | Canada | Pine, Aspen, Oak | (Vanderwel et al., 2006) |
| | Tree hollow, Deadwood | Medium decomposed | Germany, Norway, Sweden | Oak, Beech | (Jonsell and Weslien, 1998; Schauer et al., 2018a; Sverdrup-Thygeson et al., 2014) |
| | Tree hollow | Highly decomposed | France | Oak | (Gouix et al., 2015) |
| Entrance area of the tree hollow | Tree hollow | Medium sized | Germany | Beech | (Schauer et al., 2018a) |
| | Tree hollow | Large sized | Sweden, Spain | Oak, Ash | (Quinto et al., 2015; Ranius, 2002a; Ranius et al., 2009a, 2009b) |
| Distance to the ground | Tree hollow | Close or open to ground | Germany, Spain, Sweden | Oak, Beech, Ash | (Quinto et al., 2014; Schauer et al., 2018a; Taylor and Ranius, 2014) |
| | Tree hollow | High above ground | Sweden | Oak | (Ranius, 2002a) |
| Sun exposure/Temperature | Tree hollow Deadwood | High | Germany, Sweden, France, Switzerland | Beech, Oak, Spruce, Birch, Aspen | (Jonsell and Weslien, 1998; Koch Widerberg et al., 2012; Lindhe et al., 2005; Müller et al., 2015, 2015; Ranius, 2002b, 2002b; Ranius and Nilsson, 1997; Schauer et al., 2018a) |

| | | | | | |
|---|---|---|---|---|---|
| Sun exposure/Temperature | Tree hollow | Low | Germany, Italy | Beech, Oak | (Carpaneto et al., 2010; Schauer et al., 2018a) |
| Number of surrounding tree hollows/deadwood amount | Tree hollow, Deadwood | High amount | Germany, Norway, Australia, Finland, Canada | Beech, Spruce, Pine, different tropical species | (Grove, 2002b; Martikainen et al., 2000; Müller et al., 2015; Okland et al., 1996; Ranius and Wilander, 2000; Schauer et al., 2018a; Sverdrup-Thygeson et al., 2010; Vanderwel et al., 2006) |
| Tree hollow volume | Tree hollow | Medium volume | Germany | Beech | (Schauer et al., 2018a) |
| | Tree hollow | Large volume | Sweden | Oak | (Quinto et al., 2014; Ranius, 2002b; Ranius and Jansson, 2000; Sverdrup-Thygeson et al., 2010) |
| Openness | Tree hollow<br>Deadwood | High | Sweden | Oak | (Koch Widerberg et al., 2012; Ranius, 2002b; Ranius and Jansson, 2000) |
| Canopy cover | Deadwood | Low | Sweden | Oak | (Ranius and Jansson, 2000) |
| Stand age | Deadwood | Old growth | Australia, Finland | Spruce, Pine, different tropical species | (Grove, 2002b; Martikainen et al., 2000) |
| Wood mould amount | Tree hollow | High | Norway, Sweden, Spain | Oak | (Micó et al., 2015; Ranius et al., 2009a, 2009b; Sverdrup-Thygeson et al., 2014) |
| Species interactions (Ecosystem engineering species, Facilitation, Predation, Vertebrates | Tree hollow | Presence | Spain | Oak, Ash | (Micó et al., 2015; Quinto et al., 2014; Sánchez-Galván et al., 2018) |

However, comparing different forest types, it seems that the relation of deadwood amount and species richness is stronger in boreal forests compared to temperate forests (Lassauce et al., 2011; Müller et al., 2015) and the weakest relation is found in subtropical and tropical forests (Richardson et al., 2010; Schowalter et al., 2014; Ulyshen and Hanula, 2009). Nevertheless, several studies suggest, that deadwood amount is a poor predictor for saproxylic species richness, especially in forest with high heterogeneity of deadwood types (Lassauce et al., 2011), as the species richness differs between deadwood objects with different characteristics like tree species, degree of decomposition or diameter (Gossner et al., 2016; Grove, 2002a). Moreover, deadwood amount seems to be more important for species richness in ancient forests rather than but not in young forests (Brin et al., 2016).

Habitat heterogeneity is also one possible factor explaining the diversity of saproxylic species. Habitat heterogeneity of deadwood structures can increase with higher amounts of deadwood, as the amount and diversity of deadwood are highly correlated (Bouget et al., 2013; Hottola et al., 2009; Müller and Bütler, 2010; Okland et al., 1996; Similä et al., 2003). The tight link of deadwood amount and diversity was shown in temperate but also in boreal and tropical forests (Grove, 2002c; Martikainen et al., 1999; Similä et al., 2003). Moreover, habitat heterogeneity might increase with increasing size of a single deadwood object, since on a fine scale microclimate, degree of decomposition, fungal colonization, and water content can vary greatly (Graham, 1924; Leather et al., 2014; Saint-Germain et al., 2010). Many studies have underlined the importance of different deadwood types (Heilmann-Clausen and Christensen, 2005; Similä et al., 2003) and showed that deadwood diversity is the main driver of the functional composition of deadwood communities (Janssen et al., 2017). Several studies have shown that deadwood diversity could explain species richness of saproxylic beetles better than deadwood amount could (Bouget et al., 2013; Brin et al., 2009; Seibold et al., 2016; Similä et al., 2003), indicating that habitat heterogeneity is a major driver of saproxylic beetle richness. Habitat heterogeneity might also be important to evaluate the spatial distribution of deadwood objects

(Seibold et al., 2015b), as heterogeneity might be regarded as fragmentation and isolation of patches on a larger scale, influencing species richness negatively (Tews et al., 2004).

A recent study of saproxylic beetles (Seibold et al., 2017) has shown, that patch size and habitat amount in the local landscape independently positively affected the species number, without a significant interaction. This means, that there was no stronger or weaker increase in species richness with increasing patch size when the amount of habitat in the local landscape was higher than in the patch. These findings of Seibold et al. (2017) are consistent with the habitat amount hypothesis. However, the habitat amount hypothesis seems not to hold true for different taxa. Studies on plant species richness (Evju and Sverdrup-Thygeson, 2016; Haddad et al., 2017) and microarthropods (Haddad et al., 2017) revealed contradictory results not supporting the habitat amount hypothesis.

### Dispersal of saproxylic insects

Dispersal is a key trait for all species facing a changing environment. It is especially important for saproxylic species as most deadwood habitats are ephemeral and thus changing either by natural processes like decomposition or due to habitat loss and fragmentation caused by human activities (Feldhaar and Schauer, 2018; Siitonen and Jonsson, 2012a; Thomas, 2000). Dispersal allows the colonization of new habitats and thus affects species distributions, extinction risk of populations, and metapopulation dynamics (Bowler and Benton, 2005; Hanski et al., 1994).

Metapopulations are spatially discrete populations within habitat patches connected through the migration of individuals between the local populations. Extinction of local populations and the recolonization of empty habitat patches are common in metapopulations. However, to achieve a stable population the rate of extinction and recolonization has to be more or less in balance (Hanski, 1998). Metapopulation dynamics are often discussed on a large scale (Hanski, 1999; van Nouhuys, 2016; Thomas, 2000). However, for some saproxylic insects, the metapopulations dynamics take place in a way smaller dimension. Ephemeral and small habitats like logs, snags and fungal sporocarps are the habitat of many saproxylic organisms. These organisms might go extinct, once their habitat decomposes and colonization of new habitat patches is not possible because either a suitable habitat is not available or the distance for colonization is too far. Thus, forest management practices, which alter the distribution, availability, and abundance of this habitat can lead to a gap in the habitat continuity. Consequently, metapopulation dynamics might break down and result in extinctions on a landscape level (Grove, 2002a, 2002b).

Dispersal theory suggests that species inhabiting discrete and long-lasting habitats are poor dispersers compared to species associated with ephemeral habitats (Denno et al., 1996; Roff, 1994; Shaffer, 1981; Southwood, 1962; Travis and Dytham, 1999). In terms of saproxylic species, this would mean that species associated with long-lasting tree hollows should have a low dispersal propensity (Nilsson and Baranowski, 1997; Ranius and Hedin, 2001) compared to species living in ephemeral deadwood habitats like fresh deadwood or living in burnt wood, as they are adapted to their spatially and temporally dynamic habitat (Nilsson and Baranowski, 1997, 1997; Siitonen, 2012a, 2012b). Species with bad dispersing abilities are facing severe problems if new habitat patches are not in a reachable distance from the natal habitat. However, this does not hold true for all species living in tree hollows but is strongly dependent on the studied species (Feldhaar and Schauer, 2018; Schauer et al., 2018b). Forests with a long continuity and old growth forest characteristics (higher amounts of deadwood supplied continuously for decades or centuries and a high number of senescent trees) (Whitehead, 1997) are important for species dependent on these characteristics and poorly mobile species (Lachat and Müller, 2018; Ulyshen and Šobotník, 2018). Consequently, species with low dispersal abilities might be more sensitive to a break in the continuity of their habitat, as the colonization of new habitat patches might be difficult due to large distances (Ranius and Hedin, 2001). Artificial tree hollows can help to keep the continuity of habitats with similar habitat quality. However, artificial tree hollows are less colonized by some tree hollow specialists when the boxes are far away from the source habitat. This indicates that at least some of the specialists are dispersal limited (Jansson et al., 2009). Thus, some species with low dispersal inhabiting tree hollows are more common in older forests, with a higher connectivity and habitat continuity (Ulyshen and Šobotník, 2018).

Fragmentation has often been suggested to have strong negative effects on saproxylic insects (Grove, 2002a, 2002b; Siitonen, 2001). However, many saproxylic species, especially those associated with ephemeral habitats, are good dispersers and can bridge several kilometers between suitable habitats (Grove, 2002b; Kuuluvainen and Siitonen, 2003). This might be due to a preadaptation to a mosaic structure of their habitat as a result of natural disturbances (Langor et al., 2008), like fire or windthrow, which can extend over large areas (Boulanger et al., 2010). However, species inhabiting tree hollows, the most long-lasting deadwood structure, should also have good dispersal abilities because of the pre-adaptation to the naturally patchy distribution. Further, avoiding inbreeding in small populations and avoidance of competition should also favor good dispersal abilities (Perrin and Mazalov, 2000). Until today, studies on the dispersal of saproxylic species are still scarce but some of them gave evidence for good dispersal abilities of species inhabiting tree hollows (Chiari et al., 2013; Dubois et al., 2010; Schauer et al., 2018b). Thus, limited dispersal of species inhabiting tree hollows might be not as pronounced as it was assumed a long time.

In general, the absence of a species in a habitat can be explained either by dispersal limitation or habitat limitation. Often the extinction of a species is explained by poor dispersal ability. However, it might be also due to the absence of high-quality habitat or unsuitable matrix around the habitat patch, caused by forest fragmentation coupled with low connectivity and reduced habitat availability (Fahrig, 2013; Feldhaar and Schauer, 2018; Hanski et al., 1994). In large-scale studies reduced saproxylic biodiversity due to dispersal limitation was shown as fewer saproxylic species occurred in more isolated forest areas or habitat structures (Bergman et al., 2012; Ranius et al., 2011).

Concluding, dispersal abilities are strongly taxa dependent in saproxylic insects, reaching from a few meters of passalid beetles (Jackson et al., 2009) to several kilometers in some jewel beetles (Taylor et al., 2010) or cerambycid beetles (Drag et al., 2015). However, the long assumed limited dispersal ability of tree hollow inhabitants (Nilsson and Baranowski, 1997; Ranius and Hedin, 2001) is not true for all species (Chiari et al., 2013; Dubois et al., 2010; Schauer et al., 2018b). The reason why some saproxylic species are not present in some obvious habitats might not always be due to dispersal limitation, but habitat limitation or specific factors of dispersal behavior, like sex-related dispersal conditions, competition and many more (Feldhaar and Schauer, 2018).

### Trophic structure of saproxylic species

Saproxylic food webs are very complex with several trophic levels above the primary producer. Compared to other terrestrial and marine food webs the primary consumers in deadwood food webs are not herbivores but decomposers (e.g. wood decaying bacteria and fungi) and detritivores (consumers of dead matter) (Begon et al., 2006; Stokland, 2012a). Additionally, mycetophagous species and interactions between insects and fungi are pronounced in deadwood systems, due to a long history of cohabitation resulting in adaptations and interactions (Birkemoe et al., 2018). Deadwood is colonized and digested by fungi during the succession, and in late decomposition stages, the biomass of fungi and other microbes contribute a high proportion of the biomass of rotten wood (Jones and Worrall, 1995; Noll et al., 2016; Stokland, 2012b). In deadwood systems, the interactions of fungi and insects are very important but scarcely investigated. However, there is evidence, that the interactions of insects and fungi can be grouped into four main functional relationships, namely nutrition, detoxification, protection and dispersal (Birkemoe et al., 2018). Saproxylic insects feed on fungi, the nutritional value of fungi-enriched wood is increased and fungi can provide enzymes obligatory for wood digestion (Birkemoe et al., 2018; Kukor and Martin, 1986; Stokland, 2012b). Fungi can also detoxify chemical components of the tree defense and thus facilitate the uptake of otherwise toxic compounds for insects (Birkemoe et al., 2018). Fungi and insects also have protective interactions as insects protect fungi, e.g. leaf cutter ants, termites and ambrosia beetle and further fungi can serve for the fortification of nest walls and fighting microbial pathogens (Flórez et al., 2015; Schlick-Steiner et al., 2008). Further, the dispersal of fungi can be mediated by insects either passively or in special organs (Birkemoe et al., 2018).

To characterize food webs the first step is often to assign the target species to a specific feeding guild. For saproxylic insects different assignments to specific feeding guild exist (Bouget et al., 2005; Köhler, 2000; Stokland, 2012a) but it is argued that at species level these assignments are arbitrary, as saproxylic species might be qualified for multiple feeding guilds during their developmental stages or even within one stage (Ulyshen and Šobotník, 2018). Moreover, it is often not clear how the existing classification is derived and there is also not a standard usage of terms for the different feeding guild, for example, some authors use detritivorous and others use saprophagous, both probably describing the same functional group. Altogether it is often hard to assign a species to a specific feeding guild. A good example are species living in highly decayed stages of deadwood. It is hard to clearly distinguish if species allegedly feeding on wood might feed even more on the wood decaying fungi (Ulyshen and Šobotník, 2018). A combination of different methods, like stable isotope analysis, direct observations, gut content analysis, and expert knowledge are needed to get reliable information on the feeding behavior. Especially in tree hollows, it is noticeable, that a large proportion of the saproxylic community are predators. In tree hollows, there are up to 30% of species present belonging to the predatory guild and in downed deadwood even up to 41% (Pilskog et al., 2016; Quinto et al., 2014; Wende et al., 2017). However, a high trophic level, e.g. predatory species, is generally associated with a higher extinction risk in threatened species (Purvis et al., 2000). This is relevant for saproxylic species, where a high number of species is threatened. Komonen (2001) showed that parasitoids of saproxylic insects are the most sensitive of all trophic levels and disappeared first in fragmented landscapes. Consequently, intensive forest management not only reduces the biodiversity but also leads to a reduction of functional groups and reduce the complexity of interactions (Stokland, 2012a). In terms of biomass, the predatory guild in tree hollows contributes the highest biomass and thus for saproxylic beetle communities inverted Eltonian pyramids can be found (Manuscript 4). However, in terms of total biomass, the basal trophic level might contribute the highest biomass because collembolans and dipteran larvae supposedly account for the biggest proportion of biomass (Köhler, 2000).

One of the main questions in food web research is if the food web is bottom up or top down controlled. Deadwood food webs are assumed to be bottom-up controlled systems as deadwood amount and deadwood input is the energetic base and consequently available energy is limited by the amount of deadwood. Top down control seems less likely as tree mortality and thus the amount of dead wood is not influenced by most saproxylic species, except some bark beetles which can lead to the death of trees (Stokland, 2012a).

### Implications for tree hollow management

The reduction of tree hollows due to intensive management in forests has led to a decreasing habitat availability for hollow-dependent species (Andersson and Östlund, 2004; Eliasson and Nilsson, 2002; Fan et al., 2004; Lindenmayer et al., 2012b). This will negatively impact all saproxylic species using tree hollows but especially the obligate ones, finding no alternative habitat (Bergman et al., 2012; Gouix et al., 2012). Thus, as already mentioned in the introduction, intensive forest management and the resulting consequences like reduction of available habitat and fragmentation lead to endangerment of tree hollows, the keystone structure of forest biodiversity and especially of the associated species (Grove, 2002a, 2002b; Müller et al., 2014; Remm and Lõhmus, 2011; Siitonen and Jonsson, 2012a). Nowadays deadwood management is implemented and a major aim of sustainable forest management (Franklin et al., 1987; Hjältén et al., 2012; Jacobs et al., 2007; Lindenmayer et al., 2012c).

For the conservation of saproxylic biodiversity in managed forests worldwide it is crucial to protect veteran trees, deadwood in its various forms and especially tree hollows, retaining different characteristics (e.g. dimension, sun exposure, see table 1) and the full range of decomposition stages to support arthropod species diversity best (Ferro et al., 2012; Langor et al., 2008; Lee et al., 2014; Schauer et al., 2018a; Similä et al., 2003).

To improve the protection of tree hollows and establish effective management strategies it is important to understand how tree hollows develop. Tree hollow development often starts with trees being damaged, e.g., by branches breaking off and leaving cracks in the stem. These injuries provide access to sapwood and heartwood, where fungi and invertebrates initiate a combination of decaying processes. Invertebrates like beetles help to develop tree cavities as they bore galleries and help to spread decaying fungi and further facilitate the entrance of taxa unable to create their own tunnels (Gibbons and Lindenmayer, 2002; Perry et al., 1985; Siitonen and Jonsson, 2012b). However, the main decaying process is due to heart rot fungi, leaving the sapwood untouched but decaying mostly the heartwood (Siitonen and Jonsson, 2012b). Mostly, tree hollows start with small rot holes developing into bigger cavities, but the temporal development aspect is still not clear (Siitonen, 2012a). Tree age and diameter seems an important determinant for the occurrence of tree hollows (Gibbons and Lindenmayer, 2002; Horák, 2017; Ranius et al., 2009a). Ranius et al. (2009a) estimated tree hollow occurrence in different age classes in pedunculate oaks (*Quercus robur*) showing a higher probability of tree hollows in old age classes (> 200 years). Therefore, intensive forest management, where timber production depends on a shorter rotation age of trees, often does not provide enough time for trees to develop suitable deadwood habitats (Larrieu et al., 2012). Aside from tree age, silvicultural practices can have an important influence on tree hollow development. One traditional practice is pollarding, which increases the probability and speed of tree hollow formation (Sebek et al., 2013). Additionally, methods like the pruning of branches or damaging the bark to mimic natural injuries can help to speed up tree hollow formation (Carpaneto et al., 2010; Siitonen, 2012c). However, the formation of tree hollows is highly dependent on the tree species, as different tree species are not equally likely to get infected by heart rot fungi. Coniferous trees are less likely to form cavities compared to broad-leafed species (Milberg et al., 2014; Siitonen, 2012a).

Tree hollows will completely decay over time and will vanish at some point, but the development takes a long time. Thus, it must be ensured that there is a constant availability of tree hollows also in the future (Ranius et al., 2009a). Therefore, it is important to pay attention and protect existing microhabitat structures (Kraus et al., 2016) and retain structures which may develop into tree hollows in the future, like broken branches or bigger injuries at the bark. A gap in the continuity due to a long development time is especially pronounced for saproxylic species who are dependent on tree hollows with late successional characteristics like highly decayed wood mould or a large volume of wood mould, like two of the flagship species *Osmoderma eremita* and *Limoniscus violaceus* (Gouix et al., 2015; Ranius and Nilsson, 1997). Several studies showed the importance of different tree hollow characteristic for the associated species and how variable the characteristics are, depending on the landscape, history of the forest and climate (Chiari et al., 2012; Gouix et al., 2015; Quinto et al., 2014; Ranius and Nilsson, 1997; Schauer et al., 2018b). Thus, ensuring a constant availability of tree hollows in space and time with different characteristics can support a broad set of insect communities with different ecological preferences (Schauer et al., 2018a).

Generally, it is important to protect the biodiversity worldwide but besides that, a high diversity of saproxylic insects benefits forest ecosystem functioning as they provide various ecosystem services, for example, wood decomposition and nutrient cycling (Gouix et al., 2015; Grove, 2002a; Ulyshen, 2016; Ulyshen and Šobotník, 2018). A high species diversity is generally leading to a longer food chain length, supporting the more different ecosystem services (Cohen and Newman, 1991; Holt, 1993). Further, a high diversity of saproxylic insects can help to control forest pest species. A large proportion of saproxylic insects are predators and parasitoids, which can help to reduce the damage of pest species, like different bark beetle species, below economic damage levels (Fielding and Evans, 1997; Ulyshen and Šobotník, 2018; Yang et al., 2014).

Retention forestry might be one way efficiently maintaining biodiversity and ecological functions on a landscape level. The main focus of retention forestry is to keep the complexity, continuity, and composition of preharvest to postharvest forest at a significant level, meaning to protect significant elements, like structures, organisms and patches of high ecological value permanently (Gustafsson et al., 2012; Lindenmayer et al., 2012c). However, retention forestry cannot and is not meant to replace permanent reserves (Lachat and Müller, 2018; Lee et al., 2015; Lindenmayer et al., 2012c), as old forest patches of large size have the highest conservation value (Grove, 2002b; Irmler et al., 2010). Generally, there is aggregated retention, where groups of important elements retained in a larger area, and dispersed retention where single trees or small patches are retained (Franklin et al., 1997). Aggregated patches are needed to be of a certain size to maintain the long-term persistence of valuable structures and the associated microhabitats for supporting the biodiversity of sensitive interior forest species (Baker and Read, 2011; Franklin et al., 1997; Pinzon et al., 2012). However, there is still not much known on how large a sufficient aggregated patch has to be or much habitat amount it has to offer. In a study in Canada has shown that saproxylic beetle assemblages in spruce benefit from retention patches with more than 3 ha, as negative edge effects are mitigated (Lee et al., 2015). Aggregated retention patches should be located at sites having already a high ecological value to maximize the conservation effect (Lee et al., 2018). In contrast to aggregated retention, there is dispersed retention. Dispersed retention alone is problematic, as the patch size is often not large enough to counter negative edge effects and to support the diversity of interior forest species (Aubry et al., 2009; Lee et al., 2017; Matveinen-Huju et al., 2006; Pinzon et al., 2012). However, it is important to retain these valuable structures, like tree hollows. Even single trees have positive effects for threatened species and are valuable for species richness (Pilskog et al., 2016; Ulyshen and Šobotník, 2018). To maximize the benefits of retention forestry for conservation impact and maintaining biodiversity aggregated and permanently conserved patches can be connected by dispersed retention (Hämäläinen et al., 2016; Lee et al., 2017; Lindenmayer et al., 2012c; Pinzon et al., 2012). The connectivity through dispersed retention can also be actively promoted by leaving large logs and snags and complete tree crowns in harvested areas and creating high stumps and snags (Bouget et al., 2014; Jonsell et al., 2007; Jonsson et al., 2005; Siitonen, 2001). However, permanent conserves only cover a small percentage of the forested area and thus also in managed areas the conservation of deadwood and valuable structures should be promoted where ever it is possible (Franklin and Lindenmayer, 2009; Seibold and Thorn, 2018).

Connectivity is important to facilitate the dispersal among the different habitat patches. This is important for gene flow, balancing extinction through recolonization and maintaining viable populations and evolutionary potential (Bowler and Benton, 2005; Driscoll et al., 2014; Hanski et al., 1994). It is important to consider the different dispersal abilities of saproxylic species for conservation measures. For species with high dispersal abilities it is also possible to consider smaller and younger patches as they have conservation value for these species if these patches can offer the needed habitat quality (Schauer et al., 2018b; Ulyshen and Šobotník, 2018). However, some saproxylic species are limited in their dispersal, for example, some passalid beetles with dispersal distances of only a few meters (Jackson et al., 2009). For these species, it would be lethal if a reduction of habitat amount and quality around their natal habitat takes place.

Concluding I recommend the following steps for the conservation of tree hollows and deadwood in general. The first but most basic step is the reduction of deforestation and thus ensuring sources of deadwood development for the future. In general, deadwood independent of the already existing amount of deadwood and deadwood structures should be increased where ever it is possible (Seibold and Thorn, 2018). Deadwood amount is very important for the diversity, but one should keep in mind that also the heterogeneity of deadwood should be promoted to support the diversity of saproxylic species best (Brin et al., 2009; Seibold and Thorn, 2018). This also applies for key structures like tree hollows. It is important to ensure a constant availability of tree hollows with different characteristics in space and time as they need decades to develop (Ranius et al., 2009a). Every tree hollow is important as in highly managed areas even single tree hollows support species diversity and can serve as dispersed retention patches to connect more suitable habitat patches. This can be achieved by paying attention for early structures, that might develop into tree hollows, like large injuries of the breakage of limbs or by active management techniques like pruning of branches or damaging the bark to mimic natural injuries (Carpaneto et al., 2010; Siitonen, 2012c).

Conservation efforts should consider a mixed strategy for retention patches, because in ecosystems more or less mobile species are likely to coexist. Firstly, one should support and preservation of suitable habitats immediately surrounding the habitat of poorly mobile species (Huxel and Hastings, 1999). Secondly, conservation efforts can be maximized for species with high dispersal ability and colonization over long ranges by supporting even distant sites with high habitat quality, e.g. protecting areas with already existing valuable habitat structures (Ranius and Kindvall, 2006).

## Future directions

Despite saproxylic organisms are considered as keystone species for a high diversity and providers of important ecosystem services, the research on these important species has just begun (Ulyshen and Šobotník, 2018). There are still large knowledge gaps in the basic understanding of their ecology on the species level but also on the community level and their functional role within the community (Grove and Stork, 1999; Langor et al., 2008). Knowledge on the functional role of saproxylic species is very important, as the species composition will change between different regions, but the functional roles are mostly conserved by different taxa, for example click beetles (Elateridae) or rover beetles, which will be predatory irrespective of the landscape (Micó, 2018). Moreover, until today saproxylic beetles are the focus of research and most other taxa are left out. However, it is important to gain more knowledge on a wider variety of taxonomic groups, like dipterans and collembolans which contribute a high proportion to the overall diversity in tree hollows.

I could show that many different factors influence the diversity of saproxylic beetles in tree hollows. However, as shown before, they are different between study regions. It is also very likely that these characteristics differ even between different forests in the same study region, as microclimate conditions or management history might be different. Thus, it is important to continue with studies investigating the influence of tree hollow characteristics and the immediate environment to establish effective conservation measure for different regions.

Additionally, better knowledge on dispersal of saproxylic species and on habitat preferences can help to explain the absence of a specific species in a habitat and can then be contributed to either habitat limitation or dispersal limitation. Thus, future studies disentangling the problem of habitat limitation versus dispersal limitation are still needed. The study on dispersal of saproxylic beetles has just started and more studies on different species and especially species which are obligate to tree hollows are needed to estimate the distance between suitable habitats for efficient conservation. Further, factors influencing the propensity to disperse, like different dispersal capacity of sexes, body condition or competition are still poorly understood (Feldhaar and Schauer, 2018). Moreover, studies on potential differences of the dispersal capacity of individuals of the same species occurring in different landscapes are needed, as the dispersal capacity might be different due to different pre-adaptions caused by different management histories. This means, that individuals of a species with high quality and amount of deadwood with low distances between suitable habitats might show lower dispersal distances as there is no need to disperse over large distances compared to individuals of the same species pre-adapted to low quality and amount and large distances between suitable habitats.

My study on the dispersal of saproxylic insects was conducted in a highly connected area. However, in highly fragmented areas or areas surrounded by a matrix of unsuitable habitats studies are needed, to assess if geneflow is still present and species are still in genetic exchange. On landscape level studies are needed testing the suitability of aggregated and dispersed retention as step stones to connect distant sites, and thus ensuring undisrupted gene flow even on landscape scale. Additionally, to increase connectivity of tree hollows, the success of special management techniques for the creation of tree hollows like pollarding and pruning must be tested and if they are suitable even in managed forests. Further, the usage of wooden boxes mimicking tree hollows seem to be promising, but knowledge about how to maintain these artificial boxes suitable over many years is still unknown (Carlsson et al., 2016; Jansson et al., 2009).

Our study on the trophic structure of beetle communities in tree hollows was the first to our knowledge, at least using stable isotope analysis. However, to understand the food web structure it is important to investigate the associated fungi and their contribution to the nitrogen flow. Fungi in the wood mould are the basic source of energy for many of species in a tree hollow but there is still no knowledge about their trophic and isotopic niche. Further, studies are needed how ecosystem functions, e.g. decomposition and nutrient cycling is influenced by the loss of species and to which extent this loss can be compensated by the tree hollow community.

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# Appendix

Manuscript 5: Wohnungsnot in deutschen Wäldern

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Journal and status: LWF aktuell 118 (2018)

Own contribution: writing: 85%; concept and discussion: 80%; corresponding author
BS, HF and EO conceived the ideas and designed the methodology, Figures and tables were created by BS. BS led the writing of the manuscript.

**1** **Eine bodennahe Mulmhöhle in einer Buche; zahlreiche Insektenarten finden in solchen unscheinbaren Strukturen bestens geeigneten Wohnraum.**
Foto: B. Schauer

# Wohnungsnot in deutschen Wäldern

## Mulmhöhlen für die Wiederbelebung artenarmer Wirtschaftswälder

**Bastian Schauer, Heike Feldhaar und Elisabeth Obermaier**

**30 cm im Durchmesser und 80 cm hoch – Wohnraum dieser Größe hat locker Platz in einem 50 cm starken Baum. Trotz dieser »Kleinheit« und »Einfachheit« herrscht notorischer Wohnraummangel in vielen Wirtschaftswäldern. Es mangelt vor allem an sogenannten Mulmhöhlen. Das bekommen zahlreiche Waldbewohner deutlich zu spüren. Ein Mehr an Mulmhöhlen würde der Artenvielfalt, insbesondere der Vielfalt an Insekten, einen gewaltigen positiven Schub nach vorne geben.**

Ziel einer integrativen Waldbewirtschaftung ist es, die Artenvielfalt im Wald zu erhalten und zu fördern. Ein sehr wichtiges Element zur Förderung der Artenvielfalt sind Faulhöhlen im lebenden Baum, sogenannte Mulmhöhlen. Bäume mit Mulmhöhlen sind Biotopbäume und zählen zu den wichtigsten, aber auch seltensten Strukturen im Wald. Mulmhöhlen dienen einer Vielzahl von Insektenarten, darunter auch vielen bedrohten Arten, als stabiler und über Jahrzehnte bestehender Lebensraum.

### Bedeutende Strukturen im Wald

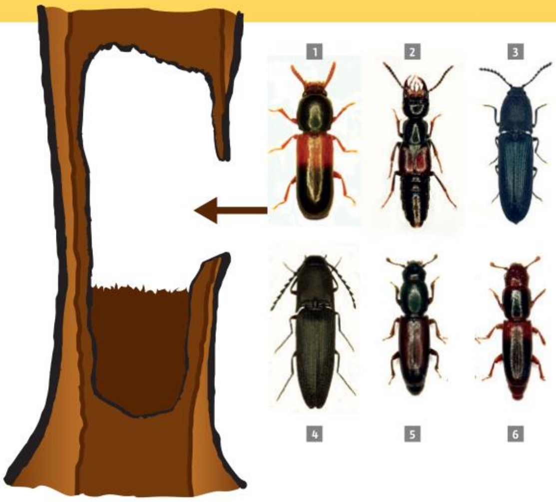
Mulmhöhlen sind langlebige Habitate, die für eine Vielzahl von Insektenarten einen stabilen Lebensraum bieten. Daher zählen sie zu den Schlüsselstrukturen für eine hohe Artenvielfalt im Wald (Müller et al. 2014). Mulmhöhlen entstehen nach Verletzungen am lebenden Baum, wie zum Beispiel durch Astabbrüche, die anschließend durch verschiedene von Insekten und Pilzen ausgelöste Zersetzungsprozesse vergrößert werden. Dies nimmt jedoch Jahrzehnte in Anspruch (Ranius et al. 2009). Aufgrund der Zersetzungsprozesse sammelt sich im Laufe der Zeit der namensgebende Mulm an, der aus zersetztem Holz, Ausscheidungen der Mulmhöhlenbewohner, Bakterien und Pilzen besteht. Je nachdem wie lange der Zersetzungsprozess schon andauert, kann man Mulmhöhlen in verschiedenen Zersetzungsstadien finden: Diese reichen von Höhlen mit anfänglich kaum bis zu fast vollständig zersetztem Mulm.

### Heimstatt zahlreicher Xylobionter

Mit Mulmhöhlen sind vor allem viele xylobionte Insekten assoziiert. Xylobionte Insekten sind entweder direkt auf Totholz angewiesen, welches als Nahrungsgrundlage der Larven und / oder Adulten dient, oder indirekt bei Arten, die sich von anderen xylobionten Arten ernähren (Speight 1989). Sie gelten als Indikator-Arten für den Zustand des Waldes, da sie gegenüber Veränderungen in der Qualität und Menge an Totholz sehr sensitiv sind (Ranius 2007; Gossner et al. 2013). In Deutschland sind circa 34 % aller im Wald lebenden Insekten xylobiont (Müller et al. 2008), wobei hier Käfer und Fliegen die artenreichsten Gruppen sind. Diese Gruppen sind sehr wichtig für den Nährstoffzyklus im Wald, da sie maßgeblich an der Zersetzung von Totholz beteiligt sind (Grove 2002). Viele dieser Arten, die auf solche stabilen und speziellen Habitate wie Mulmhöhlen angewiesen sind, sind bedroht (Müller et al. 2014).

### Seltene Strukturen der besonderen Art

Mulmhöhlen sind seltene Strukturelemente im Wald. Da in der Vergangenheit Bäume mit Mulmhöhlen aufgrund ihres fehlenden wirtschaftlichen Werts häufig aus dem Wald entfernt wurden, ist ihre Anzahl in heutigen Wirtschaftswäldern meist begrenzt. Erschwerend kommt hinzu, dass Bewohner von Mulmhöhlen spe-



**2** **Längsschnitt durch eine Mulmhöhle. Die Wände werden meist durch Braun- oder Weißfäule zersetzt und am Boden der Höhle sammelt sich der namensgebende Mulm. Die Gestalt von Mulmhöhlen ist vielfältig und durch viele Faktoren beeinflusst (z. B. der Zersetzungsgrad des Mulms). Eine hohe Vielfalt an Höhlen kann die Habitatansprüche vieler xylobionter Käferarten abdecken und trägt somit zu einem hohen Artenreichtum bei. 1:** *Corticeus fasciatus*
**2:** *Hesperus rufipennis* **3:** *Limoniscus violaceus*
**4:** *Megapenthes lugens* **5 u. 6:** *Rhizophagus sp.*
Fotos H. Bußler, LWF

zielle Habitatansprüche haben (Grove 2002) und somit nicht jede Mulmhöhle als Habitat geeignet ist und sich dadurch die Anzahl an geeigneten Habitaten nochmals verringert. Dies kann dazu führen, dass Mulmhöhlenbewohner lange Strecken zurücklegen müssen, um geeignete Habitate zu finden, um sich zu verpaaren und Eier abzulegen. Wenn diese Strecken nicht überwunden werden können, werden noch nicht besiedelte Mulmhöhlen nicht von der entsprechenden Art erreicht und es können sich kaum stabile Populationen bilden. Zudem kann es zu einem Verlust der genetischen Variabilität innerhalb von Subpopulationen kommen, was zur Folge haben kann, dass Populationen schneller aussterben, da kein ausreichender Genfluss mehr besteht.

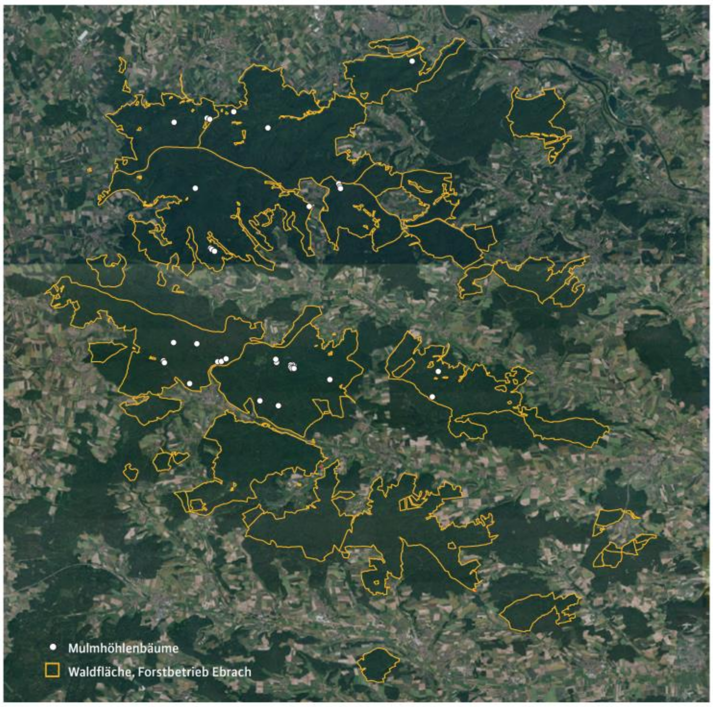
Im Rahmen einer integrativen Waldwirtschaft kann die Artenvielfalt xylobionter Gemeinschaften durch den Erhalt bzw. die Förderung von Mulmhöhlen unterstützt werden. Ähnlich wie bei der Anreicherung von Totholz ist es hierfür essenziell zu verstehen, welche Charakteristika der Mulmhöhlen und der direkten Umgebung einen positiven Einfluss auf die Biodiversität haben und wie gut sich Mulmhöhlen bewohnende Insekten ausbreiten können. Diese Informationen können dabei helfen, ein effizientes Schutzmanagement dieser Arten zu gewährleisten.

### Xylobionte Käfer in Mulmhöhlen

Im Jahr 2014 wurden im Forstbetrieb Ebrach im nördlichen Steigerwald 40 Mulmhöhlen in Rotbuchen im Rahmen des Kuratoriumsprojekts »Mulmhöhlen als Totholz-Struktur mit hoher naturschutzfachlicher Bedeutung zum Schutz der Artenvielfalt im Wald: Nahrungsbeziehungen und Ausbreitungsdistanzen von Mulmhöhlenarthropoden (L56)« ausgewählt und ein erstes Mal beprobt. Im Folgejahr wurden dann die 23 artenreichsten dieser Mulmhöhlen ein weiteres Mal untersucht. Die Insektengemeinschaften wurden mit Hilfe von Emergenzfallen von April bis August abgefangen und in Alkohol konserviert. In den bei-

**3** **Fangbereite Emergenzfalle; aus der mit schwarzem Stoff dicht verschlossenen Mulmhöhle können die Höhlenbewohner nur den Weg ans Licht über das Auffanggefäß finden, wo sie allerdings für die Wissenschaft gefangen werden.** Foto: B. Schauer

**4** **Das Untersuchungsgebiet im Forstbetrieb Ebrach im nördlichen Steigerwald**



**5 Der Eremit ist ein sehr seltener Mulmhöhlenbewohner.** Foto: H. Bußler, LWF

den Jahren konnten insgesamt 89 xylobionte Käferarten und über 3.000 Individuen gesammelt werden (55 Arten aus 28 Familien im Jahr 2014, 72 Arten aus 31 Familien im Jahr 2015). Von diesen 89 Arten sind nach der Roten Liste Bayern 33 % als bedroht eingestuft. Die Artzusammensetzung zwischen verschiedenen Mulmhöhlen, aber auch innerhalb der gleichen Mulmhöhle in zwei verschiedenen Jahren war sehr unterschiedlich. Dies zeigt, dass Käfergemeinschaften in Mulmhöhlen sehr dynamisch sind, da sie sich stark unterscheiden bzw. mehrjährige Entwicklungszyklen für einen ständigen Wechsel der schlüpfenden Käferarten sorgen. Des Weiteren wurden verschiedene Parameter der Mulmhöhlen sowie Umgebungsparameter im Radius von 50 m um die jeweils betreffende Mulmhöhle aufgenommen (Schauer et al. 2018 b).

### Mulm ist nicht gleich Mulm

Die Biodiversität xylobionter Käfer wurde unter anderem durch den Zersetzungsgrad des Mulms bestimmt. Bei einem mittleren Zersetzungsgrad, wenn der Mulm braun und mit sehr feinen, aber sichtbaren Holzstückchen durchsetzt ist, findet man die höchste Anzahl an xylobionten Käferarten. Dies kann durch eine optimale Versorgung mit Ressourcen in diesem Stadium für ein breites Spektrum an Arten erklärt werden. In späten Zersetzungsstadien nimmt die Anzahl an Arten ab, aber dennoch sind auch diese späten Stadien für bestimmte Spezialisten notwendig (Sverdrup-Thygeson et al. 2010; Gouix et al. 2015). Als Spezialist zählt auch der circa 30 mm lange Eremit *(Osmoderma eremita)*, ein xylobionter Käfer aus der Familie der Blatthornkäfer, Urwaldreliktart und prioritäre Käferart der Anhänge II + IV der FFH-Richtlinie, für den jedoch vor allem die Menge des verfügbaren Mulms wichtig ist (bevorzugt mehr als 50 l Mulm). Des Weiteren zeigte sich, dass sich eine mittlere Größe (ca. 1m$^2$) des Höhleneingangs und höhere Temperaturen innerhalb der Höhle günstig auf die Artenzahl auswirken, da sich dadurch ein optimales Mikroklima innerhalb der Höhle für die gefundenen Arten einstellt. Aber auch diese Parameter sind artspezifisch, da manche Arten Höhlen mit großen Eingängen (Ranius 2002) oder niedrigere Temperaturen bevorzugen. Außerdem waren Höhlen, die näher zum Boden lokalisiert waren, artenreicher. Jedoch kommen auch hier bestimmte Arten nur in höher gelegenen Höhlen vor (Ranius 2002). Mulmhöhlen mit großem Volumen und in Bäumen mit einem großen Durchmesser zeigen ebenfalls eine hohe Artenvielfalt. Hier ist anzunehmen, dass in großen Mulmhöhlen mehr verschiedene Mikrohabitate vorhanden sind und somit unterschiedliche Arten ein geeignetes Habitat innerhalb einer Höhle finden.

### Aufgepasst! Mulmhöhlenbewohner bevorzugen Standorte mit hoher Höhlendichte

Die Analyse der Umgebungsparameter in einem Radius von 50 m um die jeweils betreffende Mulmhöhle herum zeigte, dass sich eine hohe Sonneneinstrahlung und eine hohe Anzahl an umgebenden Höhlenbäumen positiv auf die Artenvielfalt in Mulmhöhlen auswirken. Eine hohe Anzahl an weiteren Höhlen in der Umgebung bedeutet, dass es lokal mehr bewohnbares Habitat gibt und damit größere Populationen pro Art und potenziell auch mehr Arten vorkommen können. Die Ergebnisse dieser Studie (Schauer et al. 2018b) zeigen, dass die Artenvielfalt xylobionter Käfer von vielen verschiede-

nen Parametern abhängt und eine ausreichend große Vielfalt an verschieden gestalteten Mulmhöhlen die Artenvielfalt am besten unterstützt.

