Communities of saproxylic beetles associated with the White-backed Woodpecker (*Dendrocopos leucotos*) in temperate forests of central Europe

Inaugural dissertation
of the Faculty of Science,
University of Bern

Presented by

Romain Angeleri
from Valence (FR)

Supervisor of the doctoral thesis:
Prof. Dr. R. Arlettaz
Institute of Ecology and Evolution

Prof Dr. T. Lachat
Bern University of Applied Science - HAFL

Communities of saproxylic beetles associated with the White-backed Woodpecker (*Dendrocopos leucotos*) in temperate forests of central Europe

Inaugural dissertation
of the Faculty of Science,
University of Bern

Presented by

Romain Angeleri
from Valence (FR)

Supervisor of the doctoral thesis:
Prof. Dr. R. Arlettaz
Institute of Ecology and Evolution

Prof Dr. T. Lachat
Bern University of Applied Science - HAFL

Accepted by the Faculty of Science.

Bern, 04 February 2023

The Dean
Prof. Dr. Marco Herwegh

Layout & figures: Romain Angeleri

Photo & illustration credits:

Summary: Yvonne Rogenmoser

Chapter 1: Simon Niederbacher

Chapter 2: Romain Angeleri

Chapter 3: Justin Reymond

General Discussion: Yvonne Rogenmoser

Everything you see has its roots in the unseen world […]

- Rumi -

Table of Contents

Summary

To answer the consequences of the Anthropocene and its associated erosion of biodiversity, response time, accuracy, and cost-effectiveness must be strongly considered when developing biodiversity conservation programs. Because of limited human and financial support, conservationists must prioritize relevant ecological areas, ideally with a high buffering capacity accounting for species loss. Among other conservation tools, indicator species help in assessing a specific environmental condition. From a conservation perspective, species used as indicators of naturalness would also endorse the role of an umbrella species, in the hope that the protection of the surrogate's habitat will simultaneously benefit the array of species encompassed within it.

In Fennoscandia and Eastern Europe, the White-backed Woodpecker (*Dendrocopos leucotos*) was proposed as an umbrella species for the saproxylic guild, including beetles. While the bird species went locally extinct due to intensive logging activity, it is now recolonizing its former habitat by expanding its breeding home range to extensively managed forest stands of central Europe. Because the bird species is often referenced as an old-growth deciduous forest specialist, conservationists questioned its role as a surrogate species for saproxylic beetle diversity in this specific anthropized context. The aim of the presented study is to fill in the knowledge gap regarding the relation between the central European White-backed Woodpeckers population and the saproxylic beetle communities.

From 2018 on, I characterized saproxylic beetle communities found in the White-backed Woodpecker habitat using three different sampling methods. First, passive and non-attractive flight interception traps were used to quantify flying beetle communities occurring at the woodpecker's breeding home range scale. Second, in situ eclector traps were used to directly quantify communities emerging from dead standing trees, informing on the beetle species associated to this type of dead wood, referenced as of prime importance in the bird's foraging strategy. Third, standardized fresh dead wood items were exposed for colonization along the vertical axis of the forests and set in rearing traps, informing on the colonization potential of the woodpecker's habitat by the pioneer saproxylic beetle guild. While the first two methods were capitalizing on local radio-frequency data to quantify the White-backed Woodpecker's activity, either in its breeding home range or in absence sites, the vertical stratification experiment was conducted in presence/absence sites distributed in along the western-Eurasian distribution of the woodpecker and as a collaboration between several research institutes.

I found the number of flying threatened saproxylic beetle species to be positively correlated with the White-backed Woodpecker’s activity. In addition, multiple saproxylic beetle species – including threatened ones – were to be associated with the bird’s breeding home range, emphasizing the importance of its habitat for saproxylic beetle diversity. Saproxylic beetle communities emerging from dead standing trees were highly heterogeneous, regardless of the White-backed Woodpecker activity, emphasizing the overall importance of this type of dead wood items in supporting local saproxylic beetle diversity. Experimental study of dead wood colonization along the three forest strata revealed strong partitioning of the community as a function of elevation above ground and exposure time, highlighting the importance of a diversified dead wood resource, both along a temporal continuum and in the vertical gradient of the forest.

In addition to evidencing the role of the White-backed Woodpecker as an umbrella species for threatened saproxylic beetles and indicator for forest naturalness, I propose an extensive framework for conservation programs aiming at supporting dead-wood dependent biodiversity. We believe this work will contribute to opening new opportunities for using the White-backed Woodpecker as a meaningful surrogate species for central European saproxylic diversity.

General Introduction

While past extinctions were mainly caused by natural phenomena, the massive loss of species we witness in the 21st century – known as the sixth mass extinction – is driven by a relentless anthropogenic pressure (Pimm & Raven, 2000; Vane-Wright et al., 1991; Wang-Erlandsson et al., 2022). Although being at its highest in agricultural and urban areas, it does not stop at the forest edges. While forests cover around 30% of the landmass (FOREST EUROPE 2020), they have been subject to a strong stand homogenization as an effect of intensive logging activity and dead wood removal over the last centuries (Speight, 1989). These practices have been repeatedly documented on having detrimental effects on forest biodiversity and on biome stability (Gossner et al., 2013; Müller et al., 2007; Ranius et al., 2018; Thorn et al., 2014). Due to their dependency on dead wood and their important role in the forest cycle (e.g., dead wood decay, nutrient cycling, tree regeneration; see Hilmers et al., 2018; Seibold et al., 2021), saproxylic organisms are a key component of the forest ecosystem and thus must be protected. Nevertheless, most saproxylic species lack the adaptive plasticity to respond to rapid and drastic human-induced structural and climatic changes in their habitat. If no conservation action is taken, a significant fraction of the forest-dwelling community could face local extinction. To protect this sensitive yet fundamental component of biodiversity, conservation tools allowing an acute, rapid, and cost-efficient assessment of the ecosystem must therefore be considered and evaluated.

Indicator and umbrella species?

The term "indicator species" has three distinct meanings. They are a species, or group of species, that reflect the biotic or abiotic state of an environment; reveal evidence for, or the impacts of, environmental change; or indicate the diversity of other species, taxa, or entire communities within an area (Levin, 2001).

More than a century ago, Hall & Grinnell (1919) proposed the "indicator species" concept, defined as "species being distributed across specific life-zones". While back then the association of species with a specific habitat was roughly described in terms of longitude, latitude and topography, ecological research steadily started integrating supplementary parameters characterizing ecosystems (e.g., climate, vegetation type, associated resource, trophic interaction, level of anthropization). This increased resolution on environmental characteristics improved the knowledge of the informed naturalists about where and when to find a specific species. Since then, the "indicator species" concept has evolved substantially and is now defined as "an organism whose characteristics (e.g., presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest." (Lindenmayer et al., 2000). In practice, species from many different taxonomic groups have been used as surrogate for species richness and/or ecological processes. These include epiphytes (Oswaldo et al., 2022), fungi (Müller et al., 2007), invertebrates (Bucher et al., 2019; Eckelt et al., 2018; Kašák et al., 2019; Roth & Weber, 2007), fishes (Albert et al., 2018; Branton & Richardson, 2014), reptiles (Albert et al., 2018; Hager, 1998), amphibians (Campos et al., 2014), mammals (Albert et al., 2018; Mortelliti et al., 2022; Zyśk-Gorczyńska et al., 2015) and birds (Assandri et al., 2017; Roth & Weber, 2007).

While the use of indicators species increased over time, a strong bias towards charismatic species started to develop (see Albert et al., 2018). Their excessive promotion in the public and politic spheres (Jepson & Barua, 2015) resulted in an inhomogeneous landscape of studies (Buxton et al., 2020; Oettel & Lapin, 2021), ultimately causing protection programs to focus on ecological areas that should not be prioritized (Albert et al., 2018; Cusack et al., 2022). Nonetheless, attributing a charismatic status to a neglected yet ecologically relevant species remains a valid strategy to raise public awareness and funding. Carignan & Villard (2002) proposed that ideal indicators should endorse several roles such as being (1) a flagship species (i.e., species that can easily attract public support for conservation), (2) a resource-limited species (i.e., species requiring specific resources that may be in critically short supply either temporally or spatially), (3) a process-limited species (i.e., species sensitive to the level, rate, spatial characteristics or timing of some ecological processes), (4) a dispersal-limited species (i.e., species that are limited in their ability to move from patch to patch or that face a high mortality risk in trying to do so), (5) a keystone species (i.e., species whose strong interactions with other species generate large effects in relation to their abundance), and (6) an umbrella species (i.e., species that require large areas of suitable habitat to maintain viable populations and whose requirements for persistence are believed to encapsulate those of an array of associated species).

The [White-backed] Woodpecker

Woodpeckers are well-suited as forest-related indicator species. Their fit can be attributed to their rapid identification by sight and sound (Williams & Gaston, 1994), their strong bound to the dead wood resource (Aszalós et al., 2020). Besides being attractive for birdwatchers (Mikusiński & Angelstam, 1997), they are a proved medium for the wider audience (see *Woody Woodpecker*, mascot of Universal Studios). For conservation biology, Mikusinski et al., (2001) showed that the numbers of forest bird specialists and woodland bird generalists were positively correlated with the number of woodpecker species observed within a forest stand, and proposed the use of woodpecker density as a proxy for woodland bird richness in forests lacking avian population information. In boreal forests, the Black-backed Woodpecker (*Picoides arcticus*) was associated with old-growth stands with a high temporal continuity in dead wood (Martin et al., 2021) while the Yellow-bellied Sapsucker (*Sphyropicus varius*) was principally observed foraging on moribund deciduous trees (Nappi et al., 2015). In northern Europe, Roberge & Angelstam (2006) found the Middle Spotted Woodpecker (*Dendrocopos medius*) and the Lesser Spotted Woodpecker (*Dendrocopos minor*) to be good indicators for forest bird diversity in deciduous forests, whereas the Three-toed Woodpecker (*Picoides tridactylus*) was the best fit in coniferous forests. In Fenno-Scandinavia, the White-backed Woodpecker (*Dendrocopos leucotos*) has been demonstrated to be a suitable surrogate species for forest birds and red-listed cryptogam diversity (Roberge et al., 2008) as well as for red-listed saproxylic beetles (Bell et al., 2015; Jonsell et al., 2004).

The White-backed Woodpecker is a palearctic species inhabiting a wide band of the Eurasian continent, spanning from Spain to Japan, and from Turkey to Norway (Winkler et al., 1995). While the species is represented by a dozen of forms (Campion et al., 2020), its European population can be divided into two subspecies. Whereas the *Dendrocopos leucotos lilfordi* form is an isolated subspecies (Abruzzi, Asia Minor, Armenia, Azerbaijan, Balkan Peninsula, Georgia, Pyrenees and Caucasus mountains), *Dendrocopos leucotos leucotos* form is more widespread (Gerdzhikov et al., 2018; Melletti & Penteriani, 2003). Due to intensive logging activities and dead wood removal since the beginning of the industrialization era, the species experienced a strong global population decline with some local extinctions in Northern (Carlson, 2000; Mikusiński & Angelstam, 1997; Mild & Stighäll, 2017; Virkkala et al., 1993) and Eastern Europe (Czeszczewik & Walankiewicz, 2006).

While the White-backed Woodpecker is still one of the rarest woodpecker species associated with central European broadleaved woodlands, the population of this old-growth and mature forest specialist (Carlson, 2000) is now considered to be stable. In central Europe, the species is even recolonizing its former habitat, with its expansion front lying in the Eastern Swiss Alps (Mollet et al., 2009). While the White-backed Woodpecker is told to be associated with forest's attributes typically characterizing old-growth stands (e.g., high mean diameter at breast height of live and standing dead trees, see Ettwein et al., 2020), this habitat expansion has been attributed to the overall increase of the dead wood amount in the European landscape over the last decades (Brändli & Abegg, 2009; FOREST EUROPE, 2020), thanks to the adoption of extensive forest management strategies.

The White-backed Woodpecker heavily rely on the dead wood resource for its foraging strategy (Ettwein et al., 2020; Urkijo-Letona et al., 2020). its diet mainly consists of invertebrates, especially large larvae such as those of Cerambycids (see Gustaf, 1988; Hogstad & Stenberg, 1997) found in dead standing trees (Bühler, 2009). Although firm evidence is still lacking, the role of the White-backed Woodpecker as a top-predator of saproxylic invertebrates, and consequently its association with large amounts of dead wood as found in primeval forests, suggests that it serves as an umbrella species for (threatened) saproxylic beetles (Bell, Hjältén, Nilsson, JØrgensen, et al., 2015; Jonsell et al., 2004; Martikainen et al., 1998).

Saproxylic [beetle] diversity in dead wood

Saproxylic species richness is estimated to encompass one-fourth of the taxa found in temperate forests (Lachat & Müller, 2018). The roots of the term saproxylic lie in ancient Greek, defined by *sapros* and *xylon*, meaning "rotten" and "wood". Stokland (2012) defined a saproxylic organism as "any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened or dead trees". The saproxylic guild is represented by many taxonomic groups, including epiphytes (Oswaldo et al., 2022), lichens and bryophytes (Larrieu et al., 2019), fungi (Haeler et al., 2021; Meyer et al., 2021; Müller et al., 2007), amphibians (Basham et al., 2022; Chai et al., 2021), reptiles (Shelton et al., 2020; Vasconcelos et al., 2020), airborne and terrestrial mammals (Gibbons et al., 2002; Gottfried et al., 2019; Paillet et al., 2018), cavity-nesting birds (e.g., woodpeckers, nuthatches, tits, treecreepers; Fröhlich & Ciach, 2020; Redolfi De Zan, Battisti, & Carpaneto, 2014), and invertebrates (Gossner & Damken, 2018; Grove, 2002; Jonsell et al., 1998; Speight, 1989; Stokland et al., 2012).

In central Europe, saproxylic beetles are arguably the most speciose group of the saproxylic guild (Graf et al., 2022), with 56% of all forest beetles being associated with dead wood (Köhler, 2000). Due to the high diversity of this group, they cover many functions ensuring the sustainable development of the forest ecosystem. Saproxylic beetles represent an important food source for theie predators, especially during their larval stages (Martin et al., 2021; Hogstad & Stenberg, 1997; Versluijs et al., 2020). Many species also bear the role of pollinators during their adult stage (Micó et al., 2020). However, the most important contribution of saproxylic beetles in the successional dynamic of the forest ecosystem is through dead wood decay (Seibold et al., 2021), achieved in symbiosis with other organisms (e.g., fungi, see You et al., 2015; nematodes, see Davis & Prouty, 2019).