### Ausbreitungsfähigkeit xylobionter Insekten

Die Ausbreitungsfähigkeit und die daraus resultierende Populationsstruktur xylobionter Insekten in Mulmhöhlen im Wirtschaftswald wurden populationsgenetisch mittels Mikrosatelliten analysiert. Diese Methode erlaubt es, die genetische Differenzierung und den Genfluss zwischen Subpopulationen einer Art abzuschätzen. Hierfür wurden die drei xylobionten Arten *Anaspis ruficollis* (Seidenkäfer, 77 Individuen), *Criorhina floccosa* (Schwebfliege, 99 Individuen) und *Xylomya maculata* (Holzfliege, 159 Individuen) ausgewählt, die alle drei als gefährdet gelten. Die Arten wurden in einem 14 x 14 km großen Gebiet gesammelt, welches durch einen etwa 3 km breiten Korridor aus bewohnten und landwirtschaftlich genutzten Bereichen in einen nördlichen und einen südlichen Teil getrennt wurde.

**6** **oben links: *Anaspis ruficollis* (Seidenkäfer), rechts: *Criorhina floccosa* (Schwebfliege), links: *Xylomya maculata* (Holzfliege)**
Fotos: I. Altmann, N. Pisec, F. Köhler

In dieser Studie konnten bei keiner dieser drei Arten Hinweise auf eingeschränkten Genfluss und somit eine Populationsstrukturierung gefunden werden. Dies deutet darauf hin, dass sich die Populationen jeder dieser drei Arten im Untersuchungsgebiet im Moment noch jeweils im genetischen Austausch befinden, was jedoch auch durch die relativ hohen Individuenzahlen der untersuchten Arten begünstig wird. Alle drei Arten besitzen wahrscheinlich jedoch eine gute Ausbreitungsfähigkeit und zusätzlich scheint es im Untersuchungsgebiet noch genügend Mulmhöhlenbäume zu geben, die es diesen Arten ermöglichen, geeignete Habitate (geeignete Mulmhöhlen) zu finden. Jedoch lässt sich nicht abschätzen, wie die Populationsstruktur und der Genfluss beeinflusst werden, falls es zu einer Reduktion der vorhandenen Mulmhöhlenbäume kommen sollte (Schauer et al. 2018a). Es sollten jedoch von den Ergebnissen dieser Studie keine generellen Schlüsse über die Ausbreitungsfähigkeit xylobionter Insekten gezogen werden, da xylobionte Käferarten sehr variabel in ihrer Ausbreitungsfähigkeit sind, die von wenigen Metern (*Spasalus crenatus*, Zuckerkäfer) bis hin zu mehreren Kilometern (*Bolitophagus reticulatus,* Schwarzkäfer) reicht (Übersicht in Feldhaar & Schauer 2018, in Druck). Die Ausbreitungsfähigkeit wird durch sehr viele verschiedene Faktoren beeinflusst, wie zum Beispiel die Anzahl geeigneter Habitate, die physische Fähigkeit sich auszubreiten oder auch die Vermeidung von Inzucht. Darum ist es wichtig, die Ausbreitung verschiedener Arten zu untersuchen und dabei auch verschiedene Methoden anzuwenden (z. B. genetische Untersuchungen, Besenderung, Wiederfang-Experiment), um somit geeignete Strategien zur gezielten Förderung von Arten mit verschieden Ausbreitungsfähigkeiten zu entwickeln (Feldhaar & Schauer 2018, in Druck).

### Schutz von Mulmhöhlen und ihren Insektengemeinschaften im Wald – die Vielfalt macht's

Keine Mulmhöhle gleicht der anderen, denn sie unterscheiden sich in ihren Eigenschaften, zum Beispiel dem Zersetzungsgrad des Mulms oder dem Höhlenvolumen. Die verschiedenen Eigenschaften ermöglichen es einer Vielzahl verschiedener Insektenarten trotz ihrer unterschiedlichen Habitatansprüche, ein geeignetes Habitat zu bieten. Deshalb ist es wichtig, so viele Mulmhöhlen wie möglich zu erhalten bzw. die Entstehung neuer zu fördern, da nur dadurch eine räumliche und zeitliche Mischung aus Mulmhöhlen mit verschiedenen Eigenschaften erreicht werden kann. Schon generell sollte die Bildung neuer Mulmhöhlen gefördert werden, da es Jahrzehnte dauert, bis sie sich entwickeln und die bereits bestehenden Mulmhöhlen sich im Laufe der Zeit immer weiter zersetzen und letztendlich vollkommen zerfallen und verschwinden Zur Förderung neuer Mulmhöhlen sollte eine hohe Aufmerksamkeit gegenüber bereits existierenden Habitatstrukturen im Wald bestehen, da sie sich zu künftigen Mulmhöhlen entwickeln könnten wie zum Beispiel großen Verletzungen, Astabrissen oder Spechthöhlen. Diese Strukturen sollten unbedingt erhalten und gefördert werden. Außerdem kann die Förderung durch aktiven Eingriff geschehen, indem man die Rinde von Bäumen großflächig schädigt oder Bäume über dem vitalen Ast köpft.

Ein weiterer Grund für die Bewahrung und Förderung einer hohen Anzahl an Mulmhöhlen ist, dass sich wahrscheinlich nicht alle xylobionten Arten so gut ausbreiten können wie die drei in dieser Studie näher untersuchten Arten. Deshalb ist es wichtig, dass es auch für Arten mit geringem Ausbreitungsvermögen noch möglich ist, geeignete Habitate zu erreichen. Hierfür kann man strukturreiche Gebiete über Trittsteine und/oder Biotopbäume mit Baumhöhlen miteinander verbinden, um eine hohe Konnektivität zu erzeugen, die sich positiv auch auf weniger mobile Arten auswirkt.

7 **Die Vielfalt macht's: Mulmhöhlen mit verschiedenen Eigenschaften können die Bedürfnisse vieler Arten decken.** Fotos: H. Bußler, LWF (links oben); B. Schauer

## Zusammenfassung

Mulmhöhlen bieten einer Vielzahl xylobionter Insekten über Jahrzehnte hinweg einen stabilen Lebensraum und ermöglichen auch seltenen Arten mit langen Entwicklungszeiten und besonderen Ansprüchen eine ungestörte Entwicklung. Sie gelten somit als Schlüsselstrukturen für eine hohe Artenvielfalt im Wald. Trotz dieser wichtigen Funktion sind Mulmhöhlen seltene Elemente im Wald. Um diese wichtigen Strukturen zu schützen und die Artenvielfalt im Wald zu fördern, ist es notwendig zu verstehen, welche Eigenschaften der Mulmhöhlen und der unmittelbaren Umgebung eine hohe Artenvielfalt begünstigen. Für die Besiedlung von Mulmhöhlen durch Insekten ist zudem deren Ausbreitungsfähigkeit von großer Bedeutung. Diese kann indirekt mit populationsgenetischen Methoden abgeschätzt werden. Hierfür schätzt man ab, ob zwischen einzelnen Populationen einer Art in einem Waldgebiet noch ausreichend Genfluss besteht, um stabile Populationen zu gewährleisten. Stabile Populationen von zum Teil seltenen Mulmhöhlenspezialisten können regional nur erhalten werden, wenn ein Netz von Mulmhöhlen vorhanden ist, die ein Spektrum unterschiedlicher Eigenschaften aufweisen und in einer Dichte vorkommen, die die Besiedlung ermöglicht.

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## Projekt

Das 3,5-jährige Kuratoriumsprojekt L56 »Mulmhöhlen als Totholz-Struktur mit hoher naturschutzfachlicher Bedeutung zum Schutz der Artenvielfalt im Wald: Nahrungsbeziehungen und Ausbreitungsdistanzen von Mulmhöhlenarthropoden« wurde vom Kuratorium für Forstliche Forschung und dem Bayerischen Staatsministerium für Ernährung, Landwirtschaft und Forsten finanziell gefördert. Es wurde in der Zeit von 2014 bis 2017 an der Universität Bayreuth in Kooperation mit der Bayerischen Landesanstalt für Wald und Forstwirtschaft (LWF), den Bayerischen Staatsforsten AöR (BaySF) und dem Bayreuther Zentrum für Ökologie und Umweltforschung (BayCEER) durchgeführt. Für die Erteilung der naturschutzrechtlichen Ausnahmegenehmigungen danken die Autoren den Regierungen von Oberfranken und Unterfranken.

## Manuscript 6: Mulmhöhlen – für die Artenvielfalt im Wald

Authors: Bastian Schauer, Heike Feldhaar, Anna Kanold, Elisabeth Obermaier

Journal and status: LWF Markblatt 42 (2018)

BS, AK, HF and EO conceived the ideas and designed the methodology. BS led the writing of the manuscript.

LWF Merkblatt 42
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ZENTRUM WALD FORST HOLZ
BAYERISCHE FORSTVERWALTUNG

# Mulmhöhlen – für die Artenvielfalt im Wald

**Biotopbäume mit Mulmhöhlen zählen zu den seltensten Strukturen im Wald. Mulmhöhlen bieten einer Vielzahl von Tierarten über Jahrzehnte hinweg einen Lebensraum. Hier können sich Arten mit einer langen Entwicklungszeit und besonderen Ansprüchen ungestört entwickeln. Somit gelten Mulmhöhlen als Schlüsselstrukturen für eine hohe Artenvielfalt. Bei einer integrativen Waldbewirtschaftung sollte man diese besonderen Strukturen erhalten und fördern, um die Artenvielfalt im Wald zu sichern und zu erhöhen.**

## Mulmhöhlen und ihre Entstehung

Mulmhöhlen sind Höhlen im lebenden Baum. Sie können in verschiedenen Baumarten entstehen, vor allem in Laubbäumen (z. B. Buche, Eiche, Weide, Linde). In Nadelhölzern (z. B. Tanne) finden sich solche Höhlen viel seltener. Für die Höhlenbildung sind besonders förderlich: Verletzungen, zersetzende Organismen und Zeit.

### Verletzungen

Voraussetzung für die Entstehung von Mulmhöhlen sind Verletzungen des Baumes, z. B. Astabbrüche, großflächige Schädigung der Rinde, Zwieselabrisse oder auch Spechthöhlen (Spechte legen ihre Höhlen immer an bereits geschädigten Holzstellen an – auch wenn dies von außen oft nicht erkennbar ist).

### Zersetzende Organismen

Bakterien, Pilze und Insekten können v. a. über Verletzungen in den Baum eindringen und das Holz zersetzen. So entstehen Höhlen, die sich im Lauf der Jahre vergrößern und verändern. Durch die Aktivitäten der verschiedenen Organismen sammelt sich am Boden dieser Höhlen ein Lockersubstrat, welches an Schnupftabak erinnert: der namensgebende Mulm. Mulm besteht aus zersetzten Holz- und Pflanzenresten, den Ausscheidungen der Bewohner und unterschiedlichen Stoffwechselprodukten von Bakterien, Pilzen und Insekten. Die Höhlen können ein erhebliches Volumen erreichen und große Mengen an Mulm enthalten.

### Zeit

Mulmhöhlen bilden sich über viele Jahrzehnte, meist sogar über mehr als 100 Jahre. Daher sind sie charakteristisch für alte, dicke Bäume. Die Höhlen können sehr langlebig sein und mehrere Jahrzehnte in einem lebenden Baum bestehen. Sowohl Bildung als auch Langlebigkeit einer Höhle hängen von der Baumart ab. Am dauerhaftesten bestehen Mulmhöhlen in Eichen und Linden, hier entwickeln sie sich jedoch auch nur langsam.

Spechte sind Baumhöhlenlieferanten. Es dauert dennoch sehr lange, bis eine Mulmhöhle entsteht.

Bodennahe Mulmhöhle einer Buche, hier könnte sich der Veilchenblaue Wurzelhalsschnellkäfer wohlfühlen.

Pilze sind maßgeblich für die Bildung von Mulmhöhlen.

Mulmhöhleninitialen sind z. B. Zwiesel, Astabbrüche und großflächige Verletzungen der Rinde.

## Mulmhöhlen erkennen

Das auffälligste Merkmal einer Mulmhöhle ist der Höhleneingang. Leichter zu erkennen ist dieser, wenn der Baum kein Laub trägt. Die Größe des Höhleneingangs ist variabel, er kann nur wenige Zentimeter Durchmesser haben, aber auch sehr groß sein. Dies sagt jedoch nicht zwingend etwas über die Höhlengröße selbst aus: Auch hinter kleinen Höhleneingängen können sich Höhlen mit viel Volumen verbergen. Die Größe reicht von faustgroßen Kleinhöhlen bis zu mehreren Kubikmetern fassenden Höhlen. Mulmhöhlen können am gesamten Baum, also bodennah bis in den Kronenraum entstehen.

Die Dohle ist eines der größten Tiere, die Mulmhöhlen nutzen.

Mulmhöhlen mit verschieden großen Eingängen.

## Bedeutung der Mulmhöhlen für die Artenvielfalt

Mulmhöhlen sind Lebensgrundlage für viele verschiedene Tierarten, die hier nisten bzw. Unterschlupf und Nahrung finden. Hierzu zählen neben Insekten viele Wirbeltiere wie Vögel, Fledermäuse, Marder, Bilche und Amphibien. Jede Mulmhöhle ist in ihrer Struktur einmalig und unterscheidet sich in ihren Eigenschaften ganz wesentlich von allen anderen, z. B. in Volumen, Mikroklima oder wie stark der Mulm zersetzt ist. Da die Arten, die Mulmhöhlen nutzen, ganz mannigfache Ansprüche haben, ist das Vorkommen von verschiedenen Mulmhöhlen für die Biodiversität im Wald sehr bedeutsam.

Die meisten Waldfledermausarten benötigen ein hohes Angebot an Höhlen, um ihre Quartiere häufig wechseln zu können. Durch regelmäßiges Umziehen entgehen Fledermäuse Parasiten wie Milben und Zecken oder Fressfeinden wie Mardern. Je nach Witterung werden kühlere oder wärmere Höhlen genutzt. Ihr herabfallender Kot wird von Insekten, Pilzen und Bakterien zu Mulm zersetzt.

Rund 40 % der heimischen Waldvögel zählen zu den Höhlen- und Nischenbrütern. Sie sind für ihre Brut unmittelbar auf Höhlen angewiesen. Ein Bewohner großer Höhlen ist der Raufußkauz (*Aegolius funereus*), der v. a. Schwarzspechthöhlen zur Aufzucht der Jungen nutzt. Dohlen (*Coloeus monedula*) brüten vorzugsweise in geselligen Brutkolonien und benötigen daher viele geeignete Baumhöhlen eng beisammen. Als Kletterkünstler beziehen Dohlen gerne tief ausgefaulte Höhlen, welche einen optimalen Schutz vor Feinden liefern.

Mulmhöhlen sind vor allem auch für Insekten bedeutend. 50 seltene und bedrohte Käferarten sind auf diesen über Jahrzehnte stabilen Lebensraum angewiesen. Die bekanntesten Vertreter sind der Eremit (*Osmoderma eremita*) und der Veilchenblaue Wurzelhalsschnellkäfer (*Limoniscus violaceus*). Beide kommen ausschließlich in Mulmhöhlen vor, sind vom Aussterben bedroht und zählen zu den geschützten Arten. Während der Eremit an Höhlen in jeder Stammhöhe vorkommen kann, benötigt der Veilchenblaue Wurzelhalsschnellkäfer eine Mulmhöhle mit Bodenkontakt.

Da Mulmhöhlen so vielen verschiedenen Arten als Lebensraum dienen, sind sie ein besonders bedeutsames Element im Wald und tragen dort zu einer hohen Artenvielfalt bei.

**Schutz**
Viele Höhlenbewohner zählen zu den geschützten Arten nach der Fauna-Flora-Habitat-(FFH) Richtlinie bzw. der Vogelschutzrichtlinie und sind ebenso über das Artenschutzrecht (Bundesnaturschutzgesetz §7) besonders oder streng geschützt. Ziel ist, ihren Lebensraum sowie ihre Populationen zu erhalten.

Ein Großer Abendsegler (*Nyctalus noctula*) schaut aus einer Baumhöhle.

Die Höhle in einer Buche hat der Raufußkauz für sich entdeckt.

Der Eremit oder Juchtenkäfer ist Schirmherr für zahlreiche Mulmhöhlenbewohner.

Insektenvielfalt in Mulmhöhlen

Der Längsschnitt durch eine Mulmhöhle zeigt: Die Wände sind meist durch Braun- oder Weißfäule zersetzt, am Boden der Höhle sammelt sich der namensgebende Mulm. Eine hohe Vielfalt an Höhlen kann die Habitatansprüche vieler Arten decken und trägt somit zu einem hohen Artenreichtum bei. Käfer *(Coleoptera)*, Fliegen *(Dipteren)* und parasitische Wespen *(Hymenoptera)* werden praktisch in allen Baumhöhlen gefunden. Vorkommen kann auch ein Pseudoskorpion *(Pseudoscorpiones)*.

## Mulmhöhlen fördern und erhalten

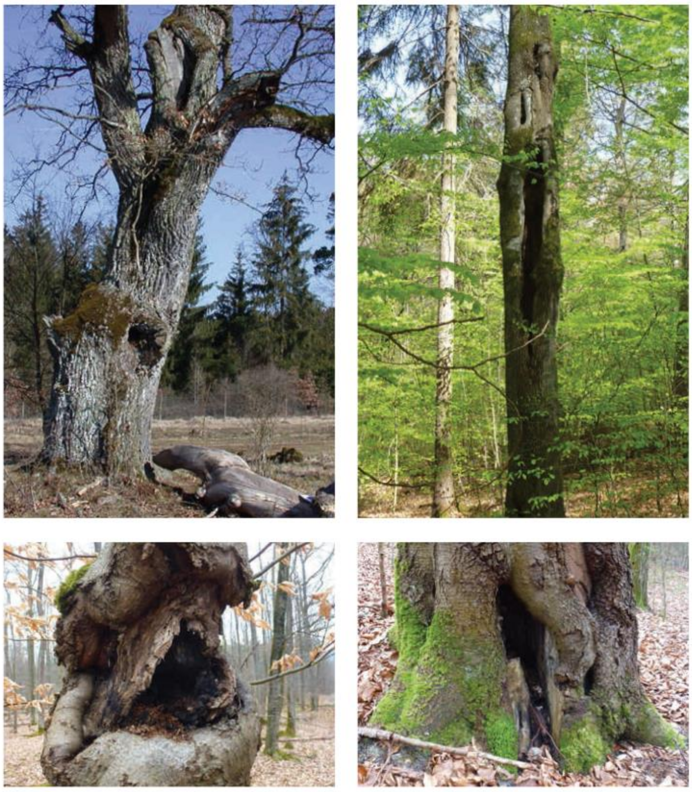
Um das Angebot an Mulmhöhlen auch dauerhaft zu sichern, sollte die Bildung neuer Mulmhöhlen (z. B. durch Belassen von verletzten Bäumen) aktiv gefördert werden. Einerseits dauert es sehr lange bis Mulmhöhlen entstehen, andererseits zersetzen sie sich im Lauf der Jahre immer weiter und zerfallen letztendlich. Um die Vielfalt von Mulmhöhlen – und damit auch deren Bewohner – im Wald zu erhalten und zu fördern, sollte Folgendes berücksichtigt werden:

Mulmhöhlen erhalten, sofern es aus sicherheitsrelevanten Aspekten möglich ist.

Bäume mit bestimmten Habitatstrukturen (großflächige Verletzungen, Astabbrüche, Zwieselabrisse und Spechthöhlen) so weit möglich im Bestand belassen; sie sind die potenziellen Mulmhöhlen von morgen.

Dort, wo entsprechende Strukturen fehlen, kann auch die Bildung von Mulmhöhlen (z. B. durch gezielte Rindenverletzungen oder Kappung der Krone über einem vitalen Ast) aktiv gefördert werden.

Achten Sie als Waldbesitzer in Ihrem Wald ganz generell aufmerksam auf Habitatstrukturen und deren Erhalt, damit unterstützen Sie die Artenvielfalt sehr einfach und wirkungsvoll.



Die Vielfalt macht's: Mulmhöhlen mit verschiedenen Eigenschaften können die Bedürfnisse vieler Arten decken.

**Beratung und finanzielle Förderung**
Im Rahmen des Vertragsnaturschutzprogramms Wald (VNP Wald) können sich Waldbesitzer mit Fördermitteln, etwa für den Erhalt von Biotopbäumen und das Belassen von Totholz, ihr freiwilliges Engagement für den Natur- und Artenschutz honorieren lassen. Informationen zum VNP Wald erhalten Sie bei Ihrem zuständigen Amt für Ernährung, Landwirtschaft und Forsten (AELF) im Internet unter *www.stmelf.bayern.de/wald*.

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## Supporting information Manuscript 1

### Supporting information Fig. S1

**Biodiversity and Conservation**

Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest

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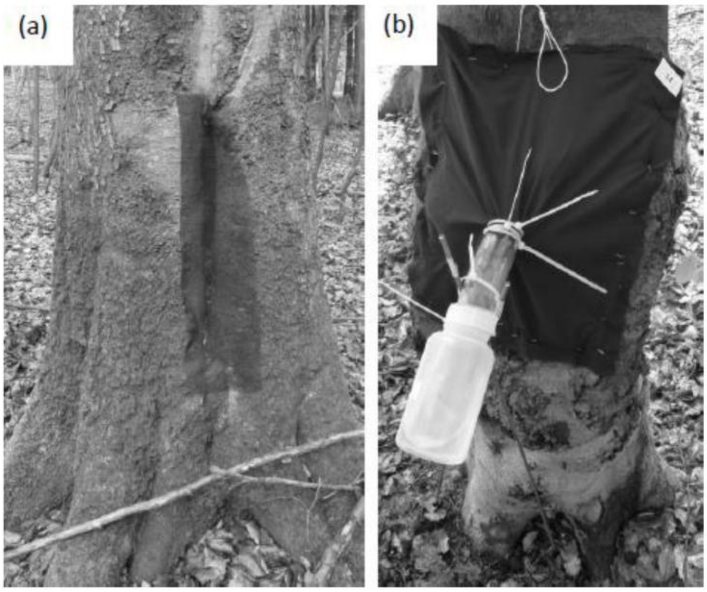

Figure S1: (a) Tree hollow closed with black acrylic mesh in the period of mid-March to mid-April to prevent the tree hollows from being used as nesting place of birds, bats and other vertebrates. (b) In April all tree hollows were closed with black fabric and emergence traps, modified from Gouix und Brustel (2012) and were attached to all hollows.

**Supporting information Fig. S2**

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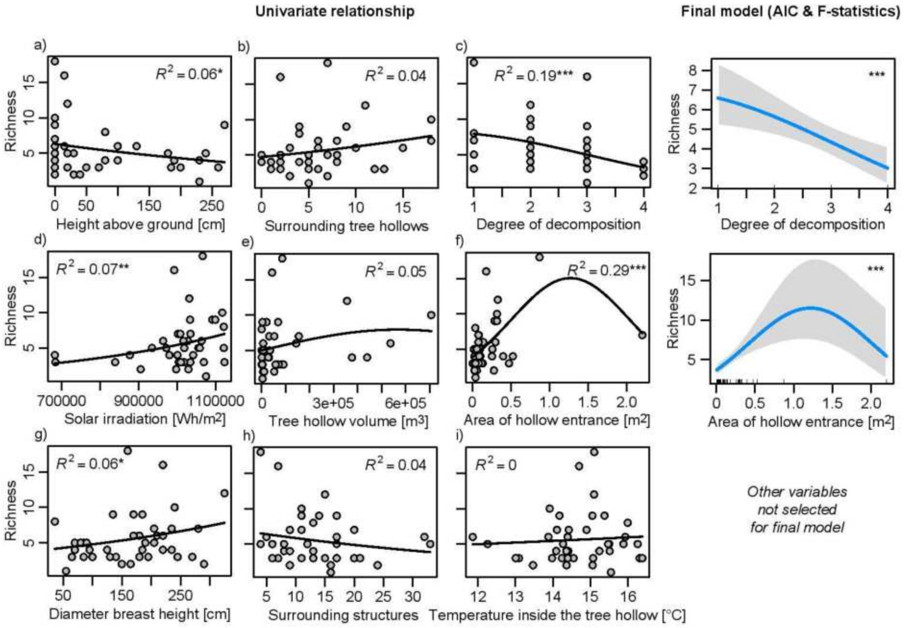

Figure S2: Conditional response of explanatory variables explaining overall species richness for the 40 tree hollows sampled in 2014. Confidence band displayed in the plot at an Alpha level (1-coverage) of 0.05.

**Supporting information Fig. S3**

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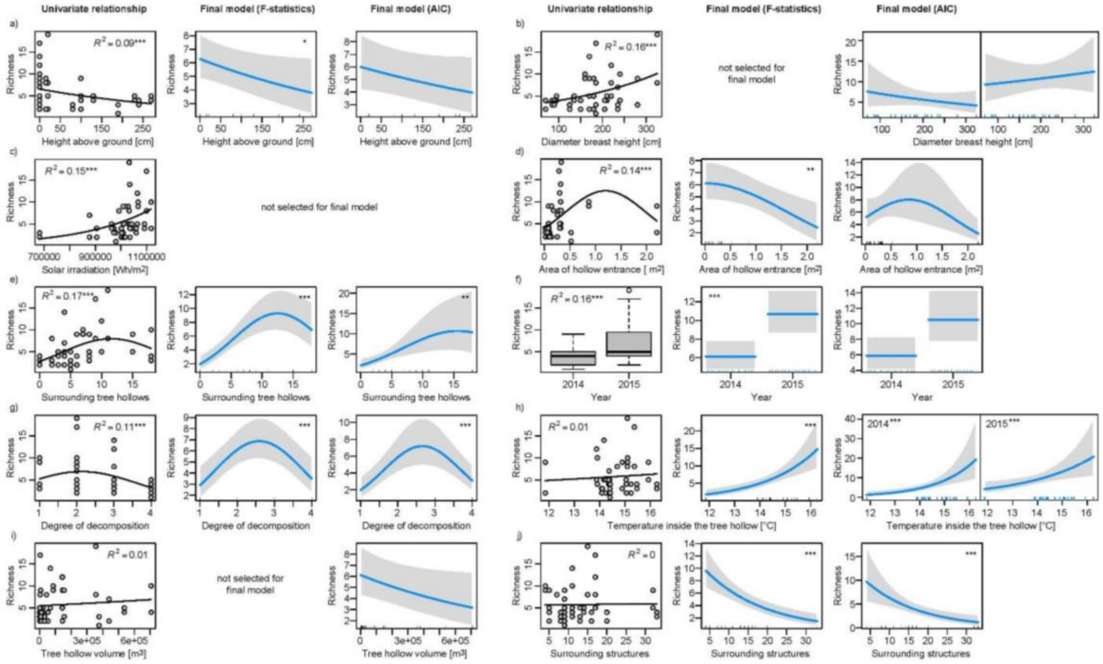

Figure S3: Conditional response of explanatory variables explaining overall species richness of non-threatened species. Confidence band displayed in the plot at an Alpha level (1-coverage) of 0.05.

**Supporting information Fig. S4**

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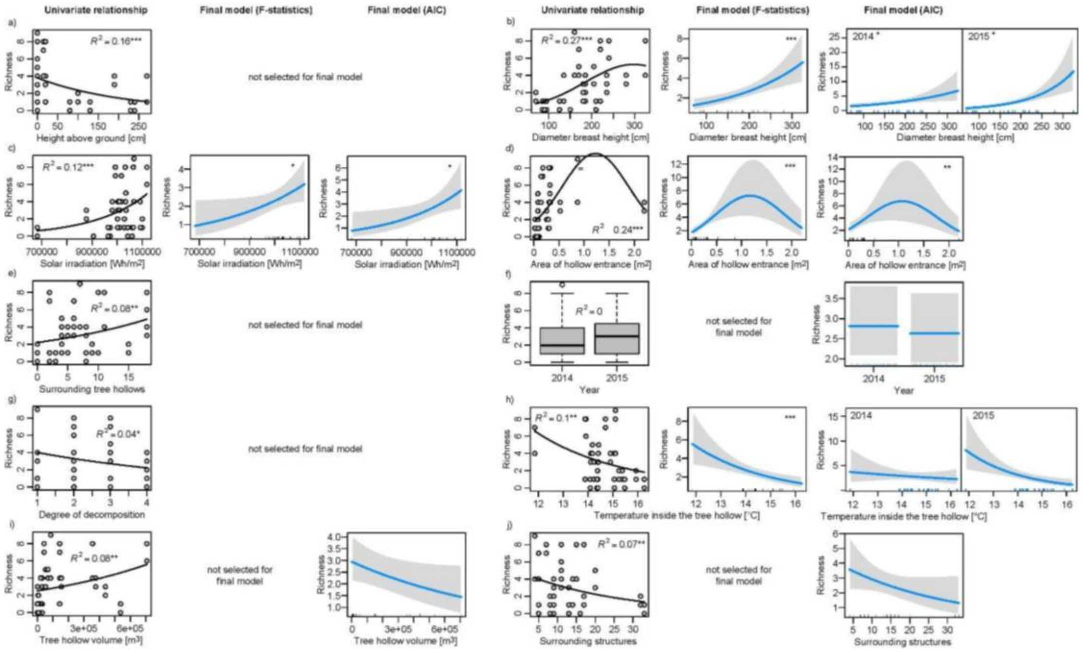

Figure S4: Conditional response of explanatory variables explaining overall species richness of red listed species. Confidence band displayed in the plot at an Alpha level (1-coverage) of 0.05.

**Supporting information Fig. S5**

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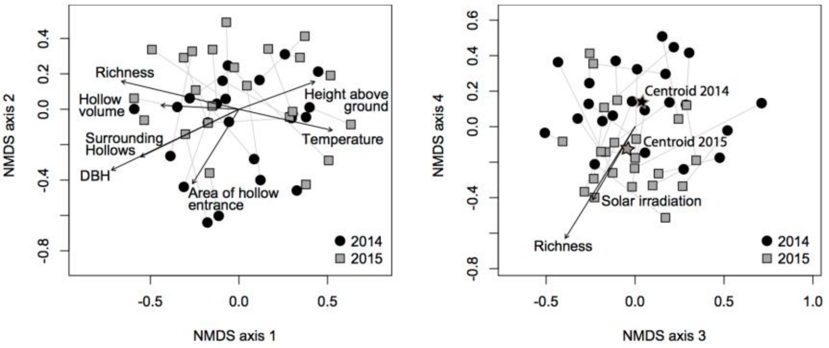

Figure S5: Nonmetric multidimensional scaling (NMDS) of similarity in species composition (Bray Curtis dissimilarity) of all species in the 23 tree hollows sampled in 2014 and 2015. Post hoc correlated environmental variables are indicated by arrows (permutation based p>0.05). This figure resembles figure 5 in the main text, but represents the result of a NMDS with 4 axes instead of two (like in figure 5).

**Supporting information Table S1**

**Biodiversity and Conservation**

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Table S1: Saproxylic beetle species, families, their Bavarian Red List status (Rote Liste Bayern, 2005), tree, week, number and year collected in 2014 and 2015 in hollows of beech trees in the northern Steigerwald. NE = not endangered, SU = status unknown, 3 = vulnerable, 2 = endangered, 1 = critically endangered.

| Species | Family | Red list | Tree | Week | Number | Year |
|---|---|---|---|---|---|---|
| *Ampedus nigroflavus* | Elateridae | 3 | 2 | 4 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 2 | 6 | 1 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 2 | 7 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 2 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 2 | 9 | 1 | 2014 |
| *Cryptophagus labilis* | Cryptophagidae | 2 | 2 | 14 | 1 | 2014 |
| *Prionocyphon serricornis* | Scirtidae | NE | 2 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 2 | 14 | 1 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 2 | 14 | 2 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 2 | 16 | 2 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 2 | 4 | 1 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 2 | 8 | 1 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 2 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 2 | 12 | 1 | 2015 |
| *Anaspis rufilabris* | Scraptiidae | NE | 2 | 12 | 1 | 2015 |
| *Scraptia fuscula* | Scraptiidae | 3 | 2 | 14 | 2 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 3 | 1 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 2 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 2 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 3 | 5 | 1 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 3 | 5 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 6 | 2 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 6 | 2 | 2014 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 3 | 8 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 3 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 8 | 6 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 8 | 2 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 3 | 9 | 3 | 2014 |
| *Plegaderus dissectus* | Histeridae | 3 | 3 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 9 | 3 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 9 | 1 | 2014 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Xyleborus germanus* | Scolytidae | NE | 3 | 10 | 2 | 2014 |
| *Ptinella aptera* | Ptiliidae | NE | 3 | 12 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 12 | 5 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 12 | 1 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 3 | 12 | 1 | 2014 |
| *Ptinella aptera* | Ptiliidae | NE | 3 | 14 | 4 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 14 | 4 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 14 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 16 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 3 | 2 | 2 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 3 | 6 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 8 | 4 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 3 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 10 | 6 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 12 | 4 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 3 | 12 | 16 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 3 | 14 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 16 | 5 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 3 | 18 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 3 | 18 | 7 | 2015 |
| *Malthodes marginatus* | Cantharidae | NE | 4 | 1 | 1 | 2014 |
| *Anaspis frontalis* | Scraptiidae | NE | 4 | 3 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 4 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 6 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 7 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 4 | 8 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 4 | 8 | 4 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 8 | 73 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 8 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 9 | 83 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 9 | 4 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 4 | 12 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 12 | 52 | 2014 |
| *Anobium nitidum* | Anobiidae | NE | 4 | 14 | 2 | 2014 |
| *Cryptophagus labilis* | Cryptophagidae | 2 | 4 | 14 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 4 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 14 | 31 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 14 | 2 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 14 | 2 | 2014 |
| *Anobium nitidum* | Anobiidae | NE | 4 | 16 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 4 | 16 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 16 | 3 | 2014 |
| *Aderus populneus* | Aderidae | 3 | 4 | 2 | 1 | 2015 |

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|---|---|---|---|---|---|---|
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 4 | 2 | 2 | 2015 |
| *Ptinella aptera* | Ptiliidae | NE | 4 | 2 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 4 | 2 | 1 | 2015 |
| *Malthodes marginatus* | Cantharidae | NE | 4 | 4 | 4 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 6 | 1 | 2015 |
| *Anaspis rufilabris* | Scraptiidae | NE | 4 | 6 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 4 | 8 | 2 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 8 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 8 | 19 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 4 | 8 | 2 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 4 | 10 | 12 | 2015 |
| *Tillus elongatus* | Cleridae | NE | 4 | 10 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 10 | 7 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 4 | 12 | 5 | 2015 |
| *Anobium nitidum* | Anobiidae | NE | 4 | 12 | 2 | 2015 |
| *Calambus bipustulatus* | Elateridae | NE | 4 | 12 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 4 | 12 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 12 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 12 | 23 | 2015 |
| *Anobium nitidum* | Anobiidae | NE | 4 | 14 | 3 | 2015 |
| *Dissoleucas niveirostris* | Anthribidae | NE | 4 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 14 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 14 | 4 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 4 | 14 | 1 | 2015 |
| *Velleius dilatatus* | Staphylinidae | NE | 4 | 14 | 1 | 2015 |
| *Anobium nitidum* | Anobiidae | NE | 4 | 16 | 2 | 2015 |
| *Anobium costatum* | Anobiidae | NE | 4 | 16 | 1 | 2015 |
| *Prionocyphon serricornis* | Scirtidae | NE | 4 | 16 | 1 | 2015 |
| *Acalles hypocrita* | Curculionidae | NE | 4 | 18 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 4 | 18 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 4 | 18 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 5 | 2 | 5 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 2 | 10 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 5 | 2 | 1 | 2014 |
| *Xyloterus signatus* | Scolytidae | NE | 5 | 2 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 5 | 4 | 1 | 2014 |
| *Ernoporicus fagi* | Scolytidae | NE | 5 | 6 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 5 | 6 | 60 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 6 | 36 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 5 | 6 | 29 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 5 | 7 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 7 | 1 | 2014 |
| *Megatoma undata* | Dermestidae | 3 | 5 | 8 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 5 | 8 | 1 | 2014 |

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|---|---|---|---|---|---|---|
| *Xyleborus germanus* | Scolytidae | NE | 5 | 8 | 34 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 5 | 8 | 3 | 2014 |
| *Melanotus castanipes* | Elateridae | NE | 5 | 9 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 5 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 9 | 8 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 5 | 9 | 4 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 10 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 12 | 13 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 5 | 12 | 2 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 5 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 14 | 2 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 5 | 14 | 5 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 5 | 16 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 5 | 16 | 1 | 2014 |
| *Malthodes marginatus* | Cantharidae | NE | 6 | 2 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 6 | 5 | 43 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 6 | 5 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 6 | 8 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 6 | 8 | 33 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 6 | 8 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 6 | 9 | 28 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 6 | 9 | 4 | 2014 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 6 | 12 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 6 | 12 | 8 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 6 | 14 | 5 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 6 | 16 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 7 | 2 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 7 | 2 | 1 | 2014 |
| *Alosterna tabacicolor* | Cerambycidae | NE | 7 | 6 | 3 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 7 | 6 | 12 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 6 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 7 | 6 | 6 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 7 | 7 | 3 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 7 | 7 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 7 | 8 | 2 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 7 | 8 | 16 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 8 | 2 | 2014 |
| *Tillus elongatus* | Cleridae | 3 | 7 | 9 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 7 | 9 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 9 | 2 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 7 | 9 | 2 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 7 | 9 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 7 | 10 | 9 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 7 | 10 | 1 | 2014 |

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|---|---|---|---|---|---|---|
| *Anisotoma humeralis* | Leiodidae | NE | 7 | 11 | 1 | 2014 |
| *Anaspis frontalis* | Scraptiidae | NE | 7 | 11 | 1 | 2014 |
| *Allecula morio* | Alleculidae | 3 | 7 | 12 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 7 | 12 | 2 | 2014 |
| *Allecula morio* | Alleculidae | 3 | 7 | 14 | 3 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 7 | 14 | 6 | 2014 |
| *Allecula morio* | Alleculidae | 3 | 7 | 16 | 2 | 2014 |
| *Prionus coriarius* | Cerambycidae | NE | 7 | 16 | 1 | 2014 |
| *Orthoperus atomus* | Corylophidae | NE | 7 | 4 | 1 | 2015 |
| *Acalles hypocrita* | Curculionidae | NE | 7 | 4 | 1 | 2015 |
| *Malachius bipustulatus* | Melyridae | NE | 7 | 4 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 4 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 7 | 4 | 1 | 2015 |
| *Anaspis rufilabris* | Scraptiidae | NE | 7 | 4 | 1 | 2015 |
| *Ampedus pomorum* | Elateridae | NE | 7 | 6 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 7 | 6 | 2 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 7 | 8 | 2 | 2015 |
| *Alosterna tabacicolor* | Cerambycidae | NE | 7 | 8 | 3 | 2015 |
| *Phloeophagus lignarius* | Curculionidae | NE | 7 | 8 | 1 | 2015 |
| *Ampedus pomorum* | Elateridae | NE | 7 | 8 | 1 | 2015 |
| *Melanotus rufipes* | Elateridae | NE | 7 | 8 | 2 | 2015 |
| *Hypebaeus flavipes* | Malachiidae | 3 | 7 | 8 | 7 | 2015 |
| *Epuraea variegata* | Nitidulidae | NE | 7 | 8 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 7 | 8 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 7 | 8 | 4 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 7 | 8 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 8 | 15 | 2015 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 7 | 8 | 1 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 7 | 8 | 1 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 7 | 10 | 1 | 2015 |
| *Cryptophagus labilis* | Cryptophagidae | 2 | 7 | 10 | 1 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 7 | 10 | 1 | 2015 |
| *Platycis cosnardi* | Lycidae | 2 | 7 | 10 | 1 | 2015 |
| *Hypebaeus flavipes* | Malachiidae | 3 | 7 | 10 | 16 | 2015 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 7 | 10 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 7 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 10 | 7 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 7 | 10 | 1 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 7 | 12 | 2 | 2015 |
| *Paromalus flavicornis* | Histeridae | NE | 7 | 12 | 1 | 2015 |
| *Hypebaeus flavipes* | Malachiidae | 3 | 7 | 12 | 6 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 7 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 12 | 25 | 2015 |
| *Arpidiphorus orbiculatus* | Sphindidae | SU | 7 | 12 | 2 | 2015 |

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|---|---|---|---|---|---|---|
| *Allecula morio* | Alleculidae | 3 | 7 | 14 | 27 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 7 | 14 | 3 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 7 | 14 | 1 | 2015 |
| *Hypebaeus flavipes* | Malachiidae | 3 | 7 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 14 | 1 | 2015 |
| *Xyloterus signatus* | Scolytidae | NE | 7 | 14 | 1 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 7 | 14 | 1 | 2015 |
| *Allecula morio* | Alleculidae | 3 | 7 | 16 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 7 | 16 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 7 | 16 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 7 | 18 | 6 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 7 | 18 | 1 | 2015 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 8 | 3 | 2 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 8 | 4 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 8 | 7 | 2 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 8 | 7 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 8 | 8 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 8 | 8 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 8 | 8 | 1 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 8 | 8 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 8 | 10 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 8 | 2 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 8 | 4 | 1 | 2015 |
| *Alosterna tabacicolor* | Cerambycidae | NE | 8 | 6 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 8 | 6 | 1 | 2015 |
| *Hypebaeus flavipes* | Malachiidae | 3 | 8 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 8 | 8 | 1 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 8 | 10 | 1 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 8 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 8 | 12 | 1 | 2015 |
| *Quedius brevicornis* | Staphylinidae | 3 | 8 | 14 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 10 | 7 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 10 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 10 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 10 | 16 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 11 | 2 | 1 | 2014 |
| *Quedius truncicola* | Staphylinidae | 3 | 11 | 8 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 11 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 11 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 11 | 12 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 11 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 11 | 14 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 11 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 11 | 8 | 1 | 2015 |

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|---|---|---|---|---|---|---|
| *Xyleborus saxeseni* | Scolytidae | NE | 11 | 8 | 4 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 11 | 12 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 11 | 12 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 11 | 12 | 6 | 2015 |
| *Xyloterus signatus* | Scolytidae | NE | 11 | 14 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 11 | 16 | 1 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 12 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 12 | 8 | 1 | 2014 |
| *Anaspis thoracica* | Scraptiidae | NE | 12 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 12 | 12 | 6 | 2014 |
| *Prionocyphon serricornis* | Scirtidae | NE | 12 | 16 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 12 | 2 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 12 | 12 | 2 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 13 | 4 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 13 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 13 | 6 | 2 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 13 | 6 | 3 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 13 | 8 | 5 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 13 | 16 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 13 | 16 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 14 | 2 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 14 | 3 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 14 | 6 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 14 | 6 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 14 | 9 | 2 | 2014 |
| *Melanotus castanipes* | Elateridae | NE | 14 | 10 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 14 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 14 | 14 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 14 | 14 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 14 | 8 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 14 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 14 | 12 | 7 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 14 | 12 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 14 | 12 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 15 | 6 | 6 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 15 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 15 | 10 | 1 | 2014 |
| *Hesperus rufipennis* | Staphylinidae | 2 | 15 | 10 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 15 | 12 | 3 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 15 | 14 | 1 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 15 | 14 | 1 | 2014 |
| *Hylecoetus dermestoides* | Lymexylidae | NE | 16 | 5 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 16 | 5 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 16 | 6 | 1 | 2014 |