While conservationists regard saproxylic beetles as keystone and/or engineer species opening new opportunities for the perennial development of the forests and its associated biodiversity, the logging industry often perceives them as a pest (Fierro et al., 2023; Müller et al., 2008; Tsikas & Karanikola, 2022). Yet insect outbreaks wiping out hectares of forest are mainly a result of extreme climatic events (Frei et al., 2022; Klesse et al., 2022) combined with stand homogenization (e.g., monoculture of exotic tree species, falling of old and senescent trees, removal of dead wood items) introduced by intensive forest management regime (Gossner et al., 2013). Ultimately, forest management generally affects structural characteristics and key ecological processes of the forest ecosystem (Müller 2007), often disrupting the dead wood phenology on which saproxylic beetles depend on (Eckelt et al., 2018; Grove, 2002; Martikainen et al., 2000; Müller et al., 2007; Siitonen, 2001). According to the European Red-

List for saproxylic beetles (Nieto & Alexander, 2010), 17.9% of the evaluated species are categorized as threatened and 12.9% of the population is thought to be declining. Due to their strong dependence on dead wood, saproxylic beetles are highly sensitive to habitat changes and are commonly used as indicators for forest naturalness (Eckelt et al., 2018; Kašák et al., 2019; Lachat et al., 2014; Schmidl & Bussler, 2004). However, the monitoring of threatened taxa is challenging as they often occur at low densities, have reduced mobility, and their identification to the species level rely on endangered taxonomists sharing identical attributes with their pinned specimens.

Considering (1) the evidenced role of the White-backed Woodpecker as an indicator species for taxonomic groups associated to its habitat, (2) its scarce occurrence at the landscape scale caused by the lack of highly qualitative forests, and (3) its dependence to saproxylic invertebrates, the species may be an ideal candidate as an umbrella – and to a broader extent, indicator – species for saproxylic communities in the recently colonized beech-dominated forests of Central Europe.

Scope of the thesis

This doctoral dissertation is part of a larger conservation project started by the Swiss Ornithological Institute in spring 2015. In cooperation with local partners, we investigated which factors enable the occurrence of White-backed Woodpeckers in managed forests in order to develop forest management measures aiming at protecting its population in Eastern Switzerland, Liechtenstein Western Austria, and to a broader extent, in its western Eurasian distribution.

While another dissertation focused on questions oriented towards the bird's habitat selection strategy, the goal of my work was to improve knowledge on saproxylic beetle communities associated with the White-backed Woodpecker along its Eurasian distribution, with a particular focus on its western-central European expansion front. Using multiple sampling methods, we characterized saproxylic beetle communities present within and outside of the woodpecker's habitat. This extensive study helps unravelling the long-lasting status quo over the White-backed Woodpecker's role as an umbrella species for threatened saproxylic beetle diversity and provides new information regarding saproxylic communities in relation to the bird's foraging ecology. Ultimately, this work will help practitioners to better target habitat management actions aiming at preserving the Eurasian White-backed Woodpecker population and its associated saproxylic beetle communities.

Outline of the thesis

In Chapter 1, we investigated the potential of the White-backed Woodpecker as an umbrella species for flying threatened saproxylic beetles. We sampled beetle communities using passive non-attractive flight interception traps in areas with different activity levels of our focal bird species. Using radio-frequency data, we identified "White-backed Woodpecker's zones of interest" (i.e., forest patches with either "high" or "low" activity of the bird) and forest patches with its ascertained absence (i.e., "control"). Overall, our results identified the White-backed Woodpecker to be a suitable umbrella species for flying threatened saproxylic beetles associated to its central European habitat.

In Chapter 2, we examined the saproxylic beetle communities which the White-backed Woodpecker could potentially excavate during its foraging activities on dead standing trees. We installed non-destructive in situ eclector traps on dead standing European beech trees and left them for two years, in the same "White-backed Woodpecker's zones of interest" as the ones used in Chapter 1. Using confirmatory path analysis, we compared the direct and indirect effects of forest characteristics on both emerging saproxylic beetle communities and radio-frequency telemetry-derived White-backed Woodpecker activity. Overall, our results bring attention on the importance of mature forest attributes for supporting the recruitment of large standing dead trees over time and thus supporting the White-backed Woodpecker population and the saproxylic beetle communities.

In Chapter 3, we explored the potential of saproxylic beetles to colonize dead wood in forest stands across Europe, comparing White-backed Woodpecker's breeding sites against uninhabited sites. Spanning along the Eurasian distribution of the bird, this large-scale experiment included five different countries (Austria, Czechia, Germany, Liechtenstein, and Switzerland). We exposed a total of 408 standardized dead wood items, for two years, in three forest strata (ground, understory, canopy). The outcome describes the importance of a diversified access to dead wood (i.e., temporal continuum and vertical positioning) in a forest stand for early colonizing saproxylic beetles. This colonizing community may in turn be used as a food source by the White-backed Woodpecker and other saproxylic predators, especially in wintertime when the majority of the dead wood items on the ground are not accessible due to snow cover.

References

Albert, C., Luque, G. M., & Courchamp, F. (2018). The twenty most charismatic species. PLoS ONE, 13(7), e0199149. https://doi.org/10.1371/journal.pone.0199149

Assandri, G., Bogliani, G., Pedrini, P., & Brambilla, M. (2017). Insectivorous birds as 'non-traditional' flagship species in vineyards: Applying a neglected conservation paradigm to agricultural systems. Ecological Indicators, 80, 275–285. https://doi.org/10.1016/j.ecolind.2017.05.012

Aszalós, R., Szigeti, V., Harmos, K., Csernák, S., Frank, T., & Ónodi, G. (2020). Foraging Activity of Woodpeckers on Various forms of Artificially Created Deadwood. Acta Ornithologica, 55(1). https://doi.org/10.3161/00016454AO2020.55.1.007

Aulén, G. (1988). Ecology and distribution history of the White-backed Woodpecker Dendrocopos leucotos in Sweden [Dissertation]. Swedish University of Agricultural Science.

Basham, E. W., González-Pinzón, M., Romero-Marcucci, A., Carl, N., Baecher, J. A., & Scheffers, B. R. (2022). Large, old trees define the vertical, horizontal, and seasonal distributions of a poison frog. Oecologia, 199(2), 257–269. https://doi.org/10.1007/s00442-022-05108-9

Bell, D., Hjältén, J., Nilsson, C., Jørgensen, D., & Johansson, T. (2015). Forest restoration to attract a putative umbrella species, the White-backed Woodpecker, benefited saproxylic beetles. Ecosphere, 6(12), 1-14(278). https://doi.org/10.1890/ES14-00551.1

Brändli, U.-B., & Abegg, M. (2009). Der Schweizer Wald wird immer natürlicher. Wald Und Holz, 90(7), 27–29.

Branton, M. A., & Richardson, J. S. (2014). A test of the umbrella species approach in restored floodplain ponds. Journal of Applied Ecology, 51(3), 776–785. https://doi.org/10.1111/1365-2664.12248

Bucher, R., Nickel, H., Kaib, S., Will, M., Carchi, J., Farwig, N., & Schabo, D. G. (2019). Birds and plants as indicators of arthropod species richness in temperate farmland. Ecological Indicators, 103, 272–279. https://doi.org/10.1016/j.ecolind.2019.04.011

Bühler, U. (2009). Totholz – existenziell für den Weissrückenspecht in Nordbünden | Dead wood – a vital necessity for the White-backed Woodpecker in the

Grisons. Schweizerische Zeitschrift für Forstwesen, 160(7), 210–217. https://doi.org/10.3188/szf.2009.0210

Buxton, R. T., Avery-Gomm, S., Lin, H.-Y., Smith, P. A., Cooke, S. J., & Bennett, J. R. (2020). Half of resources in threatened species conservation plans are allocated to research and monitoring. Nature Communications, 11(1), 4668. https://doi.org/10.1038/s41467-020-18486-6

Campion, D., Pardo, I., Elósegui, M., & Villanua, D. (2020). Gps Telemetry and Home Range of the White-backed Woodpecker Dendrocopos leucotos: Results of the First Experience. Acta Ornithologica, 55(1). https://doi.org/10.3161/00016454AO2020.55.1.008

Campos, F. S., Trindade-Filho, J., Brito, D., Llorente, G. A., & Solé, M. (2014). The efficiency of indicator groups for the conservation of amphibians in the Brazilian Atlantic Forest. Ecology and Evolution, 4(12), 2505–2514. https://doi.org/10.1002/ece3.1073

Carignan, V., & Villard, M. A. (2002). Selecting indicator species to monitor ecological integrity: A review. Environmental Monitoring and Assessment, 78(1), 45–61. https://doi.org/10.1023/A:1016136723584

Carlson, A. (2000). The effect of habitat loss on a deciduous forest specialist species: The White-backed Woodpecker (Dendrocopos leucotos). Forest Ecology and Management, 131(1–3), 215–221. https://doi.org/10.1016/S0378-1127(99)00215-7

Chai, L., Yin, C., Kamau, P. M., Luo, L., Yang, S., Lu, X., Zheng, D., & Wang, Y. (2021). Toward an understanding of tree frog (Hyla japonica) for predator deterrence. Amino Acids, 53(9), 1405–1413. https://doi.org/10.1007/s00726-021-03037-0

Cusack, J. J., Nilsen, E. B., Israelsen, M. F., Andrén, H., Grainger, M., Linnell, J. D. C., Odden, J., & Bunnefeld, N. (2022). Quantifying the checks and balances of collaborative governance systems for adaptive carnivore management. Journal of Applied Ecology, 59(4), 1038–1049. https://doi.org/10.1111/1365-2664.14113

Czeszczewik, D., & Walankiewicz, W. (2006). Logging affects the White-backed Woodpecker Dendrocopos leucotos distribution in the Białowieża Forest. Annales Zoologici Fennici, 43(2), 221–227.

Davis, A. K., & Prouty, C. (2019). The sicker the better: Nematode-infected passalus beetles provide enhanced ecosystem services. Biology Letters, 15(5), 20180842. https://doi.org/10.1098/rsbl.2018.0842

Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., Cizek, L., Frei, A., Holzer, E., Kadej, M., Kahlen, M., Köhler, F., Möller, G., Mühle, H., Sanchez, A., Schaffrath, U., Schmidl, J., Smolis, A., Szallies, A., … Seibold, S. (2018). "Primeval forest relict beetles" of Central Europe: A set of 168 umbrella species for the protection of primeval forest remnants. Journal of Insect Conservation, 22(1), 15–28. https://doi.org/10.1007/s10841-017-0028-6

Ettwein, A., Korner, P., Lanz, M., Lachat, T., Kokko, H., & Pasinelli, G. (2020). Habitat selection of an old-growth forest specialist in managed forests. Animal Conservation, 23(5), 547–560. https://doi.org/10.1111/acv.12567

Fierro, A., Vergara, P. M., Elgueta, M., Carvajal, M. A., & Alaniz, A. J. (2023). A saproxylic weevil acts as an ecosystem engineer: Impacts across multiple trophic levels. Forest Ecology and Management, 527, 120603. https://doi.org/10.1016/j.foreco.2022.120603

FOREST EUROPE. (2020). State of Europe's Forests 2020.

Frei, E. R., Gossner, M. M., Vitasse, Y., Queloz, V., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Uitentuis, I., von Arx, G., & Wohlgemuth, T. (2022). European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. Plant Biology, 24(7), 1132–1145. https://doi.org/10.1111/plb.13467

Fröhlich, A., & Ciach, M. (2020). Dead tree branches in urban forests and private gardens are key habitat components for woodpeckers in a city matrix. Landscape and Urban Planning, 202, 103869. https://doi.org/10.1016/j.landurbplan.2020.103869

Gerdzhikov, G. P., Georgiev, K. B., Plachiyski, D. G., Zlatanov, T., & Shurulinkov, P. S. (2018). Habitat Requirements of the White-backed Woodpecker Dendrocopos leucotos lilfordi (Sharpe & Dresser, 1871) (Piciformes: Picidae) in Strandzha Mountain, Bulgaria. Acta Zoologica Bulgarica, 70(4), 527–534.

Gibbons, P., Lindenmayer, D. B., Barry, S. C., & Tanton, M. T. (2002). Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. Biological Conservation, 103(1), 1–12. https://doi.org/10.1016/S0006-3207(01)00109-4

Gossner, M. M., & Damken, C. (2018). Diversity and Ecology of Saproxylic Hemiptera. In Ulyshen, M. D., (Ed.), Saproxylic Insects (Vol. 1, pp. 263–317). Springer International Publishing. https://doi.org/10.1007/978-3-319-75937-1_9

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W., & Müller, J. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology, 27(3), 605–614. https://doi.org/10.1111/cobi.12023

Gottfried, I., Gottfried, T., & Zając, K. (2019). Bats use larval galleries of the endangered beetle Cerambyx cerdo as hibernation sites. Mammalian Biology, 95, 31–34. https://doi.org/10.1016/j.mambio.2019.01.002

Graf, M., Seibold, S., Gossner, M. M., Hagge, J., Weiß, I., Bässler, C., & Müller, J. (2022). Coverage based diversity estimates of facultative saproxylic species highlight the importance of deadwood for biodiversity. Forest Ecology and Management, 517, 120275. https://doi.org/10.1016/j.foreco.2022.120275

Grove, S. J. (2002). Saproxylic Insect Ecology and the Sustainable Management of Forests. Annual Review of Ecology and Systematics, 33(1), 1–23. https://doi.org/10.1146/annurev.ecolsys.33.010802.150507

Haeler, E., Bergamini, A., Blaser, S., Ginzler, C., Hindenlang, K., Keller, C., Kiebacher, T., Kormann, U. G., Scheidegger, C., Schmidt, R., Stillhard, J., Szallies, A., Pellissier, L., & Lachat, T. (2021). Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. Landscape Ecology, 36(1), 89–104. https://doi.org/10.1007/s10980-020-01115-4

Hager, H. A. (1998). Area-sensitivity of reptiles and amphibians: Are there indicator species for habitat fragmentation? Écoscience, 5(2), 139–147. https://doi.org/10.1080/11956860.1998.11682463

Hall, H. M., & Grinnell, J. (1919). Life-zone indicators in California. Proceedings of the California Academy of Sciences, 9(2), 37–67.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018). Biodiversity along temperate forest succession. Journal of Applied Ecology, 55(6), 2756–2766. https://doi.org/10.1111/1365-2664.13238

Jepson, P., & Barua, M. (2015). A Theory of Flagship Species Action. Conservation and Society, 13(1), 95. https://doi.org/10.4103/0972-4923.161228

Jonsell, M., Weslien, J., & Ehnström, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation, 7(6), 749–764. https://doi.org/10.1023/A:1008888319031

Jonsell, M., Nittérus, K., & Stighäll, K. (2004). Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation, 118(2), 163–173. https://doi.org/10.1016/j.biocon.2003.08.017

Kašák, J., Mazalová, M., Šipoš, J., Foit, J., Hučín, M., & Kuras, T. (2019). Habitat preferences of Ceruchus chrysomelinus, an endangered relict beetle of the natural Central European montane forests. Insect Conservation and Diversity, 12(3), 206–215. https://doi.org/10.1111/icad.12338

Klesse, S., Wohlgemuth, T., Meusburger, K., Vitasse, Y., von Arx, G., Lévesque, M., Neycken, A., Braun, S., Dubach, V., Gessler, A., Ginzler, C., Gossner, M. M., Hagedorn, F., Queloz, V., Samblás Vives, E., Rigling, A., & Frei, E. R. (2022). Long-term soil water limitation and previous tree vigor drive local variability of drought-induced crown dieback in Fagus sylvatica. Science of The Total Environment, 851, 157926. https://doi.org/10.1016/j.scitotenv.2022.157926

Köhler F. (2000). Totholzkäfer in Naturwaldzellen des nördlichen Rheinlands: Vergleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung: Naturwaldzellen Teil VII. Schriftenreihe der Landesanstalt für Ökologie, Bodenordnung und Forsten, Landesamt für Agrarordnung, Nordrhein-Westfalen, Bd. 18. Landesanstalt für Ökologie, Bodenordnung und Forsten [etc.], Recklinghausen

Lachat, T., Brang, P., Bollmann, K., Brändli, U.-B., Bütler, R., Herrmann, S., Olivier, S., & Wermelinger, B. 2014: Bois mort en forêt. Formation, importance et conservation. Not. prat. 52: 12 p.

Lachat, T., & Müller, J. (2018). Importance of Primary Forests for the Conservation of Saproxylic Insects. In Ulyshen, M. D., (Ed.), Saproxylic Insects (Vol. 1, pp. 581–605). Springer International Publishing. https://doi.org/10.1007/978-3-319-75937-1_17

Larrieu, L., Gosselin, F., Archaux, F., Chevalier, R., Corriol, G., Dauffy-Richard, E., Deconchat, M., Gosselin, M., Ladet, S., Savoie, J.-M., Tillon, L., & Bouget,

C. (2019). Assessing the potential of routine stand variables from multi-taxon data as habitat surrogates in European temperate forests. Ecological Indicators, 104, 116–126. https://doi.org/10.1016/j.ecolind.2019.04.085

Levin, S. A. (Ed.). (2001). Encyclopedia of biodiversity. Academic Press.

Lindenmayer, D. B., Margules, C. R., & Botkin, D. B. (2000). Indicators of Biodiversity for Ecologically Sustainable Forest Management. Conservation Biology, 14(4), 941–950. https://doi.org/10.1046/j.1523-1739.2000.98533.x

Martikainen, P., Kaila, L., & Haila, Y. (1998). Threatened Beetles in White-backed Woodpecker Habitats. Conservation Biology, 12(2), 293–301. https://doi.org/10.1111/j.1523-1739.1998.96484.x

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation, 94(2), 199–209. https://doi.org/10.1016/S0006-3207(99)00175-5

Martin, M., Tremblay, J. A., Ibarzabal, J., & Morin, H. (2021). An indicator species highlights continuous deadwood supply is a key ecological attribute of boreal old-growth forests. Ecosphere, 12(5), 1-19. https://doi.org/10.1002/ecs2.3507

Melletti, M., & Penteriani, V. (2003). Nesting and feeding tree selection in the endangered White-backed Woodpecker, Dendrocopos leucotos lilfordi. The Wilson Bulletin, 115(3), 299–306. https://doi.org/10.1676/03-022

Meyer, S., Rusterholz, H., & Baur, B. (2021). Saproxylic insects and fungi in deciduous forests along a rural–urban gradient. Ecology and Evolution, 11(4), 1634–1652. https://doi.org/10.1002/ece3.7152

Micó, E., Ramilo, P., Thorn, S., Müller, J., Galante, E., & Carmona, C. P. (2020). Contrasting functional structure of saproxylic beetle assemblages associated to different microhabitats. Scientific Reports, 10(1520), 1-11. https://doi.org/10.1038/s41598-020-58408-6

Mikusiński, G., & Angelstam, P. (1997). European Woodpeckers and anthropogenic habitat change: A review. Vogelwelt, 118, 277–283.

Mikusinski, G., Gromadzki, M., & Chylarecki, P. (2001). Woodpeckers as Indicators of Forest Bird Diversity. Conservation Biology, 15(1), 208-217.

Mild, K. & Stighäll, K. 2005: Action Plan for the Conservation of the Swedish Population of White-backed Woodpecker (Dendrocopos leucotos). Swedish Environmental Protection Agency, Report 5486. Stockholm, Sweden. (In Swedish).

Mollet, P., Zbinden, N., & Schmid, H. (2009). Steigende Bestandszahlen bei Spechten und anderen Vogelarten dank Zunahme von Totholz? | An increase in the population of woodpeckers and other bird species thanks to an increase in the quantities of deadwood? Schweizerische Zeitschrift Fur Forstwesen, 160(11), 334–340. https://doi.org/10.3188/szf.2009.0334

Mortelliti, A., Brehm, A. M., & Evans, B. E. (2022). Umbrella effect of monitoring protocols for mammals in the Northeast US. Scientific Reports, 12(1), 1–12. https://doi.org/10.1038/s41598-022-05791-x

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., & Duelli, P. (2008). The European spruce bark beetle Ips typographus in a national park: From pest to keystone species. Biodiversity and Conservation, 17(12), 2979–3001. https://doi.org/10.1007/s10531-008-9409-1

Müller, J., Hothorn, T., & Pretzsch, H. (2007). Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech Fagus sylvatica L. Forest Ecology and Management, 242(2–3), 297–305. https://doi.org/10.1016/j.foreco.2007.01.046

Nappi, A., Drapeau, P., & Leduc, A. (2015). How important is dead wood for woodpeckers foraging in eastern North American boreal forests? Forest Ecology and Management, 346, 10–21. https://doi.org/10.1016/j.foreco.2015.02.028

Nieto, A. & Alexander, K.N.A. (2010). European Red List of Saproxylic Beetles. Publications Office of the European Union. https://data.europa.eu/doi/10.2779/84561

Oettel, J., & Lapin, K. (2021). Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. Ecological Indicators, 122, 107275. https://doi.org/10.1016/j.ecolind.2020.107275

Olav Hogstad & Ingvar Stenberg. (1997). Breeding Success, Nestling Diet and Parental Care in the White-backed Woodpecker Dendrocopos leucotos. Journal Für Ornithologie, 138, 25–38.

Oswaldo, J., Hugo, C., Wilmer, T., Ismael, P., Wilson, Q., & Omar, C. (2022). Successional forests stages influence the composition and diversity of vascular epiphytes communities from Andean Montane Forests. Ecological Indicators, 143, 109366. https://doi.org/10.1016/j.ecolind.2022.109366

Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., & Guilbert, E. (2018). The indicator side of tree microhabitats: A multi-taxon approach based on bats, birds and saproxylic beetles. Journal of Applied Ecology, 55(5), 2147–2159. https://doi.org/10.1111/1365-2664.13181

Pimm, S., Raven, P. (2000). Extinction by numbers. Nature 403, 843–845. https://doi.org/10.1038/35002708

Ranius, T., Hämäläinen, A., Egnell, G., Olsson, B., Eklöf, K., Stendahl, J., Rudolphi, J., Sténs, A., & Felton, A. (2018). The effects of logging residue extraction for energy on ecosystem services and biodiversity: A synthesis. Journal of Environmental Management, 209, 409–425. https://doi.org/10.1016/j.jenvman.2017.12.048

Redolfi De Zan, L., Battisti, C., & Carpaneto, G. (2014). Bird and beetle assemblages in relict beech forests of central Italy: A multi-taxa approach to assess the importance of dead wood in biodiversity conservation. Community Ecology, 15(2), 235–245. https://doi.org/10.1556/ComEc.15.2014.2.12

Roberge, J.-M., Angelstam, P., & Villard, M.-A. (2008). Specialised woodpeckers and naturalness in hemiboreal forests—Deriving quantitative targets for conservation planning. Biological Conservation, 141(4), 997–1012. https://doi.org/10.1016/j.biocon.2008.01.010

Roberge, J.-M., & Angelstam, P. (2006). Indicator species among resident forest birds – A cross-regional evaluation in northern Europe. Biological Conservation, 130(1), 134–147. https://doi.org/10.1016/j.biocon.2005.12.008

Roth, T., & Weber, D. (2007). Top predators as indicators for species richness? Prey species are just as useful: Predators and biodiversity. Journal of Applied Ecology, 45(3), 987–991. https://doi.org/10.1111/j.1365-2664.2007.01435.x

Schmidl, J., & Bußler, H. (2004). Ökologische Gilden xylobionter Käfer Deutschlands. Naturschutz Und Landschaftsplanung, 36, 202–218.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M. D., Lorz, J., Cadotte, M. W., Lindenmayer, D. B., Adhikari, Y. P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R. S., Birkemoe, T., … Müller, J. (2021). The contribution of insects to global forest deadwood decomposition. Nature, 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8

Shelton, M. B., Phillips, S. S., & Goldingay, R. L. (2020). Habitat requirements of an arboreal Australian snake (Hoplocephalus bitorquatus) are influenced by hollow abundance in living trees. Forest Ecology and Management, 455, 117675. https://doi.org/10.1016/j.foreco.2019.117675

Siitonen, J. (2001). Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. Ecological Bulletins, 49, 11–41.

Speight, M. C. D. (1989). Saproxylic invertebrates and their conservation (Nature and environment). Strasbourg, France: Council of Europe.

Stokland, J. N., Siitonen, J., & Jonsson, B. G. (2012). Biodiversity in dead wood. Cambridge: Cambridge University Press.

Thorn, S., Bässler, C., Gottschalk, T., Hothorn, T., Bussler, H., Raffa, K., & Müller, J. (2014). New Insights into the Consequences of Post-Windthrow Salvage Logging Revealed by Functional Structure of Saproxylic Beetles Assemblages. PLoS ONE, 9(7), e101757. https://doi.org/10.1371/journal.pone.0101757

Tsikas, A., & Karanikola, P. (2022). To Conserve or to Control? Endangered Saproxylic Beetles Considered as Forest Pests. Forests, 13(11), 1929. https://doi.org/10.3390/f13111929

Urkijo-Letona, A., Cárcamo, S., Peña, L., Fernández de Manuel, B., Onaindia, M., & Ametzaga-Arregi, I. (2020). Key elements of the White-backed Woodpecker's (Dendrocopos leucotos lilfordi) habitat in its European south-western limits. Forests, 11(8), 1–15. https://doi.org/10.3390/f11080831

Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect? - Systematics and the agony of choice. Biological Conservation, 55(3), 235–254. https://doi.org/10.1016/0006-3207(91)90030-D

Vasconcelos, R., Pujol-Buxó, E., Llorente, G. A., Saeed, A., & Carranza, S. (2020). Micro-Hotspots for Conservation: An Umbrella Tree Species for the Unique

Socotran Reptile Fauna. Forests, 11(3), 353. https://doi.org/10.3390/f11030353

Versluijs, M., Eggers, S., Mikusiński, G., Roberge, J.-M., & Hjältén, J. (2020). Foraging behavior of the Eurasian Three-toed Woodpecker (Picoides tridactylus) and its implications for ecological restoration and sustainable boreal forest management. Avian Conservation and Ecology, 15(1), art6. https://doi.org/10.5751/ACE-01477-150106

Virkkala, R., Alanko, T., Laine, T., & Tiainen, J. (1993). Population contraction of the White-backed Woodpecker Dendrocopos leucotos in Finland as a consequence of habitat alteration. Biological Conservation, 66(1), 47–53. https://doi.org/10.1016/0006-3207(93)90133-L

Wang-Erlandsson, L., Tobian, A., van der Ent, R. J., Fetzer, I., te Wierik, S., Porkka, M., Staal, A., Jaramillo, F., Dahlmann, H., Singh, C., Greve, P., Gerten, D., Keys, P. W., Gleeson, T., Cornell, S. E., Steffen, W., Bai, X., & Rockström, J. (2022). A planetary boundary for green water. Nature Reviews Earth & Environment, 3(6), 380–392. https://doi.org/10.1038/s43017-022-00287-8

Williams, P. H., & Gaston, K. J. (1994). Measuring more of biodiversity: Can higher-taxon richness predict wholesale species richness? Biological Conservation, 67, 211–217. https://doi.org/10.1016/0006-3207

Winkler, H., Christie, D. A., & Nurney, D. (1995). Woodpeckers: A Guide to the Woodpeckers, Piculets and Wrynecks of the World. Pica press.