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|---|---|---|---|---|---|---|
| *Xyleborus germanus* | Scolytidae | NE | 16 | 9 | 3 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 16 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 16 | 14 | 12 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 16 | 16 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 16 | 16 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 17 | 6 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 17 | 6 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 17 | 8 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 17 | 9 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 17 | 12 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 17 | 14 | 2 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 18 | 2 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 18 | 6 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 18 | 9 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 18 | 9 | 1 | 2014 |
| *Cerophytum elateroides* | Cerophytidae | 2 | 18 | 2 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 18 | 2 | 1 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 18 | 12 | 2 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 18 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 18 | 12 | 5 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 18 | 14 | 3 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 18 | 16 | 2 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 18 | 18 | 3 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 18 | 18 | 2 | 2015 |
| *Ischnomera spp.* | Oedemeridae | NE | 18 | 18 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 18 | 18 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 18 | 18 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 18 | 18 | 4 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 18 | 18 | 1 | 2015 |
| *Anaspis frontalis* | Scraptiidae | NE | 19 | 4 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 19 | 11 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 19 | 4 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 19 | 8 | 1 | 2015 |
| *Tillus elongatus* | Cleridae | NE | 19 | 10 | 1 | 2015 |
| *Melanotus rufipes* | Elateridae | NE | 19 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 19 | 12 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 19 | 14 | 1 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 20 | 6 | 1 | 2014 |
| *Tillus elongatus* | Cleridae | 3 | 20 | 6 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 20 | 8 | 3 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 20 | 8 | 1 | 2014 |
| *Anaspis thoracica* | Scraptiidae | NE | 20 | 8 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 20 | 9 | 7 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 9 | 1 | 2014 |

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|---|---|---|---|---|---|---|
| *Ptilinus pectinicornis* | Anobiidae | NE | 20 | 11 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 20 | 14 | 1 | 2014 |
| *Malthodes marginatus* | Cantharidae | NE | 20 | 2 | 1 | 2015 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 20 | 2 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 2 | 1 | 2015 |
| *Bibloporus bicolor* | Staphylinidae | NE | 20 | 2 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 20 | 6 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 20 | 6 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 6 | 1 | 2015 |
| *Xyloterus signatus* | Scolytidae | NE | 20 | 6 | 1 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 20 | 6 | 2 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 20 | 8 | 12 | 2015 |
| *Melanotus castanipes* | Elateridae | NE | 20 | 8 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 20 | 8 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 8 | 11 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 20 | 8 | 13 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 20 | 10 | 5 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 20 | 10 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 10 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 20 | 10 | 9 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 20 | 12 | 7 | 2015 |
| *Melanotus castanipes* | Elateridae | NE | 20 | 12 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 12 | 9 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 20 | 12 | 28 | 2015 |
| *Neuraphes plicicollis* | Scydmaenidae | NE | 20 | 12 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 14 | 13 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 20 | 14 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 16 | 7 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 20 | 16 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 20 | 18 | 36 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 20 | 18 | 3 | 2015 |
| *Malthodes marginatus* | Cantharidae | NE | 21 | 2 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 21 | 3 | 5 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 21 | 4 | 9 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 21 | 5 | 3 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 21 | 6 | 4 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 21 | 7 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 7 | 2 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 21 | 7 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 21 | 7 | 1 | 2014 |
| *Anaspis thoracica* | Scraptiidae | NE | 21 | 7 | 1 | 2014 |
| *Tillus elongatus* | Cleridae | 3 | 21 | 8 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 8 | 2 | 2014 |
| *Quedius truncicola* | Staphylinidae | 3 | 21 | 8 | 1 | 2014 |

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|---|---|---|---|---|---|---|
| *Xyleborus germanus* | Scolytidae | NE | 21 | 9 | 19 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 21 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 10 | 18 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 21 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 11 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 12 | 23 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 14 | 11 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 21 | 2 | 1 | 2015 |
| *Ischnomera sp.* | Oedemeridae | NE | 21 | 2 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 21 | 2 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 4 | 2 | 2015 |
| *Anaspis marginicollis* | Scraptiidae | 2 | 21 | 4 | 1 | 2015 |
| *Rhizophagus perforatus* | Monotomidae | SU | 21 | 6 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 6 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 21 | 6 | 1 | 2015 |
| *Phloeocharis subtilissima* | Staphylinidae | NE | 21 | 6 | 1 | 2015 |
| *Tillus elongatus* | Cleridae | NE | 21 | 8 | 2 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 21 | 8 | 1 | 2015 |
| *Rhizophagus depressus* | Monotomidae | NE | 21 | 8 | 1 | 2015 |
| *Euplectus kirbyi* | Pselaphidae | NE | 21 | 8 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 21 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 8 | 8 | 2015 |
| *Anaspis marginicollis* | Scraptiidae | 2 | 21 | 8 | 1 | 2015 |
| *Microscydmus minimus* | Scydmaenidae | NE | 21 | 8 | 1 | 2015 |
| *Arpidiphorus orbiculatus* | Sphindidae | SU | 21 | 8 | 2 | 2015 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 21 | 10 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 21 | 10 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 21 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 10 | 7 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 21 | 10 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 12 | 22 | 2015 |
| *Orchesia micans* | Melandryidae | NE | 21 | 14 | 2 | 2015 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 21 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 21 | 16 | 2 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 21 | 18 | 1 | 2015 |
| *Quedius truncicola* | Staphylinidae | NE | 21 | 18 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 2 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 22 | 2 | 2 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 22 | 3 | 5 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 22 | 4 | 1 | 2014 |
| *Triplax russica* | Erotylidae | NE | 22 | 6 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 22 | 6 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 22 | 6 | 1 | 2014 |

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|---|---|---|---|---|---|---|
| *Xyleborus dispar* | Scolytidae | NE | 22 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 6 | 1 | 2014 |
| *Anaspis frontalis* | Scraptiidae | NE | 22 | 6 | 1 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 22 | 6 | 1 | 2014 |
| *Orchesia micans* | Melandryidae | NE | 22 | 7 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 22 | 7 | 2 | 2014 |
| *Dorcatoma substriata* | Anobiidae | 2 | 22 | 8 | 2 | 2014 |
| *Plegaderus dissectus* | Histeridae | 3 | 22 | 8 | 2 | 2014 |
| *Orchesia micans* | Melandryidae | NE | 22 | 8 | 1 | 2014 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 22 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 8 | 6 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 22 | 8 | 1 | 2014 |
| *Pseudocistela ceramboides* | Tenebrionidae | 2 | 22 | 8 | 1 | 2014 |
| *Plegaderus dissectus* | Histeridae | 3 | 22 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 9 | 23 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 22 | 9 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 22 | 10 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 10 | 3 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 22 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 11 | 2 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 22 | 12 | 1 | 2014 |
| *Orchesia micans* | Melandryidae | NE | 22 | 12 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 12 | 23 | 2014 |
| *Abraeus perpusillus* | Histeridae | NE | 22 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 14 | 3 | 2014 |
| *Triplax russica* | Erotylidae | NE | 22 | 16 | 2 | 2014 |
| *Orchesia micans* | Melandryidae | NE | 22 | 16 | 2 | 2014 |
| *Abraeus perpusillus* | Histeridae | NE | 22 | 2 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 22 | 2 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 2 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 4 | 2 | 2015 |
| *Cryptophagus labilis* | Cryptophagidae | 2 | 22 | 6 | 1 | 2015 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 22 | 6 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 6 | 1 | 2015 |
| *Hypebaeus flavipes* | Malachiidae | 3 | 22 | 8 | 1 | 2015 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 22 | 8 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 22 | 8 | 2 | 2015 |
| *Hesperus rufipennis* | Staphylinidae | 2 | 22 | 8 | 3 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 22 | 10 | 1 | 2015 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 22 | 10 | 1 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 22 | 10 | 1 | 2015 |
| *Cryptophagus labilis* | Cryptophagidae | 2 | 22 | 12 | 1 | 2015 |
| *Phloeophagus lignarius* | Curculionidae | NE | 22 | 12 | 2 | 2015 |
| *Abraeus perpusillus* | Histeridae | NE | 22 | 12 | 1 | 2015 |

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|---|---|---|---|---|---|---|
| *Plegaderus dissectus* | Histeridae | 3 | 22 | 12 | 3 | 2015 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 22 | 12 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 22 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 12 | 10 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 22 | 14 | 5 | 2015 |
| *Euplectus punctatus* | Pselaphidae | NE | 22 | 16 | 1 | 2015 |
| *Abraeus perpusillus* | Histeridae | NE | 22 | 18 | 1 | 2015 |
| *Orchesia micans* | Melandryidae | NE | 22 | 18 | 1 | 2015 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 23 | 6 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 23 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 23 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 23 | 11 | 1 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 23 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 23 | 12 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 23 | 14 | 2 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 23 | 16 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 23 | 2 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 23 | 2 | 1 | 2015 |
| *Ernoporicus fagi* | Curculionidae | NE | 23 | 4 | 1 | 2015 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 23 | 4 | 2 | 2015 |
| *Cryptophagus labilis* | Cryptophagidae | 2 | 23 | 8 | 1 | 2015 |
| *Melanotus castanipes* | Elateridae | NE | 23 | 8 | 1 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 23 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 23 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 23 | 12 | 13 | 2015 |
| *Prionocyphon serricornis* | Scirtidae | NE | 23 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 23 | 14 | 6 | 2015 |
| *Abraeus perpusillus* | Histeridae | NE | 23 | 16 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 23 | 18 | 1 | 2015 |
| *Denticollis rubens* | Elateridae | 2 | 24 | 3 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 24 | 3 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 24 | 3 | 1 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 24 | 3 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 24 | 8 | 3 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 24 | 9 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 24 | 9 | 4 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 24 | 11 | 1 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 24 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 24 | 12 | 8 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 24 | 12 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 24 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 24 | 16 | 2 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 25 | 1 | 1 | 2014 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 25 | 2 | 1 | 2014 |

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|---|---|---|---|---|---|---|
| *Anaspis ruficollis* | Scraptiidae | 2 | 25 | 2 | 1 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 25 | 2 | 1 | 2014 |
| *Hesperus rufipennis* | Staphylinidae | 2 | 25 | 2 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 25 | 4 | 3 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 25 | 4 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 25 | 6 | 2 | 2014 |
| *Plegaderus dissectus* | Histeridae | 3 | 25 | 6 | 1 | 2014 |
| *Mycetophagus populi* | Mycetophagidae | 2 | 25 | 6 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 25 | 6 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 25 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 6 | 5 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 25 | 6 | 7 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 25 | 6 | 3 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 25 | 7 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 25 | 7 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 25 | 8 | 1 | 2014 |
| *Plegaderus dissectus* | Histeridae | 3 | 25 | 8 | 6 | 2014 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 25 | 8 | 1 | 2014 |
| *Ptenidium turgidum* | Ptiliidae | 3 | 25 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 8 | 25 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 25 | 8 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 25 | 8 | 4 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 25 | 9 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 9 | 16 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 25 | 9 | 1 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 25 | 9 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 25 | 10 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 10 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 25 | 10 | 1 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 25 | 10 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 11 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 12 | 22 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 25 | 12 | 2 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 25 | 12 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 14 | 7 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 25 | 14 | 1 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 25 | 14 | 2 | 2014 |
| *Siagonum quadricorne* | Staphylinidae | NE | 25 | 14 | 1 | 2014 |
| *Orchesia micans* | Melandryidae | NE | 25 | 16 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 16 | 2 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 25 | 16 | 2 | 2014 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 25 | 2 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 25 | 2 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 25 | 2 | 1 | 2015 |

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|---|---|---|---|---|---|---|
| *Cis bidentatus* | Ciidae | NE | 25 | 4 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 25 | 4 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 4 | 2 | 2015 |
| *Phloeonomus punctipennis* | Staphylinidae | NE | 25 | 4 | 1 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 25 | 8 | 3 | 2015 |
| *Rhizophagus perforatus* | Monotomidae | SU | 25 | 8 | 1 | 2015 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 25 | 8 | 1 | 2015 |
| *Xyleborus monographus* | Scolytidae | NE | 25 | 8 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 25 | 8 | 4 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 25 | 8 | 7 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 8 | 68 | 2015 |
| *Anaspis marginicollis* | Scraptiidae | 2 | 25 | 8 | 1 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 25 | 8 | 1 | 2015 |
| *Phloeonomus punctipennis* | Staphylinidae | NE | 25 | 8 | 1 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 25 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 10 | 30 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 25 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 12 | 51 | 2015 |
| *Arpidiphorus orbiculatus* | Sphindidae | SU | 25 | 12 | 4 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 14 | 4 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 25 | 14 | 3 | 2015 |
| *Arpidiphorus orbiculatus* | Sphindidae | SU | 25 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 25 | 16 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 25 | 16 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 25 | 16 | 2 | 2015 |
| *Arpidiphorus orbiculatus* | Sphindidae | SU | 25 | 16 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 25 | 18 | 2 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 25 | 18 | 3 | 2015 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 26 | 3 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 26 | 4 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 26 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 6 | 1 | 2014 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 26 | 6 | 1 | 2014 |
| *Cerophytum elateroides* | Cerophytidae | 2 | 26 | 7 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 8 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 9 | 7 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 26 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 12 | 15 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 14 | 5 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 16 | 1 | 2014 |
| *Abraeus perpusillus* | Histeridae | NE | 26 | 2 | 1 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 26 | 2 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 26 | 2 | 1 | 2015 |

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|---|---|---|---|---|---|---|
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 26 | 4 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 26 | 4 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 6 | 1 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 26 | 8 | 1 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 26 | 8 | 1 | 2015 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 26 | 8 | 1 | 2015 |
| *Ptenidium turgidum* | Ptiliidae | 3 | 26 | 8 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 26 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 10 | 2 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 26 | 10 | 1 | 2015 |
| *Crepidophorus mutilatus* | Elateridae | 2 | 26 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 26 | 12 | 24 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 26 | 12 | 1 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 26 | 12 | 1 | 2015 |
| *Ischnomera sp.* | Oedemeridae | NE | 26 | 16 | 1 | 2015 |
| *Scraptia fuscula* | Scraptiidae | 3 | 26 | 16 | 1 | 2015 |
| *Quedius truncicola* | Staphylinidae | NE | 26 | 16 | 2 | 2015 |
| *Hesperus rufipennis* | Staphylinidae | 2 | 26 | 16 | 1 | 2015 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 27 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 27 | 8 | 3 | 2014 |
| *Orchesia micans* | Melandryidae | NE | 27 | 12 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 27 | 12 | 3 | 2014 |
| *Alosterna tabacicolor* | Cerambycidae | NE | 28 | 3 | 3 | 2014 |
| *Alosterna tabacicolor* | Cerambycidae | NE | 28 | 4 | 5 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 28 | 4 | 1 | 2014 |
| *Alosterna tabacicolor* | Cerambycidae | NE | 28 | 5 | 4 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 28 | 5 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 28 | 6 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 28 | 6 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 28 | 7 | 1 | 2014 |
| *Crepidophorus mutilatus* | Elateridae | 1 | 28 | 8 | 2 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 28 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 8 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 9 | 3 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 28 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 10 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 12 | 6 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 28 | 12 | 6 | 2014 |
| *Allecula morio* | Alleculidae | 3 | 28 | 14 | 4 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 14 | 2 | 2014 |
| *Scraptia fuscula* | Scraptiidae | 3 | 28 | 14 | 4 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 28 | 16 | 1 | 2014 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 28 | 2 | 3 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 28 | 2 | 1 | 2015 |
| *Alosterna tabacicolor* | Cerambycidae | NE | 28 | 6 | 12 | 2015 |
| *Crepidophorus mutilatus* | Elateridae | 2 | 28 | 6 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 28 | 6 | 1 | 2015 |
| *Hesperus rufipennis* | Staphylinidae | 2 | 28 | 6 | 1 | 2015 |
| *Cryptophagus labilis* | Cryptophagidae | 2 | 28 | 8 | 1 | 2015 |
| *Crepidophorus mutilatus* | Elateridae | 2 | 28 | 8 | 2 | 2015 |
| *Ampedus pomorum* | Elateridae | NE | 28 | 8 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 8 | 2 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 28 | 8 | 1 | 2015 |
| *Ptenidium turgidum* | Ptiliidae | 3 | 28 | 10 | 3 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 28 | 10 | 1 | 2015 |
| *Neuraphes plicicollis* | Scydmaenidae | NE | 28 | 10 | 2 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 28 | 10 | 3 | 2015 |
| *Prionocyphon serricornis* | Scirtidae | NE | 28 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 12 | 13 | 2015 |
| *Neuraphes carinatus* | Scydmaenidae | NE | 28 | 12 | 1 | 2015 |
| *Allecula morio* | Alleculidae | 3 | 28 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 28 | 14 | 7 | 2015 |
| *Scraptia fuscula* | Scraptiidae | 3 | 28 | 14 | 1 | 2015 |
| *Neuraphes plicicollis* | Scydmaenidae | NE | 28 | 14 | 1 | 2015 |
| *Arpidiphorus orbiculatus* | Sphindidae | SU | 28 | 14 | 1 | 2015 |
| *Allecula morio* | Alleculidae | 3 | 28 | 16 | 1 | 2015 |
| *Allecula morio* | Alleculidae | 3 | 28 | 18 | 1 | 2015 |
| *Abraeus perpusillus* | Histeridae | NE | 28 | 18 | 5 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 29 | 2 | 1 | 2014 |
| *Melanotus castanipes* | Elateridae | NE | 29 | 6 | 1 | 2014 |
| *Pityophagus ferrugineus* | Nitidulidae | NE | 29 | 6 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 29 | 6 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 29 | 6 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 29 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 29 | 8 | 1 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 29 | 8 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 29 | 10 | 1 | 2014 |
| *Rhizophagus depressus* | Monotomidae | NE | 29 | 6 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 29 | 6 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 29 | 8 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 29 | 8 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 29 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 29 | 12 | 4 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 29 | 16 | 1 | 2015 |
| *Neuraphes plicicollis* | Scydmaenidae | NE | 30 | 1 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 30 | 2 | 1 | 2014 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Xyleborus germanus* | Scolytidae | NE | 30 | 2 | 4 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 30 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 30 | 6 | 9 | 2014 |
| *Rhizophagus dispar* | Monotomidae | NE | 30 | 7 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 30 | 8 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 30 | 8 | 31 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 30 | 9 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 30 | 9 | 10 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 30 | 10 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 30 | 11 | 4 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 30 | 12 | 68 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 30 | 14 | 15 | 2014 |
| *Rhizophagus depressus* | Monotomidae | NE | 31 | 3 | 1 | 2014 |
| *Melanotus castanipes* | Elateridae | NE | 31 | 7 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 31 | 7 | 3 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 31 | 8 | 4 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 31 | 8 | 7 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 31 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 31 | 14 | 2 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 31 | 2 | 2 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 31 | 6 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 31 | 6 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 31 | 8 | 1 | 2015 |
| *Choragus sheppardi* | Anthribidae | 3 | 31 | 14 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 31 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 31 | 14 | 3 | 2015 |
| *Anaspis rufilabris* | Scraptiidae | NE | 31 | 14 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 31 | 18 | 1 | 2015 |
| *Anaspis rufilabris* | Scraptiidae | NE | 32 | 2 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 32 | 9 | 1 | 2014 |
| *Prionocyphon serricornis* | Scirtidae | NE | 32 | 12 | 1 | 2014 |
| *Ischnomera caerulea/cyanea* | Oedemeridae | NE | 33 | 2 | 1 | 2014 |
| *Malthodes spp.* | Cantharidae | SU | 33 | 3 | 1 | 2014 |
| *Malthodes spp.* | Cantharidae | SU | 33 | 4 | 1 | 2014 |
| *Melanotus castanipes* | Elateridae | NE | 33 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 33 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 34 | 8 | 1 | 2014 |
| *Orchesia micans* | Melandryidae | NE | 34 | 9 | 1 | 2014 |
| *Rhizophagus depressus* | Monotomidae | NE | 34 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 35 | 5 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 35 | 6 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 35 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 35 | 9 | 1 | 2014 |
| *Phloeophagus lignarius* | Curculionidae | NE | 35 | 12 | 1 | 2014 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Xyleborus germanus* | Scolytidae | NE | 35 | 12 | 8 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 35 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 35 | 16 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 36 | 6 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 36 | 8 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 36 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 36 | 9 | 1 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 36 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 36 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 36 | 12 | 4 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 37 | 2 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 37 | 6 | 2 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 37 | 6 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 37 | 8 | 5 | 2014 |
| *Tillus elongatus* | Cleridae | 3 | 37 | 8 | 2 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 37 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 37 | 8 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 37 | 9 | 4 | 2014 |
| *Tillus elongatus* | Cleridae | 3 | 37 | 9 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 37 | 9 | 2 | 2014 |
| *Allecula morio* | Alleculidae | 3 | 37 | 12 | 4 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 37 | 12 | 1 | 2014 |
| *Hypebaeus flavipes* | Melyridae | 3 | 37 | 12 | 3 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 37 | 12 | 7 | 2014 |
| *Allecula morio* | Alleculidae | 3 | 37 | 16 | 1 | 2014 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 37 | 16 | 1 | 2014 |
| *Microscydmus minimus* | Scydmaenidae | NE | 37 | 16 | 8 | 2014 |
| *Orthoperus atomus* | Corylophidae | NE | 37 | 4 | 4 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 37 | 6 | 1 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 37 | 8 | 5 | 2015 |
| *Tillus elongatus* | Cleridae | NE | 37 | 8 | 2 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 37 | 8 | 1 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 37 | 10 | 7 | 2015 |
| *Tillus elongatus* | Cleridae | NE | 37 | 10 | 3 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 37 | 10 | 2 | 2015 |
| *Allecula morio* | Alleculidae | 3 | 37 | 14 | 1 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 37 | 14 | 41 | 2015 |
| *Tetropium castaneum* | Cerambycidae | NE | 37 | 14 | 1 | 2015 |
| *Rhizophagus perforatus* | Monotomidae | SU | 37 | 14 | 1 | 2015 |
| *Ptenidium turgidum* | Ptiliidae | 3 | 37 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 37 | 14 | 68 | 2015 |
| *Xyleborus dispar* | Scolytidae | NE | 37 | 14 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 37 | 14 | 1 | 2015 |
| *Allecula morio* | Alleculidae | 3 | 37 | 16 | 1 | 2015 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Xyleborus germanus* | Scolytidae | NE | 37 | 16 | 2 | 2015 |
| *Allecula morio* | Alleculidae | 3 | 37 | 18 | 1 | 2015 |
| *Pteryx suturalis* | Ptiliidae | NE | 38 | 3 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 6 | 1 | 2014 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 38 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 8 | 2 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 38 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 12 | 4 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 38 | 12 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 38 | 12 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 16 | 2 | 2014 |
| *Xyleborus saxeseni* | Scolytidae | NE | 38 | 8 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 8 | 5 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 38 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 10 | 3 | 2015 |
| *Phloeocharis subtilissima* | Staphylinidae | NE | 38 | 10 | 1 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 38 | 12 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 12 | 41 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 38 | 14 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 14 | 14 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 38 | 16 | 1 | 2015 |
| *Malthodes spp.* | Cantharidae | SU | 39 | 8 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 39 | 8 | 1 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 39 | 12 | 1 | 2014 |
| *Malthodes spp.* | Cantharidae | SU | 40 | 3 | 1 | 2014 |
| *Malthodes spp.* | Cantharidae | SU | 40 | 4 | 2 | 2014 |
| *Melanotus castanipes* | Elateridae | NE | 40 | 7 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 40 | 7 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 40 | 8 | 2 | 2014 |
| *Prionocyphon serricornis* | Scirtidae | NE | 40 | 12 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 40 | 12 | 2 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 40 | 14 | 2 | 2014 |
| *Prionocyphon serricornis* | Scirtidae | NE | 40 | 16 | 1 | 2014 |
| *Quedius microps* | Staphylinidae | NE | 40 | 16 | 1 | 2014 |
| *Rhagium mordax* | Cerambycidae | NE | 40 | 2 | 1 | 2015 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 40 | 2 | 4 | 2015 |
| *Rhizophagus bipustulatus* | Monotomidae | NE | 40 | 4 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 40 | 4 | 3 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 40 | 6 | 1 | 2015 |
| *Malthinus punctatus* | Cantharidae | NE | 40 | 8 | 1 | 2015 |
| *Procraerus tibialis* | Elateridae | 2 | 40 | 8 | 1 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 40 | 8 | 1 | 2015 |
| *Anaspis marginicollis* | Scraptiidae | 2 | 40 | 8 | 1 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 40 | 10 | 1 | 2015 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Xyleborus monographus* | Scolytidae | NE | 40 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 40 | 10 | 1 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 40 | 10 | 1 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 40 | 12 | 1 | 2015 |
| *Plegaderus dissectus* | Histeridae | 3 | 40 | 12 | 2 | 2015 |
| *Euplectus karsteni* | Pselaphidae | NE | 40 | 12 | 1 | 2015 |
| *Ptenidium gressneri* | Ptiliidae | 3 | 40 | 12 | 1 | 2015 |
| *Ptenidium turgidum* | Ptiliidae | 3 | 40 | 12 | 1 | 2015 |
| *Prionocyphon serricornis* | Scirtidae | NE | 40 | 12 | 2 | 2015 |
| *Cyclorhipidion bodoanus* | Scolytidae | NE | 40 | 12 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 40 | 12 | 20 | 2015 |
| *Anaspis thoracica* | Scraptiidae | NE | 40 | 12 | 1 | 2015 |
| *Neuraphes carinatus* | Scydmaenidae | NE | 40 | 12 | 1 | 2015 |
| *Arpidiphorus orbiculatus* | Sphindidae | SU | 40 | 12 | 1 | 2015 |
| *Hapalaraea pygmaea* | Staphylinidae | 3 | 40 | 12 | 1 | 2015 |
| *Ptilinus pectinicornis* | Anobiidae | NE | 40 | 14 | 1 | 2015 |
| *Prionocyphon serricornis* | Scirtidae | NE | 40 | 14 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 40 | 14 | 2 | 2015 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 41 | 2 | 1 | 2014 |
| *Hesperus rufipennis* | Staphylinidae | 2 | 41 | 2 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 41 | 5 | 1 | 2014 |
| *Ischnomera sanguinicollis* | Oedemeridae | 3 | 41 | 6 | 1 | 2014 |
| *Eucnemis capucina* | Eucnemidae | 3 | 41 | 8 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 8 | 2 | 2014 |
| *Crepidophorus mutilatus* | Elateridae | 1 | 41 | 9 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 10 | 1 | 2014 |
| *Anaspis ruficollis* | Scraptiidae | 2 | 41 | 10 | 3 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 41 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 12 | 16 | 2014 |
| *Xyleborus dispar* | Scolytidae | NE | 41 | 14 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 14 | 5 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 16 | 1 | 2014 |
| *Ischnomera sp.* | Oedemeridae | NE | 41 | 2 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 8 | 2 | 2015 |
| *Anaspis marginicollis* | Scraptiidae | 2 | 41 | 8 | 1 | 2015 |
| *Eucnemis capucina* | Eucnemidae | 3 | 41 | 10 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 10 | 2 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 41 | 12 | 2 | 2015 |
| *Xyleborus saxeseni* | Scolytidae | NE | 41 | 12 | 1 | 2015 |
| *Quedius truncicola* | Staphylinidae | NE | 41 | 18 | 1 | 2015 |
| *Hesperus rufipennis* | Staphylinidae | 2 | 41 | 18 | 1 | 2015 |
| *Xyleborus germanus* | Scolytidae | NE | 42 | 11 | 1 | 2014 |
| *Xyleborus germanus* | Scolytidae | NE | 42 | 14 | 7 | 2014 |

**Supporting information Table S2**

**Biodiversity and Conservation**

# Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest

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Table S2: Tree parameters (dbh), tree hollow parameters (height, width, depth, length, height above ground, volume, lateral surface, area of hollow entry, percentage entry to lateral surface, degree of decomposition, temperature inside tree hollow) and location parameters (surrounding tree hollows, surrounding structures, solar irradiation).

| Tree | DBH | Height [cm] | Width [cm] | Depth [cm] | Hollow length [cm] | Height above ground [cm] | Volume tree hollow[cm3] | Lateral surface [cm2] |
|---|---|---|---|---|---|---|---|---|
| 2 | 235 | 95 | 9 | 16 | 160 | 0 | 32169,91 | 8042,48 |
| 3 | 135 | 160 | 19 | 13 | 160 | 270 | 21237,17 | 6534,51 |
| 4 | 185 | 80 | 36 | 8 | 80 | 0 | 4021,24 | 2010,62 |
| 5 | 36 | 65 | 6 | 4 | 65 | 80 | 816,81 | 816,81 |
| 6 | 205 | 110 | 9 | 5 | 110 | 0 | 2159,84 | 1727,88 |
| 7 | 325 | 150 | 22 | 55 | 150 | 20 | 356374,42 | 25918,14 |
| 8 | 185 | 210 | 25 | 40 | 300 | 190 | 376991,12 | 37699,11 |
| 10 | 140 | 45 | 30 | 30 | 115 | 0 | 81288,71 | 10838,49 |
| 11 | 70 | 25 | 11 | 17 | 35 | 100 | 7944,30 | 1869,25 |
| 12 | 125 | 50 | 21 | 20 | 100 | 80 | 31415,93 | 6283,19 |
| 13 | 65 | 13 | 4 | 5 | 23 | 200 | 451,60 | 361,28 |
| 14 | 85 | 25 | 8 | 4 | 35 | 240 | 439,82 | 439,82 |
| 15 | 70 | 25 | 10 | 25 | 35 | 180 | 17180,58 | 2748,89 |
| 16 | 100 | 30 | 5 | 10 | 60 | 185 | 4712,39 | 1884,96 |
| 17 | 165 | 50 | 12 | 13 | 50 | 30 | 6636,61 | 2042,04 |
| 18 | 180 | 80 | 10 | 5 | 80 | 20 | 1570,80 | 1256,64 |
| 19 | 150 | 35 | 8 | 15 | 65 | 0 | 11486,45 | 3063,05 |
| 20 | 180 | 90 | 9 | 10 | 90 | 100 | 7068,58 | 2827,43 |
| 21 | 170 | 160 | 20 | 20 | 220 | 0 | 69115,04 | 13823,01 |
| 22 | 220 | 90 | 20 | 25 | 90 | 15 | 44178,65 | 7068,58 |
| 23 | 235 | 170 | 15 | 40 | 350 | 0 | 439822,97 | 43982,30 |
| 24 | 190 | 130 | 20 | 15 | 200 | 30 | 35342,92 | 9424,78 |
| 25 | 160 | 290 | 30 | 15 | 490 | 0 | 86590,15 | 23090,71 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 26 | 170 | 95 | 15 | 25 | 295 | 15 | 144807,79 | 23169,25 |
| 27 | 130 | 120 | 10 | 20 | 200 | 0 | 62831,85 | 12566,37 |
| 28 | 240 | 160 | 20 | 50 | 360 | 0 | 706858,35 | 56548,67 |
| 29 | 210 | 40 | 20 | 60 | 190 | 130 | 537212,34 | 35814,16 |
| 30 | 80 | 50 | 10 | 10 | 50 | 20 | 3926,99 | 1570,80 |
| 31 | 95 | 60 | 15 | 5 | 60 | 230 | 1178,10 | 942,48 |
| 32 | 270 | 95 | 50 | 35 | 95 | 260 | 91400,71 | 10445,80 |
| 33 | 220 | 160 | 25 | 15 | 160 | 0 | 28274,33 | 7539,82 |
| 34 | 85 | 20 | 25 | 15 | 20 | 70 | 3534,29 | 942,48 |
| 35 | 195 | 55 | 15 | 25 | 145 | 0 | 71176,71 | 11388,27 |
| 36 | 245 | 60 | 7 | 25 | 120 | 50 | 58904,86 | 9424,78 |
| 37 | 280 | 220 | 100 | 30 | 220 | 0 | 155508,84 | 20734,51 |
| 38 | 90 | 40 | 15 | 15 | 40 | 0 | 7068,58 | 1884,96 |
| 39 | 290 | 140 | 20 | 20 | 170 | 40 | 53407,08 | 10681,42 |
| 40 | 220 | 150 | 20 | 35 | 150 | 0 | 144316,91 | 16493,36 |
| 41 | 205 | 80 | 10 | 20 | 170 | 0 | 53407,08 | 10681,42 |
| 42 | 55 | 70 | 6 | 6 | 160 | 230 | 4523,89 | 3015,93 |

| Tree | Area of hollow entry [cm2] | Percentage entry to lateral surface | Degree of decomposition | Temperature inside tree hollow [C°] | Surrounding tree hollows | Surrounding structures | Solar irradiation 2014 [WH/m2] | Solar irradiation2015 [WH/m2] |
|---|---|---|---|---|---|---|---|---|
| 2 | 0,0855 | 0,0011 | 1,5 | 15,42 | 18 | 11 | 1002576,02 | 1002576,02 |
| 3 | 0,3040 | 0,0047 | 1,5 | 15,76 | 4 | 14 | 1091823,62 | 1091823,62 |
| 4 | 0,2880 | 0,0143 | 2 | 15,94 | 9 | 17 | 1099611,33 | 1099611,33 |
| 5 | 0,0390 | 0,0048 | 1 | 15,99 | 4 | 13 | 1121661,21 | 1121661,21 |
| 6 | 0,0990 | 0,0057 | 2 | 15,50 | 7 | 17 | 1121661,21 | 1121661,21 |
| 7 | 0,3300 | 0,0013 | 1,5 | 15,71 | 11 | 15 | 1032000,14 | 1032000,14 |
| 8 | 0,5250 | 0,0014 | 2,5 | 15,40 | 5 | 9 | 980273,84 | 980273,84 |
| 10 | 0,1350 | 0,0012 | 3 | 13,98 | 6 | 11 | 1017837,53 | 1017837,53 |
| 11 | 0,0275 | 0,0015 | 4 | 14,71 | 0 | 8 | 1001196,02 | 1001196,02 |
| 12 | 0,1050 | 0,0017 | 3 | 14,94 | 2 | 13 | 682584,32 | 682584,32 |
| 13 | 0,0052 | 0,0014 | 3 | 16,31 | 13 | 20 | 684055,10 | 684055,10 |
| 14 | 0,0200 | 0,0045 | 1 | 16,97 | 0 | 8 | 972107,09 | 972107,09 |
| 15 | 0,0250 | 0,0009 | 2 | 15,88 | 2 | 12 | 935050,70 | 935050,70 |
| 16 | 0,0150 | 0,0008 | 3 | 14,55 | 5 | 21 | 1004555,74 | 1004555,74 |
| 17 | 0,0600 | 0,0029 | 4 | 14,36 | 3 | 9 | 997702,51 | 997702,51 |
| 18 | 0,0800 | 0,0064 | 2 | 16,01 | 5 | 13 | 1010518,54 | 1010518,54 |
| 19 | 0,0280 | 0,0009 | 3,5 | 15,40 | 3 | 16 | 905637,95 | 905637,95 |
| 20 | 0,0810 | 0,0029 | 2 | 16,56 | 15 | 32 | 1028217,55 | 1028217,55 |
| 21 | 0,3200 | 0,0023 | 2,5 | 15,33 | 4 | 11 | 1034060,88 | 1034060,88 |
| 22 | 0,1800 | 0,0025 | 3 | 15,77 | 2 | 7 | 992708,52 | 992708,52 |
| 23 | 0,2550 | 0,0006 | 2,5 | 14,38 | 4 | 9 | 877203,87 | 877203,87 |
| 24 | 0,2600 | 0,0028 | 2 | 12,26 | 7 | 4 | 1018937,54 | 1018937,54 |
| 25 | 0,8700 | 0,0038 | 1,5 | 16,02 | 7 | 4 | 1066687,06 | 1066687,06 |
| 26 | 0,1425 | 0,0006 | 1,5 | 14,11 | 6 | 5 | 1016805,43 | 1016805,43 |
| 27 | 0,1200 | 0,0010 | 4 | 15,07 | 12 | 7 | 1123582,11 | 1123582,11 |
| 28 | 0,3200 | 0,0006 | 2 | 14,57 | 18 | 11 | 1117782,70 | 1117782,70 |
| 29 | 0,0800 | 0,0002 | 3 | 14,39 | 3 | 5 | 963937,10 | 963937,10 |
| 30 | 0,0500 | 0,0032 | 3 | 14,27 | 5 | 6 | 1042059,44 | 1042059,44 |
| 31 | 0,0900 | 0,0095 | 4 | 15,43 | 8 | 9 | 1034759,50 | 1034759,50 |
| 32 | 0,4750 | 0,0045 | 3 | 14,40 | 5 | 6 | 1042059,44 | 1042059,44 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 33 | 0,4000 | 0,0053 | 2 | 15,51 | 1 | 9 | 839218,60 | 839218,60 |
| 34 | 0,0500 | 0,0053 | 2 | 16,38 | 2 | 15 | 1009885,29 | 1009885,29 |
| 35 | 0,0825 | 0,0007 | 4 | 13,09 | 5 | 17 | 1069765,15 | 1069765,15 |
| 36 | 0,0420 | 0,0004 | 1 | 13,01 | 1 | 6 | 1008570,33 | 1008570,33 |
| 37 | 2,2000 | 0,0106 | 2 | 15,57 | 8 | 9 | 1059207,11 | 1059207,11 |
| 38 | 0,0600 | 0,0032 | 2 | 15,47 | 8 | 33 | 1029670,65 | 1029670,65 |
| 39 | 0,2800 | 0,0026 | 4 | 13,47 | 7 | 24 | 1063889,38 | 1063889,38 |
| 40 | 0,3000 | 0,0018 | 2,5 | 13,88 | 10 | 17 | 1035042,00 | 1035042,00 |
| 41 | 0,0800 | 0,0007 | 2,5 | 15,22 | 6 | 20 | 1075671,54 | 1075671,54 |
| 42 | 0,0420 | 0,0014 | 3 | 15,55 | 5 | 16 | 1055802,58 | 1055802,58 |

Supporting information Manuscript 2

A.1

Mean annual temperature of the region is 7-8 °C and mean annual rainfall 850 mm (Bässler, Ernst, Cadotte, Heibl & Müller 2014). The Steigerwald covers an area of approximately 1000 km$^2$ and is described as a temperate, colline to sub-montane, forested landscape. The dominating tree species is beech, *Fagus sylvatica*, with a cover of 43%, followed by oak (*Quercus petraea,* 20% cover). About 70% of the forest is covered by deciduous trees (Müller, Bußler & Kneib 2008). The study area can historically be divided into three different levels of silvicultural management intensities. The northern part of the study area belongs to an intensively managed part of the Steigerwald, which was logged intensively over a period of about 70 years until recently. Due to this intensive use these parts contained only little amounts of deadwood until ~2005. The southern part of the study area was managed more extensively with only slight logging until the 1970´s. Afterwards the forest management strategy was to maintain ecologically important structures such as deadwood and damaged trees whose injuries may turn into tree hollows or other important habitat structures for saproxylic insects. The northern and southern parts of the study area are separated by a road and a strip of agricultural area of approximately 1800 m width at maximum (Fig. 1). The third section of the forest comprises strict forest reserves, which were left unmanaged for up to 35 years. These forest reserves are scattered within the managed forest. The forest structure of these reserves is comparable to virgin beech forests with respect to tree age, tree size and amount of deadwood (Müller 2004; Müller, Bußler & Kneib 2008)

Bässler, C., Ernst, R., Cadotte, M., Heibl, C. & Müller, J. (2014) Near-to-nature logging influences fungal community assembly processes in a temperate forest. *Journal of Applied Ecology*, 51, 939–948.

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. *Journal of Insect Conservation*, 12, 107–124.

Müller, J. (2004) Welchen Beitrag leisten Naturwaldreservate zum Schutz von waldvogelarten. *Ornithologischer Anzeiger*, 43, 3–18.

A.2

Two legs of each specimen were used to extract DNA likewise with the PureGene Kit (Qiagen), with a final extraction volume of 25-50µl per individual (DNA pellet suspended in hydration solution) and stored at -20 °C.

Polymerase chain reaction (PCR) was performed in a peqSTAR 2X Gradient Thermal Cycler in a total reaction volume of 12.5 µl. It contained 2 µl (approximately 10 ng) template DNA, 7.65 µl HPLC water, 1.25 µl 1x PCR buffer (peqGOLD Taq DNA Polymerase kit), 160 µM dNTPs mix (peqGOLD Taq DNA Polymerase kit), 2.5 µM of each primer (forward primer labelled with fluorescent IR-700 or IR-800dye) and 0.5 U of Taq-Polymerase (peqGOLD Taq DNA Polymerase kit). For all loci, we used a touch-down protocol with the following cycle parameters: 3 min at 95 °C, followed by 6 cycles of 94 °C for 30 s, annealing step of 1:30 min with temperature decreasing 1°C per cycle from 60 to 55 °C, and an extension of 1 min at 72 °C. This was followed by 24 cycles of 94 °C for 30 s, annealing step of 55 °C for 1:30 s, an extension of 1 min at 72 °C and a final extension step of 3 min at 72 °C. PCR products were diluted between 1:25 and 1:35 and analyzed on a LICOR 4300 DNA Analyzer.

## A.3

Kinship coefficients for each species were calculated after Loiselle et al. (1995).The number of distance classes were constructed according to Sturges´ formula ($k = 1+log_2*n$; where $k$ = the number of distance classes and $n$ = the number of pairwise observations) (13 classes for *A. ruficollis*, 12 classes for *C. floccosa* and 14 classes for *X. maculata*). The intervals of each distance class was assigned automatically by SPAGeDI *v1.5a* (Hardy &Vekemans 2002) to ensure an evenly distribution of individual pairs to each distance class. Confidence intervals for every kinship coefficient per distance class were obtained from standard error by jackknifing the loci (20,000 permutations). The average kinship coefficient was plotted against every distance class in each species. Furthermore *Sp,* a measure for spatial genetic structure was calculated as follows $Sp= -b_F /(1-F)$, where $b_F$ is the slope of the regression of kinship on ln geographic distance and $F$ is the average kinship of distance classes. $b_F$ and $F$ were obtained from the results output of SPAGeDI *v1.5a.* The mean kinship coefficient of *A. ruficollis* over all distance classes ranges from -0.0007 to 0.1055, of *C. floccosa* over all distance classes from -0,0009 to 0.0768 and of *X. maculata* over all distance classes from -0.0059 to 0.1313. The mean *Sp* of *A. ruficollis, C. floccosa* and *X. maculata* were 0.0023 ± 0.000076 (SD), -0.0017 ± 0.000039 (SD) and 0.0002 ± 0.000001 (SD), respectively (see Appendix A: Table A4). The slopes of the regression of kinship on logarithmic geographic distance of *A. ruficollis, C. floccosa* and *X. maculata* were -0,00230749, 0,0016761 and -0,000197784, respectively.

The individual based kinship analyses using SPAGeDi showed that only within each tree hollow the kinship coefficient was significantly more positive than expected in all three species. In all other distance classes genotypes showed random spatial distribution.as individuals were related no more or less than by chance (see Appendix A: Fig. A1).

Hardy, O. J., Vekemans, X. (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Molecular Ecology Notes, 2, 618–620.

Loiselle, B.A., Sork, V.L., Nason, J. and Graham, C. (1995). Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). *American Journal of Botany,* 82, 1420-1425.

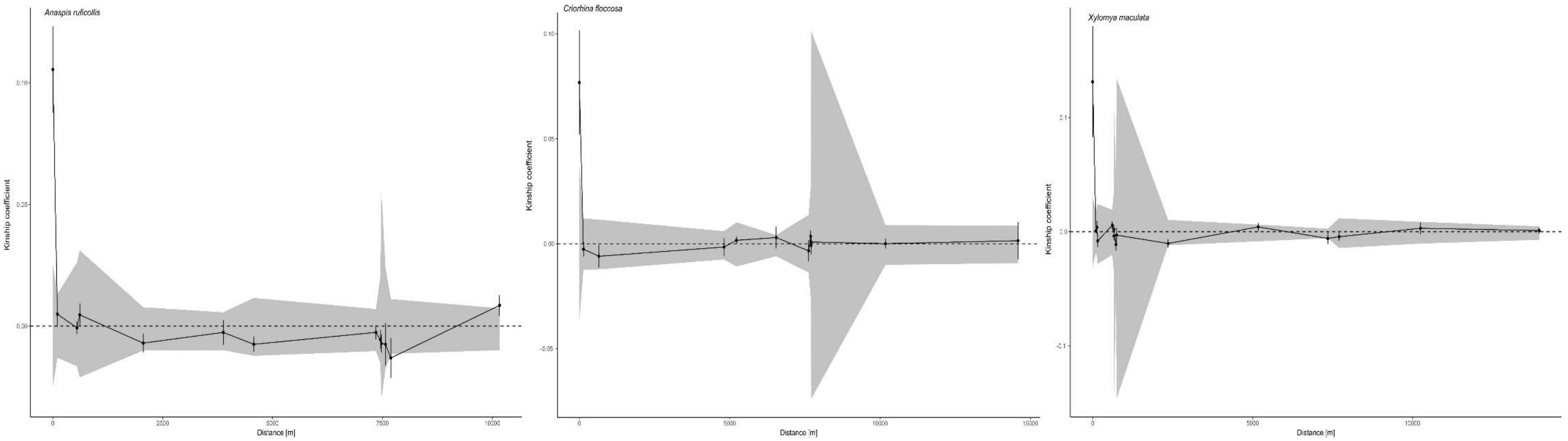

Fig A1: Average pairwise kinship coefficient of *A. ruficollis, C. floccosa* and *X. maculata* plotted against geographical distances of the populations, respectively. The observed kinship coefficient and standard error obtained by jackknifing over all loci is shown. 95% confidence interval (gray area) shows the null hypothesis of randomly distributed alleles.

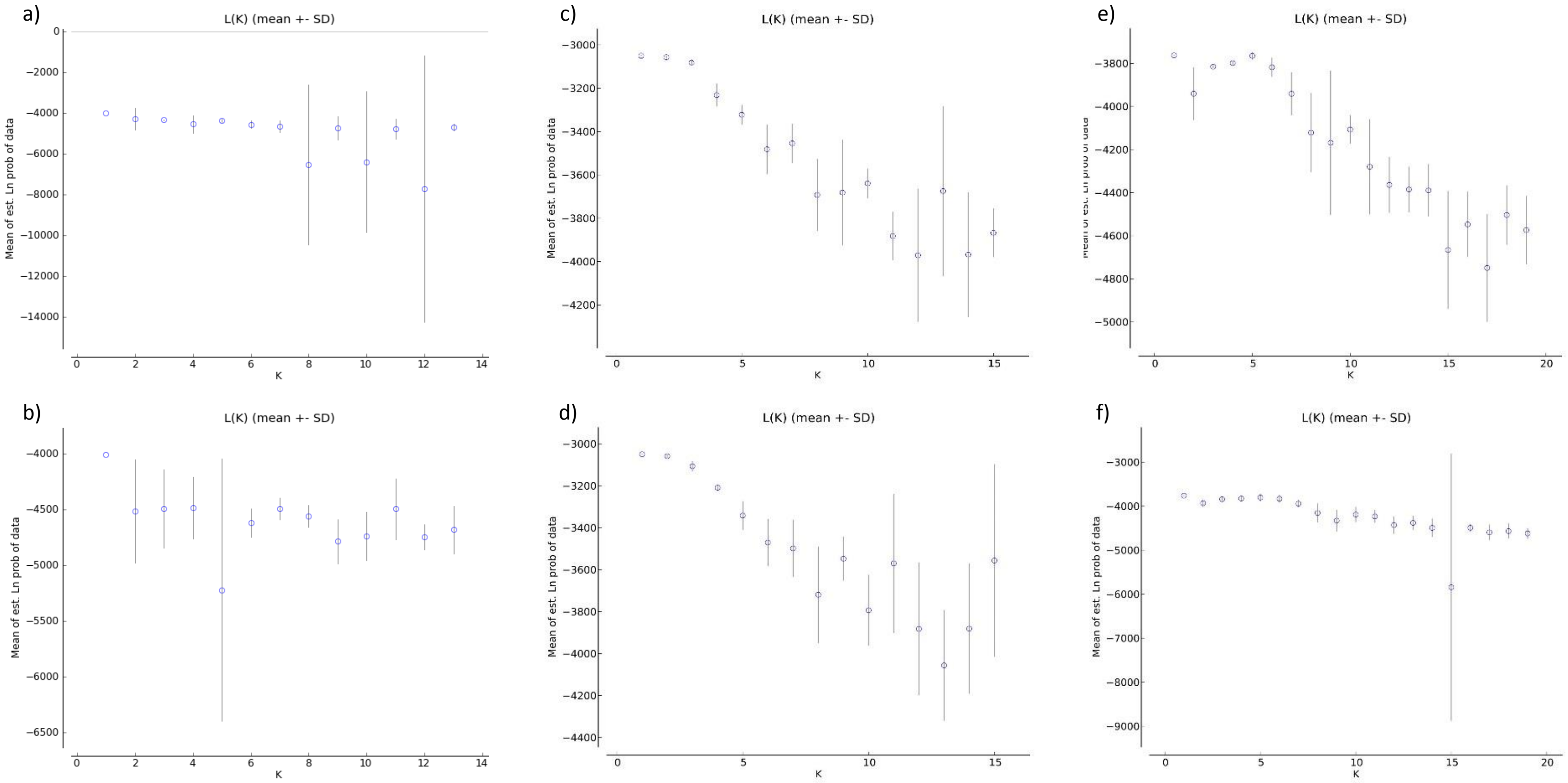

Fig A2: Probability (Ln P(D)) of potential number of cluster (K) a) *A. ruficollis* ranging from 1 to 13 with a priori location information b) *A. ruficollis* ranging from 1 to 13 without a priori location information c) *C. floccosa* ranging from 1 to 15 with a priori location information d) *C. floccosa* ranging from 1 to 15 without a priori location information e) *X. maculata* ranging from 1 to 19with a priori location information f) *X. maculata* ranging from 1 to 19 without a priori location information.

Table A1: Number of individuals per tree and year and calculated $F_{IS}$ values per population for *A. ruficollis, C. floccosa* and *X. maculata.* Populations without $F_{IS}$ value consisted of only one specimen, thus no calculation was possible.

| *A. ruficollis* | | | | *C. floccosa* | | | | *X. maculata* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Tree | # individuals 2014 | # individuals 2015 | $F_{IS}$ | Tree | # individuals 2014 | # individuals 2015 | $F_{IS}$ | Tree | # individuals 2014 | # individuals 2015 | $F_{IS}$ |
| 3 | 1 | - | - | 2 | 5 | 31 | 0.0837 | 2 | - | 2 | 0.0769 |
| 7 | 10 | - | 0.0365 | 4 | - | 1 | - | 4 | - | 2 | 0.1429 |
| 8 | 5 | - | 0.1277 | 7 | - | 2 | 0.0000 | 8 | 3 | 4 | 0.1236 |
| 21 | 23 | - | 0.0208 | 10 | 1 | - | - | 10 | 1 | - | - |
| 22 | 8 | - | 0.0886 | 18 | - | 1 | - | 11 | 2 | 5 | 0.0977 |
| 25 | 13 | - | 0.1735 | 21 | 2 | - | 0.0909 | 15 | 1 | - | - |
| 26 | 2 | - | 0.1220 | 22 | 3 | - | 0.1429 | 17 | 1 | - | - |
| 27 | 1 | - | - | 23 | 1 | 4 | -0.0377 | 19 | 1 | - | - |
| 28 | 3 | - | 0.0667 | 24 | 3 | - | -0.1494 | 21 | 3 | 12 | 0.2053 |
| 37 | 3 | - | 0.1402 | 25 | 1 | 5 | -0.0241 | 22 | 4 | 41 | 0.1605 |
| 38 | 1 | - | - | 26 | 4 | 4 | 0.1046 | 23 | 3 | 15 | 0.0290 |
| 40 | 3 | - | 0.1220 | 28 | 3 | 15 | 0.0992 | 24 | 1 | - | - |
| 41 | 4 | - | 0.2532 | 33 | 1 | - | - | 25 | - | 10 | 0.0544 |
| | | | | 40 | 2 | 8 | 0.1720 | 26 | 1 | 7 | 0.2527 |
| | | | | 41 | 1 | 1 | -0.0968 | 27 | 12 | - | 0.0007 |
| | | | | | | | | 28 | 5 | 13 | 0.1707 |
| | | | | | | | | 29 | 2 | - | -0.2000 |
| | | | | | | | | 34 | 1 | - | - |
| | | | | | | | | 35 | 7 | - | 0.0192 |

Table A.2 Pairwise calculation of $F_{ST}$- values according to Weir & Cockerham (1984) between trees of which they emerged. a) *Anaspis ruficollis.* b) *Criorhina floccosa.* c) *Xylomya maculata.* Bold numbers indicate deviation from zero after bootstrapping.

| *Anaspis ruficollis* | Tree 7 | Tree 8 | Tree 21 | Tree 22 | Tree 25 | Tree 28 | Tree 37 | Tree 40 | Tree 41 |
|---|---|---|---|---|---|---|---|---|---|
| | - | | | | | | | | |
| Tree 8 | 0.0104 | - | | | | | | | |
| Tree 21 | **0.0151** | 0.018 | - | | | | | | |
| Tree 22 | 0.0124 | 0.0134 | 0 | - | | | | | |
| Tree 25 | **0.0196** | 0.0273 | 0.0102 | 0.0012 | - | | | | |
| Tree 28 | 0.0335 | 0.0401 | 0.0241 | 0.0096 | 0.0132 | - | | | |
| Tree 37 | 0.0196 | 0.0288 | 0.0244 | 0.0043 | 0.0247 | 0.0069 | - | | |
| Tree 40 | 0.0145 | 0.0010 | 0.0020 | 0.0118 | 0.0096 | 0.0243 | 0.0165 | - | |
| Tree 41 | 0.0178 | 0.0292 | 0.0153 | 0.0145 | 0.0099 | 0.0251 | 0.0318 | 0.0044 | - |

| *Criorhina floccosa* | Tree 2 | Tree 22 | Tree 23 | Tree 24 | Tree 25 | Tree 26 | Tree 28 | Tree 40 |
|---|---|---|---|---|---|---|---|---|
| Tree 2 | - | | | | | | | |
| Tree 22 | -0.013 | - | | | | | | |
| Tree 23 | 0.0258 | 0.0083 | - | | | | | |
| Tree 24 | 0.0123 | -0.0082 | 0.0273 | - | | | | |
| Tree 25 | 0.0046 | -0.0338 | 0.0062 | 0.0015 | - | | | |
| Tree 26 | 0.0051 | -0.0102 | 0.0277 | 0.0028 | -0.0026 | - | | |
| Tree 28 | 0.0007 | -0.0147 | 0.0327 | 0.0002 | 0.0020 | 0.0123 | - | |
| Tree 40 | 0.0012 | -0.0125 | 0.0183 | 0.0125 | -0.0003 | 0.0088 | -0.0034 | - |

| *Xylomya maculata* | Tree 8 | Tree 11 | Tree 21 | Tree 22 | Tree 23 | Tree 25 | Tree 26 | Tree 27 | Tree 28 | Tree 35 |
|---|---|---|---|---|---|---|---|---|---|---|
| Tree 8 | - | | | | | | | | | |
| Tree 11 | 0.0179 | - | | | | | | | | |
| Tree 21 | 0.0217 | 0.0057 | - | | | | | | | |
| Tree 22 | 0.0215 | 0.0092 | 0.0005 | - | | | | | | |
| Tree 23 | 0.0121 | 0.0016 | 0.0005 | 0.0063 | - | | | | | |
| Tree 25 | 0.0213 | 0.0071 | 0.0023 | 0.0065 | 0.0004 | - | | | | |
| Tree 26 | 0.0184 | 0.0004 | 0.0006 | 0.0013 | 0.0037 | 0.0107 | - | | | |
| Tree 27 | 0.0175 | 0.009 | 0.0067 | 0.0152 | 0.0123 | 0.021 | 0.0026 | - | | |
| Tree 28 | 0.0162 | 0.0112 | 0.0099 | 0.0058 | 0.0128 | 0.0103 | 0.0113 | 0.0139 | - | |
| Tree 35 | 0.0177 | 0.0076 | 0.0021 | 0.0092 | 0.0079 | 0.0134 | 0.0089 | 0.0032 | 0.0091 | - |

Table A.3 Analysis of molecular variance *AMOVA* of *A. ruficollis. C. floccosa* and *X. maculata.* df = degrees of freedom. SSD = sum of square deviations. MSD = mean square deviations. Sigma = variance.

| Species | Source of Variation | df | SSD | MSD | Sigma | Total variance [%] | P - value |
|---|---|---|---|---|---|---|---|
| *A. ruficollis* | between north and south | 1 | 9.26 | 9.26 | 0.05 | 1.09 | > 0.05 |
| | between trees | 11 | 66.16 | 6.01 | 0.09 | 1.93 | < 0.01 |
| | between individuals within trees | 60 | 306.68 | 5.11 | 0.39 | 8.03 | < 0.01 |
| | within individuals | 73 | 316.07 | 4.33 | 4.33 | 88.96 | < 0.01 |
| | Total | 145 | 698.18 | 4.82 | 4.87 | 100.00 | |
| *C. floccosa* | between north and south | 1 | 3.63 | 3.63 | -0.01 | -0.19 | > 0.05 |
| | between trees | 13 | 53.13 | 4.09 | 0.01 | 0.17 | > 0.05 |
| | between individuals within trees | 84 | 338.57 | 4.03 | 0.28 | 7.33 | < 0.01 |
| | within individuals | 99 | 344.50 | 3.48 | 3.48 | 92.69 | < 0.01 |
| | Total | 197 | 739.83 | 3.76 | 3.75 | 100.00 | |
| *X. maculata* | between north and south | 1 | 3.71 | 3.71 | 0.00 | 0.09 | > 0.05 |
| | between trees | 17 | 60.02 | 3.53 | 0.04 | 1.39 | < 0.01 |
| | between individuals within trees | 140 | 414.74 | 2.96 | 0.33 | 12.14 | < 0.01 |
| | within individuals | 159 | 367.64 | 2.31 | 2.31 | 86.38 | < 0.01 |
| | Total | 317 | 846.11 | 2.67 | 2.68 | 100.00 | |

Table A.4 Description of mean kinship coefficient. standard error of mean kinship coefficient. upper and lower boundaries of 95% confidence interval and estimation of *Sp* of *A. ruficollis*. *C. floccosa* and *X. maculata.*

| Distance classes | Distance [m] | Mean kinship coefficient | SE kinship coefficient | 95% CI upper | 95% CI lower | Sp |
|---|---|---|---|---|---|---|
| *Anaspis ruficollis* | | | | | | |
| 0 | within Tree hollow | 0.1055 | 0.0178 | -0.0249171 | 0.0254055 | 0.00257964225824483 |
| 1 | 103.45 | 0.0049 | 0.0051 | -0.01304 | 0.0131228 | 0.00231885237664556 |
| 2 | 547.91 | -0.0007 | 0.0026 | -0.0164765 | 0.0261145 | 0.00230587588687918 |
| 3 | 547.91 | - | - | - | - | 0.00230749 |
| 4 | 612.00 | 0.0046 | 0.0047 | -0.0210485 | 0.0311102 | 0.00231815350612819 |
| 5 | 2057.08 | -0.0070 | 0.0039 | -0.0100248 | 0.00773698 | 0.0022914498510427 |
| 6 | 3877.30 | -0.0026 | 0.0051 | -0.00993748 | 0.00565491 | 0.00230150608418113 |
| 7 | 4571.47 | -0.0075 | 0.0032 | -0.0122252 | 0.011584 | 0.00229031265508685 |
| 8 | 7351.60 | -0.0026 | 0.0029 | -0.0102985 | 0.0069909 | 0.00230150608418113 |
| 9 | 7452.26 | -0.0055 | 0.0039 | -0.0152988 | 0.0204497 | 0.0022948682247638 |
| 10 | 7477.09 | -0.0072 | 0.0037 | -0.0297711 | 0.0557001 | 0.00229099483717236 |
| 11 | 7568.50 | -0.0075 | 0.0087 | -0.017471 | 0.0239511 | 0.00229031265508685 |
| 12 | 7690.10 | -0.0131 | 0.0082 | -0.0113797 | 0.0111021 | 0.00227765274898825 |
| 13 | 10161.47 | 0.0085 | 0.0043 | -0.00990817 | 0.00735482 | 0.0023272718103883 |
| *Criorhina floccosa* | | | | | | |
| 0 | within Tree hollow | 0.0768 | 0.0247 | -0.0365273 | 0.0369564 | -0.00181553292894281 |
| 1 | 137 | -0.0026 | 0.0035 | -0.0123475 | 0.0120771 | -0.00167175344105326 |
| 2 | 651 | -0.006 | 0.0053 | -0.0122525 | 0.0114386 | -0.00166610337972167 |
| 3 | 4813 | -0.0016 | 0.0043 | -0.00752506 | 0.00593698 | -0.00167342252396166 |
| 4 | 5228 | 0.0016 | 0.0019 | -0.010876 | 0.0101912 | -0.00167878605769231 |
| 5 | 6548 | 0.0029 | 0.0052 | -0.0059628 | 0.00411155 | -0.0016809748269983 |
| 6 | 7625 | -0.0034 | 0.0051 | -0.0137763 | 0.0136577 | -0.00167042057006179 |
| 7 | 7691 | 0.0035 | 0.0028 | -0.0248247 | 0.025946 | -0.00168198695434019 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 8 | 7707 | -0.0009 | 0.0044 | -0.043249 | 0.0568612 | -0.00167459286642022 |
| 9 | 7711 | 0.0008 | 0.0030 | -0.0739862 | 0.101292 | -0.00167744195356285 |
| 10 | 7711 | - | - | - | - | -0.0016761 |
| 11 | 10181 | 0 | 0.0023 | -0.0101139 | 0.0088477 | -0.0016761 |
| 12 | 14592 | 0.0014 | 0.0088 | -0.00925976 | 0.00848732 | -0.00167844982976167 |
| *Xylomya maculata* | | | | | | |
| 0 | within Tree hollow | 0.1313 | 0.0487 | -0.0301492 | 0.0302236 | 0.00022767813974905 |
| 1 | 103 | 0.0007 | 0.0023 | -0.0181981 | 0.0174926 | 0.000197922545782047 |
| 2 | 133 | 0.0038 | 0.0058 | -0.0216081 | 0.0217043 | 0.000198538446095162 |
| 3 | 157 | -0.0081 | 0.0054 | -0.028136 | 0.0242037 | 0.000196194821942268 |
| 4 | 612 | 0.0057 | 0.0034 | -0.0202384 | 0.0191229 | 0.00019891783164035 |
| 5 | 661 | 0.002 | 0.0032 | -0.0344283 | 0.0346806 | 0.000198180360721443 |
| 6 | 667 | -0.0038 | 0.0037 | -0.146079 | 0.10851 | 0.000197035265989241 |
| 7 | 727 | -0.0112 | 0.0055 | -0.0509141 | 0.048508 | 0.00019559335443038 |
| 8 | 749 | -0.003 | 0.0067 | -0.146079 | 0.134075 | 0.000197192422731805 |
| 9 | 2359 | -0.0103 | 0.0038 | -0.0118781 | 0.0103221 | 0.000195767593784025 |
| 10 | 5175 | 0.0042 | 0.0034 | -0.00841118 | 0.00623434 | 0.000198618196424985 |
| 11 | 7352 | -0.0059 | 0.0051 | -0.00565533 | 0.00265769 | 0.000196623918878616 |
| 12 | 7707 | -0.0044 | 0.0037 | -0.0142463 | 0.0117917 | 0.000196917562724014 |
| 13 | 10250 | 0.003 | 0.0052 | -0.0104128 | 0.00864517 | 0.000198379137412237 |
| 14 | 13962 | 0.001 | 0.0028 | -0.00706581 | 0.00469089 | 0.000197981981981982 |

## Supporting information Manuscript 4

Fig A1: NMDS plot vizualizing the Bray-Curtiss dissimilarity index of different feeding guilds calculated from the enrichment factors $\varepsilon^{13}$C and $\varepsilon^{15}$N in two dimensional space with a stress of 0.08 and 100 permutations. d = detritivorous. m = mycetophagous. m = myceto-saprophagous. x = xylophagous. xm = xylo-mycetophagous. xs = xylo-saprophagous. xz = xylo-zoophagous. zoo = zoophagous.

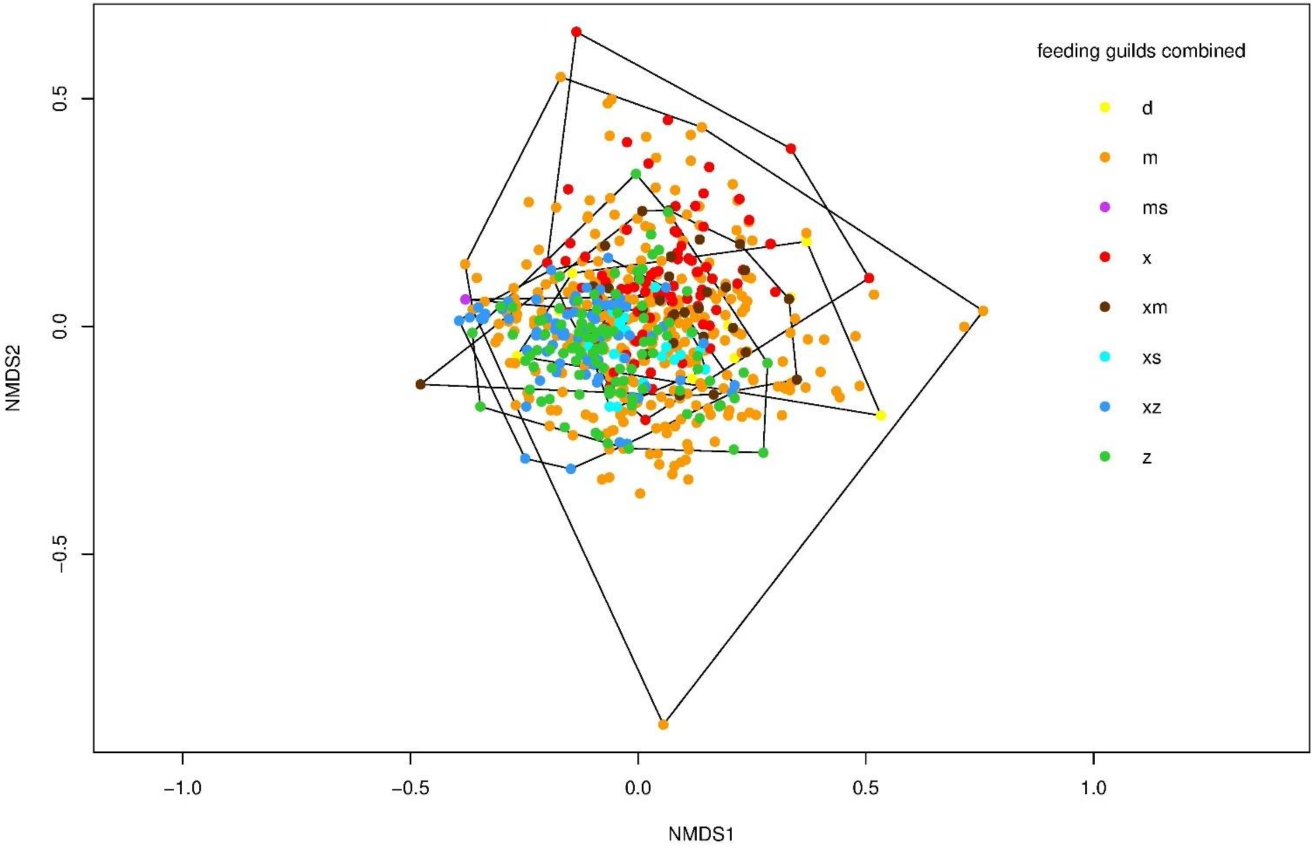

Table A1: δ$^{13}$C and δ$^{15}$N values for all wood mould samples from 2014 and 2015.

| Wood mould tree hollow | Degree of decomposition | 2014 | | 2015 | |
|---|---|---|---|---|---|
| | | δ15N | δ13C | δ15N | δ13C |
| 2 | 1.5 | -1.901 | -26.63 | -3.178 | -22.917 |
| 3 | 1.5 | -4.493 | -27.492 | 2.609 | -27.053 |
| 4 | 2 | -1.108 | -27.112 | -1.102 | -26.006 |
| 5 | 1 | -2.801 | -29.199 | - | - |
| 6 | 2 | -3.893 | -26.892 | - | - |
| 7 | 1.5 | -1.454 | -27.188 | -1.809 | -25.96 |
| 8 | 2.5 | -1.105 | -28.235 | -1.814 | -25.699 |
| 10 | 3 | -0.052 | -26.999 | - | - |
| 11 | 4 | -1.189 | -27.632 | -0.882 | -26.06 |
| 12 | 3 | -1.512 | -27.521 | -0.872 | -26.704 |
| 13 | 3 | 5.805 | -28.955 | - | - |
| 14 | 1 | -2.684 | -25.761 | -2.936 | -24.183 |
| 15 | 2 | -2.871 | -27.672 | - | - |
| 16 | 3 | -3.268 | -28.078 | - | - |
| 17 | 4 | 4.032 | -23.111 | - | - |
| 18 | 2 | -2.514 | -25.64 | -2.73 | -24.104 |
| 19 | 3.5 | -1.058 | -28.243 | -0.253 | -26.08 |
| 20 | 2 | -2.914 | -25.987 | -3.051 | -24.573 |
| 21 | 2.5 | -3.962 | -26.512 | -1.938 | -25.465 |
| 22 | 3 | -1.394 | -25.993 | 0.301 | -24.639 |
| 23 | 2.5 | 0.433 | -25.875 | 0.869 | -24.801 |
| 24 | 2 | -0.503 | -25.115 | - | - |
| 25 | 1.5 | -2.434 | -26.146 | -2.036 | -25.003 |
| 26 | 1.5 | -1.887 | -25.728 | -3.244 | -24.526 |
| 27 | 4 | -0.909 | -24.918 | - | - |
| 28 | 2 | -2.817 | -26.71 | -1.984 | -25.039 |
| 29 | 3 | -1.301 | -28.18 | -1.488 | -26.858 |
| 30 | 3 | -4.332 | -29.434 | - | - |
| 31 | 4 | -3.705 | -28.293 | -5.175 | -27.983 |
| 32 | 3 | -3.69 | -27.818 | - | - |
| 33 | 2 | -2.555 | -26.669 | - | - |
| 34 | 2 | -1.46 | -27.279 | - | - |
| 35 | 4 | -2.016 | -27.804 | - | - |
| 36 | 1 | -1.937 | -26.384 | - | - |
| 37 | 2 | -2.328 | -27.282 | -1.476 | -26.189 |
| 38 | 2 | -3.024 | -27.027 | -2.752 | -26.759 |
| 39 | 4 | 1.03 | -27.793 | - | - |
| 40 | 2.5 | -4.26 | -27.307 | -1.551 | -26.025 |
| 41 | 3 | -2.557 | -26.018 | -1.658 | -24.198 |
| 42 | 3 | 2.709 | -27.369 | - | - |

Table A2: $\delta^{13}$C. $\delta^{15}$N. $\varepsilon^{13}$C and $\varepsilon^{15}$N values for each individual per species.

| Tree hollow | Year | Species | Family | δ15N | δ13C | ε15N | ε13C |
|---|---|---|---|---|---|---|---|
| 23 | 2015 | *Abraeus perpusillus* | Histeridae | 2.38 | -22.118 | 1.511 | 2.683 |
| 22 | 2015 | *Abraeus perpusillus* | Histeridae | 1.545 | -23.643 | 1.244 | 0.996 |
| 26 | 2015 | *Abraeus perpusillus* | Histeridae | 0.667 | -22.489 | 3.911 | 2.037 |
| 28 | 2015 | *Abraeus perpusillus* | Histeridae | 0.27 | -22.845 | 2.254 | 2.194 |
| 28 | 2015 | *Abraeus perpusillus* | Histeridae | 2.276 | -23.29 | 4.26 | 1.749 |
| 7 | 2015 | *Acalles hypocrita* | Curculionidae | 1.197 | -25.329 | 3.006 | 0.631 |
| 4 | 2015 | *Acalles hypocrita* | Curculionidae | 1.754 | -23.786 | 2.856 | 2.22 |
| 4 | 2015 | *Aderus populneus* | Aderidae | 14.604 | -21.066 | 15.71 | 4.94 |
| 7 | 2014 | *Allecula morio* | Alleculidae | 0.236 | -25.092 | 1.69 | 2.096 |
| 37 | 2014 | *Allecula morio* | Alleculidae | -0.191 | -23.592 | 2.137 | 3.69 |
| 7 | 2014 | *Allecula morio* | Alleculidae | 2.105 | -24.228 | 3.559 | 2.96 |
| 7 | 2015 | *Allecula morio* | Alleculidae | -0.074 | -24.319 | 1.735 | 1.641 |
| 37 | 2015 | *Allecula morio* | Alleculidae | -0.824 | -24.25 | 0.652 | 1.939 |
| 7 | 2015 | *Allecula morio* | Alleculidae | 2.908 | -24.523 | 4.717 | 1.437 |
| 37 | 2015 | *Allecula morio* | Alleculidae | -0.426 | -25.326 | 1.05 | 0.863 |
| 28 | 2015 | *Allecula morio* | Alleculidae | 1.247 | -23.414 | 3.231 | 1.625 |
| 37 | 2015 | *Allecula morio* | Alleculidae | -0.678 | -24.794 | 0.798 | 1.395 |
| 28 | 2015 | *Allecula morio* | Alleculidae | -0.535 | -23.394 | 1.449 | 1.645 |
| 28 | 2015 | *Allecula morio* | Alleculidae | 0.064 | -23.093 | 2.048 | 1.946 |
| 28 | 2014 | *Allecula morio* | Alleculidae | -2.497 | -23.05 | 0.32 | 3.66 |
| 28 | 2014 | *Allecula morio* | Alleculidae | -0.364 | -23.083 | 2.453 | 3.627 |
| 28 | 2014 | *Allecula morio* | Alleculidae | -0.655 | -22.698 | 2.162 | 4.012 |
| 28 | 2014 | *Allecula morio* | Alleculidae | 1.405 | -22.984 | 4.222 | 3.726 |
| 37 | 2014 | *Allecula morio* | Alleculidae | -0.111 | -23.088 | 2.217 | 4.194 |
| 37 | 2014 | *Allecula morio* | Alleculidae | -0.024 | -23.188 | 2.304 | 4.094 |
| 37 | 2014 | *Allecula morio* | Alleculidae | 0.159 | -23.943 | 2.487 | 3.339 |
| 7 | 2014 | *Allecula morio* | Alleculidae | 1.891 | -24.527 | 3.345 | 2.661 |
| 7 | 2014 | *Allecula morio* | Alleculidae | 0.973 | -23.5 | 2.427 | 3.688 |
| 7 | 2015 | *Allecula morio* | Alleculidae | 3.23 | -24.36 | 5.039 | 1.6 |
| 7 | 2014 | *Alosterna tabacicolor* | Cerambycidae | 0.933 | -21.603 | 2.387 | 5.585 |
| 28 | 2014 | *Alosterna tabacicolor* | Cerambycidae | -9.475 | -24.431 | -6.658 | 2.279 |
| 28 | 2014 | *Alosterna tabacicolor* | Cerambycidae | -6.68 | -24.222 | -3.863 | 2.488 |
| 7 | 2015 | *Alosterna tabacicolor* | Cerambycidae | -3.814 | -21.95 | -2.005 | 4.01 |
| 28 | 2015 | *Alosterna tabacicolor* | Cerambycidae | -6.315 | -22.202 | -4.331 | 2.837 |
| 8 | 2015 | *Alosterna tabacicolor* | Cerambycidae | -6.696 | -22.129 | -4.882 | 3.57 |
| 7 | 2015 | *Alosterna tabacicolor* | Cerambycidae | -4.684 | -21.749 | -2.875 | 4.211 |
| 7 | 2015 | *Alosterna tabacicolor* | Cerambycidae | 1.909 | -20.7 | 3.718 | 5.26 |
| 28 | 2015 | *Alosterna tabacicolor* | Cerambycidae | -2.145 | -22.314 | -0.161 | 2.725 |
| 28 | 2015 | *Alosterna tabacicolor* | Cerambycidae | 0.496 | -22.217 | 2.48 | 2.822 |
| 28 | 2014 | *Alosterna tabacicolor* | Cerambycidae | 0.222 | -22.846 | 3.039 | 3.864 |
| 28 | 2014 | *Alosterna tabacicolor* | Cerambycidae | -2.085 | -22.891 | 0.732 | 3.819 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 2 | 2014 | *Ampedus nigroflavus* | Elateridae | -0.577 | -22.144 | 1.324 | 4.486 |
| 28 | 2015 | *Ampedus pomorum* | Elateridae | 2.095 | -22.587 | 4.079 | 2.452 |
| 7 | 2015 | *Ampedus pomorum* | Elateridae | 2.016 | -25.387 | 3.825 | 0.573 |
| 7 | 2015 | *Ampedus pomorum* | Elateridae | 1.23 | -24.66 | 3.039 | 1.3 |
| 19 | 2014 | *Anaspis frontalis* | Scraptiidae | 4.642 | -22.968 | 5.7 | 5.275 |
| 22 | 2014 | *Anaspis frontalis* | Scraptiidae | 0.472 | -21.785 | 1.866 | 4.208 |
| 7 | 2014 | *Anaspis frontalis* | Scraptiidae | 1.092 | -20.065 | 2.546 | 7.123 |
| 24 | 2015 | *Anaspis marginicollis* | Scraptiidae | 4.109 | -22.048 | 4.612 | 3.067 |
| 21 | 2015 | *Anaspis marginicollis* | Scraptiidae | -0.677 | -22.809 | 1.261 | 2.656 |
| 40 | 2015 | *Anaspis marginicollis* | Scraptiidae | 6.026 | -22.428 | 7.577 | 3.597 |
| 41 | 2015 | *Anaspis marginicollis* | Scraptiidae | 1.65 | -21.572 | 3.308 | 2.626 |
| 22 | 2014 | *Anaspis ruficollis* | Scraptiidae | 2.082 | -20.92 | 3.476 | 5.073 |
| 40 | 2014 | *Anaspis ruficollis* | Scraptiidae | 0.045 | -24.195 | 4.305 | 3.112 |
| 25 | 2014 | *Anaspis ruficollis* | Scraptiidae | 2.195 | -21.48 | 4.629 | 4.666 |
| 25 | 2014 | *Anaspis ruficollis* | Scraptiidae | -0.769 | -21.864 | 1.665 | 4.282 |
| 7 | 2014 | *Anaspis ruficollis* | Scraptiidae | 1.616 | -21.759 | 3.07 | 5.429 |
| 21 | 2014 | *Anaspis ruficollis* | Scraptiidae | 3.028 | -21.752 | 6.99 | 4.76 |
| 26 | 2014 | *Anaspis ruficollis* | Scraptiidae | 2.726 | -20.107 | 4.613 | 5.621 |
| 27 | 2014 | *Anaspis ruficollis* | Scraptiidae | -0.358 | -23.438 | 0.551 | 1.48 |
| 7 | 2014 | *Anaspis ruficollis* | Scraptiidae | 1.397 | -21.67 | 2.851 | 5.518 |
| 21 | 2014 | *Anaspis ruficollis* | Scraptiidae | -2.053 | -22.365 | 1.909 | 4.147 |
| 3 | 2014 | *Anaspis ruficollis* | Scraptiidae | 1.509 | -18.94 | 6.002 | 8.552 |
| 8 | 2014 | *Anaspis ruficollis* | Scraptiidae | 4.047 | -20.734 | 5.152 | 7.501 |
| 22 | 2014 | *Anaspis ruficollis* | Scraptiidae | -1.35 | -22.587 | 0.044 | 3.406 |
| 22 | 2014 | *Anaspis ruficollis* | Scraptiidae | 1.663 | -21.464 | 3.057 | 4.529 |
| 8 | 2014 | *Anaspis ruficollis* | Scraptiidae | 4.435 | -20.796 | 5.54 | 7.439 |
| 8 | 2014 | *Anaspis ruficollis* | Scraptiidae | 3.244 | -24.07 | 4.349 | 4.165 |
| 37 | 2014 | *Anaspis ruficollis* | Scraptiidae | 8.93 | -25.146 | 11.26 | 2.136 |
| 28 | 2014 | *Anaspis ruficollis* | Scraptiidae | 0.38 | -22.857 | 3.197 | 3.853 |
| 37 | 2014 | *Anaspis ruficollis* | Scraptiidae | 0.124 | -22.526 | 2.452 | 4.756 |
| 28 | 2014 | *Anaspis ruficollis* | Scraptiidae | 3.656 | -23.19 | 6.473 | 3.52 |
| 26 | 2014 | *Anaspis ruficollis* | Scraptiidae | 1.205 | -21.389 | 3.092 | 4.339 |
| 7 | 2014 | *Anaspis ruficollis* | Scraptiidae | 0.488 | -22.163 | 1.942 | 5.025 |
| 7 | 2015 | *Anaspis ruficollis* | Scraptiidae | 3.809 | -21.51 | 5.618 | 4.45 |
| 40 | 2014 | *Anaspis ruficollis* | Scraptiidae | -0.475 | -22.112 | 3.785 | 5.195 |
| 41 | 2014 | *Anaspis ruficollis* | Scraptiidae | -0.299 | -20.565 | 2.258 | 5.453 |
| 32 | 2014 | *Anaspis rufilabris* | Scraptiidae | 1.107 | -23.209 | 4.797 | 4.609 |
| 4 | 2015 | *Anaspis rufilabris* | Scraptiidae | 3.44 | -20.817 | 4.542 | 5.189 |
| 7 | 2015 | *Anaspis rufilabris* | Scraptiidae | 4.343 | -21.619 | 6.152 | 4.341 |
| 31 | 2015 | *Anaspis rufilabris* | Scraptiidae | 0.703 | -22.82 | 5.878 | 5.163 |
| 12 | 2014 | *Anaspis thoracica* | Scraptiidae | 0.791 | -23.065 | 2.303 | 4.456 |
| 20 | 2014 | *Anaspis thoracica* | Scraptiidae | 0.582 | -22.28 | 3.496 | 3.707 |
| 21 | 2014 | *Anaspis thoracica* | Scraptiidae | -0.139 | -22.158 | 3.823 | 4.354 |
| 7 | 2015 | *Anaspis thoracica* | Scraptiidae | -1.112 | -20.381 | 0.697 | 5.579 |
| 37 | 2015 | *Anaspis thoracica* | Scraptiidae | 3.363 | -21.206 | 4.839 | 4.983 |
| 2 | 2015 | *Anaspis thoracica* | Scraptiidae | 5.433 | -22.061 | 8.611 | 0.856 |
| 4 | 2015 | *Anaspis thoracica* | Scraptiidae | 3.638 | -21.458 | 4.74 | 4.548 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 4 | 2015 | *Anaspis thoracica* | Scraptiidae | 4.13 | -23.075 | 5.232 | 2.931 |
| 28 | 2015 | *Anaspis thoracica* | Scraptiidae | 7.229 | -21.839 | 9.213 | 3.2 |
| 26 | 2015 | *Anaspis thoracica* | Scraptiidae | 1.55 | -20.952 | 4.794 | 3.574 |
| 40 | 2015 | *Anaspis thoracica* | Scraptiidae | 5.397 | -21.21 | 6.948 | 4.815 |
| 40 | 2015 | *Anaspis thoracica* | Scraptiidae | -0.93 | -26.048 | 0.621 | -0.023 |
| 4 | 2015 | *Anaspis thoracica* | Scraptiidae | 1.013 | -21.676 | 2.115 | 4.33 |
| 7 | 2014 | *Anisotoma humeralis* | Leiodidae | 6.097 | -21.162 | 7.551 | 6.026 |
| 4 | 2015 | *Anobium costatum* | Anobiidae | 0.457 | -24.433 | 1.559 | 1.573 |
| 4 | 2014 | *Anobium nitidum* | Anobiidae | -9.682 | -20.913 | -8.574 | 6.199 |
| 4 | 2014 | *Anobium nitidum* | Anobiidae | -5.321 | -21.054 | -4.213 | 6.058 |
| 4 | 2015 | *Anobium nitidum* | Anobiidae | 0.477 | -24.591 | 1.579 | 1.415 |
| 4 | 2015 | *Anobium nitidum* | Anobiidae | -4.676 | -24.144 | -3.574 | 1.862 |
| 4 | 2015 | *Anobium nitidum* | Anobiidae | -2.892 | -24.046 | -1.79 | 1.96 |
| 24 | 2015 | *Arpidiphorus orbiculatus* | Sphindidae | 4.55 | -20.41 | 5.053 | 4.705 |
| 21 | 2015 | *Arpidiphorus orbiculatus* | Sphindidae | 4.876 | -22.583 | 6.814 | 2.882 |
| 24 | 2015 | *Arpidiphorus orbiculatus* | Sphindidae | 3.882 | -21.735 | 4.385 | 3.38 |
| 7 | 2015 | *Arpidiphorus orbiculatus* | Sphindidae | 4.698 | -20.05 | 6.507 | 5.91 |
| 40 | 2015 | *Arpidiphorus orbiculatus* | Sphindidae | 6.421 | -20.144 | 7.972 | 5.881 |
| 28 | 2015 | *Arpidiphorus orbiculatus* | Sphindidae | 3.432 | -19.375 | 5.416 | 5.664 |
| 4 | 2015 | *Calambus bipustulatus* | Elateridae | 0.859 | -24.991 | 1.961 | 1.015 |
| 26 | 2014 | *Cerophytum elateroides* | Cerophytidae | -3.301 | -22.487 | -1.414 | 3.241 |
| 31 | 2015 | *Choragus sheppardi* | Anthribidae | -3.151 | -22.693 | 2.024 | 5.29 |
| 24 | 2015 | *Cis bidentatus* | Cisidae | -1.954 | -19.807 | -1.451 | 5.308 |
| 28 | 2014 | *Crepidophorus mutilatus* | Elateridae | 1.989 | -22.818 | 4.806 | 3.892 |
| 41 | 2014 | *Crepidophorus mutilatus* | Elateridae | 4.22 | -20.233 | 6.777 | 5.785 |
| 28 | 2015 | *Crepidophorus mutilatus* | Elateridae | 0.646 | -22.659 | 2.63 | 2.38 |
| 28 | 2015 | *Crepidophorus mutilatus* | Elateridae | -1.385 | -23.095 | 0.599 | 1.944 |
| 26 | 2015 | *Crepidophorus mutilatus* | Elateridae | 0.517 | -22.09 | 3.761 | 2.436 |
| 28 | 2015 | *Crepidophorus mutilatus* | Elateridae | -0.598 | -22.682 | 1.386 | 2.357 |
| 4 | 2014 | *Cryptophagus labilis* | Cryptophagidae | 4.58 | -17.449 | 5.688 | 9.663 |
| 28 | 2015 | *Cryptophagus labilis* | Cryptophagidae | -1.595 | -21.761 | 0.389 | 3.278 |
| 23 | 2015 | *Cryptophagus labilis* | Cryptophagidae | 2.208 | -21.27 | 1.339 | 3.531 |
| 7 | 2015 | *Cryptophagus labilis* | Cryptophagidae | 0.443 | -21.902 | 2.252 | 4.058 |
| 30 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | 3.125 | -25.486 | 7.457 | 3.948 |
| 25 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -0.962 | -25.666 | 1.472 | 0.48 |
| 22 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -0.686 | -22.336 | 0.708 | 3.657 |
| 3 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -0.594 | -23.09 | 3.899 | 4.402 |
| 38 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -0.836 | -22.228 | 2.188 | 4.799 |
| 4 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -1.82 | -21.514 | -0.712 | 5.598 |
| 5 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | 2.678 | -20.618 | 5.479 | 8.581 |
| 4 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -0.649 | -18.339 | 0.459 | 8.773 |
| 4 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | 1.443 | -20.49 | 2.551 | 6.622 |
| 24 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | 0.797 | -22.995 | 1.3 | 2.12 |
| 11 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -5.749 | -17.342 | -4.56 | 10.29 |
| 24 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 0.867 | -23.109 | 1.37 | 2.006 |
| 18 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 0.137 | -23.177 | 2.867 | 0.927 |
| 24 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -1.19 | -23.455 | -0.687 | 1.66 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 23 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 1.485 | -22.193 | 0.616 | 2.608 |
| 20 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 3.004 | -22.939 | 6.055 | 1.634 |
| 18 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -0.098 | -24.1 | 2.632 | 0.004 |
| 20 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 2.658 | -23.649 | 5.709 | 0.924 |
| 24 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 0.443 | -21.602 | 0.946 | 3.513 |
| 26 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -2.631 | -24.182 | 0.613 | 0.344 |
| 7 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 2.603 | -22.119 | 4.412 | 3.841 |
| 21 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -0.196 | -23.501 | 1.742 | 1.964 |
| 31 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -2.688 | -23.955 | 2.487 | 4.028 |
| 4 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -2.631 | -23.146 | -1.529 | 2.86 |
| 40 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 1.663 | -23.108 | 3.214 | 2.917 |
| 4 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | 6.563 | -23.475 | 7.665 | 2.531 |
| 18 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -0.558 | -21.392 | 2.172 | 2.712 |
| 29 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -4.932 | -22.543 | -3.444 | 4.315 |
| 3 | 2015 | *Cyclorhipidion bodoanus* | Scolytidae | -2.318 | -21.818 | -4.927 | 5.235 |
| 6 | 2014 | *Cyclorhipidion bodoanus* | Scolytidae | -0.022 | -23.027 | 3.871 | 3.865 |
| 24 | 2014 | *Denticollis rubens* | Elateridae | 1.362 | -22.471 | 1.865 | 2.644 |
| 4 | 2015 | *Dissoleucas niveirostris* | Anthribidae | -3.368 | -22.69 | -2.266 | 3.316 |
| 22 | 2014 | *Dorcatoma substriata* | Anobiidae | 3.199 | -18.513 | 4.593 | 7.48 |
| 7 | 2015 | *Epuraea variegata* | Nitidulidae | 2.192 | -21.946 | 4.001 | 4.014 |
| 23 | 2015 | *Ernoporicus fagi* | Scolytidae | -3.734 | -24.913 | -4.603 | -0.112 |
| 28 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.431 | -20.757 | 0.386 | 5.953 |
| 28 | 2014 | *Eucnemis capucina* | Eucnemidae | -3.006 | -24.404 | -0.189 | 2.306 |
| 25 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.814 | -22.621 | -0.38 | 3.525 |
| 25 | 2014 | *Eucnemis capucina* | Eucnemidae | -3.859 | -24.019 | -1.425 | 2.127 |
| 41 | 2014 | *Eucnemis capucina* | Eucnemidae | 1.105 | -22.065 | 3.662 | 3.953 |
| 12 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.355 | -25.089 | -0.843 | 2.432 |
| 25 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.033 | -24.523 | 0.401 | 1.623 |
| 22 | 2014 | *Eucnemis capucina* | Eucnemidae | -3.97 | -21.624 | -2.576 | 4.369 |
| 11 | 2014 | *Eucnemis capucina* | Eucnemidae | -3.054 | -22.417 | -1.865 | 5.215 |
| 21 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.614 | -23.027 | 1.348 | 3.485 |
| 23 | 2015 | *Eucnemis capucina* | Eucnemidae | -1.639 | -24.022 | -2.508 | 0.779 |
| 26 | 2015 | *Eucnemis capucina* | Eucnemidae | -3.805 | -23.255 | -0.561 | 1.271 |
| 18 | 2015 | *Eucnemis capucina* | Eucnemidae | -3.544 | -25.044 | -0.814 | -0.94 |
| 22 | 2015 | *Eucnemis capucina* | Eucnemidae | -2.661 | -22.222 | -2.962 | 2.417 |
| 40 | 2015 | *Eucnemis capucina* | Eucnemidae | -2.622 | -22.228 | -1.071 | 3.797 |
| 11 | 2015 | *Eucnemis capucina* | Eucnemidae | -3.21 | -24.044 | -2.328 | 2.016 |
| 41 | 2015 | *Eucnemis capucina* | Eucnemidae | -0.343 | -24.095 | 1.315 | 0.103 |
| 8 | 2015 | *Eucnemis capucina* | Eucnemidae | -1.199 | -23.008 | 0.615 | 2.691 |
| 3 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.233 | -26.844 | 2.26 | 0.648 |
| 3 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.833 | -22.662 | 1.66 | 4.83 |
| 18 | 2014 | *Eucnemis capucina* | Eucnemidae | -2.224 | -23.129 | 0.29 | 2.511 |
| 18 | 2014 | *Eucnemis capucina* | Eucnemidae | -1.916 | -22.343 | 0.598 | 3.297 |
| 18 | 2015 | *Eucnemis capucina* | Eucnemidae | -1.342 | -22.038 | 1.388 | 2.066 |
| 18 | 2015 | *Eucnemis capucina* | Eucnemidae | -3.039 | -23.565 | -0.309 | 0.539 |
| 25 | 2014 | *Hapalaraea pygmaea* | Staphylinidae | 2.696 | -18.984 | 5.13 | 7.162 |
| 3 | 2014 | *Hapalaraea pygmaea* | Staphylinidae | 3.021 | -23.014 | 7.514 | 4.478 |