You, L., Simmons, D. R., Bateman, C. C., Short, D. P. G., Kasson, M. T., Rabaglia, R. J., & Hulcr, J. (2015). New Fungus-Insect Symbiosis: Culturing, Molecular, and Histological Methods Determine Saprophytic Polyporales Mutualists of Ambrosiodmus Ambrosia Beetles. PLoS ONE, 10(9), e0137689. https://doi.org/10.1371/journal.pone.0137689

Zyśk-Gorczyńska, E., Jakubiec, Z., & Wuczyński, A. (2015). Brown bears (Ursus arctos) as ecological engineers: The prospective role of trees damaged by bears in forest ecosystems. Canadian Journal of Zoology, 93(2), 133–141. https://doi.org/10.1139/cjz-2014-0139

Chapter 1

The White-backed Woodpecker (*Dendrocopos leucotos*) as an umbrella species for threatened saproxylic beetle communities in Central European beech forests

The White-backed Woodpecker (*Dendrocopos leucotos*) as an umbrella species for threatened saproxylic beetle communities in Central European beech forests

Romain Angeleri [1,2,3], Urs G. Kormann [1,4], Nicolas Roth [1,3], Antonia Ettwein [4], Gilberto Pasinelli [4], Raphaël Arlettaz [2], Thibault Lachat [1,3]

[1] Bern University of Applied Sciences, School of Agricultural, Forest and Food Sciences, Länggasse 85, 3052 Zollikofen, Switzerland

[2] University of Bern, Institute of Ecology and Evolution – Conservation Biology, Baltzerstrasse 6, 3012 Bern, Switzerland

[3] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[4] Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

Chapter status: *Submitted to "Ecological Indicators" (In revision)*

Abstract

The umbrella species concept is a popular conservation planning tool which postulates that conservation schemes targeting a specific species will indirectly benefit many other sympatric species. In Scandinavia and Central Europe, the White-backed Woodpecker (*Dendrocopos leucotos*) is considered an umbrella species for woodland birds and cryptogam species of conservation concern. Whether this also applies to saproxylic beetles, a group of high conservation concern, remains open. Therefore, we tested that umbrella function in Central European beech forests that are currently recolonized by this woodpecker. Relying on radiotracking data, we compared saproxylic beetle communities within the breeding home ranges of White-backed Woodpeckers (high and low activity of the bird) against forests with ascertained absence of the bird (control). Bayesian inference for linear regressions identified that species richness of threatened saproxylic beetles was 1.51 (lower and upper 5% PPCrI = [1.09; 2.01]) times higher in sites with high White-backed Woodpecker activity compared to the control. Community composition analyses on threatened saproxylic beetles showed a reduced β-diversity at low and high White-backed Woodpecker sites compared to the control. Finally, an indicator species analysis showed that 17 saproxylic beetle species, including 4 threatened species, were positively associated with White-backed Woodpecker's breeding home ranges, while only 3 species, all not threatened, were associated with the control sites. Overall, our results suggest that the White-backed Woodpecker plays the role of an umbrella species for threatened saproxylic beetle communities, opening new opportunities for conservation planning in European beech forests.

Keywords

Dendrocopos leucotos; Red-listed saproxylic beetles; Indicator species; Bayesian inference for GLM; Community identity; Multi-level pattern analysis

Introduction

Umbrella species are defined as organisms that need large expanses of habitat or habitat of high quality so that they can serve as surrogates for the overall biodiversity value of an ecosystem. In effect, their presence de facto encapsulates an array of other organisms that have similar but less stringent ecological requirements (Roberge & Angelstam, 2004; Suter et al., 2002). Umbrella species are therefore often selected for making conservation-related decisions and suggesting management measures that, if successful, are presumed to guarantee the persistence of a rich and diverse ecological community beyond the persistence of that very species (Favreau et al., 2006; Wilcox, 1984). Umbrella species roles have been evidenced among birds (Suter et al., 2002), fish (Branton & Richardson, 2014), mammals (Mortelliti et al., 2022) and arthropods (Kašák et al., 2019). In addition to their umbrella function, these species may also sometimes play the role of a keystone species that make them superior indicators of ecological integrity (Carignan & Villard, 2002). Finally, some of these species can even play the additional role of flagship species that are helpful to raise public awareness and conservation support (Gregr et al., 2020). For conservation practitioners, the reliance on umbrella species is often key to developing effective action plans for a suite of other species that are more difficult to monitor. This approach is now widely employed as conservation efforts chronically suffer from restricted funding (Buxton et al., 2020) and because even basic ecological knowledge on numerous taxa is still lacking (Dobson, 1997; Nieto & Alexander, 2010; Ulyshen, 2018). However, the caveat remains that a species' umbrella role should be clearly demonstrated beforehand (Suter et al., 2002), which needs in-depth research.

The White-backed Woodpecker (*Dendrocopos leucotos*) depends heavily on dead wood resources (Urkijo-Letona et al., 2020), which have thus been promoted in specific conservation action plans (Stighäll & Olsson, 2015). More generally, the species is referenced as an old-growth and mature forest specialist (Carlson, 2000) and previous research in Scandinavia has demonstrated its umbrella function for other forest birds and cryptogam species of conservation concern (Roberge, Angelstam, et al., 2008). Additionally, the species has been suggested to play a similar role for threatened saproxylic beetle communities (Bell et al., 2015; Martikainen et al., 1998) although firm evidence is still lacking. Consequently, it may be an ideal candidate as an umbrella species for saproxylic communities in beech-dominated forests of Central Europe. White-backed

Woodpecker populations have declined strongly in Northern (Carlson, 2000; Virkkala et al., 1993) and Eastern Europe (Czeszczewik & Walankiewicz, 2006), but the species is currently expanding across Central Europe from the East, with its expansion front lying in the Eastern Swiss Alps (Mollet et al., 2009). There, the species occurs mainly in managed forests as old-growth forests are absent. Yet its presence is still positively correlated with a structure that typically characterizes old-growth forest stands (e.g., mean diameter at breast height of live trees and standing dead wood, see (Ettwein et al., 2020) for details). Additionally, Ettwein et al. (2020) demonstrated that the density of emergence holes of saproxylic insects on both standing and lying dead wood was positively correlated to the occupancy probability of the White-backed Woodpecker. Given the relationship between this old-growth forest specialist and insects that inhabit dead-wood, we examine the potential of this woodpecker as an umbrella species for saproxylic beetle communities in Central Europe, with an emphasis on species of conservation concern.

Saproxylic beetles are defined as those that are "dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight, 1989). They are a key component of forest ecosystems through their contribution to dead wood decay, spore dissemination and trophic interactions (Grove, 2002; Seibold et al., 2021; Ulyshen, 2018). Saproxylic beetle species are negatively affected by intensive forest management, a widespread practice in Central European forests (Larsson Ekström et al., 2021; Lindenmayer et al., 2006). According to the European Red-List for saproxylic beetles (Nieto & Alexander, 2010), 17.9% of the evaluated species are categorized as threatened and 12.9% of the population is thought to be declining, which is why saproxylic beetles are considered a conservation focus in European forests. Due to their ecological requirements for dead wood, saproxylic beetles are highly sensitive to habitat changes and are therefore widely used as indicators for undisturbed forest (Bouget et al., 2014; Brunet & Isacsson, 2009; Eckelt et al., 2018; Lachat et al., 2014; Schmidl & Bussler, 2004). Yet, saproxylic beetles – and especially rare species – are inherently hard to monitor because they often occur at low densities, are represented by numerous species, their identification to the species level is challenging and skilled taxonomic specialists are rare. In contrast, birds are well suited for monitoring programs because they can be quickly and easily identified by sight and sound (Carignan & Villard, 2002; Williams & Gaston, 1994). Additionally, birds show promise as indicators for a wide range of taxa, including arthropods (Bell et al., 2015; Roth & Weber, 2008; Vallino et al., 2021), demonstrating their potential role as umbrella species.

Here, we examine the potential of the White-backed Woodpecker as a useful umbrella species for the saproxylic beetle community in beech-dominated forests of Central Europe. First, we hypothesize that at the community level, specimen abundance and species richness of saproxylic beetles are positively correlated with White-backed Woodpecker habitat use. Second, we expect predictable co-occurrence patterns between target woodpecker species and saproxylic species, resulting in pronounced changes in the saproxylic beetle community along the gradient of woodpecker habitat use.

Material and method

Study area

The study took place in Eastern Switzerland (cantons Grisons and St. Gallen), Western Austria (province Vorarlberg) and the Principality of Liechtenstein, in an area of approximately 40 km^2 (46.8 - 47.4°N, 9.2 - 10.2°E; Figure 1). All sampling sites were in beech-dominated forest stands between 630 and 1230 m above sea level. The climate of the region is representative of the Central European Alps and described as ranging from a temperate climate, without dry seasons and with hot summers, to a cold climate, without dry seasons and with cold summers (Beck et al., 2018).

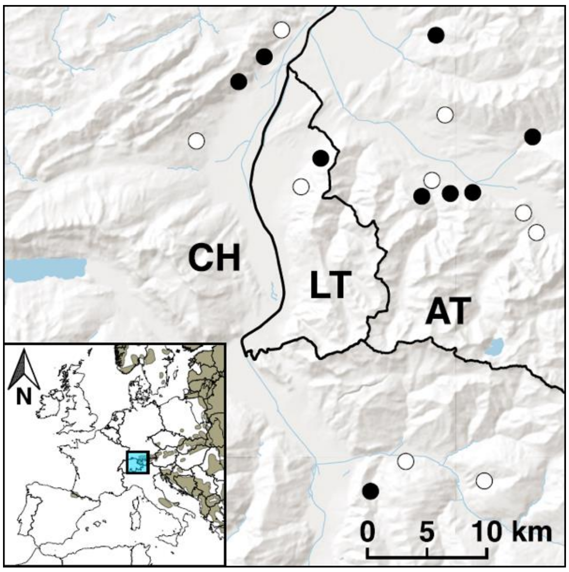


Figure 1. Overview of the White-backed Woodpecker distribution in Western European (khaki area), the study region (blue square) and the study sites (dots). Black dots represent the White-backed Woodpecker breeding home range sites whereas white dots represent sites with a controlled absence of the target bird species. CH = Switzerland, LT = Liechtenstein, AT = Austria. Source: BirdLife International and Handbook of the Birds of the World (2020) 2020. *Dendrocopos leucotos*. The IUCN Red List of Threatened Species. Version 2021-3. Downloaded on 09 March 2022.

Sites selection

The site selection was designed to represent 3 levels of White-backed Woodpecker activity: high (i.e., sites within a White-backed Woodpecker breeding home range and with high White-backed Woodpecker activity), low (i.e., sites within a White-backed Woodpecker breeding home range but with little White-backed Woodpecker activity) and control (i.e., sites where White-backed Woodpeckers did not occur). To identify these sites, we applied a two-step approach.

First, we used White-backed Woodpecker telemetry data collected in 2016 and 2017 (Ettwein et al.– under revision) to identify forest surfaces with high and low White-backed Woodpecker activity within 9 monitored breeding home ranges. We identified high and low White-backed Woodpecker activity by creating a heatmap-type layer based on the number of telemetry locations using a hexagon approach of 500 m^2 in Quantum GIS (v.2.18) with the plugin QMarxan Toolbox (v.0.3.4). Second, out of these hexagons, we selected four sampling plots each with the highest and lowest woodpecker activity per territory, respectively, called "High" and "Low". We then selected 9 forests without known White-backed Woodpecker observations as absence sites following the procedure described in (Ettwein et al., 2020). The absence sites had a size of 550x550 m (= 30.25 ha), which approximately corresponds to the average breeding home range size of the tracked White-backed Woodpeckers (Ettwein et al. – under revision). From February to March 2018, we confirmed the absence of the White-backed Woodpecker by using playbacks every 200 m. Four sampling plots were selected in each of the 9 absence sites. In both breeding home ranges and control sites, sampling plots with overlapping rock cliffs and river streams were not selected for accessibility reasons, and the next sampling plot with high (or low) White-backed Woodpecker activity was selected from the created heatmaps in breeding home ranges. Within the breeding home ranges, sampling plots were installed at least 150 m away from the currently active breeding cavity of the tagged White-backed Woodpecker. This avoided the potentially confounding effect of visits to the nest on bird activity. We then distributed 4 sampling plots around the center of every control site, called "Control". To avoid spatial autocorrelation, sampling plots were installed 50 m apart within each site. Slope aspect, slope gradient and cardinal orientation of all sampling plots were equally distributed across White-backed Woodpecker activity levels (i.e., High, Low, Control).

Beetle sampling

To quantify the saproxylic beetle community, flying insects were collected using non-baited flight interception traps (Polytrap^{TM}), a widely used and standardized method to study saproxylic beetles. A trap was made from two transparent acrylic glass sheets above a funnel leading into a collecting bottle filled with water and antifungal agent (ROCIMA^{TM} GT Biocid; 0.5%). We installed one trap per sampling plot, for a total of 108 traps equally distributed among the three activity levels (Control, Low, High = 36 traps each). A trap was hung between 2 European beech trees at approximately 1.5 m from the ground. Traps were emptied monthly from mid-April 2018 to mid-August 2018.

Beetle identification

Beetle specimens were identified to species level by specialized taxonomists. Species were classified as saproxylic following an enhanced list of Schmidl & Bussler (2004). Conservation status such as primeval forest relict species (Eckelt et al., 2018) and threatened species (i.e., Vulnerable, Endangered and Critically Endangered) were attributed to every saproxylic species. Due to the lack of completeness of the Swiss red list for saproxylic beetles (Monnerat et al., 2016), we considered the more comprehensive list for red-listed saproxylic beetles developed for the Baden-Württemberg region, a neighboring German federal state (Bense, 2001). Samples were pooled across all months and non-saproxylic species were excluded from further analyses.

Habitat characterization

We inventoried habitat characteristics in summer 2018 on plots of 500 m^2 centered on every trap. We recorded the species and diameter at breast height (DBH hereafter) of all living trees (DBH ≥ 7 cm). For all dead wood items (snag = height > 130 cm & DBH ≥ 7 cm; stump = height ≤ 130 cm & diameter at mid height ≥ 7 cm; logs = diameter at mid length ≥ 7 cm), we recorded their diameter with a slide caliper, decay stage (Keller, 2011) and when possible- originating species. Snag height was measured with a Haglöf Sweden® Vertex IV. Stump height and log length were measured with a logging tape. The volume of standing dead wood was estimated using either the formula of a cone for non-broken snags or the formula of a truncated cone for the broken ones. The volume of logs and stumps was estimated using the formula of a cylinder.