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|---|---|---|---|---|---|---|---|
| 22 | 2014 | *Hapalaraea pygmaea* | Staphylinidae | 3.609 | -20.277 | 5.003 | 5.716 |
| 8 | 2014 | *Hapalaraea pygmaea* | Staphylinidae | 4.308 | -20.594 | 5.413 | 7.641 |
| 28 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | 2.786 | -21.388 | 4.77 | 3.651 |
| 7 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | 2.286 | -21.628 | 4.095 | 4.332 |
| 24 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | 2.453 | -19.783 | 2.956 | 5.332 |
| 3 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | -0.508 | -21.358 | -3.117 | 5.695 |
| 20 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | 1.047 | -23.362 | 4.098 | 1.211 |
| 37 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | -0.097 | -26.473 | 1.379 | -0.284 |
| 22 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | 1.876 | -21.383 | 1.575 | 3.256 |
| 28 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | 1.754 | -21.638 | 3.738 | 3.401 |
| 21 | 2015 | *Hapalaraea pygmaea* | Staphylinidae | 2.097 | -22.003 | 4.035 | 3.462 |
| 3 | 2014 | *Hapalaraea pygmaea* | Staphylinidae | -0.956 | -23.278 | 3.537 | 4.214 |
| 41 | 2014 | *Hesperus rufipennis* | Staphylinidae | 2.216 | -24.064 | 4.773 | 1.954 |
| 25 | 2014 | *Hesperus rufipennis* | Staphylinidae | 1.357 | -22.319 | 3.791 | 3.827 |
| 15 | 2014 | *Hesperus rufipennis* | Staphylinidae | 9.183 | -23.811 | 12.05 | 3.861 |
| 26 | 2015 | *Hesperus rufipennis* | Staphylinidae | -0.04 | -20.874 | 3.204 | 3.652 |
| 41 | 2015 | *Hesperus rufipennis* | Staphylinidae | 0.708 | -24.157 | 2.366 | 0.041 |
| 28 | 2015 | *Hesperus rufipennis* | Staphylinidae | -1.124 | -25.367 | 0.86 | -0.328 |
| 22 | 2015 | *Hesperus rufipennis* | Staphylinidae | 2.556 | -21.985 | 2.255 | 2.654 |
| 22 | 2015 | *Hesperus rufipennis* | Staphylinidae | 2.289 | -22.104 | 1.988 | 2.535 |
| 22 | 2015 | *Hesperus rufipennis* | Staphylinidae | 4.588 | -21.231 | 4.287 | 3.408 |
| 16 | 2014 | *Hylecoetus dermestoides* | Lymexylidae | -0.785 | -25.785 | 2.483 | 2.293 |
| 22 | 2014 | *Hypebaeus flavipes* | Malachiidae | 7.03 | -22.446 | 8.424 | 3.547 |
| 37 | 2014 | *Hypebaeus flavipes* | Malachiidae | 2.891 | -23.785 | 5.219 | 3.497 |
| 7 | 2014 | *Hypebaeus flavipes* | Malachiidae | 5.055 | -22.598 | 6.509 | 4.59 |
| 8 | 2014 | *Hypebaeus flavipes* | Malachiidae | 4.359 | -23.23 | 5.464 | 5.005 |
| 7 | 2014 | *Hypebaeus flavipes* | Malachiidae | 5.625 | -22.651 | 7.079 | 4.537 |
| 22 | 2014 | *Hypebaeus flavipes* | Malachiidae | 4.116 | -22.957 | 5.51 | 3.036 |
| 8 | 2014 | *Hypebaeus flavipes* | Malachiidae | 4.811 | -23.882 | 5.916 | 4.353 |
| 7 | 2014 | *Hypebaeus flavipes* | Malachiidae | 4.057 | -23.232 | 5.511 | 3.956 |
| 37 | 2014 | *Hypebaeus flavipes* | Malachiidae | 4.223 | -23.553 | 6.551 | 3.729 |
| 22 | 2014 | *Hypebaeus flavipes* | Malachiidae | 5.983 | -21.884 | 7.377 | 4.109 |
| 8 | 2014 | *Hypebaeus flavipes* | Malachiidae | 3.296 | -23.218 | 4.401 | 5.017 |
| 14 | 2014 | *Hypebaeus flavipes* | Malachiidae | 5.01 | -22.816 | 7.694 | 2.945 |
| 7 | 2015 | *Hypebaeus flavipes* | Malachiidae | 1.54 | -23.748 | 3.349 | 2.212 |
| 7 | 2015 | *Hypebaeus flavipes* | Malachiidae | 4.285 | -23.447 | 6.094 | 2.513 |
| 22 | 2015 | *Hypebaeus flavipes* | Malachiidae | 5.24 | -24.591 | 4.939 | 0.048 |
| 7 | 2015 | *Hypebaeus flavipes* | Malachiidae | 2.537 | -23.169 | 4.346 | 2.791 |
| 33 | 2014 | *Ischnomera caerulea/cyanea* | Oedemeridae | -1.668 | -22.471 | 0.887 | 4.198 |
| 28 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | -0.054 | -24.962 | 2.763 | 1.748 |
| 29 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | 1.014 | -23.325 | 2.315 | 4.855 |
| 41 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | -2.081 | -22.572 | 0.476 | 3.446 |
| 25 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | -0.109 | -22.499 | 2.325 | 3.647 |
| 24 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | -4.096 | -23.259 | -3.593 | 1.856 |
| 2 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | -0.467 | -21.294 | 1.434 | 5.336 |
| 23 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | -0.978 | -22.528 | -1.411 | 3.347 |

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|---|---|---|---|---|---|---|---|
| 26 | 2014 | *Ischnomera sanguinicollis* | Oedemeridae | -1.186 | -23.029 | 0.701 | 2.699 |
| 26 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -3.127 | -22.629 | 0.117 | 1.897 |
| 40 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -1.356 | -22.909 | 0.195 | 3.116 |
| 24 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -0.527 | -23.368 | -0.024 | 1.747 |
| 23 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -3.017 | -21.21 | -3.886 | 3.591 |
| 21 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -5.237 | -21.763 | -3.299 | 3.702 |
| 23 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -5.105 | -20.311 | -5.974 | 4.49 |
| 4 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | 2.078 | -23.315 | 3.18 | 2.691 |
| 20 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | 1.534 | -22.434 | 4.585 | 2.139 |
| 28 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -2.22 | -22.67 | -0.236 | 2.369 |
| 40 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -1.261 | -23.038 | 0.29 | 2.987 |
| 40 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -1.689 | -22.064 | -0.138 | 3.961 |
| 23 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -1.536 | -23.665 | -2.405 | 1.136 |
| 4 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | 0.839 | -21.724 | 1.941 | 4.282 |
| 28 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -3.331 | -22.505 | -1.347 | 2.534 |
| 28 | 2015 | *Ischnomera sanguinicollis* | Oedemeridae | -2.567 | -22.526 | -0.583 | 2.513 |
| 26 | 2015 | *Ischnomera sp.* | Oedemeridae | -3.463 | -21.456 | -0.219 | 3.07 |
| 41 | 2015 | *Ischnomera sp.* | Oedemeridae | 1.615 | -20.869 | 3.273 | 3.329 |
| 21 | 2015 | *Ischnomera sp.* | Oedemeridae | -6.226 | -22.211 | -4.288 | 3.254 |
| 18 | 2015 | *Ischnomera sp.* | Oedemeridae | -1.632 | -23.58 | 1.098 | 0.524 |
| 7 | 2015 | *Malachius bipustulatus* | Malachiidae | 6.396 | -22.922 | 8.205 | 3.038 |
| 40 | 2015 | *Malthinus punctatus* | Cantharidae | 0.068 | -27.614 | 1.619 | -1.589 |
| 4 | 2014 | *Malthodes marginatus* | Cantharidae | -0.116 | -25.808 | 0.992 | 1.304 |
| 6 | 2014 | *Malthodes marginatus* | Cantharidae | -1.726 | -26.13 | 2.167 | 0.762 |
| 21 | 2014 | *Malthodes marginatus* | Cantharidae | -2.632 | -26.79 | 1.33 | -0.278 |
| 4 | 2015 | *Malthodes marginatus* | Cantharidae | -0.938 | -25.888 | 0.164 | 0.118 |
| 20 | 2015 | *Malthodes marginatus* | Cantharidae | -2.023 | -26.67 | 1.028 | -2.097 |
| 4 | 2015 | *Malthodes marginatus* | Cantharidae | -1.677 | -26.078 | -0.575 | -0.072 |
| 4 | 2015 | *Malthodes marginatus* | Cantharidae | 0.056 | -25.506 | 1.158 | 0.5 |
| 5 | 2014 | *Megatoma undata* | Dermestidae | 4.893 | -24.385 | 7.694 | 4.814 |
| 29 | 2014 | *Melanotus castanipes* | Elateridae | 0.434 | -24.257 | 1.735 | 3.923 |
| 31 | 2014 | *Melanotus castanipes* | Elateridae | 1.873 | -23.297 | 5.578 | 4.996 |
| 40 | 2014 | *Melanotus castanipes* | Elateridae | 0.469 | -24.018 | 4.729 | 3.289 |
| 5 | 2014 | *Melanotus castanipes* | Elateridae | 3.173 | -22.519 | 5.974 | 6.68 |
| 33 | 2014 | *Melanotus castanipes* | Elateridae | 2.44 | -24.168 | 4.995 | 2.501 |
| 14 | 2014 | *Melanotus castanipes* | Elateridae | 2.115 | -23.168 | 4.799 | 2.593 |
| 23 | 2015 | *Melanotus castanipes* | Elateridae | 1.698 | -24.961 | 0.829 | -0.16 |
| 20 | 2015 | *Melanotus castanipes* | Elateridae | 2.201 | -24.163 | 5.252 | 0.41 |
| 20 | 2015 | *Melanotus castanipes* | Elateridae | 1.888 | -24.355 | 4.939 | 0.218 |
| 7 | 2015 | *Melanotus rufipes* | Elateridae | 4.217 | -22.249 | 6.026 | 3.711 |
| 19 | 2015 | *Melanotus rufipes* | Elateridae | 2.265 | -22.968 | 2.518 | 3.112 |
| 7 | 2015 | *Melanotus rufipes* | Elateridae | 1.405 | -24.504 | 3.214 | 1.456 |
| 22 | 2014 | *Mycetophagus populi* | Mycetophagidae | 0.826 | -21.706 | 2.22 | 4.287 |
| 25 | 2014 | *Mycetophagus populi* | Mycetophagidae | 1.649 | -22.404 | 4.083 | 3.742 |
| 22 | 2015 | *Mycetophagus populi* | Mycetophagidae | 0.945 | -21.236 | 0.644 | 3.403 |
| 22 | 2015 | *Mycetophagus populi* | Mycetophagidae | 0.528 | -21.847 | 0.227 | 2.792 |
| 21 | 2015 | *Mycetophagus populi* | Mycetophagidae | 1.178 | -21.045 | 3.116 | 4.42 |

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| 22 | 2015 | *Mycetophagus populi* | Mycetophagidae | 2.087 | -21.722 | 1.786 | 2.917 |
| 21 | 2015 | *Mycetophagus populi* | Mycetophagidae | 1.386 | -20.497 | 3.324 | 4.968 |
| 40 | 2015 | *Neuraphes carinatus* | Scydmaenidae | 3.105 | -24.067 | 4.656 | 1.958 |
| 22 | 2014 | *Orchesia micans* | Melandryidae | 3.553 | -18.916 | 4.947 | 7.077 |
| 22 | 2014 | *Orchesia micans* | Melandryidae | 5.365 | -18.375 | 6.759 | 7.618 |
| 22 | 2014 | *Orchesia micans* | Melandryidae | 4.257 | -18.895 | 5.651 | 7.098 |
| 25 | 2014 | *Orchesia micans* | Melandryidae | 3.72 | -19.592 | 6.154 | 6.554 |
| 22 | 2014 | *Orchesia micans* | Melandryidae | 4.03 | -19.346 | 5.424 | 6.647 |
| 34 | 2014 | *Orchesia micans* | Melandryidae | 3.023 | -21.269 | 4.483 | 6.01 |
| 27 | 2014 | *Orchesia micans* | Melandryidae | 5.762 | -18.204 | 6.671 | 6.714 |
| 22 | 2015 | *Orchesia micans* | Melandryidae | 1.382 | -18.832 | 1.081 | 5.807 |
| 21 | 2015 | *Orchesia micans* | Melandryidae | 3.245 | -19.616 | 5.183 | 5.849 |
| 21 | 2015 | *Orchesia micans* | Melandryidae | 3.761 | -19.002 | 5.699 | 6.463 |
| 37 | 2015 | *Orthoperus atomus* | Corylophidae | 2.967 | -23.088 | 4.443 | 3.101 |
| 7 | 2015 | *Paromalus flavicornis* | Histeridae | 2.925 | -22.284 | 4.734 | 3.676 |
| 24 | 2015 | *Phloeonomus punctipennis* | Staphylinidae | 0.501 | -20.086 | 1.004 | 5.029 |
| 7 | 2015 | *Phloeophagus lignarius* | Curculionidae | -4.573 | -22.607 | -2.764 | 3.353 |
| 22 | 2015 | *Phloeophagus lignarius* | Curculionidae | -1.994 | -22.582 | -2.295 | 2.057 |
| 22 | 2015 | *Phloeophagus lignarius* | Curculionidae | -0.876 | -21.674 | -1.177 | 2.965 |
| 29 | 2014 | *Pityophagus ferrugineus* | Nitidulidae | -0.805 | -23.961 | 0.496 | 4.219 |
| 7 | 2015 | *Platycis cosnardi* | Lycidae | 0.899 | -21.405 | 2.708 | 4.555 |
| 25 | 2014 | *Plegaderus dissectus* | Histeridae | 2.304 | -22.201 | 4.738 | 3.945 |
| 24 | 2015 | *Plegaderus dissectus* | Histeridae | 2.992 | -21.181 | 3.495 | 3.934 |
| 26 | 2015 | *Plegaderus dissectus* | Histeridae | 0.06 | -19.701 | 3.304 | 4.825 |
| 40 | 2015 | *Plegaderus dissectus* | Histeridae | 3.32 | -20.363 | 4.871 | 5.662 |
| 40 | 2015 | *Plegaderus dissectus* | Histeridae | 2.107 | -21.472 | 3.658 | 4.553 |
| 22 | 2015 | *Plegaderus dissectus* | Histeridae | 3.202 | -21.059 | 2.901 | 3.58 |
| 22 | 2014 | *Plegaderus dissectus* | Histeridae | 1.683 | -22.257 | 3.077 | 3.736 |
| 12 | 2014 | *Prionocyphon serricornis* | Scirtidae | 3.41 | -24 | 4.922 | 3.521 |
| 2 | 2014 | *Prionocyphon serricornis* | Scirtidae | -6.258 | -25.332 | -4.357 | 1.298 |
| 40 | 2014 | *Prionocyphon serricornis* | Scirtidae | -0.364 | -21.762 | 3.896 | 5.545 |
| 32 | 2014 | *Prionocyphon serricornis* | Scirtidae | -1.536 | -21.512 | 2.154 | 6.306 |
| 40 | 2015 | *Prionocyphon serricornis* | Scirtidae | -4.139 | -25.244 | -2.588 | 0.781 |
| 4 | 2015 | *Prionocyphon serricornis* | Scirtidae | -1.016 | -25.407 | 0.086 | 0.599 |
| 40 | 2015 | *Prionocyphon serricornis* | Scirtidae | 0.347 | -24.312 | 1.898 | 1.713 |
| 28 | 2015 | *Prionocyphon serricornis* | Scirtidae | -3.293 | -28.216 | -1.309 | -3.177 |
| 23 | 2015 | *Prionocyphon serricornis* | Scirtidae | 0.367 | -23.393 | -0.502 | 1.408 |
| 40 | 2015 | *Prionocyphon serricornis* | Scirtidae | 0.034 | -25.155 | 1.585 | 0.87 |
| 40 | 2015 | *Procraerus tibialis* | Elateridae | 2.258 | -22.443 | 3.809 | 3.582 |
| 22 | 2014 | *Pseudocistela ceramboides* | Tenebrionidae | 1.48 | -22.484 | 2.874 | 3.509 |
| 37 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -0.119 | -23.467 | 2.209 | 3.815 |
| 20 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -2.592 | -22.611 | 0.322 | 3.376 |
| 20 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -1.768 | -21.662 | 1.146 | 4.325 |
| 4 | 2014 | *Ptilinus pectinicornis* | Anobiidae | 0.173 | -20.769 | 1.281 | 6.343 |
| 37 | 2014 | *Ptilinus pectinicornis* | Anobiidae | 0.049 | -19.777 | 2.377 | 7.505 |
| 37 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -0.43 | -20.396 | 1.898 | 6.886 |
| 37 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -1.13 | -20.06 | 1.198 | 7.222 |

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| 25 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -2.857 | -17.47 | -0.423 | 8.676 |
| 20 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -1.379 | -20.912 | 1.535 | 5.075 |
| 20 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -3.682 | -20.478 | -0.768 | 5.509 |
| 40 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -2.61 | -22.261 | -1.059 | 3.764 |
| 37 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -2.826 | -22.504 | -1.35 | 3.685 |
| 7 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -2.083 | -22.077 | -0.274 | 3.883 |
| 7 | 2015 | *Ptilinus pectinicornis* | Anobiidae | 2.332 | -22.271 | 4.141 | 3.689 |
| 37 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -2.621 | -22.598 | -1.145 | 3.591 |
| 20 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -0.954 | -21.71 | 2.097 | 2.863 |
| 4 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -1.89 | -23.432 | -0.788 | 2.574 |
| 20 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -2.13 | -21.924 | 0.921 | 2.649 |
| 37 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -3.485 | -22.254 | -2.009 | 3.935 |
| 4 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -0.683 | -22.008 | 0.419 | 3.998 |
| 7 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -1.765 | -21.959 | 0.044 | 4.001 |
| 20 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -1.661 | -21.44 | 1.39 | 3.133 |
| 7 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -3.011 | -24.354 | -1.557 | 2.834 |
| 7 | 2014 | *Ptilinus pectinicornis* | Anobiidae | -5.32 | -21.958 | -3.866 | 5.23 |
| 4 | 2015 | *Ptilinus pectinicornis* | Anobiidae | -1.298 | -22.755 | -0.196 | 3.251 |
| 8 | 2015 | *Quedius brevicornis* | Staphylinidae | 2.118 | -24.323 | 3.932 | 1.376 |
| 40 | 2014 | *Quedius microps* | Staphylinidae | 4.192 | -20.319 | 8.452 | 6.988 |
| 21 | 2014 | *Quedius truncicola* | Staphylinidae | 3.808 | -24.537 | 7.77 | 1.975 |
| 11 | 2014 | *Quedius truncicola* | Staphylinidae | 0.454 | -23.126 | 1.643 | 4.506 |
| 26 | 2015 | *Quedius truncicola* | Staphylinidae | 3.013 | -23.351 | 6.257 | 1.175 |
| 41 | 2015 | *Quedius truncicola* | Staphylinidae | 0.427 | -24.47 | 2.085 | -0.272 |
| 21 | 2015 | *Quedius truncicola* | Staphylinidae | 2.811 | -21.52 | 4.749 | 3.945 |
| 26 | 2015 | *Quedius truncicola* | Staphylinidae | 2.598 | -23.893 | 5.842 | 0.633 |
| 40 | 2015 | *Rhagium mordax* | Cerambycidae | -1.048 | -21.775 | 0.503 | 4.25 |
| 3 | 2014 | *Rhizophagus bipustulatus* | Monotomidae | -2.943 | -23.952 | 1.55 | 3.54 |
| 24 | 2015 | *Rhizophagus bipustulatus* | Monotomidae | -1.712 | -22.168 | -1.209 | 2.947 |
| 40 | 2015 | *Rhizophagus bipustulatus* | Monotomidae | 1.597 | -23.746 | 3.148 | 2.279 |
| 26 | 2015 | *Rhizophagus bipustulatus* | Monotomidae | -2.755 | -23.284 | 0.489 | 1.242 |
| 7 | 2015 | *Rhizophagus bipustulatus* | Monotomidae | 0.681 | -23.11 | 2.49 | 2.85 |
| 22 | 2015 | *Rhizophagus bipustulatus* | Monotomidae | -0.288 | -22.706 | -0.589 | 1.933 |
| 31 | 2014 | *Rhizophagus depressus* | Monotomidae | 0.972 | -26.233 | 4.677 | 2.06 |
| 21 | 2015 | *Rhizophagus depressus* | Monotomidae | 1.911 | -22.152 | 3.849 | 3.313 |
| 29 | 2015 | *Rhizophagus depressus* | Monotomidae | -2.766 | -22.197 | -1.278 | 4.661 |
| 30 | 2014 | *Rhizophagus dispar* | Monotomidae | -0.548 | -23.823 | 3.784 | 5.611 |
| 37 | 2015 | *Rhizophagus perforatus* | Monotomidae | -1.85 | -23.322 | -0.374 | 2.867 |
| 24 | 2015 | *Rhizophagus perforatus* | Monotomidae | 2.872 | -23.647 | 3.375 | 1.468 |
| 21 | 2015 | *Rhizophagus perforatus* | Monotomidae | 2.291 | -23.3 | 4.229 | 2.165 |
| 25 | 2014 | *Scraptia fuscula* | Scraptiidae | 2.465 | -18.545 | 4.899 | 7.601 |
| 15 | 2014 | *Scraptia fuscula* | Scraptiidae | 3.451 | -19.818 | 6.322 | 7.854 |
| 24 | 2014 | *Scraptia fuscula* | Scraptiidae | 2.363 | -21.761 | 2.866 | 3.354 |
| 25 | 2014 | *Scraptia fuscula* | Scraptiidae | 1.641 | -19.492 | 4.075 | 6.654 |
| 26 | 2015 | *Scraptia fuscula* | Scraptiidae | 0.672 | -23.091 | 3.916 | 1.435 |
| 28 | 2015 | *Scraptia fuscula* | Scraptiidae | 1.738 | -23.74 | 3.722 | 1.299 |
| 28 | 2014 | *Scraptia fuscula* | Scraptiidae | 4.902 | -18.24 | 7.719 | 8.47 |

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|---|---|---|---|---|---|---|---|
| 28 | 2014 | *Scraptia fuscula* | Scraptiidae | 4.004 | -18.976 | 6.821 | 7.734 |
| 28 | 2014 | *Scraptia fuscula* | Scraptiidae | 4.215 | -18.418 | 7.032 | 8.292 |
| 28 | 2014 | *Scraptia fuscula* | Scraptiidae | 3.978 | -19.132 | 6.795 | 7.578 |
| 25 | 2014 | *Siagonum quadricorne* | Staphylinidae | 0.149 | -19.518 | 2.583 | 6.628 |
| 37 | 2015 | *Tetropium castaneum* | Cerambycidae | -3.137 | -22.514 | -1.661 | 3.675 |
| 21 | 2014 | *Tillus elongatus* | Cleridae | 1.003 | -22.554 | 4.965 | 3.958 |
| 20 | 2014 | *Tillus elongatus* | Cleridae | 0.246 | -22.106 | 3.16 | 3.881 |
| 37 | 2014 | *Tillus elongatus* | Cleridae | -0.061 | -22.236 | 2.267 | 5.046 |
| 7 | 2014 | *Tillus elongatus* | Cleridae | -0.478 | -24.565 | 0.976 | 2.623 |
| 21 | 2015 | *Tillus elongatus* | Cleridae | -0.697 | -21.88 | 1.241 | 3.585 |
| 37 | 2015 | *Tillus elongatus* | Cleridae | -2.45 | -21.975 | -0.974 | 4.214 |
| 19 | 2015 | *Tillus elongatus* | Cleridae | -2.75 | -21.702 | -2.497 | 4.378 |
| 37 | 2015 | *Tillus elongatus* | Cleridae | -2.135 | -21.872 | -0.659 | 4.317 |
| 21 | 2015 | *Tillus elongatus* | Cleridae | 0.242 | -21.482 | 2.18 | 3.983 |
| 37 | 2015 | *Tillus elongatus* | Cleridae | -1.171 | -21.746 | 0.305 | 4.443 |
| 4 | 2015 | *Tillus elongatus* | Cleridae | -1.012 | -21.663 | 0.09 | 4.343 |
| 22 | 2014 | *Triplax russica* | Erotylidae | 1.517 | -20.299 | 2.911 | 5.694 |
| 22 | 2014 | *Triplax russica* | Erotylidae | 2.58 | -19.408 | 3.974 | 6.585 |
| 4 | 2015 | *Velleius dilatatus* | Staphylinidae | 5.042 | -24.972 | 6.144 | 1.034 |
| 29 | 2014 | *Xyleborus dispar* | Scolytidae | -2.629 | -26.768 | -1.328 | 1.412 |
| 31 | 2014 | *Xyleborus dispar* | Scolytidae | 6.065 | -24.892 | 9.77 | 3.401 |
| 25 | 2014 | *Xyleborus dispar* | Scolytidae | -2.825 | -27.003 | -0.391 | -0.857 |
| 15 | 2014 | *Xyleborus dispar* | Scolytidae | -2.974 | -25.655 | -0.103 | 2.017 |
| 4 | 2014 | *Xyleborus dispar* | Scolytidae | -2.723 | -29.309 | -1.615 | -2.197 |
| 13 | 2014 | *Xyleborus dispar* | Scolytidae | 1.839 | -22.05 | -3.966 | 6.905 |
| 5 | 2014 | *Xyleborus dispar* | Scolytidae | -2.913 | -25.342 | -0.112 | 3.857 |
| 30 | 2014 | *Xyleborus dispar* | Scolytidae | -1.476 | -26.089 | 2.856 | 3.345 |
| 5 | 2014 | *Xyleborus dispar* | Scolytidae | 0.857 | -24.048 | 3.658 | 5.151 |
| 7 | 2014 | *Xyleborus dispar* | Scolytidae | -2.065 | -23.99 | -0.611 | 3.198 |
| 35 | 2014 | *Xyleborus dispar* | Scolytidae | -3.121 | -24.937 | -1.105 | 2.867 |
| 20 | 2014 | *Xyleborus dispar* | Scolytidae | 1.674 | -24.774 | 4.588 | 1.213 |
| 30 | 2014 | *Xyleborus dispar* | Scolytidae | -3.692 | -27.301 | 0.64 | 2.133 |
| 5 | 2014 | *Xyleborus dispar* | Scolytidae | -0.966 | -25.709 | 1.835 | 3.49 |
| 31 | 2014 | *Xyleborus dispar* | Scolytidae | -3.035 | -29.378 | 0.67 | -1.085 |
| 21 | 2014 | *Xyleborus dispar* | Scolytidae | -5.361 | -27.696 | -1.399 | -1.184 |
| 10 | 2014 | *Xyleborus dispar* | Scolytidae | 6.287 | -25.132 | 6.339 | 1.867 |
| 39 | 2014 | *Xyleborus dispar* | Scolytidae | 1.978 | -25.089 | 0.948 | 2.704 |
| 18 | 2014 | *Xyleborus dispar* | Scolytidae | 1.045 | -23.827 | 3.559 | 1.813 |
| 7 | 2014 | *Xyleborus dispar* | Scolytidae | 0.583 | -24.734 | 2.037 | 2.454 |
| 30 | 2014 | *Xyleborus dispar* | Scolytidae | -2.653 | -24.309 | 1.679 | 5.125 |
| 36 | 2014 | *Xyleborus dispar* | Scolytidae | -4.772 | -27.401 | -2.835 | -1.017 |
| 41 | 2014 | *Xyleborus dispar* | Scolytidae | -1.785 | -26.942 | 0.772 | -0.924 |
| 31 | 2014 | *Xyleborus dispar* | Scolytidae | 1.328 | -25.114 | 5.033 | 3.179 |
| 39 | 2014 | *Xyleborus dispar* | Scolytidae | -2.074 | -25.342 | -3.104 | 2.451 |
| 41 | 2014 | *Xyleborus dispar* | Scolytidae | 2.106 | -21.669 | 4.663 | 4.349 |
| 37 | 2015 | *Xyleborus dispar* | Scolytidae | 1.233 | -25.563 | 2.709 | 0.626 |
| 7 | 2015 | *Xyleborus dispar* | Scolytidae | -2.414 | -24.969 | -0.605 | 0.991 |

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|---|---|---|---|---|---|---|---|
| 31 | 2015 | *Xyleborus dispar* | Scolytidae | -2.965 | -23.83 | 2.21 | 4.153 |
| 24 | 2015 | *Xyleborus dispar* | Scolytidae | -1.623 | -27.199 | -1.12 | -2.084 |
| 31 | 2015 | *Xyleborus dispar* | Scolytidae | 3.174 | -23.268 | 8.349 | 4.715 |
| 21 | 2015 | *Xyleborus dispar* | Scolytidae | -2.295 | -24.933 | -0.357 | 0.532 |
| 4 | 2015 | *Xyleborus dispar* | Scolytidae | -0.092 | -26.906 | 1.01 | -0.9 |
| 18 | 2015 | *Xyleborus dispar* | Scolytidae | -2.653 | -24.289 | 0.077 | -0.185 |
| 3 | 2015 | *Xyleborus dispar* | Scolytidae | -1.972 | -25.651 | -4.581 | 1.402 |
| 12 | 2015 | *Xyleborus dispar* | Scolytidae | -4.188 | -24.479 | -3.316 | 2.225 |
| 26 | 2015 | *Xyleborus dispar* | Scolytidae | -1.951 | -25.164 | 1.293 | -0.638 |
| 7 | 2015 | *Xyleborus dispar* | Scolytidae | -3.741 | -26.23 | -1.932 | -0.27 |
| 17 | 2014 | *Xyleborus dispar* | Scolytidae | -0.73 | -25.885 | -4.762 | -2.774 |
| 31 | 2015 | *Xyleborus dispar* | Scolytidae | -1.874 | -24.402 | 3.301 | 3.581 |
| 28 | 2014 | *Xyleborus germanus* | Scolytidae | 5.165 | -24.052 | 7.982 | 2.658 |
| 29 | 2014 | *Xyleborus germanus* | Scolytidae | 6.82 | -23.58 | 8.121 | 4.6 |
| 22 | 2014 | *Xyleborus germanus* | Scolytidae | 1.973 | -25.105 | 3.367 | 0.888 |
| 35 | 2014 | *Xyleborus germanus* | Scolytidae | 1.864 | -23.79 | 3.88 | 4.014 |
| 21 | 2014 | *Xyleborus germanus* | Scolytidae | 0.36 | -24.737 | 4.322 | 1.775 |
| 25 | 2014 | *Xyleborus germanus* | Scolytidae | -0.981 | -25.542 | 1.453 | 0.604 |
| 37 | 2014 | *Xyleborus germanus* | Scolytidae | -1.847 | -23.291 | 0.481 | 3.991 |
| 22 | 2014 | *Xyleborus germanus* | Scolytidae | -0.36 | -24.121 | 1.034 | 1.872 |
| 4 | 2014 | *Xyleborus germanus* | Scolytidae | 0.08 | -24.924 | 1.188 | 2.188 |
| 13 | 2014 | *Xyleborus germanus* | Scolytidae | -0.35 | -25.202 | -6.155 | 3.753 |
| 14 | 2014 | *Xyleborus germanus* | Scolytidae | 3.625 | -26.15 | 6.309 | -0.389 |
| 16 | 2014 | *Xyleborus germanus* | Scolytidae | -0.132 | -25.112 | 3.136 | 2.966 |
| 7 | 2014 | *Xyleborus germanus* | Scolytidae | -0.746 | -24.33 | 0.708 | 2.858 |
| 5 | 2014 | *Xyleborus germanus* | Scolytidae | -2.536 | -22.65 | 0.265 | 6.549 |
| 6 | 2014 | *Xyleborus germanus* | Scolytidae | 1.291 | -26.733 | 5.184 | 0.159 |
| 3 | 2014 | *Xyleborus germanus* | Scolytidae | 0.638 | -23.405 | 5.131 | 4.087 |
| 38 | 2014 | *Xyleborus germanus* | Scolytidae | 1.314 | -24.641 | 4.338 | 2.386 |
| 30 | 2014 | *Xyleborus germanus* | Scolytidae | -1.422 | -25.111 | 2.91 | 4.323 |
| 36 | 2014 | *Xyleborus germanus* | Scolytidae | 0.606 | -23.497 | 2.543 | 2.887 |
| 26 | 2014 | *Xyleborus germanus* | Scolytidae | 3.444 | -24.851 | 5.331 | 0.877 |
| 11 | 2014 | *Xyleborus germanus* | Scolytidae | 0.322 | -24.063 | 1.511 | 3.569 |
| 3 | 2014 | *Xyleborus germanus* | Scolytidae | 1.743 | -24.088 | 6.236 | 3.404 |
| 41 | 2014 | *Xyleborus germanus* | Scolytidae | -2.628 | -24.864 | -0.071 | 1.154 |
| 12 | 2014 | *Xyleborus germanus* | Scolytidae | -0.194 | -24.107 | 1.318 | 3.414 |
| 5 | 2014 | *Xyleborus germanus* | Scolytidae | -1.979 | -24.678 | 0.822 | 4.521 |
| 34 | 2014 | *Xyleborus germanus* | Scolytidae | -1.291 | -24.426 | 0.169 | 2.853 |
| 17 | 2014 | *Xyleborus germanus* | Scolytidae | -0.028 | -25.987 | -4.06 | -2.876 |
| 30 | 2014 | *Xyleborus germanus* | Scolytidae | 0.591 | -24.116 | 4.923 | 5.318 |
| 3 | 2014 | *Xyleborus germanus* | Scolytidae | -4.095 | -24.622 | 0.398 | 2.87 |
| 24 | 2014 | *Xyleborus germanus* | Scolytidae | -0.364 | -26.616 | 0.139 | -1.501 |
| 4 | 2014 | *Xyleborus germanus* | Scolytidae | -0.708 | -22.462 | 0.4 | 4.65 |
| 31 | 2014 | *Xyleborus germanus* | Scolytidae | 0.065 | -25.018 | 3.77 | 3.275 |
| 8 | 2014 | *Xyleborus germanus* | Scolytidae | 0.242 | -23.201 | 1.347 | 5.034 |
| 21 | 2014 | *Xyleborus germanus* | Scolytidae | 0.77 | -25.611 | 4.732 | 0.901 |
| 4 | 2014 | *Xyleborus germanus* | Scolytidae | -2.975 | -23.418 | -1.867 | 3.694 |

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|---|---|---|---|---|---|---|---|
| 4 | 2014 | *Xyleborus germanus* | Scolytidae | -2.589 | -22.346 | -1.481 | 4.766 |
| 27 | 2014 | *Xyleborus germanus* | Scolytidae | -0.224 | -25.012 | 0.685 | -0.094 |
| 17 | 2014 | *Xyleborus germanus* | Scolytidae | -0.222 | -23.582 | -4.254 | -0.471 |
| 17 | 2014 | *Xyleborus germanus* | Scolytidae | 1.876 | -22.773 | -2.156 | 0.338 |
| 38 | 2014 | *Xyleborus germanus* | Scolytidae | -1.803 | -23.999 | 1.221 | 3.028 |
| 26 | 2014 | *Xyleborus germanus* | Scolytidae | 1.685 | -25.571 | 3.572 | 0.157 |
| 28 | 2014 | *Xyleborus germanus* | Scolytidae | 3.059 | -26.274 | 5.876 | 0.436 |
| 35 | 2014 | *Xyleborus germanus* | Scolytidae | -0.552 | -23.714 | 1.464 | 4.09 |
| 22 | 2014 | *Xyleborus germanus* | Scolytidae | -1.522 | -18.794 | -0.128 | 7.199 |
| 25 | 2014 | *Xyleborus germanus* | Scolytidae | -3.534 | -23.368 | -1.1 | 2.778 |
| 10 | 2014 | *Xyleborus germanus* | Scolytidae | 2.43 | -23.16 | 2.482 | 3.839 |
| 33 | 2014 | *Xyleborus germanus* | Scolytidae | 0.217 | -19.939 | 2.772 | 6.73 |
| 2 | 2014 | *Xyleborus germanus* | Scolytidae | -2.822 | -20.43 | -0.921 | 6.2 |
| 24 | 2014 | *Xyleborus germanus* | Scolytidae | 2.484 | -26.3 | 2.987 | -1.185 |
| 36 | 2014 | *Xyleborus germanus* | Scolytidae | -2.087 | -21.849 | -0.15 | 4.535 |
| 32 | 2014 | *Xyleborus germanus* | Scolytidae | -3.169 | -21.782 | 0.521 | 6.036 |
| 16 | 2014 | *Xyleborus germanus* | Scolytidae | -0.53 | -24.253 | 2.738 | 3.825 |
| 16 | 2014 | *Xyleborus germanus* | Scolytidae | -1.428 | -25.487 | 1.84 | 2.591 |
| 6 | 2014 | *Xyleborus germanus* | Scolytidae | 4.781 | -23.391 | 8.674 | 3.501 |
| 41 | 2014 | *Xyleborus germanus* | Scolytidae | 0.304 | -21.762 | 2.861 | 4.256 |
| 28 | 2014 | *Xyleborus germanus* | Scolytidae | -0.332 | -34.86 | 2.485 | -8.15 |
| 23 | 2014 | *Xyleborus germanus* | Scolytidae | 1.022 | -22.643 | 0.589 | 3.232 |
| 15 | 2014 | *Xyleborus germanus* | Scolytidae | 0.393 | -23.922 | 3.264 | 3.75 |
| 7 | 2014 | *Xyleborus germanus* | Scolytidae | -2.142 | -22.57 | -0.688 | 4.618 |
| 18 | 2014 | *Xyleborus germanus* | Scolytidae | 5.027 | -24.035 | 7.541 | 1.605 |
| 28 | 2014 | *Xyleborus germanus* | Scolytidae | -0.24 | -20.825 | 2.577 | 5.885 |
| 2 | 2014 | *Xyleborus germanus* | Scolytidae | -0.942 | -16.446 | 0.959 | 10.184 |
| 42 | 2014 | *Xyleborus germanus* | Scolytidae | -0.024 | -23.921 | -2.733 | 3.448 |
| 42 | 2014 | *Xyleborus germanus* | Scolytidae | -1.567 | -22.403 | -4.276 | 4.966 |
| 19 | 2014 | *Xyleborus germanus* | Scolytidae | 1.075 | -20.007 | 2.133 | 8.236 |
| 23 | 2014 | *Xyleborus germanus* | Scolytidae | -0.722 | -24.477 | -1.155 | 1.398 |
| 11 | 2014 | *Xyleborus germanus* | Scolytidae | 4.227 | -26.74 | 5.416 | 0.892 |
| 20 | 2014 | *Xyleborus germanus* | Scolytidae | 1.196 | -18.045 | 4.11 | 7.942 |
| 14 | 2014 | *Xyleborus germanus* | Scolytidae | 0.147 | -20.814 | 2.831 | 4.947 |
| 40 | 2015 | *Xyleborus germanus* | Scolytidae | 0.185 | -26.378 | 1.736 | -0.353 |
| 7 | 2015 | *Xyleborus germanus* | Scolytidae | -5.121 | -23.33 | -3.312 | 2.63 |
| 37 | 2015 | *Xyleborus germanus* | Scolytidae | -0.994 | -23.946 | 0.482 | 2.243 |
| 7 | 2015 | *Xyleborus germanus* | Scolytidae | 0.04 | -24.805 | 1.849 | 1.155 |
| 24 | 2015 | *Xyleborus germanus* | Scolytidae | 2.977 | -26.534 | 3.48 | -1.419 |
| 37 | 2015 | *Xyleborus germanus* | Scolytidae | 1.693 | -23.863 | 3.169 | 2.326 |
| 21 | 2015 | *Xyleborus germanus* | Scolytidae | -0.632 | -26.117 | 1.306 | -0.652 |
| 29 | 2015 | *Xyleborus germanus* | Scolytidae | -2.031 | -25.719 | -0.543 | 1.139 |
| 28 | 2015 | *Xyleborus germanus* | Scolytidae | -0.574 | -23.583 | 1.41 | 1.456 |
| 7 | 2015 | *Xyleborus germanus* | Scolytidae | -3.362 | -24.468 | -1.553 | 1.492 |
| 24 | 2015 | *Xyleborus germanus* | Scolytidae | 2.639 | -26.303 | 3.142 | -1.188 |
| 21 | 2015 | *Xyleborus germanus* | Scolytidae | 1.354 | -25.613 | 3.292 | -0.148 |
| 3 | 2015 | *Xyleborus germanus* | Scolytidae | -3.137 | -23.07 | -5.746 | 3.983 |

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| 4 | 2015 | *Xyleborus germanus* | Scolytidae | 0.06 | -24.811 | 1.162 | 1.195 |
| 37 | 2015 | *Xyleborus germanus* | Scolytidae | -0.084 | -24.307 | 1.392 | 1.882 |
| 11 | 2015 | *Xyleborus germanus* | Scolytidae | 0.066 | -25.97 | 0.948 | 0.09 |
| 3 | 2015 | *Xyleborus germanus* | Scolytidae | -1.183 | -24.575 | -3.792 | 2.478 |
| 38 | 2015 | *Xyleborus germanus* | Scolytidae | -0.134 | -22.586 | 2.618 | 4.173 |
| 8 | 2015 | *Xyleborus germanus* | Scolytidae | -2.692 | -23.568 | -0.878 | 2.131 |
| 41 | 2015 | *Xyleborus germanus* | Scolytidae | 1.596 | -24.137 | 3.254 | 0.061 |
| 22 | 2015 | *Xyleborus germanus* | Scolytidae | -0.168 | -25.696 | -0.469 | -1.057 |
| 8 | 2015 | *Xyleborus germanus* | Scolytidae | -1.704 | -22.816 | 0.11 | 2.883 |
| 40 | 2015 | *Xyleborus germanus* | Scolytidae | -1.457 | -24.523 | 0.094 | 1.502 |
| 22 | 2015 | *Xyleborus germanus* | Scolytidae | -0.119 | -25.592 | -0.42 | -0.953 |
| 8 | 2015 | *Xyleborus germanus* | Scolytidae | 2.487 | -22.328 | 4.301 | 3.371 |
| 4 | 2015 | *Xyleborus germanus* | Scolytidae | 0.185 | -22.077 | 1.287 | 3.929 |
| 20 | 2015 | *Xyleborus germanus* | Scolytidae | -1.699 | -23.274 | 1.352 | 1.299 |
| 26 | 2015 | *Xyleborus germanus* | Scolytidae | -3.15 | -24.747 | 0.094 | -0.221 |
| 4 | 2015 | *Xyleborus germanus* | Scolytidae | 0.772 | -21.932 | 1.874 | 4.074 |
| 20 | 2015 | *Xyleborus germanus* | Scolytidae | -1.855 | -25.112 | 1.196 | -0.539 |
| 23 | 2015 | *Xyleborus germanus* | Scolytidae | 0.23 | -25.721 | -0.639 | -0.92 |
| 18 | 2015 | *Xyleborus germanus* | Scolytidae | 4.038 | -24.375 | 6.768 | -0.271 |
| 21 | 2015 | *Xyleborus germanus* | Scolytidae | 0.855 | -26.234 | 2.793 | -0.769 |
| 41 | 2015 | *Xyleborus germanus* | Scolytidae | 1.355 | -25.979 | 3.013 | -1.781 |
| 26 | 2015 | *Xyleborus germanus* | Scolytidae | -1.245 | -25.642 | 1.999 | -1.116 |
| 24 | 2015 | *Xyleborus germanus* | Scolytidae | -1.727 | -23.28 | -1.224 | 1.835 |
| 20 | 2015 | *Xyleborus germanus* | Scolytidae | 0.778 | -23.372 | 3.829 | 1.201 |
| 38 | 2015 | *Xyleborus germanus* | Scolytidae | -0.253 | -23.153 | 2.499 | 3.606 |
| 26 | 2015 | *Xyleborus germanus* | Scolytidae | 0.645 | -25.461 | 3.889 | -0.935 |
| 38 | 2015 | *Xyleborus germanus* | Scolytidae | 1.442 | -25.701 | 4.194 | 1.058 |
| 40 | 2015 | *Xyleborus germanus* | Scolytidae | 0.459 | -25.462 | 2.01 | 0.563 |
| 11 | 2015 | *Xyleborus germanus* | Scolytidae | 2.05 | -26.15 | 2.932 | -0.09 |
| 41 | 2015 | *Xyleborus germanus* | Scolytidae | -2.859 | -26.091 | -1.201 | -1.893 |
| 3 | 2015 | *Xyleborus germanus* | Scolytidae | -1.636 | -24.187 | -4.245 | 2.866 |
| 18 | 2015 | *Xyleborus germanus* | Scolytidae | 1.944 | -25.686 | 4.674 | -1.582 |
| 12 | 2015 | *Xyleborus germanus* | Scolytidae | 3.162 | -25.355 | 4.034 | 1.349 |
| 14 | 2015 | *Xyleborus germanus* | Scolytidae | 0.915 | -24.778 | 3.851 | -0.595 |
| 19 | 2015 | *Xyleborus germanus* | Scolytidae | -0.229 | -24.563 | 0.024 | 1.517 |
| 22 | 2015 | *Xyleborus germanus* | Scolytidae | -1.919 | -25.197 | -2.22 | -0.558 |
| 23 | 2015 | *Xyleborus germanus* | Scolytidae | -1.322 | -22.911 | -2.191 | 1.89 |
| 28 | 2015 | *Xyleborus germanus* | Scolytidae | 0.253 | -25.383 | 2.237 | -0.344 |
| 29 | 2015 | *Xyleborus germanus* | Scolytidae | -2.393 | -24.533 | -0.905 | 2.325 |
| 19 | 2015 | *Xyleborus germanus* | Scolytidae | -1.183 | -26.381 | -0.93 | -0.301 |
| 28 | 2015 | *Xyleborus germanus* | Scolytidae | -0.954 | -23.582 | 1.03 | 1.457 |
| 23 | 2015 | *Xyleborus germanus* | Scolytidae | 0.061 | -26.069 | -0.808 | -1.268 |
| 31 | 2015 | *Xyleborus germanus* | Scolytidae | -2.063 | -25.158 | 3.112 | 2.825 |
| 11 | 2015 | *Xyleborus germanus* | Scolytidae | 1.922 | -27.002 | 2.804 | -0.942 |
| 18 | 2015 | *Xyleborus germanus* | Scolytidae | 0.654 | -25.304 | 3.384 | -1.2 |
| 14 | 2015 | *Xyleborus germanus* | Scolytidae | 1.203 | -24.668 | 4.139 | -0.485 |
| 14 | 2015 | *Xyleborus germanus* | Scolytidae | -1.233 | -24.331 | 1.703 | -0.148 |

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|---|---|---|---|---|---|---|---|
| 24 | 2015 | *Xyleborus monographus* | Scolytidae | -3.34 | -21.269 | -2.837 | 3.846 |
| 40 | 2015 | *Xyleborus monographus* | Scolytidae | -1.211 | -22.685 | 0.34 | 3.34 |
| 29 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.067 | -22.922 | 1.234 | 5.258 |
| 29 | 2014 | *Xyleborus saxeseni* | Scolytidae | 0.204 | -21.857 | 1.505 | 6.323 |
| 25 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.958 | -23.164 | 1.476 | 2.982 |
| 22 | 2014 | *Xyleborus saxeseni* | Scolytidae | 1.842 | -23.64 | 3.236 | 2.353 |
| 13 | 2014 | *Xyleborus saxeseni* | Scolytidae | 0.253 | -22.421 | -5.552 | 6.534 |
| 14 | 2014 | *Xyleborus saxeseni* | Scolytidae | 0.067 | -23.554 | 2.751 | 2.207 |
| 5 | 2014 | *Xyleborus saxeseni* | Scolytidae | 0.397 | -22.339 | 3.198 | 6.86 |
| 6 | 2014 | *Xyleborus saxeseni* | Scolytidae | 4.885 | -23.558 | 8.778 | 3.334 |
| 14 | 2014 | *Xyleborus saxeseni* | Scolytidae | 0.937 | -23.845 | 3.621 | 1.916 |
| 5 | 2014 | *Xyleborus saxeseni* | Scolytidae | -1.062 | -23.461 | 1.739 | 5.738 |
| 13 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.061 | -22.696 | -5.866 | 6.259 |
| 10 | 2014 | *Xyleborus saxeseni* | Scolytidae | -3.421 | -23.391 | -3.369 | 3.608 |
| 15 | 2014 | *Xyleborus saxeseni* | Scolytidae | -1.021 | -22.293 | 1.85 | 5.379 |
| 38 | 2014 | *Xyleborus saxeseni* | Scolytidae | 0.136 | -21.765 | 3.16 | 5.262 |
| 21 | 2014 | *Xyleborus saxeseni* | Scolytidae | -1.762 | -21.875 | 2.2 | 4.637 |
| 4 | 2014 | *Xyleborus saxeseni* | Scolytidae | -3.423 | -22.86 | -2.315 | 4.252 |
| 3 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.525 | -16.265 | 3.968 | 11.227 |
| 3 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.11 | -17.444 | 4.383 | 10.048 |
| 3 | 2014 | *Xyleborus saxeseni* | Scolytidae | 1.786 | -18.789 | 6.279 | 8.703 |
| 4 | 2014 | *Xyleborus saxeseni* | Scolytidae | -1.289 | -21.55 | -0.181 | 5.562 |
| 16 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.338 | -22.209 | 2.93 | 5.869 |
| 6 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.167 | -20.032 | 3.726 | 6.86 |
| 20 | 2014 | *Xyleborus saxeseni* | Scolytidae | -4.292 | -19.358 | -1.378 | 6.629 |
| 3 | 2014 | *Xyleborus saxeseni* | Scolytidae | -1.591 | -19.233 | 2.902 | 8.259 |
| 25 | 2014 | *Xyleborus saxeseni* | Scolytidae | -0.43 | -21.05 | 2.004 | 5.096 |
| 7 | 2015 | *Xyleborus saxeseni* | Scolytidae | 2.509 | -23.26 | 4.318 | 2.7 |
| 37 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.711 | -24.062 | -1.235 | 2.127 |
| 18 | 2015 | *Xyleborus saxeseni* | Scolytidae | 2.012 | -22.942 | 4.742 | 1.162 |
| 24 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.748 | -23.325 | -2.245 | 1.79 |
| 7 | 2015 | *Xyleborus saxeseni* | Scolytidae | -1.662 | -23.756 | 0.147 | 2.204 |
| 20 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.322 | -22.167 | 0.729 | 2.406 |
| 18 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.043 | -22.801 | 0.687 | 1.303 |
| 20 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.706 | -22.293 | 2.345 | 2.28 |
| 7 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.489 | -21.988 | -0.68 | 3.972 |
| 28 | 2015 | *Xyleborus saxeseni* | Scolytidae | 0.711 | -22.87 | 2.695 | 2.169 |
| 24 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.232 | -24.964 | -1.729 | 0.151 |
| 4 | 2015 | *Xyleborus saxeseni* | Scolytidae | -1.033 | -23.558 | 0.069 | 2.448 |
| 31 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.142 | -22.654 | 3.033 | 5.329 |
| 19 | 2015 | *Xyleborus saxeseni* | Scolytidae | 1.856 | -24.354 | 2.109 | 1.726 |
| 29 | 2015 | *Xyleborus saxeseni* | Scolytidae | 2.613 | -25.03 | 4.101 | 1.828 |
| 11 | 2015 | *Xyleborus saxeseni* | Scolytidae | 0.261 | -23.64 | 1.143 | 2.42 |
| 38 | 2015 | *Xyleborus saxeseni* | Scolytidae | -4.261 | -24.573 | -1.509 | 2.186 |
| 21 | 2015 | *Xyleborus saxeseni* | Scolytidae | 2.302 | -23.918 | 4.24 | 1.547 |
| 23 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.697 | -23.124 | -1.566 | 1.677 |
| 8 | 2015 | *Xyleborus saxeseni* | Scolytidae | 6.769 | -23.376 | 8.583 | 2.323 |

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|---|---|---|---|---|---|---|---|
| 22 | 2015 | *Xyleborus saxeseni* | Scolytidae | 2.269 | -24.52 | 1.968 | 0.119 |
| 26 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.932 | -23.959 | 2.312 | 0.567 |
| 3 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.481 | -22.133 | -3.09 | 4.92 |
| 4 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.117 | -20.954 | 0.985 | 5.052 |
| 20 | 2015 | *Xyleborus saxeseni* | Scolytidae | -3.249 | -23.976 | -0.198 | 0.597 |
| 22 | 2015 | *Xyleborus saxeseni* | Scolytidae | -1.34 | -22.762 | -1.641 | 1.877 |
| 4 | 2015 | *Xyleborus saxeseni* | Scolytidae | -1.814 | -18.557 | -0.712 | 7.449 |
| 41 | 2015 | *Xyleborus saxeseni* | Scolytidae | -3.414 | -21.366 | -1.756 | 2.832 |
| 38 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.673 | -23.199 | 2.079 | 3.56 |
| 11 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.019 | -22.619 | 0.863 | 3.441 |
| 3 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.071 | -24.01 | -4.68 | 3.043 |
| 14 | 2015 | *Xyleborus saxeseni* | Scolytidae | -1.052 | -22.233 | 1.884 | 1.95 |
| 3 | 2015 | *Xyleborus saxeseni* | Scolytidae | -2.208 | -23.059 | -4.817 | 3.994 |
| 4 | 2014 | *Xyleborus saxeseni* | Scolytidae | -2.524 | -22.167 | -1.416 | 4.945 |
| 11 | 2015 | *Xyleborus saxeseni* | Scolytidae | -0.437 | -22.128 | 0.445 | 3.932 |
| 5 | 2014 | *Xyloterus signatus* | Scolytidae | -2.855 | -22.036 | -0.054 | 7.163 |
| 20 | 2015 | *Xyloterus signatus* | Scolytidae | -3.351 | -25.345 | -0.3 | -0.772 |
| 11 | 2015 | *Xyloterus signatus* | Scolytidae | 1.458 | -25.19 | 2.34 | 0.87 |

Table A3: Body length. pronotum width. feeding guild and estimated dry weight after Rogers et al. (1976) for all individuals per species.

| Species | Tree hollow | Year | Bodylength [mm] | Width Pronotum [mm] | Estimated dry weight after Rogers (1976) |
|---|---|---|---|---|---|
| *Abraeus perpusillus* | 22 | 2015 | 1.374 | 0.850 | 0.070117283 |
| *Abraeus perpusillus* | 22 | 2015 | 1.33 | 0.989 | 0.064385955 |
| *Abraeus perpusillus* | 23 | 2015 | 1.485 | 1.023 | 0.085945501 |
| *Abraeus perpusillus* | 26 | 2015 | 1.264 | 0.860 | 0.056347827 |
| *Abraeus perpusillus* | 28 | 2015 | 1.318 | 0.887 | 0.062875031 |
| *Abraeus perpusillus* | 28 | 2015 | 1.399 | 0.973 | 0.073509294 |
| *Abraeus perpusillus* | 28 | 2015 | 1.405 | 0.980 | 0.07433816 |
| *Abraeus perpusillus* | 28 | 2015 | 1.567 | 1.067 | 0.098941983 |
| *Acalles hypocrita* | 4 | 2015 | 4.732 | 2.214 | 1.790263872 |
| *Acalles hypocrita* | 7 | 2015 | 5.509 | 2.325 | 2.666309149 |
| *Aderus populneus* | 4 | 2015 | 1.794 | 0.437 | 0.141031014 |
| *Allecula morio* | 7 | 2014 | 6.897 | 1.776 | 4.803852138 |
| *Allecula morio* | 7 | 2014 | 8.538 | 2.078 | 8.403359699 |
| *Allecula morio* | 7 | 2014 | 7.005 | 1.811 | 5.003445403 |
| *Allecula morio* | 7 | 2014 | 8.447 | 1.852 | 8.170720867 |
| *Allecula morio* | 7 | 2015 | 7.924 | 2.036 | 6.910895763 |
| *Allecula morio* | 7 | 2015 | 7.645 | 1.941 | 6.291422664 |
| *Allecula morio* | 7 | 2015 | 6.321 | 1.593 | 3.822597839 |
| *Allecula morio* | 28 | 2014 | 8.546 | 2.018 | 8.42400483 |
| *Allecula morio* | 28 | 2014 | 7.331 | 1.902 | 5.636733139 |
| *Allecula morio* | 28 | 2014 | 7.241 | 1.662 | 5.457227183 |
| *Allecula morio* | 28 | 2014 | 6.656 | 1.496 | 4.37641724 |
| *Allecula morio* | 28 | 2015 | 7.694 | 1.946 | 6.3976217 |
| *Allecula morio* | 28 | 2015 | 7.346 | 2.168 | 5.667000621 |
| *Allecula morio* | 28 | 2015 | 7.894 | 1.911 | 6.842555035 |
| *Allecula morio* | 37 | 2014 | 6.549 | 1.689 | 4.1944818 |
| *Allecula morio* | 37 | 2014 | 6.977 | 1.680 | 4.951216233 |
| *Allecula morio* | 37 | 2014 | 6.364 | 1.479 | 3.891104436 |
| *Allecula morio* | 37 | 2015 | 6.592 | 1.648 | 4.267022176 |
| *Allecula morio* | 37 | 2015 | 6.983 | 1.807 | 4.962379676 |
| *Allecula morio* | 37 | 2015 | 7.319 | 1.922 | 5.612591276 |
| *Alosterna tabacicolor* | 7 | 2014 | 6.329 | 1.185 | 3.835286308 |
| *Alosterna tabacicolor* | 7 | 2015 | 6.467 | 1.417 | 4.058273714 |
| *Alosterna tabacicolor* | 7 | 2015 | 6.498 | 1.387 | 4.109440263 |
| *Alosterna tabacicolor* | 7 | 2015 | 6.201 | 1.231 | 3.635378007 |
| *Alosterna tabacicolor* | 8 | 2015 | 6.155 | 1.350 | 3.565146243 |
| *Alosterna tabacicolor* | 28 | 2014 | 6.217 | 1.958 | 3.660005279 |
| *Alosterna tabacicolor* | 28 | 2014 | 7.817 | 1.458 | 6.66906473 |
| *Alosterna tabacicolor* | 28 | 2014 | 5.944 | 1.080 | 3.253765855 |
| *Alosterna tabacicolor* | 28 | 2014 | 5.884 | 1.283 | 3.168416156 |
| *Alosterna tabacicolor* | 28 | 2015 | 5.809 | 1.191 | 3.063694421 |
| *Alosterna tabacicolor* | 28 | 2015 | 6.412 | 1.402 | 3.968467657 |
| *Alosterna tabacicolor* | 28 | 2015 | 7.915 | 1.635 | 6.890349443 |

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|---|---|---|---|---|---|
| *Ampedus nigroflavus* | 2 | 2014 | 9.178 | 2.585 | 10.15546326 |
| *Ampedus pomorum* | 7 | 2015 | 10.891 | 3.452 | 15.90074107 |
| *Ampedus pomorum* | 7 | 2015 | 9.822 | 2.983 | 12.13007973 |
| *Ampedus pomorum* | 28 | 2015 | 10.178 | 2.843 | 13.31605098 |
| *Anaspis frontalis* | 7 | 2014 | 3.352 | 1.056 | 0.725431393 |
| *Anaspis frontalis* | 19 | 2014 | 3.622 | 1.090 | 0.888678693 |
| *Anaspis frontalis* | 22 | 2014 | 3.427 | 1.041 | 0.768731705 |
| *Anaspis marginicollis* | 21 | 2015 | 3.268 | 1.035 | 0.678764007 |
| *Anaspis marginicollis* | 21 | 2015 | 3.191 | 0.891 | 0.637658372 |
| *Anaspis marginicollis* | 25 | 2015 | 3.798 | 1.156 | 1.006314744 |
| *Anaspis marginicollis* | 40 | 2015 | 2.954 | 0.920 | 0.52092515 |
| *Anaspis marginicollis* | 41 | 2015 | 3.489 | 1.056 | 0.805705595 |
| *Anaspis ruficollis* | 3 | 2014 | 3.24 | 1.051 | 0.663632683 |
| *Anaspis ruficollis* | 7 | 2014 | 3.184 | 0.994 | 0.633999994 |
| *Anaspis ruficollis* | 7 | 2014 | 2.823 | 1.042 | 0.462553893 |
| *Anaspis ruficollis* | 7 | 2014 | 3.376 | 0.968 | 0.739118762 |
| *Anaspis ruficollis* | 7 | 2014 | 3.187 | 1.052 | 0.635566277 |
| *Anaspis ruficollis* | 7 | 2014 | 3.416 | 1.092 | 0.762283708 |
| *Anaspis ruficollis* | 7 | 2014 | 3.24 | 1.072 | 0.663632683 |
| *Anaspis ruficollis* | 7 | 2014 | 3.2 | 1.004 | 0.642381141 |
| *Anaspis ruficollis* | 7 | 2014 | 3.346 | 0.969 | 0.722034241 |
| *Anaspis ruficollis* | 7 | 2014 | 2.658 | 0.834 | 0.395033456 |
| *Anaspis ruficollis* | 7 | 2014 | 3.277 | 1.024 | 0.683672507 |
| *Anaspis ruficollis* | 7 | 2015 | 3.029 | 1.034 | 0.556293436 |
| *Anaspis ruficollis* | 8 | 2014 | 3.056 | 0.856 | 0.569379224 |
| *Anaspis ruficollis* | 8 | 2014 | 3.561 | 0.927 | 0.849998991 |
| *Anaspis ruficollis* | 8 | 2014 | 3.165 | 0.903 | 0.624135623 |
| *Anaspis ruficollis* | 8 | 2014 | 2.711 | 0.804 | 0.416005599 |
| *Anaspis ruficollis* | 8 | 2014 | 3.27 | 1.055 | 0.679852895 |
| *Anaspis ruficollis* | 21 | 2014 | 3.392 | 1.112 | 0.748331712 |
| *Anaspis ruficollis* | 21 | 2014 | 3.233 | 0.994 | 0.659882765 |
| *Anaspis ruficollis* | 21 | 2014 | 3.401 | 1.118 | 0.753545039 |
| *Anaspis ruficollis* | 21 | 2014 | 3.42 | 0.979 | 0.764624549 |
| *Anaspis ruficollis* | 21 | 2014 | 3.971 | 1.162 | 1.130882656 |
| *Anaspis ruficollis* | 21 | 2014 | 3.232 | 0.996 | 0.659348135 |
| *Anaspis ruficollis* | 21 | 2014 | 3.403 | 0.994 | 0.754706597 |
| *Anaspis ruficollis* | 21 | 2014 | 3.794 | 1.097 | 1.00354034 |
| *Anaspis ruficollis* | 21 | 2014 | 3.055 | 0.954 | 0.568891207 |
| *Anaspis ruficollis* | 21 | 2014 | 3.129 | 0.909 | 0.605706752 |
| *Anaspis ruficollis* | 21 | 2014 | 3.643 | 0.856 | 0.902241643 |
| *Anaspis ruficollis* | 21 | 2014 | 3.668 | 0.931 | 0.918553965 |
| *Anaspis ruficollis* | 21 | 2014 | 3.117 | 0.958 | 0.599639539 |
| *Anaspis ruficollis* | 21 | 2014 | 3.01 | 0.931 | 0.547197441 |
| *Anaspis ruficollis* | 21 | 2014 | 3.075 | 1.030 | 0.578700762 |
| *Anaspis ruficollis* | 21 | 2014 | 3.326 | 1.003 | 0.710781509 |
| *Anaspis ruficollis* | 21 | 2014 | 3.047 | 0.971 | 0.564996385 |
| *Anaspis ruficollis* | 21 | 2014 | 3.245 | 1.038 | 0.666319244 |

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|---|---|---|---|---|---|
| *Anaspis ruficollis* | 21 | 2014 | 3.283 | 1.015 | 0.686956998 |
| *Anaspis ruficollis* | 21 | 2014 | 3.193 | 1.069 | 0.638706015 |
| *Anaspis ruficollis* | 21 | 2014 | 3.223 | 0.991 | 0.654548512 |
| *Anaspis ruficollis* | 22 | 2014 | 3.469 | 1.155 | 0.793661119 |
| *Anaspis ruficollis* | 22 | 2014 | 2.95 | 0.914 | 0.519079074 |
| *Anaspis ruficollis* | 22 | 2014 | 1.023 | 0.590 | 0.032372333 |
| *Anaspis ruficollis* | 22 | 2014 | 2.909 | 0.715 | 0.500389732 |
| *Anaspis ruficollis* | 22 | 2014 | 3.128 | 0.954 | 0.605199708 |
| *Anaspis ruficollis* | 22 | 2014 | 2.861 | 0.950 | 0.479045348 |
| *Anaspis ruficollis* | 22 | 2014 | 2.825 | 0.861 | 0.463412969 |
| *Anaspis ruficollis* | 22 | 2014 | 2.963 | 0.962 | 0.52509365 |
| *Anaspis ruficollis* | 25 | 2014 | 3.48 | 1.030 | 0.800271699 |
| *Anaspis ruficollis* | 25 | 2014 | 2.807 | 0.878 | 0.455716717 |
| *Anaspis ruficollis* | 25 | 2014 | 2.734 | 0.782 | 0.425316211 |
| *Anaspis ruficollis* | 25 | 2014 | 3.069 | 0.969 | 0.575747004 |
| *Anaspis ruficollis* | 25 | 2014 | 2.878 | 0.810 | 0.486539056 |
| *Anaspis ruficollis* | 25 | 2014 | 2.977 | 0.950 | 0.531618868 |
| *Anaspis ruficollis* | 25 | 2014 | 3.092 | 1.026 | 0.587120562 |
| *Anaspis ruficollis* | 25 | 2014 | 2.679 | 0.832 | 0.403262974 |
| *Anaspis ruficollis* | 25 | 2014 | 3.386 | 1.067 | 0.744868585 |
| *Anaspis ruficollis* | 25 | 2014 | 2.812 | 0.885 | 0.457846573 |
| *Anaspis ruficollis* | 25 | 2014 | 3.238 | 1.010 | 0.662559937 |
| *Anaspis ruficollis* | 25 | 2014 | 2.581 | 0.831 | 0.365750064 |
| *Anaspis ruficollis* | 26 | 2014 | 3.236 | 0.996 | 0.661488264 |
| *Anaspis ruficollis* | 26 | 2014 | 3.69 | 0.924 | 0.933058597 |
| *Anaspis ruficollis* | 27 | 2014 | 3.211 | 0.960 | 0.648182707 |
| *Anaspis ruficollis* | 28 | 2014 | 3.094 | 0.941 | 0.588116075 |
| *Anaspis ruficollis* | 28 | 2014 | 3.165 | 1.015 | 0.624135623 |
| *Anaspis ruficollis* | 28 | 2014 | 3.704 | 0.963 | 0.942362079 |
| *Anaspis ruficollis* | 37 | 2014 | 2.904 | 0.816 | 0.49813948 |
| *Anaspis ruficollis* | 37 | 2014 | 2.893 | 0.971 | 0.493210979 |
| *Anaspis ruficollis* | 37 | 2014 | 2.745 | 0.811 | 0.429814233 |
| *Anaspis ruficollis* | 37 | 2014 | 3.35 | 0.993 | 0.724297913 |
| *Anaspis ruficollis* | 38 | 2014 | 3.334 | 1.041 | 0.715269488 |
| *Anaspis ruficollis* | 40 | 2014 | 3.421 | 0.993 | 0.765210453 |
| *Anaspis ruficollis* | 40 | 2014 | 2.812 | 0.867 | 0.457846573 |
| *Anaspis ruficollis* | 40 | 2014 | 3.293 | 1.015 | 0.692452797 |
| *Anaspis ruficollis* | 41 | 2014 | 2.754 | 0.888 | 0.43351622 |
| *Anaspis ruficollis* | 41 | 2014 | 3.471 | 0.950 | 0.794860521 |
| *Anaspis ruficollis* | 41 | 2014 | 3.119 | 0.874 | 0.600648119 |
| *Anaspis ruficollis* | 41 | 2014 | 3.347 | 0.994 | 0.722599748 |
| *Anaspis rufilabris* | 2 | 2015 | 3.178 | 1.081 | 0.630874595 |
| *Anaspis rufilabris* | 4 | 2015 | 3.573 | 1.049 | 0.857524115 |
| *Anaspis rufilabris* | 7 | 2015 | 3.742 | 1.188 | 0.967902811 |
| *Anaspis rufilabris* | 31 | 2015 | 3.173 | 0.993 | 0.628277386 |
| *Anaspis rufilabris* | 32 | 2014 | 3.287 | 1.114 | 0.689152069 |
| *Anaspis thoracica* | 2 | 2015 | 3.23 | 1.032 | 0.658279678 |

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|---|---|---|---|---|---|
| *Anaspis thoracica* | 4 | 2015 | 3.732 | 1.126 | 0.961140601 |
| *Anaspis thoracica* | 4 | 2015 | 3.127 | 1.016 | 0.604692926 |
| *Anaspis thoracica* | 4 | 2015 | 3.099 | 0.908 | 0.590609419 |
| *Anaspis thoracica* | 7 | 2015 | 3.003 | 0.988 | 0.543869632 |
| *Anaspis thoracica* | 7 | 2015 | 3.005 | 0.939 | 0.544819154 |
| *Anaspis thoracica* | 21 | 2014 | 3.164 | 0.961 | 0.623619093 |
| *Anaspis thoracica* | 28 | 2015 | 3.479 | 1.140 | 0.799669335 |
| *Anaspis thoracica* | 37 | 2015 | 3.243 | 1.001 | 0.665243814 |
| *Anaspis thoracica* | 40 | 2015 | 3.202 | 0.975 | 0.643433573 |
| *Anaspis thoracica* | 40 | 2015 | 2.864 | 0.721 | 0.480362543 |
| *Anisotoma humeralis* | 7 | 2014 | 3.514 | 2.069 | 0.820919256 |
| *Anobium costatum* | 4 | 2015 | 3.587 | 1.098 | 0.866355319 |
| *Anobium nitidum* | 4 | 2014 | 2.56 | 0.800 | 0.358004552 |
| *Anobium nitidum* | 4 | 2014 | 2.892 | 0.782 | 0.492764435 |
| *Anobium nitidum* | 4 | 2015 | 2.464 | 0.760 | 0.323890703 |
| *Anobium nitidum* | 4 | 2015 | 2.899 | 0.918 | 0.495895496 |
| *Anobium nitidum* | 4 | 2015 | 2.59 | 0.810 | 0.369101 |
| *Anobium nitidum* | 4 | 2015 | 2.486 | 0.756 | 0.331522329 |
| *Anobium nitidum* | 4 | 2015 | 3.047 | 0.949 | 0.564996385 |
| *Anobium nitidum* | 4 | 2015 | 2.808 | 0.871 | 0.456142197 |
| *Arpidiphorus orbiculatus* | 7 | 2015 | 1.133 | 0.612 | 0.042304075 |
| *Arpidiphorus orbiculatus* | 7 | 2015 | 1.492 | 0.700 | 0.087010999 |
| *Arpidiphorus orbiculatus* | 21 | 2015 | 1.452 | 0.766 | 0.081031219 |
| *Arpidiphorus orbiculatus* | 21 | 2015 | 1.333 | 0.744 | 0.064767157 |
| *Arpidiphorus orbiculatus* | 25 | 2015 | 1.315 | 0.631 | 0.062500762 |
| *Arpidiphorus orbiculatus* | 25 | 2015 | 1.419 | 0.749 | 0.076294585 |
| *Arpidiphorus orbiculatus* | 25 | 2015 | 1.362 | 0.675 | 0.068524182 |
| *Arpidiphorus orbiculatus* | 25 | 2015 | 1.223 | 0.687 | 0.051684124 |
| *Arpidiphorus orbiculatus* | 28 | 2015 | 1.205 | 0.736 | 0.049714824 |
| *Arpidiphorus orbiculatus* | 40 | 2015 | 1.175 | 0.648 | 0.046537071 |
| *Calambus bipustulatus* | 4 | 2015 | 7.485 | 2.180 | 5.9522665 |
| *Cerophytum elateroides* | 26 | 2014 | 7.449 | 2.230 | 5.877552701 |
| *Choragus sheppardi* | 31 | 2015 | 1.533 | 0.651 | 0.093415789 |
| *Cis bidentatus* | 25 | 2015 | 2.322 | 0.942 | 0.277241885 |
| *Crepidophorus mutilatus* | 26 | 2015 | 11.639 | 3.079 | 18.92338782 |
| *Crepidophorus mutilatus* | 28 | 2014 | 11.996 | 3.247 | 20.48214125 |
| *Crepidophorus mutilatus* | 28 | 2015 | 12.448 | 3.343 | 22.56631978 |
| *Crepidophorus mutilatus* | 28 | 2015 | 12.941 | 3.564 | 24.98363192 |
| *Crepidophorus mutilatus* | 28 | 2015 | 10.925 | 2.797 | 16.03112598 |
| *Crepidophorus mutilatus* | 41 | 2014 | 11.306 | 3.014 | 17.53756808 |
| *Cryptophagus labilis* | 2 | 2014 | 1.826 | 0.654 | 0.147717471 |
| *Cryptophagus labilis* | 4 | 2014 | 1.728 | 0.646 | 0.127839315 |
| *Cryptophagus labilis* | 7 | 2015 | 1.696 | 0.641 | 0.121729422 |
| *Cryptophagus labilis* | 22 | 2015 | 1.939 | 0.860 | 0.172883561 |
| *Cryptophagus labilis* | 22 | 2015 | 1.877 | 0.763 | 0.158772847 |
| *Cryptophagus labilis* | 23 | 2015 | 2.018 | 0.758 | 0.191952284 |
| *Cryptophagus labilis* | 28 | 2015 | 2.048 | 0.706 | 0.199519025 |

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|---|---|---|---|---|---|
| *Cyclorhipidion bodoanus* | 3 | 2014 | 2.157 | 0.728 | 0.228553154 |
| *Cyclorhipidion bodoanus* | 3 | 2015 | 2.346 | 0.783 | 0.284812614 |
| *Cyclorhipidion bodoanus* | 3 | 2015 | 2.103 | 0.692 | 0.213864516 |
| *Cyclorhipidion bodoanus* | 4 | 2014 | 2.324 | 0.773 | 0.277867967 |
| *Cyclorhipidion bodoanus* | 4 | 2014 | 1.928 | 0.659 | 0.170325729 |
| *Cyclorhipidion bodoanus* | 4 | 2014 | 2.182 | 0.748 | 0.235558768 |
| *Cyclorhipidion bodoanus* | 4 | 2015 | 2.193 | 0.725 | 0.238682762 |
| *Cyclorhipidion bodoanus* | 4 | 2015 | 2.122 | 0.710 | 0.218964008 |
| *Cyclorhipidion bodoanus* | 4 | 2015 | 2.008 | 0.707 | 0.189470131 |
| *Cyclorhipidion bodoanus* | 6 | 2014 | 2.172 | 0.732 | 0.232740825 |
| *Cyclorhipidion bodoanus* | 6 | 2014 | 2.205 | 0.715 | 0.242119827 |
| *Cyclorhipidion bodoanus* | 7 | 2015 | 1.926 | 0.700 | 0.1698632 |
| *Cyclorhipidion bodoanus* | 11 | 2014 | 2.122 | 0.724 | 0.218964008 |
| *Cyclorhipidion bodoanus* | 11 | 2015 | 2.069 | 0.716 | 0.204923764 |
| *Cyclorhipidion bodoanus* | 11 | 2015 | 2.215 | 0.738 | 0.245007294 |
| *Cyclorhipidion bodoanus* | 14 | 2015 | 2.125 | 0.746 | 0.219775991 |
| *Cyclorhipidion bodoanus* | 18 | 2015 | 2.244 | 0.756 | 0.253501021 |
| *Cyclorhipidion bodoanus* | 18 | 2015 | 2.025 | 0.697 | 0.193701691 |
| *Cyclorhipidion bodoanus* | 18 | 2015 | 2.202 | 0.738 | 0.241257711 |
| *Cyclorhipidion bodoanus* | 18 | 2015 | 2.15 | 0.729 | 0.226614975 |
| *Cyclorhipidion bodoanus* | 20 | 2015 | 2.272 | 0.755 | 0.261872356 |
| *Cyclorhipidion bodoanus* | 20 | 2015 | 2.076 | 0.744 | 0.206745228 |
| *Cyclorhipidion bodoanus* | 20 | 2015 | 2.238 | 0.760 | 0.251729002 |
| *Cyclorhipidion bodoanus* | 20 | 2015 | 2.106 | 0.752 | 0.214664763 |
| *Cyclorhipidion bodoanus* | 21 | 2015 | 2.356 | 0.825 | 0.288004378 |
| *Cyclorhipidion bodoanus* | 21 | 2015 | 2.039 | 0.732 | 0.197229998 |
| *Cyclorhipidion bodoanus* | 22 | 2014 | 2.216 | 0.713 | 0.245297205 |
| *Cyclorhipidion bodoanus* | 23 | 2015 | 2.32 | 0.759 | 0.276616677 |
| *Cyclorhipidion bodoanus* | 24 | 2014 | 2.228 | 0.747 | 0.248792697 |
| *Cyclorhipidion bodoanus* | 24 | 2014 | 2.308 | 0.802 | 0.272883733 |
| *Cyclorhipidion bodoanus* | 25 | 2014 | 2.23 | 0.741 | 0.249378254 |
| *Cyclorhipidion bodoanus* | 25 | 2015 | 2.093 | 0.746 | 0.21121036 |
| *Cyclorhipidion bodoanus* | 25 | 2015 | 2.226 | 0.716 | 0.248207991 |
| *Cyclorhipidion bodoanus* | 25 | 2015 | 2.078 | 0.756 | 0.207267478 |
| *Cyclorhipidion bodoanus* | 25 | 2015 | 2.094 | 0.703 | 0.211474854 |
| *Cyclorhipidion bodoanus* | 25 | 2015 | 2.169 | 0.747 | 0.231899528 |
| *Cyclorhipidion bodoanus* | 25 | 2015 | 1.888 | 0.654 | 0.161222278 |
| *Cyclorhipidion bodoanus* | 26 | 2015 | 2.204 | 0.737 | 0.241832244 |
| *Cyclorhipidion bodoanus* | 26 | 2015 | 2.183 | 0.738 | 0.235841716 |
| *Cyclorhipidion bodoanus* | 29 | 2015 | 2.181 | 0.728 | 0.23527603 |
| *Cyclorhipidion bodoanus* | 30 | 2014 | 2.37 | 0.754 | 0.292509857 |
| *Cyclorhipidion bodoanus* | 31 | 2015 | 2.078 | 0.698 | 0.207267478 |
| *Cyclorhipidion bodoanus* | 31 | 2015 | 2.116 | 0.719 | 0.217345612 |
| *Cyclorhipidion bodoanus* | 40 | 2015 | 2.062 | 0.700 | 0.203112256 |
| *Cyclorhipidion bodoanus* | 40 | 2015 | 2.226 | 0.746 | 0.248207991 |
| *Denticollis rubens* | 24 | 2014 | 10.135 | 2.019 | 13.16915994 |
| *Dissoleucas niveirostris* | 4 | 2015 | 3.632 | 1.544 | 0.895121399 |