Statistical analysis

Differences in explanatory variables among the three activity levels were controlled a priori. A Shapiro-Wilk test of Normality was performed on all explanatory variables. If data was normally distributed, we used a Welch's test followed with a Games-Howell post-hoc pairwise test with Holm correction for multiple testing, whereas if data was non-normal, we used a Kruskall-Wallis test followed with a Dunn post-hoc pairwise test with Holm correction for multiple testing) (ggbetweenstats {ggstatsplot}). Additionally, all variables were controlled for collinearity with an exclusion threshold set at 0.8 (tab_corr {sjPlot}). Then, we first tested whether species richness and specimen abundance of overall saproxylic beetles and of threatened saproxylic beetles, respectively, differed between the three activity levels (Control, Low, High), using Bayesian generalized linear models with group-specific terms via Stan (stan_glmer.nb {rstanarm}) fitted on a negative binomial distribution (fitdist {fitdistrplus}). Estimates of the models were retrieved using the {bayestestR} and {effectsize} packages. Second, we assessed whether the three activity levels differed in their saproxylic beetle community composition, using (1) a Bray-Curtis similarity based permutational test for homogeneity of multivariate dispersion (betadisper {vegan}) followed with Tukey Honest Significant Differences test corrected for multiple comparisons (TukeyHSD {stats}) and (2) a permutational multivariate analysis of variance (adonis2 {vegan}). Third, to assess whether certain individual species were associated with any of the three activity levels, we performed a multi-level pattern analysis (multipatt {indicspecies}). All statistical analyses were performed using R Version 4.1.1 (R Core Team 2021) and figures were created using the {bayesplot}, {ggstatsplot}, {gridExtra}, {patchwork} and {tidyverse} packages.

Forest characteristics, saproxylic beetles and White-backed Woodpecker

Using four Bayesian generalized linear models with group-specific terms via Stan we analyzed how species richness and specimen abundance of overall and threatened saproxylic beetles, respectively, varied as a function of the White-backed Woodpecker activity levels (Control, Low, High) and the habitat characteristics (volume of standing dead wood, volume of lying dead wood, mean diameter at breast height of live tree) as a proxy for forest naturalness. All four models were run under a negative binomial distribution, implementing 4 chains with 2000 iterations each (warmup = 1000; sampling = 1000) and default prior for 108 observations (i.e., sampling unit) and 18 groups (i.e., sites as random intercepts to account for the hierarchical design of the study).

Community composition

Two complementary multivariate analyses were done to investigate compositional differences of the saproxylic beetle communities (overall or threatened) among the three activity levels. First, we tested whether the three groups (i.e., activity levels) differed in species composition, using a permutational multivariate analysis of variance (Anderson, 2017). This method tests whether the group centroids (i.e., the average identity of saproxylic beetle species composing the community of a given activity level) in multivariate species space differed between groups, where overlapping group centroids indicates a degree of community similarity across the groups. Second, we tested whether or not groups differed in their compositional variance (i.e., β-diversity), that is, the degree of variation in species identities among groups, using permutational test for homogeneity of multivariate dispersion with 9999 permutations (Anderson et al., 2006, 2011). This method statistically assesses the degree of biotic homogenization among treatments, where large treatment-wise dispersion indicates a large variation in species identities within a group and thus a low species overlap between sampling plots representing a group (i.e., high β-diversity); as opposed to small group-wise dispersion (i.e., low β-diversity). Differences in β-diversity among groups were assessed using a pairwise Tukey Honest Significant Differences test corrected for multiple comparisons. For both analyses, sampling site was used as the blocking factor to account for the hierarchical design of the study.

Multi-level pattern analysis

To test if some saproxylic beetle species were associated with a given activity level (hereafter site group), we performed a multi-level pattern analysis with 9999 permutations (De Cáceres et al., 2010, 2012; De Cáceres & Legendre, 2009; Dufrêne & Legendre, 1997). This method provides two outputs: the specificity index (the conditional probability of a positive predictive value of a given species as an indicator of the target site group) and the fidelity index (the conditional probability that a given species will be found in a newly surveyed site belonging to the same site group (Sattler et al., 2014)). A good indicator species should therefore be both ecologically restricted to the target site group (specificity index = 1) and frequent within it (fidelity index = 1). The species-sites group association (i.e., saproxylic beetle species-White-backed Woodpecker activity treatments) followed an abundance matrix represented by equal site group size. These analyses were conducted for the three activity groups (Control, Low, High) independently and for the Low and High activity groups pooled together, representing the breeding home range of the White-backed Woodpecker as a site. A total of four site groups (i.e., [Control] OR [Low] OR [High] OR [Low AND High]) were screened during this analysis.

Results

Specimen abundance and species richness of overall, threatened and primeval saproxylic beetles

In total, the sampling effort yielded 21552 (579 threatened) saproxylic beetle specimens, represented by 400 (49 threatened) saproxylic beetle species. The Control sites yielded 6285 (136) specimens for 291 (28) species, the Low White-backed Woodpecker activity level yielded 8’563 (229) specimens for 301 (34) species and the High White-backed Woodpecker activity level yielded 6704 (214) specimens for 305 (37) species (Table 1). Additionally, 8 primeval relict saproxylic beetle species (Eckelt et al., 2018) were sampled: *Ceruchus chrysomelinus* (Control = 6 specimens; Low = 0 specimen; High = 1 specimen), *Cryptophagus confusus* (1; 5; 2), *Cryptophagus quercinus* (0; 1; 0), *Grynocharis oblonga* (1; 4; 4), *Ischnodes sanguinicollis* (4; 4; 4), *Pryonichus melanarius* (0; 0; 1), *Prostomis mandibularis* (0; 1; 1), *Triplax elongata* (0; 2; 0). Due to their low incidence, the statistical analysis of primeval forest relict species was not possible.

Table 1. Specimen abundance and species richness of the studied saproxylic beetle suites per White-backed Woodpecker activity treatment (Control: absence site, Low and High: presence sites). Values represent samples pooled per White-backed Woodpecker activity levels.

Saproxylic beetles set	**Observation**	**White-backed Woodpecker activity level** Control	Low	High	**Total**
Overall	Specimen abundance	6285	8563	6704	21552
	Species richness	291	301	305	400
Threatened	Specimen abundance	136	229	214	579
	Species richness	28	34	37	49
Primeval forest relict species	Specimen abundance	12	17	13	42
	Species richness	4	6	6	8

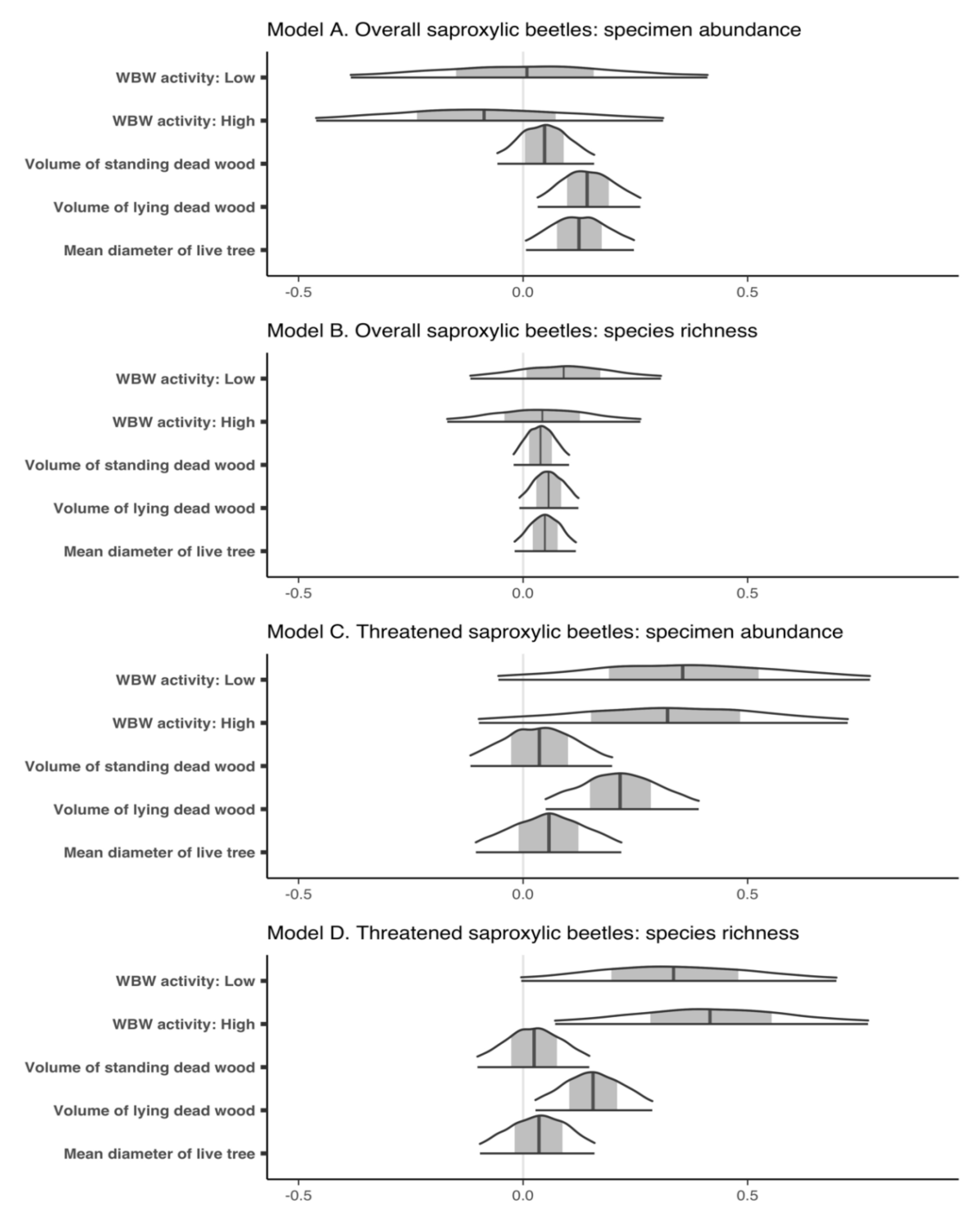


Figure 2. Summary of parameter estimates for the effects of White-backed Woodpecker activity levels (WBW activity, "Control" as reference level), volume of standing dead wood, volume of lying dead wood and mean diameter of live trees on a) Overall saproxylic beetles: specimen abundance; b) Overall saproxylic beetles: species richness; c) Threatened saproxylic beetles: specimen abundance and d) Threatened saproxylic beetles: species richness. Vertical lines represent the parameter estimates. The grey area under curve, the total area under curve and the border of the area under curve represent the 50%, the 90% and the distribution of the HDI posterior probability, respectively.

Drivers of saproxylic beetle species richness and specimen abundance

First, sites representing a High White-backed Woodpecker activity had 1.5 times more threatened saproxylic beetle species compared to the Control sites (Posterior Probability Credible Interval median [lower and upper 5%] = 0.416 [0.092, 0.786]; Figure 2, Model D; Table 2, Model D) whereas no difference in species richness of threatened saproxylic beetles was demonstrated between the sites representing a Low White-backed Woodpecker activity and the Control sites. Second, we did not detect differences between sites representing a Low and a High White-backed Woodpecker activity for the abundance and species richness of saproxylic beetles, regardless of their conservation status (overall or threatened) (see Supplementary materials S5). Third, the volume of lying dead wood had a positive effect on abundance of overall saproxylic beetles (0.143 [0.03, 0.258]; Figure 2, Model A; Table 2, Model A), as well as on the abundance (0.216 [0.048, 0.387]; Figure 2, Model C; Table 2, Model C) and species richness (0.156 [0.024, 0.282]; Figure 2, Model D; Table 2, Model D) of threatened saproxylic beetles. Finally, the mean diameter of live trees also had a positive effect on the overall specimen abundance (0.124 [0.009, 0.249]; Figure 2, Model A; Table 2, Model A).

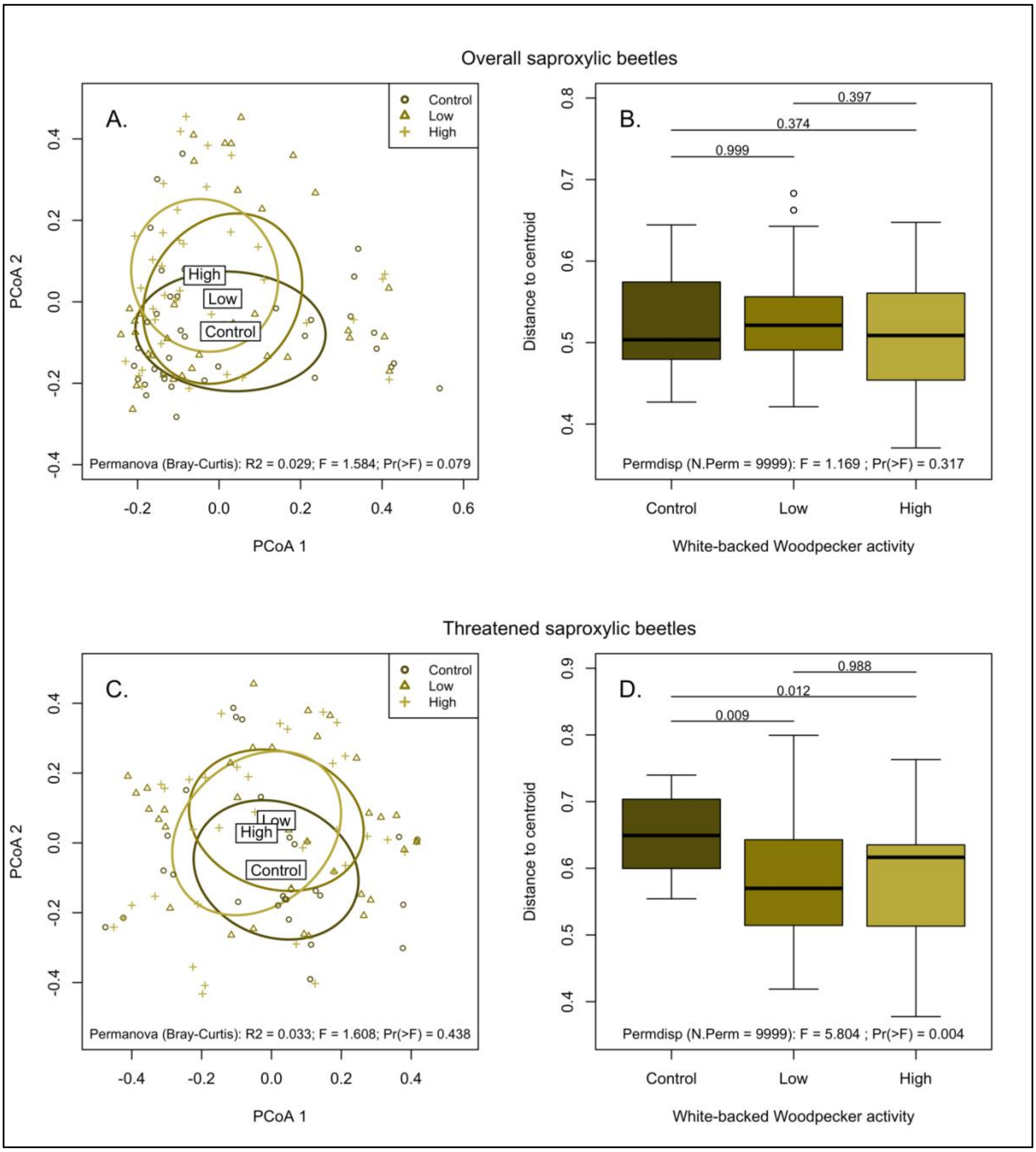
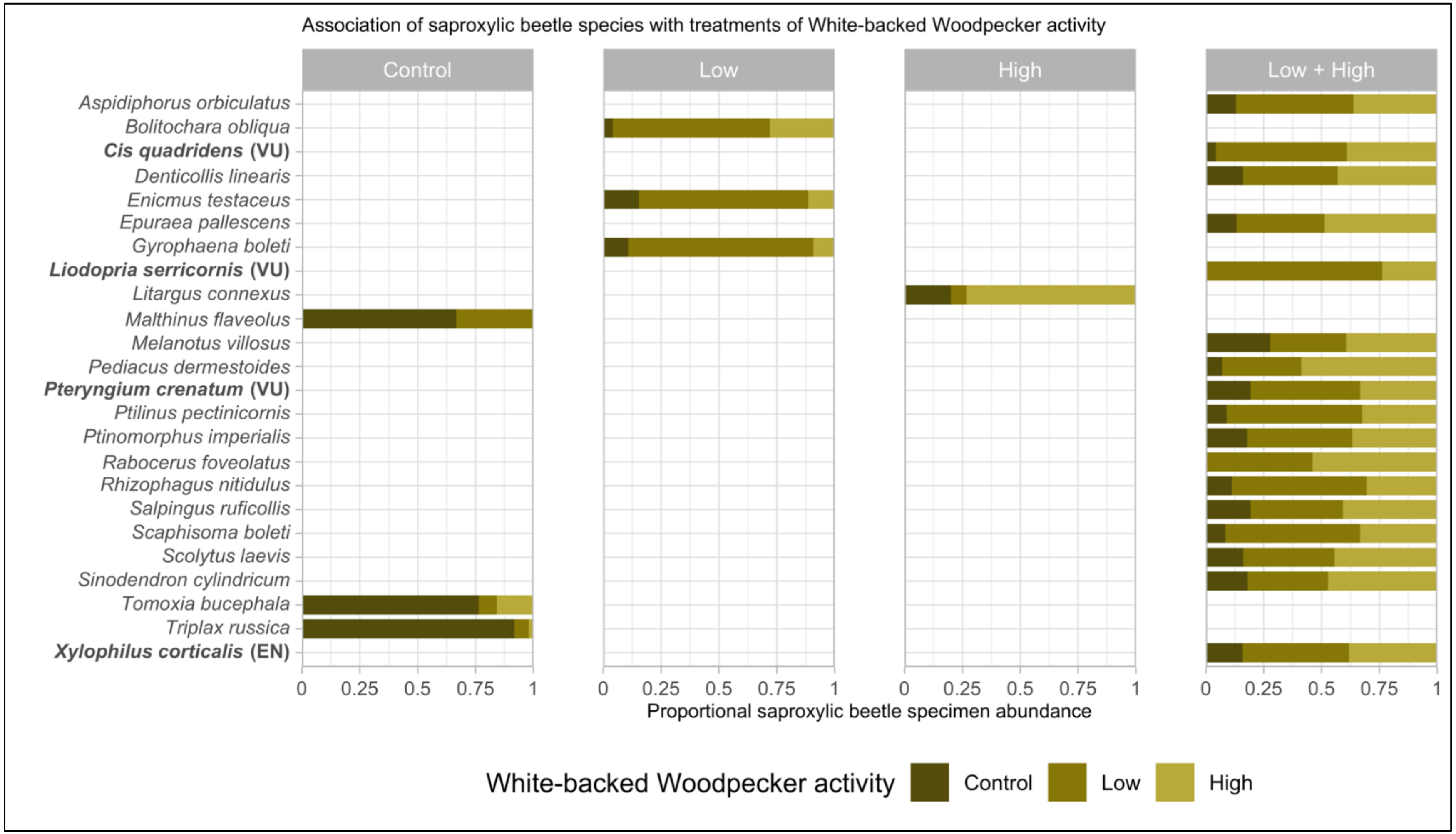


Figure 3. Summary of the community composition analyses for the overall saproxylic beetle suite (A; B) and threatened saproxylic beetle suite (C; D). Group centroid position was tested with a permutational multivariate analysis of variance (A; C) and average distance to group centroid was tested with a permutational test for homogeneity of multivariate dispersions (B; D). Numbers above boxplots are p. values resulting of a pairwise Tukey Honest Significant Difference test.

Community composition

Neither community composition (Figure 3.A) nor β-diversity (Figure 3.B) of the overall saproxylic beetle community differed across the three White-backed Woodpecker activity levels. Additionally, community composition of the threatened saproxylic beetle community did not differ across the three White-backed Woodpecker activity levels (Figure 3.C). However, White-backed Woodpecker activity levels significantly differed in β-diversity of threatened saproxylic beetles (Df = 2, Sum sq = 0.088, Mean sq = 0.044, F = 5.804, N.Perm = 9999, Pr(>F) = 0.004; Figure 3.D). Specifically, post-hoc pairwise testing revealed that communities found in High and Low White-backed Woodpecker activity sites had a reduced β-diversity compared to control sites ($p < 0.05$ for both cases).

Figure 4. Summary of the multi-level pattern analysis per species-sites group association (Control, Low, High, Low + High). Species' proportional specimen abundance per White-backed Woodpecker activity levels (Control, Low, High) is displayed within the corresponding site group association. Threatened species are displayed in bold.



Multi-level pattern analysis

Out of the 400 identified species, 24 were identified as indicator of at least one of the White-backed Woodpecker activity level (i.e., site group). First, 3 saproxylic beetle species were significantly associated with sites representing the control level. Their specificity index ranged from 0.667 to 0.918 and their fidelity index ranged from 0.250 to 0.306. Second, 3 saproxylic beetle species were significantly associated with sites representing the Low White-backed Woodpecker activity level. Their specificity index ranged from 0.680 to 0.800 and their fidelity index ranged from 0.222 to 0.472. Third, 1 saproxylic beetle species was significantly associated with sites representing the High White-backed Woodpecker activity level. It had a specificity index of 0.733 and a fidelity index of 0.194. Finally, 17 saproxylic beetle species – including 4 threatened taxa (*Cis quadriens, Liodopria serricornis, Pteryngium crenatum, Xylophilus corticalis*) – were significantly associated with the combination of the sites representing the Low and High White-backed Woodpecker activity levels. Their specificity index ranged from 0.722 to 1 and their fidelity index ranged from 0.125 to 0.958 (Figure 4, Table 3).

Table 2. Summary table of the Bayesian generalized linear mixed models. Explanatory variables with a non-null predicted effect (90% of the HDI posterior probability excluding 0) are displayed in bold.

Model	Saproxylic beetles set	Response variable	Explanatory variable	Model output CrI 90% HDI posterior probability: median (min; max)	Effect size exponential(CrI 90% HDI posterior probability): median (min; max)
A	Overall	Specimen abundance	WBW activity: Low	0.009 (-0.391; 0.401)	1.009 (0.676; 1.493)
			WBW activity: High	-0.087 (-0.462; 0.312)	0.917 (0.63; 1.366)
			Volume of standing dead wood	0.048 (-0.057; 0.158)	1.049 (0.945; 1.171)
			Volume of lying dead wood	**0.143 (0.03; 0.258)**	**1.154 (1.03; 1.294)**
			Mean diameter of live tree	**0.124 (0.009; 0.249)**	**1.132 (1.009; 1.283)**
B	Overall	Species richness	WBW activity: Low	0.09 (-0.117; 0.307)	1.094 (0.89; 1.359)
			WBW activity: High	0.043 (-0.171; 0.257)	1.044 (0.843; 1.293)
			Volume of standing dead wood	0.039 (-0.022; 0.101)	1.04 (0.978; 1.106)
			Volume of lying dead wood	0.057 (-0.007; 0.125)	1.059 (0.993; 1.133)
			Mean diameter of live tree	0.048 (-0.023; 0.113)	1.049 (0.977; 1.12)
C	Threatened	Specimen abundance	WBW activity: Low	0.355 (-0.059; 0.764)	1.426 (0.943; 2.147)
			WBW activity: High	0.322 (-0.108; 0.714)	1.38 (0.898; 2.042)
			Volume of standing dead wood	0.036 (-0.116; 0.199)	1.037 (0.89; 1.22)
			Volume of lying dead wood	**0.216 (0.048; 0.387)**	**1.241 (1.049; 1.473)**
			Mean diameter of live tree	0.058 (-0.1; 0.223)	1.06 (0.905; 1.25)
D	Threatened	Species richness	WBW activity: Low	0.335 (-0.012; 0.681)	1.398 (0.988; 1.976)
			WBW activity: High	**0.416 (0.092; 0.786)**	**1.516 (1.096; 2.195)**
			Volume of standing dead wood	0.024 (-0.097; 0.152)	1.024 (0.908; 1.164)
			Volume of lying dead wood	**0.156 (0.024; 0.282)**	**1.169 (1.024; 1.326)**
			Mean diameter of live tree	0.035 (-0.097; 0.158)	1.036 (0.908; 1.171)

Table 3. Summary table of the multi-level pattern analysis per species-sites group association. Threatened species are displayed in bold.

Habitat association	Species	Family	Red List Status	IndVal stat	IndVal P-Value	Specificity	Fidelity	Control: Specimen abundance (Species incidence)	Low: Specimen abundance (Species incidence)	High: Specimen abundance (Species incidence)	Low + High: Average specimen abundance (combined species incidence)
Control	Malthinus flaveolus	Cantharidae	NE	0.451	0.005	0.667	0.306	12 (31%)	6 (14%)	0 (0%)	3 (7%)
	Tomoxia bucephala	Mordellidae	LC	0.46	0.014	0.763	0.278	29 (28%)	3 (8%)	6 (14%)	4 (11%)
	Triplax russica	Erotylidae	LC	0.479	0.003	0.918	0.25	45 (25%)	3 (8%)	1 (3%)	2 (6%)
Low	Bolitochara obliqua	Staphylinidae	LC	0.389	0.031	0.68	0.222	1 (3%)	17 (22%)	7 (8%)	12 (15%)
	Enicmus testaceus	Latridiidae	NE	0.473	0.002	0.731	0.306	4 (6%)	19 (31%)	3 (6%)	11 (18%)
	Gyrophaena boleti	Staphylinidae	LC	0.615	0.014	0.8	0.472	22 (22%)	164 (47%)	19 (31%)	92 (39%)
High	Litargus connexus	Mycetophagidae	LC	0.378	0.038	0.733	0.194	3 (8%)	1 (3%)	11 (19%)	6 (11%)
Low + High	Aspidiphorus orbiculatus	Sphindidae	NE	0.631	0.003	0.87	0.458	9 (19%)	35 (47%)	25 (44%)	30 (46%)
	Cis quadridens	**Ciidae**	**VU**	**0.446**	**0.012**	**0.957**	**0.208**	**1 (3%)**	**13 (22%)**	**9 (19%)**	**11 (21%)**
	Denticollis linearis	Elateridae	LC	0.771	0.002	0.84	0.708	36 (50%)	92 (61%)	97 (81%)	94 (71%)
	Epuraea pallescens	Nitidulidae	LC	0.64	0.002	0.867	0.472	15 (19%)	43 (47%)	55 (47%)	49 (47%)
	Liodopria serricornis	**Leiodidae**	**VU**	**0.441**	**0.006**	**1**	**0.194**	**0 (0%)**	**16 (25%)**	**5 (14%)**	**10 (19%)**
	Melanotus villosus	Elateridae	NE	0.832	0.003	0.722	0.958	105 (69%)	124 (94%)	149 (97%)	136 (96%)
	Pediacus dermestoides	Cucujidae	NE	0.601	0.004	0.929	0.389	6 (17%)	29 (39%)	50 (39%)	40 (39%)
	Pteryngium crenatum	**Cryptophagidae**	**VU**	**0.599**	**0.009**	**0.807**	**0.444**	**11 (19%)**	**27 (44%)**	**19 (44%)**	**23 (44%)**
	Ptilinus pectinicornis	Ptinidae	LC	0.907	0.001	0.91	0.903	360 (81%)	2349 (92%)	1302 (89%)	1826 (90%)
	Ptinomorphus imperialis	Ptinidae	NE	0.684	0.011	0.821	0.569	19 (39%)	48 (58%)	39 (56%)	44 (57%)
	Rabocerus foveolatus	Salpingidae	LC	0.354	0.044	1	0.125	0 (0%)	6 (8%)	7 (17%)	6 (12%)
	Rhizophagus nitidulus	Monotomidae	LC	0.555	0.018	0.887	0.347	7 (19%)	36 (44%)	19 (25%)	28 (35%)
	Salpingus ruficollis	Salpingidae	LC	0.778	0.004	0.807	0.75	47 (56%)	97 (72%)	99 (78%)	98 (75%)
	Scaphisoma boleti	Staphylinidae	LC	0.422	0.04	0.917	0.194	2 (6%)	14 (25%)	8 (14%)	11 (19%)
	Scolytus laevis	Curculionidae	DD	0.629	0.041	0.838	0.472	32 (31%)	78 (53%)	88 (42%)	83 (47%)
	Sinodendron cylindricum	Lucanidae	LC	0.594	0.02	0.819	0.431	13 (25%)	25 (42%)	34 (44%)	30 (43%)
	Xylophilus corticalis	**Eucnemidae**	**EN**	**0.611**	**0.002**	**0.841**	**0.444**	**10 (17%)**	**29 (44%)**	**24 (44%)**	**26 (44%)**

Discussion

Umbrella species for threatened saproxylic beetles

Based on three main results, we provide evidence that the White-backed Woodpecker is an effective umbrella species for threatened saproxylic beetles in Central Europe. First, sites with a high White-backed Woodpecker activity harbored on average 1.5 times as many red-listed saproxylic beetle species compared to the control sites. Second, threatened saproxylic beetle communities of the High and Low activity levels had reduced β-diversity compared to the control. Third, at the species level, 5.7 times as many species were associated with White-backed Woodpecker's breeding home ranges than with absence sites, of which 4 species were red-listed. Our findings therefore suggest that the protection of White-backed Woodpecker breeding sites, presenting old-growth forest characteristics (high dead wood volume and live trees of large diameter) can support the achievement of a major conservation goal in European forests, namely the protection of red-listed dead-wood dependent beetles.