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|---|---|---|---|---|---|
| *Dorcatoma substriata* | 22 | 2014 | 2.061 | 1.120 | 0.202854281 |
| *Epuraea variegata* | 7 | 2015 | 2.526 | 1.427 | 0.345680759 |
| *Ernoporicus fagi* | 23 | 2015 | 1.645 | 0.598 | 0.112371067 |
| *Eucnemis capucina* | 3 | 2014 | 5.544 | 1.954 | 2.710919865 |
| *Eucnemis capucina* | 3 | 2014 | 5.419 | 1.916 | 2.553689054 |
| *Eucnemis capucina* | 3 | 2014 | 5.221 | 1.818 | 2.316405117 |
| *Eucnemis capucina* | 7 | 2015 | 5.459 | 1.836 | 2.603371502 |
| *Eucnemis capucina* | 8 | 2015 | 5.394 | 1.921 | 2.522937591 |
| *Eucnemis capucina* | 11 | 2014 | 5.053 | 1.747 | 2.126174968 |
| *Eucnemis capucina* | 11 | 2015 | 5.22 | 1.750 | 2.31524288 |
| *Eucnemis capucina* | 18 | 2014 | 5.651 | 2.030 | 2.850152805 |
| *Eucnemis capucina* | 18 | 2014 | 5.303 | 1.941 | 2.412939886 |
| *Eucnemis capucina* | 18 | 2014 | 6.031 | 2.061 | 3.380024747 |
| *Eucnemis capucina* | 18 | 2015 | 6.296 | 2.216 | 3.783113787 |
| *Eucnemis capucina* | 18 | 2015 | 5.915 | 2.048 | 3.212338344 |
| *Eucnemis capucina* | 18 | 2015 | 4.654 | 1.767 | 1.713976852 |
| *Eucnemis capucina* | 21 | 2014 | 5.06 | 1.714 | 2.133900639 |
| *Eucnemis capucina* | 22 | 2015 | 5.558 | 1.919 | 2.728892455 |
| *Eucnemis capucina* | 23 | 2015 | 5.667 | 1.920 | 2.871344201 |
| *Eucnemis capucina* | 25 | 2014 | 5.09 | 1.698 | 2.167207171 |
| *Eucnemis capucina* | 25 | 2014 | 5.577 | 1.930 | 2.753401394 |
| *Eucnemis capucina* | 25 | 2014 | 5.502 | 1.988 | 2.657441879 |
| *Eucnemis capucina* | 26 | 2015 | 6.049 | 2.065 | 3.406519119 |
| *Eucnemis capucina* | 28 | 2014 | 5.643 | 2.003 | 2.839593485 |
| *Eucnemis capucina* | 28 | 2014 | 5.602 | 2.001 | 2.785856699 |
| *Eucnemis capucina* | 40 | 2015 | 5.952 | 2.054 | 3.265251942 |
| *Eucnemis capucina* | 41 | 2014 | 5.415 | 1.826 | 2.548753335 |
| *Eucnemis capucina* | 41 | 2015 | 5.417 | 1.833 | 2.551220457 |
| *Hapalaraea pygmaea* | 2 | 2014 | 2.302 | 0.658 | 0.271029008 |
| *Hapalaraea pygmaea* | 2 | 2015 | 2.197 | 0.771 | 0.239825075 |
| *Hapalaraea pygmaea* | 3 | 2014 | 3.028 | 0.754 | 0.555812386 |
| *Hapalaraea pygmaea* | 3 | 2014 | 2.613 | 0.766 | 0.377750539 |
| *Hapalaraea pygmaea* | 3 | 2014 | 2.976 | 0.727 | 0.531151128 |
| *Hapalaraea pygmaea* | 3 | 2015 | 2.101 | 0.663 | 0.213332045 |
| *Hapalaraea pygmaea* | 3 | 2015 | 2.513 | 0.774 | 0.341039089 |
| *Hapalaraea pygmaea* | 7 | 2015 | 2.325 | 0.655 | 0.278181335 |
| *Hapalaraea pygmaea* | 8 | 2015 | 2.461 | 0.711 | 0.322858532 |
| *Hapalaraea pygmaea* | 20 | 2015 | 1.935 | 0.710 | 0.171950712 |
| *Hapalaraea pygmaea* | 20 | 2015 | 2.035 | 0.711 | 0.196217891 |
| *Hapalaraea pygmaea* | 21 | 2015 | 2.664 | 0.667 | 0.397374045 |
| *Hapalaraea pygmaea* | 21 | 2015 | 2.486 | 0.731 | 0.331522329 |
| *Hapalaraea pygmaea* | 22 | 2014 | 2.068 | 0.737 | 0.204664368 |
| *Hapalaraea pygmaea* | 22 | 2015 | 2.15 | 0.745 | 0.226614975 |
| *Hapalaraea pygmaea* | 25 | 2014 | 1.88 | 0.724 | 0.159438575 |
| *Hapalaraea pygmaea* | 25 | 2014 | 2.215 | 0.725 | 0.245007294 |
| *Hapalaraea pygmaea* | 25 | 2015 | 2.135 | 0.696 | 0.222496039 |
| *Hapalaraea pygmaea* | 28 | 2015 | 2.236 | 0.770 | 0.251140037 |

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|---|---|---|---|---|---|
| *Hapalaraea pygmaea* | 28 | 2015 | 2.248 | 0.781 | 0.25468664 |
| *Hapalaraea pygmaea* | 28 | 2015 | 2.235 | 0.735 | 0.250845874 |
| *Hapalaraea pygmaea* | 37 | 2015 | 2.291 | 0.745 | 0.267648968 |
| *Hapalaraea pygmaea* | 37 | 2015 | 2.325 | 0.814 | 0.278181335 |
| *Hapalaraea pygmaea* | 40 | 2015 | 2.337 | 0.770 | 0.281958808 |
| *Hesperus rufipennis* | 15 | 2014 | 7.768 | 1.585 | 6.56009287 |
| *Hesperus rufipennis* | 22 | 2015 | 6.581 | 1.700 | 4.248392106 |
| *Hesperus rufipennis* | 22 | 2015 | 6.932 | 1.440 | 4.86798522 |
| *Hesperus rufipennis* | 22 | 2015 | 7.775 | 1.546 | 6.575592347 |
| *Hesperus rufipennis* | 25 | 2014 | 7.204 | 1.553 | 5.384469784 |
| *Hesperus rufipennis* | 26 | 2015 | 7.768 | 1.694 | 6.56009287 |
| *Hesperus rufipennis* | 28 | 2015 | 7.96 | 1.504 | 6.993459704 |
| *Hesperus rufipennis* | 41 | 2014 | 6.992 | 1.635 | 4.979154 |
| *Hylecoetus dermestoides* | 16 | 2014 | 12.761 | 2.223 | 24.08339873 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.895 | 0.647 | 0.162793095 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.734 | 0.672 | 0.12900557 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.992 | 0.624 | 0.185540146 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.665 | 0.636 | 0.115985886 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.604 | 0.582 | 0.10518051 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.072 | 0.641 | 0.205703171 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.727 | 0.616 | 0.127645575 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.718 | 0.609 | 0.125910085 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.688 | 0.595 | 0.120230773 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.003 | 0.652 | 0.188236538 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.806 | 0.610 | 0.143516004 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.677 | 0.654 | 0.118188838 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.094 | 0.648 | 0.211474854 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.887 | 0.615 | 0.160998644 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.98 | 0.675 | 0.182626013 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.057 | 0.727 | 0.201824406 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.935 | 0.676 | 0.171950712 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.163 | 0.727 | 0.230222582 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.628 | 0.589 | 0.109353923 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.119 | 0.657 | 0.218153882 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.113 | 0.687 | 0.216539197 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.166 | 0.688 | 0.231060115 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.847 | 0.652 | 0.152209972 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.897 | 0.654 | 0.163243631 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.874 | 0.652 | 0.158108841 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.983 | 0.633 | 0.183351873 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.028 | 0.663 | 0.194454443 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.859 | 0.651 | 0.154814573 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.242 | 0.693 | 0.252909494 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.796 | 0.657 | 0.141443316 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.987 | 0.664 | 0.184322457 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.994 | 0.643 | 0.186028611 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.004 | 0.662 | 0.188482858 |

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| *Hypebaeus flavipes* | 7 | 2014 | 1.802 | 0.659 | 0.142684691 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.07 | 0.663 | 0.205183363 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.785 | 0.603 | 0.139184854 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.084 | 0.686 | 0.208839119 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.913 | 0.660 | 0.166875685 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.005 | 0.659 | 0.188729377 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.754 | 0.600 | 0.132940517 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.752 | 0.610 | 0.132543729 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.943 | 0.642 | 0.173819532 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.057 | 0.664 | 0.201824406 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.871 | 0.538 | 0.157446555 |
| *Hypebaeus flavipes* | 7 | 2014 | 2.021 | 0.689 | 0.192700828 |
| *Hypebaeus flavipes* | 7 | 2014 | 1.829 | 0.639 | 0.148354166 |
| *Hypebaeus flavipes* | 7 | 2015 | 2.26 | 0.712 | 0.258264046 |
| *Hypebaeus flavipes* | 7 | 2015 | 1.839 | 0.645 | 0.150488728 |
| *Hypebaeus flavipes* | 7 | 2015 | 2.105 | 0.665 | 0.214397808 |
| *Hypebaeus flavipes* | 8 | 2014 | 1.986 | 0.659 | 0.184079514 |
| *Hypebaeus flavipes* | 8 | 2014 | 1.821 | 0.573 | 0.146660073 |
| *Hypebaeus flavipes* | 8 | 2014 | 2.045 | 0.672 | 0.198754201 |
| *Hypebaeus flavipes* | 8 | 2014 | 2.083 | 0.687 | 0.208576669 |
| *Hypebaeus flavipes* | 8 | 2015 | 2.08 | 0.665 | 0.207790543 |
| *Hypebaeus flavipes* | 14 | 2014 | 2.011 | 0.663 | 0.19021268 |
| *Hypebaeus flavipes* | 22 | 2014 | 2.219 | 0.749 | 0.246168212 |
| *Hypebaeus flavipes* | 22 | 2014 | 2.17 | 0.713 | 0.232179751 |
| *Hypebaeus flavipes* | 22 | 2014 | 1.921 | 0.589 | 0.168710276 |
| *Hypebaeus flavipes* | 22 | 2014 | 1.953 | 0.679 | 0.176173149 |
| *Hypebaeus flavipes* | 22 | 2014 | 2.062 | 0.642 | 0.203112256 |
| *Hypebaeus flavipes* | 22 | 2015 | 2.131 | 0.661 | 0.221405537 |
| *Hypebaeus flavipes* | 37 | 2014 | 2.107 | 0.716 | 0.214931922 |
| *Hypebaeus flavipes* | 37 | 2014 | 1.914 | 0.636 | 0.167104331 |
| *Hypebaeus flavipes* | 37 | 2014 | 1.997 | 0.675 | 0.186762797 |
| *Hypebaeus flavipes* | 37 | 2014 | 1.928 | 0.644 | 0.170325729 |
| *Hypebaeus flavipes* | 37 | 2014 | 1.813 | 0.629 | 0.144977994 |
| *Hypebaeus flavipes* | 37 | 2014 | 2.138 | 0.691 | 0.22331609 |
| *Ischnomera caerulea/cyanea* | 33 | 2014 | 7.593 | 1.445 | 6.179921336 |
| *Ischnomera sanguinicollis* | 2 | 2014 | 9.161 | 1.501 | 10.10625363 |
| *Ischnomera sanguinicollis* | 2 | 2015 | 9.543 | 1.740 | 11.24797493 |
| *Ischnomera sanguinicollis* | 4 | 2015 | 8.258 | 1.474 | 7.700377584 |
| *Ischnomera sanguinicollis* | 4 | 2015 | 7.76 | 1.428 | 6.542406867 |
| *Ischnomera sanguinicollis* | 20 | 2015 | 8.897 | 1.513 | 9.360909502 |
| *Ischnomera sanguinicollis* | 21 | 2015 | 7.576 | 1.334 | 6.143736067 |
| *Ischnomera sanguinicollis* | 23 | 2014 | 6.811 | 1.274 | 4.648494759 |
| *Ischnomera sanguinicollis* | 23 | 2015 | 8.451 | 1.451 | 8.180861982 |
| *Ischnomera sanguinicollis* | 23 | 2015 | 8.442 | 1.526 | 8.158055408 |
| *Ischnomera sanguinicollis* | 23 | 2015 | 9.44 | 1.676 | 10.93267567 |
| *Ischnomera sanguinicollis* | 24 | 2014 | 8.643 | 1.802 | 8.6768255 |

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|---|---|---|---|---|---|
| *Ischnomera sanguinicollis* | 25 | 2014 | 9.406 | 1.565 | 10.82981087 |
| *Ischnomera sanguinicollis* | 25 | 2015 | 9.82 | 1.768 | 12.12360944 |
| *Ischnomera sanguinicollis* | 26 | 2014 | 6.954 | 1.262 | 4.908566935 |
| *Ischnomera sanguinicollis* | 26 | 2015 | 8.867 | 1.604 | 9.278436835 |
| *Ischnomera sanguinicollis* | 28 | 2014 | 8.757 | 1.675 | 8.979886667 |
| *Ischnomera sanguinicollis* | 28 | 2015 | 8.184 | 1.494 | 7.520899158 |
| *Ischnomera sanguinicollis* | 28 | 2015 | 9.24 | 1.667 | 10.3361881 |
| *Ischnomera sanguinicollis* | 28 | 2015 | 9.374 | 1.703 | 10.73354561 |
| *Ischnomera sanguinicollis* | 29 | 2014 | 9.289 | 1.742 | 10.48041601 |
| *Ischnomera sanguinicollis* | 40 | 2015 | 7.901 | 1.311 | 6.858463651 |
| *Ischnomera sanguinicollis* | 40 | 2015 | 8.674 | 1.562 | 8.758600427 |
| *Ischnomera sanguinicollis* | 40 | 2015 | 6.925 | 1.311 | 4.855116518 |
| *Ischnomera sanguinicollis* | 41 | 2014 | 9.398 | 1.629 | 10.80569472 |
| *Ischnomera sp.* | 21 | 2015 | 6.447 | 1.380 | 4.02547316 |
| *Ischnomera sp.* | 26 | 2015 | 5.504 | 1.233 | 2.659973521 |
| *Ischnomera sp.* | 41 | 2015 | 7.246 | 1.462 | 5.467105607 |
| *Ischnomera spp.* | 18 | 2015 | 7.733 | 1.647 | 6.482934384 |
| *Malachius bipustulatus* | 7 | 2015 | 5.203 | 1.675 | 2.295539992 |
| *Malthinus punctatus* | 40 | 2015 | 3.62 | 0.716 | 0.887393604 |
| *Malthodes marginatus* | 4 | 2014 | 3.505 | 0.668 | 0.815422062 |
| *Malthodes marginatus* | 4 | 2015 | 3.639 | 0.771 | 0.899648427 |
| *Malthodes marginatus* | 4 | 2015 | 4.853 | 0.833 | 1.912699757 |
| *Malthodes marginatus* | 4 | 2015 | 5.06 | 0.833 | 2.133900639 |
| *Malthodes marginatus* | 6 | 2014 | 3.686 | 0.728 | 0.930410936 |
| *Malthodes marginatus* | 20 | 2015 | 3.707 | 0.743 | 0.944363112 |
| *Malthodes marginatus* | 21 | 2014 | 3.69 | 0.705 | 0.933058597 |
| *Megatoma undata* | 5 | 2014 | 3.908 | 1.482 | 1.084478068 |
| *Melanotus castanipes* | 5 | 2014 | 10.392 | 3.472 | 14.0621453 |
| *Melanotus castanipes* | 14 | 2014 | 13.937 | 3.436 | 30.34054694 |
| *Melanotus castanipes* | 20 | 2015 | 14.09 | 3.822 | 31.22098792 |
| *Melanotus castanipes* | 20 | 2015 | 15.462 | 4.286 | 39.82684391 |
| *Melanotus castanipes* | 23 | 2015 | 15.312 | 4.277 | 38.82249752 |
| *Melanotus castanipes* | 29 | 2014 | 14.392 | 3.847 | 33.00481124 |
| *Melanotus castanipes* | 31 | 2014 | 15.61 | 4.096 | 40.83339082 |
| *Melanotus castanipes* | 33 | 2014 | 15.084 | 4.024 | 37.32614437 |
| *Melanotus castanipes* | 40 | 2014 | 14.549 | 4.031 | 33.95648096 |
| *Melanotus rufipes* | 7 | 2015 | 12.559 | 3.614 | 23.09734693 |
| *Melanotus rufipes* | 7 | 2015 | 13.963 | 3.851 | 30.48906688 |
| *Melanotus rufipes* | 19 | 2015 | 12.282 | 3.192 | 21.7863694 |
| *Mycetophagus populi* | 21 | 2015 | 3.849 | 1.611 | 1.042104728 |
| *Mycetophagus populi* | 21 | 2015 | 3.998 | 1.625 | 1.151139479 |
| *Mycetophagus populi* | 22 | 2014 | 3.422 | 1.403 | 0.765796634 |
| *Mycetophagus populi* | 22 | 2015 | 3.704 | 1.568 | 0.942362079 |
| *Mycetophagus populi* | 22 | 2015 | 3.063 | 1.447 | 0.572802587 |
| *Mycetophagus populi* | 22 | 2015 | 3.815 | 1.506 | 1.018158849 |
| *Mycetophagus populi* | 25 | 2014 | 3.7 | 1.493 | 0.939698117 |
| *Neuraphes carinatus* | 40 | 2015 | 1.27 | 0.375 | 0.057051306 |

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|---|---|---|---|---|---|
| *Orchesia micans* | 21 | 2015 | 4.38 | 1.624 | 1.462049272 |
| *Orchesia micans* | 21 | 2015 | 4.555 | 1.536 | 1.620090959 |
| *Orchesia micans* | 22 | 2014 | 4.293 | 1.434 | 1.387181752 |
| *Orchesia micans* | 22 | 2014 | 4.135 | 1.450 | 1.257377503 |
| *Orchesia micans* | 22 | 2014 | 4.354 | 1.504 | 1.439419932 |
| *Orchesia micans* | 22 | 2014 | 4.254 | 1.601 | 1.354407193 |
| *Orchesia micans* | 22 | 2015 | 4.443 | 1.534 | 1.517790325 |
| *Orchesia micans* | 25 | 2014 | 3.338 | 1.351 | 0.717520032 |
| *Orchesia micans* | 27 | 2014 | 4.095 | 1.400 | 1.225758951 |
| *Orchesia micans* | 34 | 2014 | 4.718 | 1.536 | 1.776419914 |
| *Orthoperus atomus* | 37 | 2015 | 0.757 | 0.441 | 0.014707235 |
| *Orthoperus atomus* | 37 | 2015 | 0.733 | 0.413 | 0.013516749 |
| *Orthoperus atomus* | 37 | 2015 | 0.791 | 0.454 | 0.016501454 |
| *Orthoperus atomus* | 37 | 2015 | 0.691 | 0.441 | 0.011580634 |
| *Paromalus flavicornis* | 7 | 2015 | 1.716 | 0.986 | 0.125526414 |
| *Phloeonomus punctipennis* | 25 | 2015 | 1.623 | 0.453 | 0.108476175 |
| *Phloeonomus punctipennis* | 25 | 2015 | 1.374 | 0.436 | 0.070117283 |
| *Phloeophagus lignarius* | 7 | 2015 | 3.096 | 0.971 | 0.58911263 |
| *Phloeophagus lignarius* | 22 | 2015 | 3.359 | 1.154 | 0.729407206 |
| *Phloeophagus lignarius* | 22 | 2015 | 3.305 | 1.133 | 0.699083536 |
| *Pityophagus ferrugineus* | 29 | 2014 | 3.806 | 1.267 | 1.011877766 |
| *Platycis cosnardi* | 7 | 2015 | 6.164 | 1.284 | 3.578820613 |
| *Plegaderus dissectus* | 22 | 2014 | 1.246 | 0.670 | 0.054269661 |
| *Plegaderus dissectus* | 22 | 2014 | 1.33 | 0.718 | 0.064385955 |
| *Plegaderus dissectus* | 22 | 2014 | 1.356 | 0.715 | 0.067736106 |
| *Plegaderus dissectus* | 22 | 2015 | 1.27 | 0.704 | 0.057051306 |
| *Plegaderus dissectus* | 22 | 2015 | 1.257 | 0.710 | 0.055533912 |
| *Plegaderus dissectus* | 25 | 2014 | 1.211 | 0.646 | 0.050366004 |
| *Plegaderus dissectus* | 25 | 2014 | 1.414 | 0.690 | 0.075592253 |
| *Plegaderus dissectus* | 25 | 2014 | 1.261 | 0.643 | 0.05599811 |
| *Plegaderus dissectus* | 25 | 2014 | 1.321 | 0.685 | 0.063250683 |
| *Plegaderus dissectus* | 25 | 2015 | 1.212 | 0.709 | 0.050475044 |
| *Plegaderus dissectus* | 25 | 2015 | 1.087 | 0.651 | 0.037950827 |
| *Plegaderus dissectus* | 25 | 2015 | 1.255 | 0.731 | 0.055302708 |
| *Plegaderus dissectus* | 25 | 2015 | 1.226 | 0.675 | 0.052016948 |
| *Plegaderus dissectus* | 26 | 2015 | 1.163 | 0.669 | 0.045302137 |
| *Plegaderus dissectus* | 40 | 2015 | 1.167 | 0.669 | 0.045711501 |
| *Plegaderus dissectus* | 40 | 2015 | 1.314 | 0.764 | 0.062376312 |
| *Plegaderus dissectus* | 40 | 2015 | 1.22 | 0.683 | 0.051352619 |
| *Prionocyphon serricornis* | 2 | 2014 | 4.145 | 1.808 | 1.265360056 |
| *Prionocyphon serricornis* | 4 | 2015 | 3.588 | 1.674 | 0.866988261 |
| *Prionocyphon serricornis* | 12 | 2014 | 3.94 | 1.851 | 1.107898414 |
| *Prionocyphon serricornis* | 23 | 2015 | 3.491 | 1.621 | 0.806916216 |
| *Prionocyphon serricornis* | 28 | 2015 | 4.103 | 1.913 | 1.232042853 |
| *Prionocyphon serricornis* | 32 | 2014 | 4.392 | 1.983 | 1.472567285 |
| *Prionocyphon serricornis* | 40 | 2014 | 3.589 | 1.552 | 0.867621489 |
| *Prionocyphon serricornis* | 40 | 2015 | 4.349 | 1.952 | 1.435093137 |

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|---|---|---|---|---|---|
| *Prionocyphon serricornis* | 40 | 2015 | 3.775 | 1.745 | 0.990426528 |
| *Prionocyphon serricornis* | 40 | 2015 | 4.217 | 1.942 | 1.323760061 |
| *Procraerus tibialis* | 40 | 2015 | 7.319 | 2.053 | 5.612591276 |
| *Pseudocistela ceramboides* | 22 | 2014 | 9.812 | 3.270 | 12.09774965 |
| *Ptilinus pectinicornis* | 4 | 2015 | 4.459 | 1.425 | 1.53215258 |
| *Ptilinus pectinicornis* | 4 | 2015 | 3.785 | 1.208 | 0.997315239 |
| *Ptilinus pectinicornis* | 4 | 2015 | 3.988 | 1.299 | 1.143611019 |
| *Ptilinus pectinicornis* | 7 | 2014 | 3.89 | 1.224 | 1.071439849 |
| *Ptilinus pectinicornis* | 7 | 2014 | 3.823 | 1.268 | 1.023762223 |
| *Ptilinus pectinicornis* | 7 | 2015 | 3.236 | 1.033 | 0.661488264 |
| *Ptilinus pectinicornis* | 7 | 2015 | 4.014 | 1.320 | 1.163248614 |
| *Ptilinus pectinicornis* | 7 | 2015 | 3.73 | 1.181 | 0.959791675 |
| *Ptilinus pectinicornis* | 20 | 2014 | 3.884 | 1.165 | 1.067115428 |
| *Ptilinus pectinicornis* | 20 | 2014 | 3.608 | 1.062 | 0.879707197 |
| *Ptilinus pectinicornis* | 20 | 2014 | 3.741 | 1.121 | 0.967225271 |
| *Ptilinus pectinicornis* | 20 | 2014 | 3.867 | 1.156 | 1.054921564 |
| *Ptilinus pectinicornis* | 20 | 2015 | 3.446 | 1.112 | 0.77994837 |
| *Ptilinus pectinicornis* | 20 | 2015 | 3.261 | 1.027 | 0.674961393 |
| *Ptilinus pectinicornis* | 20 | 2015 | 2.997 | 0.934 | 0.541027208 |
| *Ptilinus pectinicornis* | 20 | 2015 | 3.223 | 0.967 | 0.654548512 |
| *Ptilinus pectinicornis* | 20 | 2015 | 4.125 | 1.280 | 1.249426163 |
| *Ptilinus pectinicornis* | 20 | 2015 | 3.665 | 1.225 | 0.916586939 |
| *Ptilinus pectinicornis* | 25 | 2014 | 2.951 | 0.890 | 0.519540213 |
| *Ptilinus pectinicornis* | 37 | 2014 | 3.531 | 1.123 | 0.831365234 |
| *Ptilinus pectinicornis* | 37 | 2014 | 3.299 | 1.023 | 0.695763283 |
| *Ptilinus pectinicornis* | 37 | 2014 | 3.96 | 1.199 | 1.122693547 |
| *Ptilinus pectinicornis* | 37 | 2015 | 3.306 | 1.026 | 0.699637863 |
| *Ptilinus pectinicornis* | 37 | 2015 | 4.099 | 1.282 | 1.228898419 |
| *Ptilinus pectinicornis* | 37 | 2015 | 4.011 | 1.273 | 1.160972182 |
| *Ptilinus pectinicornis* | 37 | 2015 | 3.394 | 1.021 | 0.749488295 |
| *Ptilinus pectinicornis* | 37 | 2015 | 3.826 | 1.165 | 1.025868393 |
| *Ptilinus pectinicornis* | 37 | 2015 | 4.16 | 1.331 | 1.277392511 |
| *Ptilinus pectinicornis* | 40 | 2015 | 2.974 | 0.893 | 0.530216411 |
| *Quedius brevicornis* | 8 | 2015 | 9.495 | 2.509 | 11.10034964 |
| *Quedius microps* | 40 | 2014 | 1.035 | 5.639 | 0.033376712 |
| *Quedius truncicola* | 11 | 2014 | 10.064 | 1.864 | 12.92881988 |
| *Quedius truncicola* | 21 | 2014 | 9.103 | 2.163 | 9.939472611 |
| *Quedius truncicola* | 21 | 2015 | 9.443 | 1.981 | 10.94178085 |
| *Quedius truncicola* | 26 | 2015 | 9.205 | 2.098 | 10.23392374 |
| *Quedius truncicola* | 26 | 2015 | 10.967 | 1.997 | 16.19309968 |
| *Quedius truncicola* | 41 | 2015 | 9.329 | 2.071 | 10.59907056 |
| *Rhagium mordax* | 40 | 2015 | 11.813 | 3.152 | 19.67358807 |
| *Rhizophagus bipustulatus* | 3 | 2014 | 2.618 | 0.646 | 0.379647288 |
| *Rhizophagus bipustulatus* | 6 | 2014 | 2.083 | 0.581 | 0.208576669 |
| *Rhizophagus bipustulatus* | 7 | 2015 | 2.336 | 0.749 | 0.281642815 |
| *Rhizophagus bipustulatus* | 22 | 2015 | 2.131 | 0.663 | 0.221405537 |
| *Rhizophagus bipustulatus* | 25 | 2014 | 2.241 | 0.603 | 0.252614051 |

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|---|---|---|---|---|---|
| *Rhizophagus bipustulatus* | 25 | 2015 | 2.048 | 0.619 | 0.199519025 |
| *Rhizophagus bipustulatus* | 26 | 2015 | 2.564 | 0.722 | 0.359471988 |
| *Rhizophagus bipustulatus* | 40 | 2015 | 2.156 | 0.656 | 0.228275646 |
| *Rhizophagus depressus* | 21 | 2015 | 2.318 | 0.730 | 0.275992341 |
| *Rhizophagus depressus* | 29 | 2015 | 2.604 | 0.845 | 0.37435118 |
| *Rhizophagus depressus* | 31 | 2014 | 3.045 | 0.895 | 0.564025264 |
| *Rhizophagus dispar* | 30 | 2014 | 2.614 | 0.685 | 0.378129419 |
| *Rhizophagus perforatus* | 21 | 2015 | 2.318 | 0.759 | 0.275992341 |
| *Rhizophagus perforatus* | 25 | 2015 | 2.368 | 0.745 | 0.291863569 |
| *Rhizophagus perforatus* | 37 | 2015 | 2.9 | 0.852 | 0.496343791 |
| *Scraptia fuscula* | 2 | 2015 | 2.459 | 0.883 | 0.322171549 |
| *Scraptia fuscula* | 15 | 2014 | 2.653 | 0.850 | 0.393089492 |
| *Scraptia fuscula* | 24 | 2014 | 2.366 | 0.799 | 0.291218164 |
| *Scraptia fuscula* | 24 | 2014 | 2.6 | 0.842 | 0.372846449 |
| *Scraptia fuscula* | 24 | 2014 | 2.556 | 0.822 | 0.356540825 |
| *Scraptia fuscula* | 25 | 2014 | 2.398 | 0.683 | 0.301650943 |
| *Scraptia fuscula* | 25 | 2014 | 2.327 | 0.728 | 0.278808727 |
| *Scraptia fuscula* | 25 | 2014 | 2.269 | 0.864 | 0.260967376 |
| *Scraptia fuscula* | 25 | 2014 | 2.55 | 0.836 | 0.354352183 |
| *Scraptia fuscula* | 26 | 2015 | 2.505 | 0.816 | 0.338201938 |
| *Scraptia fuscula* | 28 | 2014 | 2.184 | 0.756 | 0.236124875 |
| *Scraptia fuscula* | 28 | 2014 | 2.283 | 0.783 | 0.26520721 |
| *Scraptia fuscula* | 28 | 2014 | 2.421 | 0.839 | 0.30929022 |
| *Scraptia fuscula* | 28 | 2014 | 2.4 | 0.811 | 0.302310543 |
| *Scraptia fuscula* | 28 | 2014 | 2.811 | 0.844 | 0.457420111 |
| *Scraptia fuscula* | 28 | 2014 | 2.459 | 0.767 | 0.322171549 |
| *Scraptia fuscula* | 28 | 2014 | 2.791 | 0.753 | 0.448942387 |
| *Scraptia fuscula* | 28 | 2014 | 2.729 | 0.773 | 0.42328132 |
| *Scraptia fuscula* | 28 | 2015 | 2.513 | 0.856 | 0.341039089 |
| *Siagonum quadricorne* | 25 | 2014 | 2.939 | 0.738 | 0.51402324 |
| *Tetropium castaneum* | 37 | 2015 | 2.955 | 11.627 | 0.521387303 |
| *Tillus elongatus* | 4 | 2015 | 7.951 | 1.392 | 6.972761866 |
| *Tillus elongatus* | 4 | 2015 | 7.558 | 1.473 | 6.105565361 |
| *Tillus elongatus* | 7 | 2014 | 7.595 | 1.295 | 6.184187068 |
| *Tillus elongatus* | 19 | 2015 | 6.733 | 1.158 | 4.510310173 |
| *Tillus elongatus* | 20 | 2014 | 8.083 | 1.508 | 7.280144438 |
| *Tillus elongatus* | 21 | 2014 | 6.928 | 1.272 | 4.860629097 |
| *Tillus elongatus* | 21 | 2015 | 6.37 | 1.129 | 3.900723368 |
| *Tillus elongatus* | 21 | 2015 | 6.213 | 1.084 | 3.653838822 |
| *Tillus elongatus* | 37 | 2014 | 7.667 | 1.590 | 6.338967908 |
| *Tillus elongatus* | 37 | 2015 | 6.94 | 1.254 | 4.882718107 |
| *Tillus elongatus* | 37 | 2015 | 8.014 | 1.543 | 7.11844453 |
| *Tillus elongatus* | 37 | 2015 | 7.262 | 1.503 | 5.498790835 |
| *Triplax russica* | 22 | 2014 | 6.252 | 2.578 | 3.714236376 |
| *Triplax russica* | 22 | 2014 | 5.253 | 2.221 | 2.353787377 |
| *Velleius dilatatus* | 4 | 2015 | 16.012 | 5.207 | 43.64628284 |
| *Xyleborus dispar* | 3 | 2015 | 3.43 | 1.452 | 0.770496081 |

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|---|---|---|---|---|---|
| *Xyleborus dispar* | 4 | 2014 | 3.385 | 1.385 | 0.744292363 |
| *Xyleborus dispar* | 4 | 2015 | 3.512 | 1.474 | 0.819695684 |
| *Xyleborus dispar* | 5 | 2014 | 3.53 | 1.413 | 0.830748503 |
| *Xyleborus dispar* | 5 | 2014 | 3.437 | 1.415 | 0.774622689 |
| *Xyleborus dispar* | 5 | 2014 | 3.332 | 1.358 | 0.714145856 |
| *Xyleborus dispar* | 5 | 2014 | 3.262 | 1.302 | 0.675503815 |
| *Xyleborus dispar* | 5 | 2014 | 3.313 | 1.345 | 0.703525756 |
| *Xyleborus dispar* | 5 | 2014 | 3.275 | 1.356 | 0.682579839 |
| *Xyleborus dispar* | 7 | 2014 | 3.048 | 1.230 | 0.565482334 |
| *Xyleborus dispar* | 7 | 2014 | 3.289 | 1.395 | 0.690251228 |
| *Xyleborus dispar* | 7 | 2015 | 3.366 | 1.472 | 0.733396464 |
| *Xyleborus dispar* | 7 | 2015 | 3.317 | 1.442 | 0.705753393 |
| *Xyleborus dispar* | 10 | 2014 | 3.436 | 1.424 | 0.774032339 |
| *Xyleborus dispar* | 12 | 2015 | 3.244 | 1.447 | 0.665781395 |
| *Xyleborus dispar* | 13 | 2014 | 3.245 | 1.346 | 0.666319244 |
| *Xyleborus dispar* | 15 | 2014 | 2.05 | 0.814 | 0.200029917 |
| *Xyleborus dispar* | 15 | 2014 | 3.339 | 1.444 | 0.71808335 |
| *Xyleborus dispar* | 17 | 2014 | 3.298 | 1.400 | 0.695210857 |
| *Xyleborus dispar* | 17 | 2014 | 3.101 | 1.339 | 0.591608584 |
| *Xyleborus dispar* | 18 | 2014 | 3.459 | 1.388 | 0.787680895 |
| *Xyleborus dispar* | 18 | 2015 | 3.474 | 1.458 | 0.796661725 |
| *Xyleborus dispar* | 20 | 2014 | 3.432 | 1.385 | 0.771673721 |
| *Xyleborus dispar* | 21 | 2014 | 3.425 | 1.402 | 0.767556843 |
| *Xyleborus dispar* | 21 | 2015 | 3.426 | 1.451 | 0.768144135 |
| *Xyleborus dispar* | 22 | 2014 | 3.212 | 1.438 | 0.648711722 |
| *Xyleborus dispar* | 25 | 2014 | 3.485 | 1.482 | 0.803287723 |
| *Xyleborus dispar* | 25 | 2015 | 3.409 | 1.443 | 0.758197909 |
| *Xyleborus dispar* | 26 | 2015 | 3.294 | 1.470 | 0.693003867 |
| *Xyleborus dispar* | 29 | 2014 | 3.396 | 1.429 | 0.750645983 |
| *Xyleborus dispar* | 30 | 2014 | 3.05 | 1.287 | 0.566455005 |
| *Xyleborus dispar* | 30 | 2014 | 3.503 | 1.470 | 0.814203564 |
| *Xyleborus dispar* | 30 | 2014 | 3.485 | 1.482 | 0.803287723 |
| *Xyleborus dispar* | 31 | 2014 | 3.438 | 1.432 | 0.775213317 |
| *Xyleborus dispar* | 31 | 2014 | 3.341 | 1.454 | 0.719210809 |
| *Xyleborus dispar* | 31 | 2014 | 3.259 | 1.376 | 0.673877357 |
| *Xyleborus dispar* | 31 | 2015 | 3.425 | 1.444 | 0.767556843 |
| *Xyleborus dispar* | 31 | 2015 | 3.193 | 1.435 | 0.638706015 |
| *Xyleborus dispar* | 31 | 2015 | 3.541 | 1.495 | 0.837548119 |
| *Xyleborus dispar* | 36 | 2014 | 3.421 | 1.428 | 0.765210453 |
| *Xyleborus dispar* | 37 | 2015 | 3.293 | 1.390 | 0.692452797 |
| *Xyleborus dispar* | 39 | 2014 | 3.328 | 1.444 | 0.711901866 |
| *Xyleborus dispar* | 39 | 2014 | 3.244 | 1.362 | 0.665781395 |
| *Xyleborus dispar* | 41 | 2014 | 3.439 | 1.482 | 0.775804224 |
| *Xyleborus germanus* | 2 | 2014 | 2.365 | 0.962 | 0.290895792 |
| *Xyleborus germanus* | 2 | 2014 | 2.239 | 0.946 | 0.252023805 |
| *Xyleborus germanus* | 2 | 2014 | 2.345 | 0.980 | 0.284494647 |
| *Xyleborus germanus* | 2 | 2015 | 2.421 | 0.987 | 0.30929022 |

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|---|---|---|---|---|---|
| *Xyleborus germanus* | 3 | 2014 | 2.247 | 0.944 | 0.254389914 |
| *Xyleborus germanus* | 3 | 2014 | 2.346 | 0.975 | 0.284812614 |
| *Xyleborus germanus* | 3 | 2014 | 2.354 | 0.959 | 0.287364265 |
| *Xyleborus germanus* | 3 | 2015 | 2.21 | 0.971 | 0.243560915 |
| *Xyleborus germanus* | 3 | 2015 | 2.358 | 0.969 | 0.288645371 |
| *Xyleborus germanus* | 3 | 2015 | 2.288 | 0.969 | 0.266731687 |
| *Xyleborus germanus* | 3 | 2015 | 2.404 | 1.003 | 0.303632415 |
| *Xyleborus germanus* | 3 | 2015 | 2.366 | 0.975 | 0.291218164 |
| *Xyleborus germanus* | 3 | 2015 | 2.299 | 0.981 | 0.270104577 |
| *Xyleborus germanus* | 4 | 2014 | 2.36 | 0.998 | 0.289287246 |
| *Xyleborus germanus* | 4 | 2014 | 2.321 | 0.982 | 0.276929172 |
| *Xyleborus germanus* | 4 | 2014 | 2.454 | 0.945 | 0.320458048 |
| *Xyleborus germanus* | 4 | 2014 | 2.28 | 0.974 | 0.264295116 |
| *Xyleborus germanus* | 4 | 2014 | 2.247 | 0.954 | 0.254389914 |
| *Xyleborus germanus* | 4 | 2014 | 2.349 | 0.982 | 0.285767834 |
| *Xyleborus germanus* | 4 | 2015 | 2.288 | 0.979 | 0.266731687 |
| *Xyleborus germanus* | 4 | 2015 | 2.302 | 1.011 | 0.271029008 |
| *Xyleborus germanus* | 4 | 2015 | 2.347 | 1.000 | 0.285130801 |
| *Xyleborus germanus* | 4 | 2015 | 2.217 | 0.963 | 0.245587329 |
| *Xyleborus germanus* | 4 | 2015 | 2.371 | 0.999 | 0.292833333 |
| *Xyleborus germanus* | 5 | 2014 | 2.251 | 0.964 | 0.255578099 |
| *Xyleborus germanus* | 5 | 2014 | 2.225 | 0.952 | 0.247915956 |
| *Xyleborus germanus* | 5 | 2014 | 2.434 | 1.001 | 0.313660437 |
| *Xyleborus germanus* | 5 | 2014 | 2.257 | 1.016 | 0.257366801 |
| *Xyleborus germanus* | 5 | 2014 | 2.183 | 0.713 | 0.235841716 |
| *Xyleborus germanus* | 6 | 2014 | 2.283 | 0.999 | 0.26520721 |
| *Xyleborus germanus* | 6 | 2014 | 2.191 | 0.983 | 0.238112869 |
| *Xyleborus germanus* | 6 | 2014 | 2.205 | 0.954 | 0.242119827 |
| *Xyleborus germanus* | 6 | 2014 | 2.29 | 0.970 | 0.267342991 |
| *Xyleborus germanus* | 7 | 2014 | 2.248 | 0.950 | 0.25468664 |
| *Xyleborus germanus* | 7 | 2014 | 2.335 | 0.963 | 0.281327041 |
| *Xyleborus germanus* | 7 | 2014 | 2.306 | 0.978 | 0.272264622 |
| *Xyleborus germanus* | 7 | 2014 | 2.307 | 0.973 | 0.272574069 |
| *Xyleborus germanus* | 7 | 2015 | 2.348 | 0.995 | 0.285449208 |
| *Xyleborus germanus* | 7 | 2015 | 2.336 | 1.020 | 0.281642815 |
| *Xyleborus germanus* | 7 | 2015 | 2.256 | 0.975 | 0.257068148 |
| *Xyleborus germanus* | 7 | 2015 | 2.253 | 0.987 | 0.256173476 |
| *Xyleborus germanus* | 8 | 2014 | 2.333 | 0.984 | 0.280696149 |
| *Xyleborus germanus* | 8 | 2015 | 2.37 | 1.026 | 0.292509857 |
| *Xyleborus germanus* | 8 | 2015 | 2.163 | 0.994 | 0.230222582 |
| *Xyleborus germanus* | 8 | 2015 | 2.252 | 0.996 | 0.255875681 |
| *Xyleborus germanus* | 10 | 2014 | 2.29 | 1.000 | 0.267342991 |
| *Xyleborus germanus* | 10 | 2014 | 2.24 | 0.939 | 0.252318821 |
| *Xyleborus germanus* | 11 | 2014 | 2.313 | 0.967 | 0.274435315 |
| *Xyleborus germanus* | 11 | 2014 | 2.361 | 1.002 | 0.289608514 |
| *Xyleborus germanus* | 11 | 2014 | 2.349 | 0.966 | 0.285767834 |
| *Xyleborus germanus* | 11 | 2014 | 2.383 | 0.994 | 0.296732305 |

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|---|---|---|---|---|---|
| *Xyleborus germanus* | 11 | 2015 | 2.299 | 0.956 | 0.270104577 |
| *Xyleborus germanus* | 11 | 2015 | 2.321 | 0.990 | 0.276929172 |
| *Xyleborus germanus* | 11 | 2015 | 2.122 | 0.976 | 0.218964008 |
| *Xyleborus germanus* | 11 | 2015 | 2.31 | 0.987 | 0.273503713 |
| *Xyleborus germanus* | 11 | 2015 | 2.358 | 0.988 | 0.288645371 |
| *Xyleborus germanus* | 12 | 2014 | 2.268 | 0.957 | 0.260666146 |
| *Xyleborus germanus* | 12 | 2014 | 2.351 | 1.000 | 0.286405747 |
| *Xyleborus germanus* | 12 | 2015 | 2.36 | 0.993 | 0.289287246 |
| *Xyleborus germanus* | 12 | 2015 | 2.46 | 0.999 | 0.322514927 |
| *Xyleborus germanus* | 13 | 2014 | 2.263 | 1.010 | 0.259163222 |
| *Xyleborus germanus* | 13 | 2014 | 2.321 | 0.988 | 0.276929172 |
| *Xyleborus germanus* | 14 | 2014 | 2.333 | 0.987 | 0.280696149 |
| *Xyleborus germanus* | 14 | 2014 | 2.448 | 1.005 | 0.318409299 |
| *Xyleborus germanus* | 14 | 2014 | 2.26 | 0.987 | 0.258264046 |
| *Xyleborus germanus* | 14 | 2015 | 2.286 | 0.966 | 0.266121248 |
| *Xyleborus germanus* | 14 | 2015 | 2.238 | 0.979 | 0.251729002 |
| *Xyleborus germanus* | 14 | 2015 | 2.323 | 0.986 | 0.277554817 |
| *Xyleborus germanus* | 14 | 2015 | 2.341 | 0.936 | 0.283224972 |
| *Xyleborus germanus* | 14 | 2015 | 2.369 | 0.981 | 0.292186602 |
| *Xyleborus germanus* | 14 | 2015 | 2.35 | 0.986 | 0.28608668 |
| *Xyleborus germanus* | 15 | 2014 | 2.263 | 0.949 | 0.259163222 |
| *Xyleborus germanus* | 16 | 2014 | 2.38 | 0.984 | 0.295754572 |
| *Xyleborus germanus* | 16 | 2014 | 2.359 | 1.003 | 0.288966198 |
| *Xyleborus germanus* | 16 | 2014 | 2.317 | 1.000 | 0.2756805 |
| *Xyleborus germanus* | 16 | 2014 | 2.33 | 0.976 | 0.279751454 |
| *Xyleborus germanus* | 16 | 2014 | 2.385 | 0.986 | 0.297385236 |
| *Xyleborus germanus* | 17 | 2014 | 2.146 | 0.994 | 0.225512022 |
| *Xyleborus germanus* | 17 | 2014 | 2.29 | 0.979 | 0.267342991 |
| *Xyleborus germanus* | 17 | 2014 | 2.391 | 1.003 | 0.299349356 |
| *Xyleborus germanus* | 17 | 2014 | 2.444 | 1.030 | 0.317047978 |
| *Xyleborus germanus* | 17 | 2014 | 2.359 | 0.968 | 0.288966198 |
| *Xyleborus germanus* | 17 | 2014 | 2.122 | 0.949 | 0.218964008 |
| *Xyleborus germanus* | 18 | 2014 | 2.29 | 0.982 | 0.267342991 |
| *Xyleborus germanus* | 18 | 2015 | 2.279 | 0.983 | 0.263991517 |
| *Xyleborus germanus* | 18 | 2015 | 2.354 | 0.978 | 0.287364265 |
| *Xyleborus germanus* | 18 | 2015 | 2.354 | 0.983 | 0.287364265 |
| *Xyleborus germanus* | 18 | 2015 | 2.376 | 0.971 | 0.29445403 |
| *Xyleborus germanus* | 18 | 2015 | 2.393 | 0.996 | 0.300005841 |
| *Xyleborus germanus* | 18 | 2015 | 2.305 | 0.973 | 0.271955393 |
| *Xyleborus germanus* | 19 | 2015 | 2.378 | 0.973 | 0.295103858 |
| *Xyleborus germanus* | 19 | 2015 | 2.433 | 0.992 | 0.31332292 |
| *Xyleborus germanus* | 20 | 2014 | 2.584 | 0.816 | 0.366864943 |
| *Xyleborus germanus* | 20 | 2015 | 2.222 | 0.980 | 0.247041128 |
| *Xyleborus germanus* | 20 | 2015 | 2.339 | 0.942 | 0.282591452 |
| *Xyleborus germanus* | 20 | 2015 | 2.386 | 0.988 | 0.297712034 |
| *Xyleborus germanus* | 20 | 2015 | 2.276 | 0.966 | 0.263082012 |
| *Xyleborus germanus* | 20 | 2015 | 2.186 | 0.941 | 0.236691822 |