Generally, our findings are in line with previous studies that proposed the White-backed Woodpecker as an umbrella species for forest species. Bell et al. (Bell et al., 2015) demonstrated that a higher number of red listed – but including near threatened (NT) – saproxylic beetle species were associated with forest patches restored to meet White-backed Woodpecker's habitat requirements compared to managed forest stands. Prior to it, peers already proposed the White-backed Woodpecker as an umbrella species for saproxylic beetles but yielded uncertain results. (Martikainen et al., 1998), identified threatened saproxylic beetle species within White-backed Woodpecker territories, but lacked control sites to validate the umbrella species hypothesis. Similarly, (Roberge, Mikusiński, et al., 2008) tried to answer the question addressed by Martikainen et al. (1998), without significant results in favor of saproxylic beetles. Yet, they did observe an umbrella effect of the White-backed Woodpecker for forest birds of conservation concern and red-listed cryptogam species. Nonetheless, it is important to stress that the present validation of the White-backed Woodpecker as an umbrella species for threatened saproxylic beetles was made possible by using the comprehensive red-list for saproxylic beetles of the geographically close Baden-Württemberg region (Bense, 2001). Preliminary analyses performed with the Swiss red-list for saproxylic beetles (Monnerat et al., 2016) did not show any relation between White-backed Woodpecker occurrence and threatened saproxylic beetles. From our understanding, this disparity in analysis outputs of both prior and present research could be explained by the different levels of completeness of the two red lists. Additionally, as demonstrated in the European red list of saproxylic beetles (Nieto & Alexander, 2010), most of the assessed taxa suffer from data deficiency regarding their conservation statuses and population trends, pointing out the fundamental need for enhanced red lists for saproxylic beetles, at both local and continental scale.

Importance of the habitat

Our results also highlight the importance of forest structure for the conservation of saproxylic beetles. The entire saproxylic beetle community and the threatened species both profited from the volume of lying dead wood and the presence of trees of large diameter. Sampling plots representing White-backed Woodpecker's breeding home range were characterized by a higher volume of lying dead wood (Supplementary materials S3) and by larger live trees compared to control sites (Supplementary materials S4); two characteristics of old-growth forests which both White-backed Woodpeckers and many saproxylic beetles specialized on.

Backing up those observations, previous studies delivered similar results in mature and old-growth forests characterized by a high structural complexity, an increasing density and diversity of tree-related microhabitats (Paillet et al., 2017) as well as an increasing proportion of dead branches in the tree crown, having in turn a positive effect on dead wood availability in the surroundings (Keren & Diaci, 2018; Lachat & Müller, 2018). Additionally, our results are in line with general findings of European studies reporting positive effects of mean live tree diameter and volume of lying dead wood on White-backed Woodpecker occurrence (Czeszczewik, 2009; Czeszczewik et al., 2013; Czeszczewik & Walankiewicz, 2006; Ettwein et al., 2020; Gerdzhikov et al., 2018; Mollet et al., 2009; Roberge, Angelstam & Villard, 2008; Urkijo-Letona et al., 2020) and on saproxylic beetle communities, including species of conservation concern (Gossner et al., 2013; Haeler et al., 2021; Jonsell et al., 1998; Lachat et al., 2014; Parisi et al., 2019; Roth et al., 2019). Finally, one should not overlook the importance of forest structures for both saproxylic beetles and White-backed Woodpeckers, as wood-living insect larvae represent the majority of invertebrates brought to the nestlings (Hogstad & Stenberg, 1997).

Conclusions

The presented results support the idea that the White-backed Woodpecker is a suitable umbrella species for threatened saproxylic beetles in beech-dominated forests of Central Europe, underlining the importance of protecting sites where our selected surrogate species occurs. Biodiversity conservation programs aiming at protecting and promoting this woodpecker species and its associated biodiversity should first protect sites with known White-backed Woodpecker occurrence (Campion et al., 2020). By doing this, conservation programs would also promote saproxylic beetles' persistence through habitat quality improvement enabling forests to reach late successional stages. Secondly, conservation programs should identify forest sites adjacent to existing White-backed Woodpecker territories to implement conservation actions such as limiting logging activity (Czeszczewik & Walankiewicz, 2006) and implementing dead wood enrichment protocols (Doerfler et al., 2017; Roth et al., 2019) to match White-backed Woodpecker habitat requirements in this geographical context (Ettwein et al., 2020). Such conservation measures are expected to benefit not only our surrogate species but also its associated fauna such as saproxylic beetles. Additionally, combining the role of this umbrella species with the status of a flagship species could facilitate the acceptance for conservation measures that can sometimes be restrictive for forest users, and free up financial resources for protection (Floyd & Martin, 2016; Stighäll & Olsson, 2015). Finally, testing the umbrella function of the White-backed Woodpecker and other highly specialized surrogate species on a broader spectrum of organisms and their response to habitat parameters could help in building more comprehensive and integrative biodiversity protection programs.

Acknowledgements

We are grateful to Vasyl and Maksym Chumak who have coordinated the saproxylic beetle identification process. We also acknowledge the work of Michael Lanz for the general coordination of the project "The White-backed Woodpecker in managed forests" and of Ueli Bühler for his early support in the development of this project in the Graubünden region. We thank Sarah Degenhart, David Hasler, Simon Niedersachsen, Nicolaj Novikov, Valentin Sylvoz and Silas Zurbuchen for their help, and especially Pierre Cardineau and Nina Marjanovic for their enduring involvement in the fieldwork. Finally, Elena Haeler for the stimulating discussions and Felicity Newell for proof reading support. This work was supported by the Swiss Federal Office for the Environment, the Swiss Ornithological Institute and Inatura – Erlebnis Naturschau GmbH Dornbirn.

References

Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef: Statistics Reference Online, 1–15. https://doi.org/10.1002/9781118445112.stat07841

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. Ecology Letters, 14(1), 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9(6), 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. Scientific Data, 5, 1–12. https://doi.org/10.1038/sdata.2018.214

Bell, D., Hjältén, J., Nilsson, C., JØrgensen, D., & Johansson, T. (2015). Forest restoration to attract a putative umbrella species, the White-backed Woodpecker, benefited saproxylic beetles. Ecosphere, 6(12). https://doi.org/10.1890/ES14-00551.1

Bense, U. (2002). Verzeichnis und Rote Liste der Totholzkäfer Baden-Württembergs. Landesanstalt für Umweltschutz Baden-Württemberg (LfU), 1–77.

Bouget, C., Larrieu, L., & Brin, A. (2014). Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecological Indicators, 36, 656–664. https://doi.org/10.1016/j.ecolind.2013.09.031

Branton, M. A., & Richardson, J. S. (2014). A test of the umbrella species approach in restored floodplain ponds. Journal of Applied Ecology, 51(3), 776–785. https://doi.org/10.1111/1365-2664.12248

Brunet, J., & Isacsson, G. (2009). Influence of snag characteristics on saproxylic beetle assemblages in a south Swedish beech forest. Journal of Insect Conservation, 13(5), 515–528. https://doi.org/10.1007/s10841-008-9200-3

Buxton, R. T., Avery-Gomm, S., Lin, H. Y., Smith, P. A., Cooke, S. J., & Bennett, J. R. (2020). Half of resources in threatened species conservation plans are allocated to research and monitoring. Nature Communications, 11(1), 1–8. https://doi.org/10.1038/s41467-020-18486-6

Campion, D., Pardo, I., Elósegui, M., & Villanua, D. (2020). GPS telemetry and home range of the White-backed Woodpecker Dendrocopos leucotos: Results of the first experience. Acta Ornithologica, 55(1), 77–87. https://doi.org/10.3161/00016454AO2020.55.1.008

Carignan, V., & Villard, M. A. (2002). Selecting indicator species to monitor ecological integrity: A review. Environmental Monitoring and Assessment, 78(1), 45–61. https://doi.org/10.1023/A:1016136723584

Carlson, A. (2000). The effect of habitat loss on a deciduous forest specialist species: The White-backed Woodpecker (Dendrocopos leucotos). Forest Ecology and Management, 131(1–3), 215–221. https://doi.org/10.1016/S0378-1127(99)00215-7

Czeszczewik, D. (2009). Foraging behaviour of White-backed Woodpeckers Dendrocopos leucotos in a primeval forest (Białowieża National Park, NE Poland): Dependence on habitat resources and season. Acta Ornithologica, 44(2), 109–118. https://doi.org/10.3161/000164509x482687

Czeszczewik, D., & Walankiewicz, W. (2006). Logging affects the White-backed Woodpecker Dendrocopos leucotos distribution in the Białowieża Forest. Annales Zoologici Fennici, 43(2), 221–227.

Czeszczewik, D., Walankiewicz, W., Mitrus, C., Tumiel, T., Stański, T., Sahel, M., & Bednarczyk, G. (2013). Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. Bird Conservation International, 23(4), 414–425. https://doi.org/10.1017/S0959270912000354

De Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. Ecology, 90(12), 3566–3574. https://doi.org/10.1890/08-1823.1

De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. Oikos, 119(10), 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

De Cáceres, M., Legendre, P., Wiser, S. K., & Brotons, L. (2012). Using species combinations in indicator value analyses. Methods in Ecology and Evolution, 3(6), 973–982. https://doi.org/10.1111/j.2041-210X.2012.00246.x

Dobson, A. (1997). Global biodiversity assessment. Trends in Ecology & Evolution, 12(1), 39–40. https://doi.org/10.1016/s0169-5347(97)88395-4

Doerfler, I., Müller, J., Gossner, M. M., Hofner, B., & Weisser, W. W. (2017). Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. Forest Ecology and Management, 400, 607–620. https://doi.org/10.1016/j.foreco.2017.06.013

Dufrêne, M., & Legendre, P. (1997). Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. Ecological Monographs, 67(3), 345–366.

Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., Cizek, L., Frei, A., Holzer, E., Kadej, M., Kahlen, M., Köhler, F., Möller, G., Mühle, H., Sanchez, A., Schaffrath, U., Schmidl, J., Smolis, A., Szallies, A., … Seibold, S. (2018). "Primeval forest relict beetles" of Central Europe: A set of 168 umbrella species for the protection of primeval forest remnants. Journal of

Insect Conservation, 22(1), 15–28. https://doi.org/10.1007/s10841-017-0028-6

Ettwein, A., Korner, P., Lanz, M., Lachat, T., Kokko, H., & Pasinelli, G. (2020). Habitat selection of an old-growth forest specialist in managed forests. Animal Conservation, 23(5), 547–560. https://doi.org/10.1111/acv.12567

Favreau, J. M., Drew, C. A., Hess, G. R., Rubino, M. J., Koch, F. H., & Eschelbach, K. A. (2006). Recommendations for Assessing the Effectiveness of Surrogate Species Approaches. Biodiversity and Conservation, 15(12), 3949–3969. https://doi.org/10.1007/s10531-005-2631-1

Floyd, C., & Martin, K. (2016). Avian Ecosystem Engineers: Birds That Excavate Cavities. In Ç. H. Şekercioğlu, D. G. Wenny, & C. J. Whelan (Eds.), Why Birds Matter: Avian Ecological Function and Ecosystem Services (pp. 298–320). The University of Chicago Press.

Gerdzhikov, G. P., Georgiev, K. B., Plachiyski, D. G., Zlatanov, T., & Shurulinkov, P. S. (2018). Habitat requirements of the White-backed Woodpecker Dendrocopos leucotos lilfordi (Sharpe & Dresser, 1871) (Piciformes: Picidae) in Strandzha mountain, Bulgaria. Acta Zoologica Bulgarica, 70(4), 527–534.

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W., & Müller, J. (2013). Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests. Conservation Biology, 27(3), 605–614. https://doi.org/10.1111/cobi.12023

Gregr, E. J., Christensen, V., Nichol, L., Martone, R. G., Markel, R. W., Watson, J. C., Harley, C. D. G., Pakhomov, E. A., Shurin, J. B., & Chan, K. M. A. (2020). Cascading social-ecological costs and benefits triggered by a recovering keystone predator. Science, 368(6496), 1243–1247. https://doi.org/10.1126/science.aay5342

Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics, 33(1), 1–23. https://doi.org/10.1146/annurev.ecolsys.33.010802.150507

Haeler, E., Bergamini, A., Blaser, S., Ginzler, C., Hindenlang, K., Keller, C., Kiebacher, T., Kormann, U. G., Scheidegger, C., Schmidt, R., Stillhard, J., Szallies, A., Pellissier, L., & Lachat, T. (2021). Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. Landscape Ecology, 36(1), 89–104. https://doi.org/10.1007/s10980-020-01115-4

Hogstad, O., & Stenberg, I. (1997). Breeding success, nestling diet and parental care in the White-backed Woodpecker Dendrocopos leucotos. Journal of Ornithology, 138(1), 25–38. https://doi.org/10.1007/BF01651649

Jonsell, M., Weslien, J., & Ehnström, B. (1998). Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation, 7(6), 749–764. https://doi.org/10.1023/A:1008888319031

Kašák, J., Mazalová, M., Šipoš, J., Foit, J., Hučín, M., & Kuras, T. (2019). Habitat preferences of Ceruchus chrysomelinus, an endangered relict beetle of the natural Central European montane forests. Insect Conservation and Diversity, 12(3), 206–215. https://doi.org/10.1111/icad.12338

K Keller, M. (ed.) 2011: Swiss National Forest Inventory. Manual of the Field Survey 2004–2007 [published online March 2011]. Available from World Wide Web <http://www.wsl.ch/publikationen/pdf/10919.pdf>. Birmensdorf, Swiss Federal Research Institute WSL, 269 pp.

Keren, S., & Diaci, J. (2018). Comparing the quantity and structure of deadwood in selection managed and old-growth forests in South-East Europe. Forests, 9(2), 1–16. https://doi.org/10.3390/f9020076

Lachat, T., Brang, P., Bollmann, K., Brändli, U.-B., Bütler, R., Herrmann, S., Olivier, S., & Wermelinger, B. 2014: Bois mort en forêt. Formation, importance et conservation. Not. prat. 52: 12 p.