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| *Xyleborus germanus* | 20 | 2015 | 2.203 | 0.964 | 0.241544872 |
| *Xyleborus germanus* | 21 | 2014 | 2.233 | 1.017 | 0.250258187 |
| *Xyleborus germanus* | 21 | 2014 | 2.308 | 0.967 | 0.272883733 |
| *Xyleborus germanus* | 21 | 2014 | 2.352 | 0.976 | 0.286725033 |
| *Xyleborus germanus* | 21 | 2015 | 2.18 | 0.987 | 0.234993502 |
| *Xyleborus germanus* | 21 | 2015 | 2.313 | 0.988 | 0.274435315 |
| *Xyleborus germanus* | 21 | 2015 | 2.296 | 0.967 | 0.269182099 |
| *Xyleborus germanus* | 21 | 2015 | 2.284 | 0.950 | 0.265511674 |
| *Xyleborus germanus* | 21 | 2015 | 2.26 | 0.994 | 0.258264046 |
| *Xyleborus germanus* | 21 | 2015 | 2.217 | 0.968 | 0.245587329 |
| *Xyleborus germanus* | 22 | 2014 | 2.355 | 0.975 | 0.287684211 |
| *Xyleborus germanus* | 22 | 2014 | 2.36 | 0.969 | 0.289287246 |
| *Xyleborus germanus* | 22 | 2014 | 2.227 | 0.982 | 0.248500237 |
| *Xyleborus germanus* | 22 | 2014 | 2.351 | 0.977 | 0.286405747 |
| *Xyleborus germanus* | 22 | 2014 | 2.303 | 0.962 | 0.271337586 |
| *Xyleborus germanus* | 22 | 2015 | 2.307 | 0.984 | 0.272574069 |
| *Xyleborus germanus* | 22 | 2015 | 2.223 | 0.969 | 0.247332525 |
| *Xyleborus germanus* | 22 | 2015 | 2.323 | 0.994 | 0.277554817 |
| *Xyleborus germanus* | 22 | 2015 | 2.329 | 0.967 | 0.279436993 |
| *Xyleborus germanus* | 22 | 2015 | 2.211 | 0.964 | 0.243849767 |
| *Xyleborus germanus* | 23 | 2014 | 2.333 | 0.987 | 0.280696149 |
| *Xyleborus germanus* | 23 | 2014 | 2.364 | 1.003 | 0.290573642 |
| *Xyleborus germanus* | 23 | 2014 | 2.327 | 0.987 | 0.278808727 |
| *Xyleborus germanus* | 23 | 2014 | 2.264 | 0.967 | 0.259463377 |
| *Xyleborus germanus* | 23 | 2015 | 2.398 | 1.024 | 0.301650943 |
| *Xyleborus germanus* | 23 | 2015 | 2.362 | 1.012 | 0.289930003 |
| *Xyleborus germanus* | 23 | 2015 | 2.32 | 1.012 | 0.276616677 |
| *Xyleborus germanus* | 23 | 2015 | 2.411 | 1.016 | 0.305954278 |
| *Xyleborus germanus* | 23 | 2015 | 2.296 | 0.967 | 0.269182099 |
| *Xyleborus germanus* | 24 | 2014 | 2.245 | 0.918 | 0.253797105 |
| *Xyleborus germanus* | 24 | 2014 | 2.146 | 0.970 | 0.225512022 |
| *Xyleborus germanus* | 24 | 2014 | 2.386 | 1.002 | 0.297712034 |
| *Xyleborus germanus* | 24 | 2014 | 2.25 | 0.976 | 0.255280732 |
| *Xyleborus germanus* | 25 | 2014 | 2.286 | 0.976 | 0.266121248 |
| *Xyleborus germanus* | 25 | 2014 | 2.291 | 0.954 | 0.267648968 |
| *Xyleborus germanus* | 25 | 2014 | 2.392 | 1.028 | 0.299677487 |
| *Xyleborus germanus* | 25 | 2014 | 2.333 | 0.976 | 0.280696149 |
| *Xyleborus germanus* | 25 | 2015 | 2.298 | 0.974 | 0.269796868 |
| *Xyleborus germanus* | 25 | 2015 | 2.34 | 1.005 | 0.282908102 |
| *Xyleborus germanus* | 25 | 2015 | 2.318 | 0.997 | 0.275992341 |
| *Xyleborus germanus* | 25 | 2015 | 2.419 | 1.023 | 0.308621242 |
| *Xyleborus germanus* | 25 | 2015 | 2.353 | 0.969 | 0.287044539 |
| *Xyleborus germanus* | 25 | 2015 | 2.282 | 0.991 | 0.264902963 |
| *Xyleborus germanus* | 26 | 2014 | 2.386 | 1.022 | 0.297712034 |
| *Xyleborus germanus* | 26 | 2014 | 2.213 | 0.984 | 0.244428107 |
| *Xyleborus germanus* | 26 | 2014 | 2.354 | 0.997 | 0.287364265 |
| *Xyleborus germanus* | 26 | 2015 | 2.193 | 0.963 | 0.238682762 |

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| *Xyleborus germanus* | 26 | 2015 | 2.289 | 0.981 | 0.267037231 |
| *Xyleborus germanus* | 26 | 2015 | 2.341 | 0.969 | 0.283224972 |
| *Xyleborus germanus* | 26 | 2015 | 2.389 | 0.992 | 0.298693761 |
| *Xyleborus germanus* | 26 | 2015 | 2.182 | 0.949 | 0.235558768 |
| *Xyleborus germanus* | 27 | 2014 | 2.419 | 1.010 | 0.308621242 |
| *Xyleborus germanus* | 27 | 2014 | 2.325 | 0.991 | 0.278181335 |
| *Xyleborus germanus* | 28 | 2014 | 2.373 | 0.995 | 0.293480948 |
| *Xyleborus germanus* | 28 | 2014 | 2.438 | 0.985 | 0.315012753 |
| *Xyleborus germanus* | 28 | 2014 | 2.414 | 1.003 | 0.306952713 |
| *Xyleborus germanus* | 28 | 2014 | 2.265 | 0.969 | 0.259763747 |
| *Xyleborus germanus* | 28 | 2014 | 2.344 | 0.960 | 0.284176899 |
| *Xyleborus germanus* | 28 | 2014 | 2.246 | 0.960 | 0.254093403 |
| *Xyleborus germanus* | 28 | 2014 | 2.316 | 0.969 | 0.275368877 |
| *Xyleborus germanus* | 28 | 2014 | 2.295 | 0.971 | 0.268875039 |
| *Xyleborus germanus* | 28 | 2015 | 2.301 | 0.987 | 0.270720648 |
| *Xyleborus germanus* | 28 | 2015 | 2.296 | 1.014 | 0.269182099 |
| *Xyleborus germanus* | 28 | 2015 | 2.2 | 0.997 | 0.240684024 |
| *Xyleborus germanus* | 28 | 2015 | 2.266 | 0.992 | 0.260064332 |
| *Xyleborus germanus* | 28 | 2015 | 2.39 | 1.001 | 0.299021448 |
| *Xyleborus germanus* | 28 | 2015 | 2.371 | 0.994 | 0.292833333 |
| *Xyleborus germanus* | 29 | 2014 | 2.305 | 0.997 | 0.271955393 |
| *Xyleborus germanus* | 29 | 2015 | 2.309 | 0.980 | 0.273193614 |
| *Xyleborus germanus* | 29 | 2015 | 2.331 | 0.993 | 0.280066134 |
| *Xyleborus germanus* | 29 | 2015 | 2.396 | 0.991 | 0.300992235 |
| *Xyleborus germanus* | 29 | 2015 | 2.222 | 0.968 | 0.247041128 |
| *Xyleborus germanus* | 30 | 2014 | 2.336 | 0.971 | 0.281642815 |
| *Xyleborus germanus* | 30 | 2014 | 2.353 | 0.974 | 0.287044539 |
| *Xyleborus germanus* | 30 | 2014 | 2.375 | 0.972 | 0.294129448 |
| *Xyleborus germanus* | 30 | 2014 | 2.326 | 1.028 | 0.278494922 |
| *Xyleborus germanus* | 31 | 2014 | 2.334 | 1.008 | 0.281011486 |
| *Xyleborus germanus* | 31 | 2014 | 2.436 | 0.987 | 0.314336145 |
| *Xyleborus germanus* | 31 | 2015 | 2.394 | 1.023 | 0.300334416 |
| *Xyleborus germanus* | 31 | 2015 | 2.294 | 0.983 | 0.268568197 |
| *Xyleborus germanus* | 32 | 2014 | 2.375 | 1.003 | 0.294129448 |
| *Xyleborus germanus* | 33 | 2014 | 2.305 | 0.967 | 0.271955393 |
| *Xyleborus germanus* | 34 | 2014 | 2.345 | 0.982 | 0.284494647 |
| *Xyleborus germanus* | 35 | 2014 | 2.377 | 0.973 | 0.294778833 |
| *Xyleborus germanus* | 35 | 2014 | 2.275 | 0.971 | 0.262779275 |
| *Xyleborus germanus* | 35 | 2014 | 2.37 | 0.959 | 0.292509857 |
| *Xyleborus germanus* | 36 | 2014 | 2.334 | 0.944 | 0.281011486 |
| *Xyleborus germanus* | 36 | 2014 | 2.259 | 0.944 | 0.25796475 |
| *Xyleborus germanus* | 36 | 2014 | 2.268 | 0.931 | 0.260666146 |
| *Xyleborus germanus* | 36 | 2014 | 2.294 | 0.954 | 0.268568197 |
| *Xyleborus germanus* | 37 | 2014 | 2.263 | 0.966 | 0.259163222 |
| *Xyleborus germanus* | 37 | 2014 | 2.324 | 0.970 | 0.277867967 |
| *Xyleborus germanus* | 37 | 2015 | 2.465 | 1.018 | 0.324235213 |
| *Xyleborus germanus* | 37 | 2015 | 2.35 | 1.022 | 0.28608668 |

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| *Xyleborus germanus* | 37 | 2015 | 2.277 | 0.974 | 0.263384965 |
| *Xyleborus germanus* | 37 | 2015 | 2.316 | 0.952 | 0.275368877 |
| *Xyleborus germanus* | 37 | 2015 | 2.293 | 0.974 | 0.26826157 |
| *Xyleborus germanus* | 38 | 2014 | 2.316 | 0.966 | 0.275368877 |
| *Xyleborus germanus* | 38 | 2014 | 2.31 | 0.967 | 0.273503713 |
| *Xyleborus germanus* | 38 | 2014 | 2.353 | 0.984 | 0.287044539 |
| *Xyleborus germanus* | 38 | 2014 | 2.41 | 1.000 | 0.305621914 |
| *Xyleborus germanus* | 38 | 2015 | 2.327 | 1.057 | 0.278808727 |
| *Xyleborus germanus* | 38 | 2015 | 2.305 | 1.005 | 0.271955393 |
| *Xyleborus germanus* | 38 | 2015 | 2.294 | 0.972 | 0.268568197 |
| *Xyleborus germanus* | 38 | 2015 | 2.369 | 0.977 | 0.292186602 |
| *Xyleborus germanus* | 38 | 2015 | 2.458 | 1.015 | 0.321828396 |
| *Xyleborus germanus* | 38 | 2015 | 2.346 | 0.992 | 0.284812614 |
| *Xyleborus germanus* | 40 | 2014 | 2.267 | 1.021 | 0.260365131 |
| *Xyleborus germanus* | 40 | 2014 | 2.435 | 0.976 | 0.313998179 |
| *Xyleborus germanus* | 40 | 2015 | 2.305 | 1.007 | 0.271955393 |
| *Xyleborus germanus* | 40 | 2015 | 2.177 | 0.909 | 0.234147176 |
| *Xyleborus germanus* | 40 | 2015 | 2.337 | 0.990 | 0.281958808 |
| *Xyleborus germanus* | 40 | 2015 | 2.299 | 0.937 | 0.270104577 |
| *Xyleborus germanus* | 40 | 2015 | 2.408 | 1.024 | 0.304957855 |
| *Xyleborus germanus* | 40 | 2015 | 2.268 | 0.995 | 0.260666146 |
| *Xyleborus germanus* | 41 | 2014 | 2.199 | 0.921 | 0.240397496 |
| *Xyleborus germanus* | 41 | 2014 | 2.3 | 0.974 | 0.270412504 |
| *Xyleborus germanus* | 41 | 2014 | 2.196 | 0.960 | 0.23953918 |
| *Xyleborus germanus* | 41 | 2014 | 2.374 | 0.979 | 0.293805087 |
| *Xyleborus germanus* | 41 | 2015 | 2.358 | 1.020 | 0.288645371 |
| *Xyleborus germanus* | 41 | 2015 | 2.348 | 0.962 | 0.285449208 |
| *Xyleborus germanus* | 41 | 2015 | 2.331 | 0.954 | 0.280066134 |
| *Xyleborus germanus* | 41 | 2015 | 2.293 | 0.983 | 0.26826157 |
| *Xyleborus germanus* | 41 | 2015 | 2.402 | 0.982 | 0.302971033 |
| *Xyleborus germanus* | 41 | 2015 | 2.204 | 0.948 | 0.241832244 |
| *Xyleborus germanus* | 42 | 2014 | 2.246 | 0.966 | 0.254093403 |
| *Xyleborus germanus* | 42 | 2014 | 2.342 | 0.950 | 0.283542062 |
| *Xyleborus germanus* | 42 | 2014 | 2.41 | 0.998 | 0.305621914 |
| *Xyleborus monographus* | 25 | 2015 | 2.969 | 0.983 | 0.527884071 |
| *Xyleborus monographus* | 40 | 2015 | 3.183 | 1.012 | 0.633478431 |
| *Xyleborus saxeseni* | 3 | 2014 | 2.459 | 0.767 | 0.322171549 |
| *Xyleborus saxeseni* | 3 | 2014 | 2.316 | 0.754 | 0.275368877 |
| *Xyleborus saxeseni* | 3 | 2014 | 2.38 | 0.777 | 0.295754572 |
| *Xyleborus saxeseni* | 3 | 2014 | 2.354 | 0.749 | 0.287364265 |
| *Xyleborus saxeseni* | 3 | 2015 | 2.279 | 0.784 | 0.263991517 |
| *Xyleborus saxeseni* | 3 | 2015 | 2.423 | 0.807 | 0.309960094 |
| *Xyleborus saxeseni* | 3 | 2015 | 2.544 | 0.816 | 0.352171867 |
| *Xyleborus saxeseni* | 3 | 2015 | 2.448 | 0.804 | 0.318409299 |
| *Xyleborus saxeseni* | 3 | 2015 | 2.422 | 0.792 | 0.309625045 |
| *Xyleborus saxeseni* | 4 | 2014 | 2.405 | 0.772 | 0.30396344 |
| *Xyleborus saxeseni* | 4 | 2014 | 2.362 | 0.808 | 0.289930003 |

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| *Xyleborus saxeseni* | 4 | 2014 | 2.372 | 0.782 | 0.29315703 |
| *Xyleborus saxeseni* | 4 | 2014 | 2.464 | 0.825 | 0.323890703 |
| *Xyleborus saxeseni* | 4 | 2014 | 2.303 | 0.744 | 0.271337586 |
| *Xyleborus saxeseni* | 4 | 2015 | 2.204 | 0.755 | 0.241832244 |
| *Xyleborus saxeseni* | 4 | 2015 | 2.314 | 0.773 | 0.274746285 |
| *Xyleborus saxeseni* | 4 | 2015 | 2.487 | 0.825 | 0.331871835 |
| *Xyleborus saxeseni* | 4 | 2015 | 2.273 | 0.791 | 0.262174447 |
| *Xyleborus saxeseni* | 4 | 2015 | 2.246 | 0.760 | 0.254093403 |
| *Xyleborus saxeseni* | 4 | 2015 | 2.368 | 0.767 | 0.291863569 |
| *Xyleborus saxeseni* | 5 | 2014 | 2.422 | 0.808 | 0.309625045 |
| *Xyleborus saxeseni* | 5 | 2014 | 2.368 | 0.785 | 0.291863569 |
| *Xyleborus saxeseni* | 5 | 2014 | 2.316 | 0.785 | 0.275368877 |
| *Xyleborus saxeseni* | 5 | 2014 | 2.42 | 0.792 | 0.308955619 |
| *Xyleborus saxeseni* | 6 | 2014 | 2.415 | 0.776 | 0.307285971 |
| *Xyleborus saxeseni* | 6 | 2014 | 2.367 | 0.792 | 0.291540756 |
| *Xyleborus saxeseni* | 6 | 2014 | 2.444 | 0.807 | 0.317047978 |
| *Xyleborus saxeseni* | 7 | 2015 | 2.132 | 0.699 | 0.221677852 |
| *Xyleborus saxeseni* | 7 | 2015 | 2.376 | 0.788 | 0.29445403 |
| *Xyleborus saxeseni* | 7 | 2015 | 2.339 | 0.773 | 0.282591452 |
| *Xyleborus saxeseni* | 7 | 2015 | 2.171 | 0.751 | 0.232460184 |
| *Xyleborus saxeseni* | 7 | 2015 | 2.287 | 0.775 | 0.26642636 |
| *Xyleborus saxeseni* | 7 | 2015 | 2.444 | 0.821 | 0.317047978 |
| *Xyleborus saxeseni* | 7 | 2015 | 2.262 | 0.760 | 0.258863282 |
| *Xyleborus saxeseni* | 8 | 2015 | 2.252 | 0.836 | 0.255875681 |
| *Xyleborus saxeseni* | 10 | 2014 | 2.351 | 0.758 | 0.286405747 |
| *Xyleborus saxeseni* | 11 | 2015 | 2.403 | 0.781 | 0.303301612 |
| *Xyleborus saxeseni* | 11 | 2015 | 2.251 | 0.782 | 0.255578099 |
| *Xyleborus saxeseni* | 11 | 2015 | 2.347 | 0.802 | 0.285130801 |
| *Xyleborus saxeseni* | 11 | 2015 | 2.468 | 0.798 | 0.325270102 |
| *Xyleborus saxeseni* | 11 | 2015 | 2.428 | 0.822 | 0.311638702 |
| *Xyleborus saxeseni* | 13 | 2014 | 2.368 | 0.814 | 0.291863569 |
| *Xyleborus saxeseni* | 13 | 2014 | 2.444 | 0.799 | 0.317047978 |
| *Xyleborus saxeseni* | 13 | 2014 | 2.404 | 0.784 | 0.303632415 |
| *Xyleborus saxeseni* | 14 | 2014 | 2.266 | 0.800 | 0.260064332 |
| *Xyleborus saxeseni* | 14 | 2014 | 2.391 | 0.806 | 0.299349356 |
| *Xyleborus saxeseni* | 14 | 2014 | 2.376 | 0.748 | 0.29445403 |
| *Xyleborus saxeseni* | 14 | 2015 | 2.323 | 0.790 | 0.277554817 |
| *Xyleborus saxeseni* | 15 | 2014 | 2.213 | 0.766 | 0.244428107 |
| *Xyleborus saxeseni* | 15 | 2014 | 2.334 | 0.774 | 0.281011486 |
| *Xyleborus saxeseni* | 16 | 2014 | 2.307 | 0.758 | 0.272574069 |
| *Xyleborus saxeseni* | 16 | 2014 | 2.462 | 0.816 | 0.323202363 |
| *Xyleborus saxeseni* | 18 | 2015 | 2.311 | 0.778 | 0.27381403 |
| *Xyleborus saxeseni* | 18 | 2015 | 2.322 | 0.758 | 0.277241885 |
| *Xyleborus saxeseni* | 18 | 2015 | 2.405 | 0.813 | 0.30396344 |
| *Xyleborus saxeseni* | 18 | 2015 | 2.181 | 0.745 | 0.23527603 |
| *Xyleborus saxeseni* | 19 | 2015 | 2.294 | 0.775 | 0.268568197 |
| *Xyleborus saxeseni* | 19 | 2015 | 2.419 | 0.796 | 0.308621242 |

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| *Xyleborus saxeseni* | 20 | 2014 | 2.351 | 0.781 | 0.286405747 |
| *Xyleborus saxeseni* | 20 | 2015 | 2.346 | 0.752 | 0.284812614 |
| *Xyleborus saxeseni* | 20 | 2015 | 2.323 | 0.775 | 0.277554817 |
| *Xyleborus saxeseni* | 20 | 2015 | 2.36 | 0.814 | 0.289287246 |
| *Xyleborus saxeseni* | 20 | 2015 | 2.224 | 0.775 | 0.247624134 |
| *Xyleborus saxeseni* | 20 | 2015 | 2.097 | 0.744 | 0.212269564 |
| *Xyleborus saxeseni* | 20 | 2015 | 2.199 | 0.761 | 0.240397496 |
| *Xyleborus saxeseni* | 21 | 2015 | 2.339 | 0.819 | 0.282591452 |
| *Xyleborus saxeseni* | 21 | 2015 | 2.3 | 0.759 | 0.270412504 |
| *Xyleborus saxeseni* | 22 | 2014 | 2.325 | 0.761 | 0.278181335 |
| *Xyleborus saxeseni* | 22 | 2014 | 2.402 | 0.798 | 0.302971033 |
| *Xyleborus saxeseni* | 22 | 2015 | 2.444 | 0.815 | 0.317047978 |
| *Xyleborus saxeseni* | 22 | 2015 | 2.224 | 0.779 | 0.247624134 |
| *Xyleborus saxeseni* | 22 | 2015 | 2.409 | 0.834 | 0.305289773 |
| *Xyleborus saxeseni* | 23 | 2015 | 2.504 | 0.807 | 0.337848325 |
| *Xyleborus saxeseni* | 25 | 2014 | 2.44 | 0.809 | 0.315690261 |
| *Xyleborus saxeseni* | 25 | 2014 | 2.513 | 0.792 | 0.341039089 |
| *Xyleborus saxeseni* | 25 | 2014 | 2.375 | 0.774 | 0.294129448 |
| *Xyleborus saxeseni* | 25 | 2014 | 2.384 | 0.764 | 0.29705866 |
| *Xyleborus saxeseni* | 25 | 2015 | 2.419 | 0.789 | 0.308621242 |
| *Xyleborus saxeseni* | 25 | 2015 | 2.27 | 0.781 | 0.261268821 |
| *Xyleborus saxeseni* | 25 | 2015 | 2.369 | 0.788 | 0.292186602 |
| *Xyleborus saxeseni* | 25 | 2015 | 2.413 | 0.803 | 0.306619678 |
| *Xyleborus saxeseni* | 26 | 2015 | 2.344 | 0.799 | 0.284176899 |
| *Xyleborus saxeseni* | 26 | 2015 | 2.254 | 0.786 | 0.256471486 |
| *Xyleborus saxeseni* | 28 | 2015 | 2.399 | 0.788 | 0.301980632 |
| *Xyleborus saxeseni* | 28 | 2015 | 2.386 | 0.795 | 0.297712034 |
| *Xyleborus saxeseni* | 29 | 2014 | 2.452 | 0.827 | 0.319774229 |
| *Xyleborus saxeseni* | 29 | 2014 | 2.393 | 0.811 | 0.300005841 |
| *Xyleborus saxeseni* | 29 | 2014 | 2.331 | 0.782 | 0.280066134 |
| *Xyleborus saxeseni* | 29 | 2014 | 2.37 | 0.814 | 0.292509857 |
| *Xyleborus saxeseni* | 29 | 2015 | 2.312 | 0.778 | 0.274124564 |
| *Xyleborus saxeseni* | 29 | 2015 | 2.378 | 0.785 | 0.295103858 |
| *Xyleborus saxeseni* | 31 | 2015 | 2.375 | 0.810 | 0.294129448 |
| *Xyleborus saxeseni* | 31 | 2015 | 2.532 | 0.783 | 0.347836167 |
| *Xyleborus saxeseni* | 37 | 2015 | 2.268 | 0.749 | 0.260666146 |
| *Xyleborus saxeseni* | 38 | 2014 | 2.247 | 0.727 | 0.254389914 |
| *Xyleborus saxeseni* | 38 | 2015 | 2.403 | 0.814 | 0.303301612 |
| *Xyleborus saxeseni* | 38 | 2015 | 2.394 | 0.804 | 0.300334416 |
| *Xyleborus saxeseni* | 38 | 2015 | 2.397 | 0.802 | 0.301321478 |
| *Xyleborus saxeseni* | 38 | 2015 | 2.371 | 0.789 | 0.292833333 |
| *Xyleborus saxeseni* | 38 | 2015 | 2.383 | 0.771 | 0.296732305 |
| *Xyleborus saxeseni* | 38 | 2015 | 2.46 | 0.830 | 0.322514927 |
| *Xyleborus saxeseni* | 41 | 2015 | 2.463 | 0.805 | 0.32354642 |
| *Xyloterus signatus* | 7 | 2015 | 3.787 | 1.433 | 0.998696525 |
| *Xyloterus signatus* | 20 | 2015 | 3.234 | 1.321 | 0.660417663 |

Table A4: SEA and SEAc of all guilds and species and niche breadth overlap calculated by overlap of standard ellipse areas with corrections for small sample sizes (SEAc) between species within feeding guilds. For the calculation of SEAc overlap species with less than five individuals were excluded. as the results would not be statistically meaningful.

**All guilds**

| | d | m | ms | x | xm | xs | xz | z |
|---|---|---|---|---|---|---|---|---|
| SEA | 22.52328 | 25.25623 | 5.065180 | 12.93676 | 17.73199 | 4.241013 | 13.73718 | 14.68040 |
| SEAc | 25.02587 | 25.34333 | 7.597771 | 13.09262 | 18.41399 | 4.453064 | 13.93066 | 14.82869 |

**SEAc overlap**

| | d | m | ms | x | xm | xs | xz | z |
|---|---|---|---|---|---|---|---|---|
| d | - | | | | | | | |
| m | 0.6476736 | - | | | | | | |
| ms | 0.2133423 | 0.1985852 | - | | | | | |
| x | 0.3882073 | 0.474838 | 0.2010404 | - | | | | |
| xm | 0.5787741 | 0.6139861 | 0.1880438 | 0.6292845 | - | | | |
| xs | 0.1779384 | 0.1757095 | 0.1942392 | 0.3366191 | 0.2418305 | - | | |
| xz | 0.5220514 | 0.475678 | 0.2406666 | 0.348772 | 0.4668505 | 0.3196592 | - | |
| z | 0.5360222 | 0.5522014 | 0.2167253 | 0.4390977 | 0.5824696 | 0.3003006 | 0.7030734 | - |

**Detrivorous**

| | | |
|---|---|---|
| *Prionocyphon serricornis* | | no overlap calculated because only one species in the detrivorous species |
| SEA | 19.51880 | |
| SEAc | 21.9586 | |

**Mycetophagous**

| | *Arpidiphorus orbiculatus* | *Cyclorhipidion bodoanus* | *Mycetophagus populi* | *Orchesia micans* | *Xyleborus dispar* | *Xyleborus germanus* | *Xyleborus saxeseni* |
|---|---|---|---|---|---|---|---|
| SEA | 5.152145 | 23.43791 | 2.630245 | 2.285614 | 21.89875 | 22.39303 | 23.10006 |
| SEAc | 6.440181 | 24.27498 | 3.156295 | 2.571316 | 22.47503 | 22.56936 | 23.49834 |

**SEAc overlap**

| | *Arpidiphorus orbiculatus* | *Cyclorhipidion bodoanus* | *Mycetophagus populi* | *Orchesia micans* | *Xyleborus dispar* | *Xyleborus germanus* | *Xyleborus saxeseni* |
|---|---|---|---|---|---|---|---|
| *Arpidiphorus orbiculatus* | - | | | | | | |
| *Cyclorhipidion bodoanus* | 0.2039874 | - | | | | | |
| *Mycetophagus populi* | 0.1672921 | 0.1300225 | - | | | | |
| *Orchesia micans* | 0.2605336 | 0.07678569 | 0.06537816 | - | | | |
| *Xyleborus dispar* | 0.2136307 | 0.5683714 | 0.1404356 | 0.07457385 | - | | |
| *Xyleborus germanus* | 0.1723118 | 0.6773071 | 0.1398487 | 0.06333957 | 0.702979 | - | |
| *Xyleborus saxeseni* | 0.2212372 | 0.7853915 | 0.1343199 | 0.08992152 | 0.6035455 | 0.6480986 | - |

**Xylophagous**

| | *Alosterna tabacicolor* | *Anobium nitidum* | *Ischnomera sanguinicollis* | *Ptilinus pectinicornis* | *Rhizophagus bipustulatus* |
|---|---|---|---|---|---|
| SEA | 9.420625 | 16.73651 | 8.653401 | 8.878990 | 4.362227 |
| SEAc | 10.362688 | 22.31535 | 9.065468 | 9.265033 | 5.452784 |

**SEAc overlap**

| | *Alosterna tabacicolor* | *Anobium nitidum* | *Ischnomera sanguinicollis* | *Ptilinus pectinicornis* | *Rhizophagus bipustulatus* |
|---|---|---|---|---|---|
| *Alosterna tabacicolor* | - | | | | |
| *Anobium nitidum* | 0.2504669 | - | | | |
| *Ischnomera sanguinicollis* | 0.544235 | 0.3004965 | - | | |
| *Ptilinus pectinicornis* | 0.4019317 | 0.2147513 | 0.5038816 | - | |
| *Rhizophagus bipustulatus* | 0.2825775 | 0.1940335 | 0.5926129 | 0.409714 | - |

**Xylomycetophagous**

no SEAc overlap calculated because only one species in the xylomycetophagous species

| | *Eucnemis capucina* |
|---|---|
| SEA | 8.753792 |
| SEAc | 9.151691 |

**Xylosaprophagous**

no SEAc overlap calculated because only one species in the xylosaprophagous species

| | *Allecula morio* |
|---|---|
| SEA | 4.376949 |
| SEAc | 4.607314 |

**Xylozoophagous**

| | *Anaspis ruficollis* | *Anaspis thoracica* | *Melanotus castanipes* | *Scraptia fuscula* |
|---|---|---|---|---|
| SEA | 11.29401 | 13.53610 | 11.88731 | 8.984655 |
| SEAc | 11.78505 | 14.76665 | 13.58549 | 10.107737 |

**SEAc overlap**

| | *Anaspis ruficollis* | *Anaspis thoracica* | *Melanotus castanipes* | *Scraptia fuscula* |
|---|---|---|---|---|
| *Anaspis ruficollis* | - | | | |
| *Anaspis thoracica* | 0.6620034 | - | | |
| *Melanotus castanipes* | 0.521213 | 0.5291206 | - | |
| *Scraptia fuscula* | 0.3710539 | 0.3019253 | 0.4227485 | - |

**Zoophagous**

| | *Abraeus perpusillus* | *Crepidophorus mutilatus* | *Hapalaraea pygmaea* | *Hesperus rufipennis* | *Hypebaeus flavipes* | *Malthodes marginatus* | *Plegaderus dissectus* | *Quedius truncicola* | *Tillus elongatus* |
|---|---|---|---|---|---|---|---|---|---|
| SEA | 2.696310 | 4.213025 | 16.11938 | 13.77710 | 5.123099 | 2.941074 | 1.485690 | 14.06044 | 3.952966 |
| SEAc | 3.595080 | 5.266282 | 17.46267 | 15.74525 | 5.489035 | 3.529289 | 1.782828 | 17.57555 | 4.392185 |

**SEAc overlap**

| | *Abraeus perpusillus* | *Crepidophorus mutilatus* | *Hapalaraea pygmaea* | *Hesperus rufipennis* | *Hypebaeus flavipes* | *Malthodes marginatus* | *Plegaderus dissectus* | *Quedius truncicola* | *Tillus elongatus* |
|---|---|---|---|---|---|---|---|---|---|
| *Abraeus perpusillus* | - | | | | | | | | |
| *Crepidophorus mutilatus* | 0.3291006 | - | | | | | | | |
| *Hapalaraea pygmaea* | 0.2058724 | 0.2750809 | - | | | | | | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Hesperus rufipennis* | 0.2283279 | 0.3186902 | 0.5149267 | - | | | | | |
| *Hypebaeus flavipes* | 0.2232315 | 0.3365681 | 0.3143297 | 0.3406034 | - | | | | |
| *Malthodes marginatus* | 0.2551148 | 0.2195687 | 0.1282091 | 0.1831436 | 0.005759011 | - | | | |
| *Plegaderus dissectus* | 0.1039951 | 0.2298219 | 0.1020937 | 0.1099234 | 0.201762 | 0.006320428 | - | | |
| *Quedius truncicola* | 0.2045501 | 0.2355313 | 0.5388812 | 0.5421116 | 0.2988147 | 0.1423351 | 0.101438 | - | |
| *Tillus elongatus* | 0.1265621 | 0.2038233 | 0.2170613 | 0.168328 | 0.1431633 | 0.01426689 | 0.2678567 | 0.1889157 | - |

Table A5: SEA and SEAc of all families and species. and niche breadth overlap calculated by overlap of standard ellipse areas with corrections for small sample sizes (SEAc) between species within families. For the calculation of SEAc overlap species with less than five individuals were excluded. as the results would not be statistically meaningful.

**All families**

| | Alleculidae | Anobiidae | Cantharidae | Cerambycidae | Cleridae | Curculionidae | Elateridae | Eucnemidae | Histeridae | Malachiidae | Melandryidae | Monotomidae | Mycetophagidae | Oedemeridae | Scirtidae | Scolytidae | Scraptiidae | Sphindidae | Staphylinidae |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SEA | 4.376949 | 15.31710 | 3.080418 | 8.115922 | 3.952966 | 6.448730 | 8.730380 | 8.753792 | 4.186518 | 5.325755 | 2.285614 | 8.506971 | 2.630245 | 8.877633 | 19.51880 | 24.54771 | 13.37847 | 5.152145 | 18.48798 |
| SEAc | 4.607314 | 15.82767 | 3.593821 | 8.792248 | 4.392185 | 8.598306 | 9.109962 | 9.151691 | 4.567111 | 5.680806 | 2.571316 | 9.280332 | 3.156295 | 9.219080 | 21.95865 | 24.64105 | 13.61318 | 6.440181 | 19.06573 |

**SEAc overlap**

| | Alleculidae | Anobiidae | Cantharidae | Cerambycidae | Cleridae | Curculionidae | Elateridae | Eucnemidae | Histeridae | Malachiidae | Melandryidae | Monotomidae | Mycetophagidae | Oedemeridae | Scirtidae | Scolytidae | Scraptiidae | Sphindidae | Staphylinidae |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Alleculidae | - | | | | | | | | | | | | | | | | | | |
| Anobiidae | 0.2749886 | - | | | | | | | | | | | | | | | | | |
| Cantharidae | 0.1970227 | 0.1029116 | - | | | | | | | | | | | | | | | | |
| Cerambycidae | 0.2255757 | 0.422577 | 0.02469998 | - | | | | | | | | | | | | | | | |
| Cleridae | 0.3538985 | 0.2764522 | 0.01056419 | 0.4588442 | - | | | | | | | | | | | | | | |
| Curculionidae | 0.3084092 | 0.3671796 | 0.163739 | 0.320605 | 0.1795057 | - | | | | | | | | | | | | | |
| Elateridae | 0.4654702 | 0.3089845 | 0.232337 | 0.2395095 | 0.224477 | 0.2927703 | - | | | | | | | | | | | | |
| Eucnemidae | 0.3375927 | 0.4742053 | 0.2494664 | 0.3694843 | 0.3394344 | 0.3990813 | 0.2882269 | - | | | | | | | | | | | |
| Histeridae | 0.5802472 | 0.2830024 | 0.1438604 | 0.2403049 | 0.2874935 | 0.1945191 | 0.5013315 | 0.2230214 | - | | | | | | | | | | |
| Malachiidae | 0.2066439 | 0.1299763 | 0 | 0.137231 | 0.1443739 | 0.1083778 | 0.4169467 | 0.05074946 | 0.3061304 | - | | | | | | | | | |
| Melandryidae | 0.01332724 | 0.08259325 | 0 | 0.0720115 | 0.02454198 | 0 | 0.109499 | 0.02656699 | 0.1152017 | 0.05819752 | - | | | | | | | | |
| Monotomidae | 0.4964601 | 0.4591221 | 0.1608108 | 0.4114069 | 0.4238851 | 0.4713106 | 0.5462436 | 0.5340217 | 0.3965074 | 0.2761704 | 0.03712061 | - | | | | | | | |
| Mycetophagidae | 0.4501549 | 0.1994162 | 0.06380249 | 0.3401559 | 0.4206321 | 0.141547 | 0.291434 | 0.2276119 | 0.400933 | 0.1533313 | 0.06537816 | 0.311767 | - | | | | | | |
| Oedemeridae | 0.4559087 | 0.5660742 | 0.1269317 | 0.5378978 | 0.4478418 | 0.535167 | 0.3306848 | 0.5810043 | 0.3250458 | 0.1530523 | 0.01527985 | 0.6427942 | 0.2738333 | - | | | | | |
| Scirtidae | 0.2098178 | 0.4415369 | 0.1629489 | 0.2745749 | 0.1879536 | 0.2578905 | 0.3824407 | 0.3998978 | 0.2079869 | 0.169813 | 0.1000714 | 0.4047827 | 0.1437381 | 0.3539941 | - | | | | |
| Scolytidae | 0.1869772 | 0.5665912 | 0.1458469 | 0.287171 | 0.1782467 | 0.3080173 | 0.3696867 | 0.3714003 | 0.1853457 | 0.1942615 | 0.07284129 | 0.3766209 | 0.1280909 | 0.366774 | 0.6343973 | - | | | |
| Scraptiidae | 0.3297487 | 0.3674201 | 0.07948435 | 0.2475028 | 0.2212562 | 0.2057601 | 0.503647 | 0.2443003 | 0.3309248 | 0.3945834 | 0.1886398 | 0.4421042 | 0.2207199 | 0.297062 | 0.434394 | 0.4008066 | - | | |
| Sphindidae | 0.1799669 | 0.1496156 | 0 | 0.1534619 | 0.1481506 | 0.060352 | 0.3987817 | 0.04894755 | 0.3272551 | 0.6010881 | 0.2605336 | 0.2298419 | 0.1672921 | 0.1424094 | 0.2104632 | 0.1876726 | 0.4730842 | - | |
| Staphylinidae | 0.2416543 | 0.3992541 | 0.1438346 | 0.239011 | 0.1937593 | 0.2734545 | 0.4778188 | 0.3286553 | 0.2395456 | 0.297959 | 0.1298298 | 0.4417485 | 0.1655481 | 0.3106155 | 0.523042 | 0.5672025 | 0.6569769 | 0.3327375 | - |

**Anobiidae**

| | *Anobium nitidum* | *Ptilinus pectinicornis* |
|---|---|---|
| SEA | 1.673.651 | 8.878.990 |
| SEAc | 22.31535 | 9.265033 |

**SEAc overlap**

| | *Anobium nitidum* | *Ptilinus pectinicornis* |
|---|---|---|
| *Anobium nitidum* | - | |
| *Ptilinus pectinicornis* | 0.2147513 | - |

**Histeridae**

| | *Abraeus perpusillus* | *Plegaderus dissectus* |
|---|---|---|
| SEA | 2.696.310 | 1.485.690 |
| SEAc | 3.595080 | 1.782828 |

**SEAc overlap**

| | *Abraeusperpusillus* | *Plegaderus dissectus* |
|---|---|---|
| *Abraeusperpusillus* | - | |
| *Plegaderus dissectus* | 0.1039951 | - |

**Elateridae**

| | *Crepidophorus mutilatus* | *Melanotus castanipes* |
|---|---|---|
| SEA | 4.213025 | 1.188731 |
| SEAc | 5.266282 | 1.358549 |

**SEAc overlap**

| | *Crepidophorus mutilatus* | *Melanotus castanipes* |
|---|---|---|
| *Crepidophorus mutilatus* | - | |
| *Melanotus castanipes* | 0.2969738 | - |

**Scolitidae**

| | *Cyclorhipidion bodoanus* | *Xyleborus dispar* | *Xyleborus germanus* |
|---|---|---|---|
| SEA | 23.43791 | 21.89875 | 22.39303 |
| SEAc | 24.27498 | 22.47503 | 22.56936 |

**SEAc overlap**

| | *Cyclorhipidion bodoanus* | *Xyleborus dispar* | *Xyleborus germanus* | *Xyleborus saxeseni* |
|---|---|---|---|---|
| *Cyclorhipidion bodoanus* | - | | | |
| *Xyleborus dispar* | 0.5683714 | - | | |
| *Xyleborus germanus* | 0.6773071 | 0.702979 | - | |
| *Xyleborus saxeseni* | 0.7853915 | 0.603546 | 0.648099 | - |

**Scraptiidae**

| | *Anaspis ruficollis* | *Anaspis thoracica* | *Scraptia fuscula* |
|---|---|---|---|
| SEA | 11.29401 | 13.53610 | 8.984655 |
| SEAc | 11.78505 | 14.76665 | 10.10773 |

**SEAc overlap**

| | *Anaspis ruficollis* | *Anaspis thoracica* | *Scraptia fuscula* |
|---|---|---|---|
| *Anaspis ruficollis* | - | | |
| *Anaspis thoracica* | 0.6620034 | - | |
| *Scraptia fuscula* | 0.3710539 | 0.3019253 | - |

**Staphilinidae**

| | *Hapalaraea pygmaea* | *Hesperus rufipennis* | *Quedius truncicola* |
|---|---|---|---|
| SEA | 16.11938 | 13.77710 | 14.06044 |
| SEAc | 17.46267 | 15.74525 | 17.57555 |

**SEAc overlap**

| | *Hapalaraea pygmaea* | *Hesperus rufipennis* | *Quedius truncicola* |
|---|---|---|---|
| *Hapalaraea pygmaea* | - | | |
| *Hesperus rufipennis* | 0.5149267 | - | |
| *Quedius truncicola* | 0.5388812 | 0.542112 | - |

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(§ 9 Satz 2 Nr. 3 PromO BayNAT)

Hiermit versichere ich eidesstattlich. dass ich die Arbeit selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

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