Lachat, T., & Müller, J. (2018). Importance of Primary Forests for the Conservation of Saproxylic Insects. In Ulyshen, M. D., (Ed.), Saproxylic Insects (Vol. 1, pp. 581–605). Springer International Publishing. https://doi.org/10.1007/978-3-319-75937-1_17

Larsson Ekström, A., Bergmark, P., & Hekkala, A. M. (2021). Can multifunctional forest landscapes sustain a high diversity of saproxylic beetles? Forest Ecology and Management, 490, 119107. https://doi.org/10.1016/j.foreco.2021.119107

Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation, 131(3), 433–445. https://doi.org/10.1016/j.biocon.2006.02.019

Martikainen, P., Kaila, L., & Haila, Y. (1998). Threatened Beetles in White-backed Woodpecker Habitats. Conservation Biology, 12(2), 293–301. https://doi.org/10.1111/j.1523-1739.1998.96484.x

Mollet, P., Zbinden, N., & Schmid, H. (2009). Steigende Bestandszahlen bei Spechten und anderen Vogelarten dank Zunahme von Totholz? | An increase in the population of woodpeckers and other bird species thanks to an increase in the quantities of deadwood? Schweizerische Zeitschrift Fur Forstwesen, 160(11), 334–340. https://doi.org/10.3188/szf.2009.0334

Monnerat, C., Barbalat, S., Lachat, T., & Gonseth, Y. (2016). Critères et procédure d'élaboration de listes taxonomiques nationales: le cas des Buprestidae, Cerambycidae, Cetoniidae et Lucanidae (Coleoptera) de Suisse | Criteria and procedure for developing national taxonomic lists: the case of Buprestidae, Cerambycidae, Cetoniidae and Lucanidae (Coleoptera) in Switzerland. Bulletin de la Société Entomologique Suisse, 88, 155-172. https://dx.doi.org/10.5169/seals-514999

Mortelliti, A., Brehm, A. M., & Evans, B. E. (2022). Umbrella effect of monitoring protocols for mammals in the Northeast US. Scientific Reports, 12(1), 1–12. https://doi.org/10.1038/s41598-022-05791-x

Nieto, A. & Alexander, K.N.A. (2010). European Red List of Saproxylic Beetles. Publications Office of the European Union. https://data.europa.eu/doi/10.2779/84561

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., & Guilbert, E. (2017). Snags and large trees drive higher tree microhabitat densities in strict forest reserves. Forest Ecology and

Management, 389, 176–186. https://doi.org/10.1016/j.foreco.2016.12.014

Parisi, F., Di Febbraro, M., Lombardi, F., Biscaccianti, A. B., Campanaro, A., Tognetti, R., & Marchetti, M. (2019). Relationships between stand structural attributes and saproxylic beetle abundance in a Mediterranean broadleaved mixed forest. Forest Ecology and Management, 432, 957–966. https://doi.org/10.1016/j.foreco.2018.10.040

Roberge, J.-M., & Angelstam, P. E. R. (2004). Usefulness of the Umbrella Species Concept. Conservation Biology, 18(1), 76–85.

Roberge, J.-M., Angelstam, P., & Villard, M. A. (2008). Specialised woodpeckers and naturalness in hemiboreal forests—Deriving quantitative targets for conservation planning. Biological Conservation, 141(4), 997–1012. https://doi.org/10.1016/j.biocon.2008.01.010

Roberge, J.-M., Mikusiński, G., & Svensson, S. (2008). The white-backed woodpecker: Umbrella species for forest conservation planning? Biodiversity and Conservation, 17(10), 2479–2494. https://doi.org/10.1007/s10531-008-9394-4

Roth, N., Doerfler, I., Bässler, C., Blaschke, M., Bussler, H., Gossner, M. M., Heideroth, A., Thorn, S., Weisser, W. W., & Müller, J. (2019). Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity. Diversity and Distributions, 25(3), 430–441. https://doi.org/10.1111/ddi.12870

Roth, T., & Weber, D. (2008). Top predators as indicators for species richness? Prey species are just as useful. Journal of Applied Ecology, 45(3), 987–991. https://doi.org/10.1111/j.1365-2664.2007.01435.x

Sattler, T., Pezzatti, G. B., Nobis, M. P., Obrist, M. K., Roth, T., & Moretti, M. (2014). Selection of multiple umbrella species for functional and taxonomic diversity to represent urban biodiversity. Conservation Biology, 28(2), 414–426. https://doi.org/10.1111/cobi.12213

Schmidl, J., & Bußler, H. (2004). Ökologische Gilden xylobionter Käfer Deutschlands. Naturschutz Und Landschaftsplanung, 36, 202–218.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M. D., Lorz, J., Cadotte, M. W., Lindenmayer, D. B., Adhikari, Y. P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R. S., Birkemoe, T., … Müller, J. (2021). The contribution of insects to global forest deadwood decomposition. Nature, 597(7874), 77–81. https://doi.org/10.1038/s41586-021-03740-8

Speight, M. C. D. (1989). Saproxylic invertebrates and their conservation (Nature and environment). Strasbourg, France: Council of Europe.

Stighäll, K. (2015). Habitat composition and restocking for conservation of the white-backed woodpecker in Sweden [Dissertation]. School of Science and Technology, Örebro University.

Suter, W., Graf, R. F., & Hess, R. (2002). Capercaillie (Tetrao urogallus) and avian biodiversity: Testing the umbrella-species concept. Conservation Biology, 16(3), 778–788. https://doi.org/10.1046/j.1523-1739.2002.01129.x

Ulyshen MD (2018) Saproxylic Insects - Diversity, Ecology and Conservation. Springer

Urkijo-Letona, A., Cárcamo, S., Peña, L., de Manuel, B. F., Onaindia, M., & Ametzaga-Arregi, I. (2020). Key elements of the White-backed Woodpecker's (Dendrocopos leucotos lilfordi) habitat in its European south-western limits. Forests, 11(8), 1–15. https://doi.org/10.3390/f11080831

Vallino, C., Caprio, E., Genco, F., Chamberlain, D., Palestrini, C., Roggero, A., Bocca, M., & Rolando, A. (2021). F Flocking of foraging Yellow-Billed Choughs Pyrrhocorax Graculus reflects the availability of grasshoppers and the extent of human influence in high elevation ecosystems. Ardeola, 68(1), 53–70. https://doi.org/10.13157/arla.68.1.2021.ra4

Virkkala, R., Alanko, T., Laine, T., & Tiainen, J. (1993). Population contraction of the White-backed Woodpecker Dendrocopos leucotos in Finland as a consequence of habitat alteration. Biological Conservation, 66(1), 47–53. https://doi.org/10.1016/0006-3207(93)90133-L

Wilcox, B. A. (1984). In situ conservation of genetic resources: Determinants of minimum area requirements. In McNeely J.A. and Miller K.R (Ed.), National Parks, Conservation, and Development: The Role of Protected Areas in Sustaining Society (Smithsonia, p. 825).

Williams, P. H., & Gaston, K. J. (1994). Measuring more of biodiversity: Can higher-taxon richness predict wholesale species richness? Biological Conservation, 67, 211–217. https://doi.org/10.1016/0006-3207

R packages

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Lüdecke D (2021). _sjPlot: Data Visualization for Statistics in Social Science_. R package version 2.8.9, https://CRAN.R-project.org/package=sjPlot.

Wickham et al., (2019). Welcome to the tidyverse. Journal of Open Source Software, 4(43), 1686, https://doi.org/10.21105/joss.01686

Patil, I. (2021). Visualizations with statistical details: The 'ggstatsplot' approach. Journal of Open Source Software, 6(61), 3167, doi:10.21105/joss.03167

Goodrich B, Gabry J, Ali I & Brilleman S. (2020). rstanarm: Bayesian applied regression modeling via Stan. R package version 2.21.1 https://mc-stan.org/rstanarm.

Gabry J, Mahr T (2022). "bayesplot: Plotting for Bayesian Models." R package version 1.9.0, <URL: https://mc stan.org/bayesplot/>.

Thomas Lin Pedersen (2020). patchwork: The Composer of Plots. R package version 1.1.1. https://CRAN.R project.org/package=patchwork

Makowski, D., Ben-Shachar, M., & Lüdecke, D. (2019). bayestestR: Describing Effects and their Uncertainty, Existence and Significance within the Bayesian Framework. Journal of Open Source Software, 4(40), 1541.doi:10.21105/joss.01541

Ben-Shachar M, Lüdecke D, Makowski D (2020). effectsize: Estimation of Effect Size Indices and Standardized Parameters. Journal of Open Source Software, 5(56), 2815. doi: 10.21105/joss.02815

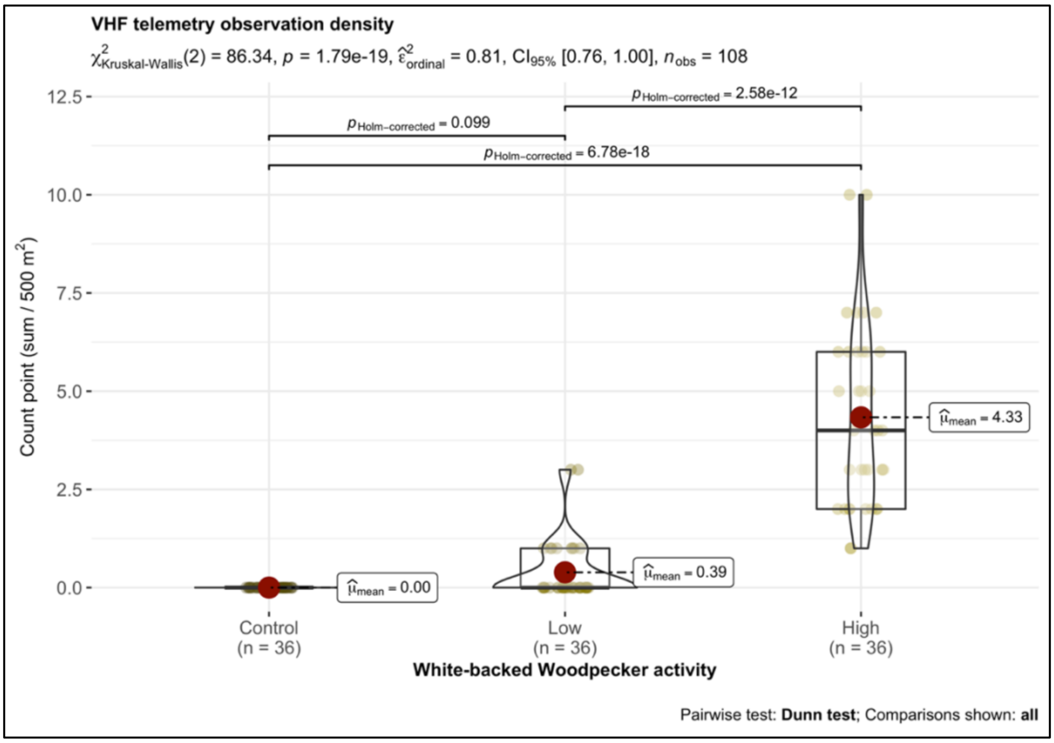
Baptiste Auguie (2017). gridExtra: Miscellaneous Functions for "Grid" Graphics. R package version 2.3. https://CRAN.R-project.org/package=gridExtra

Jari Oksanen, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs and Helene Wagner (2020). vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R project.org/package=vegan

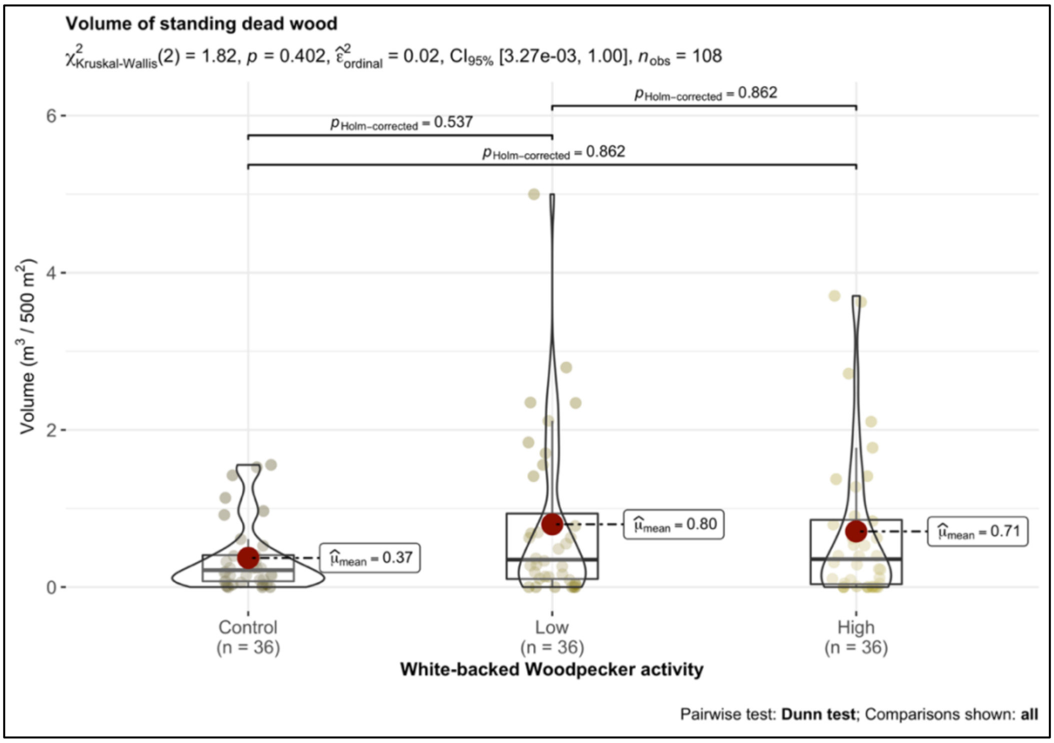
De Caceres, M., Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. Ecology, URL http://sites.google.com/site/miqueldecaceres/

Marie Laure Delignette-Muller, Christophe Dutang (2015). fitdistrplus: An R Package for Fitting Distributions. Journal of Statistical Software, 64(4), 1-34. URL http://www.jstatsoft.org/v64/i04/

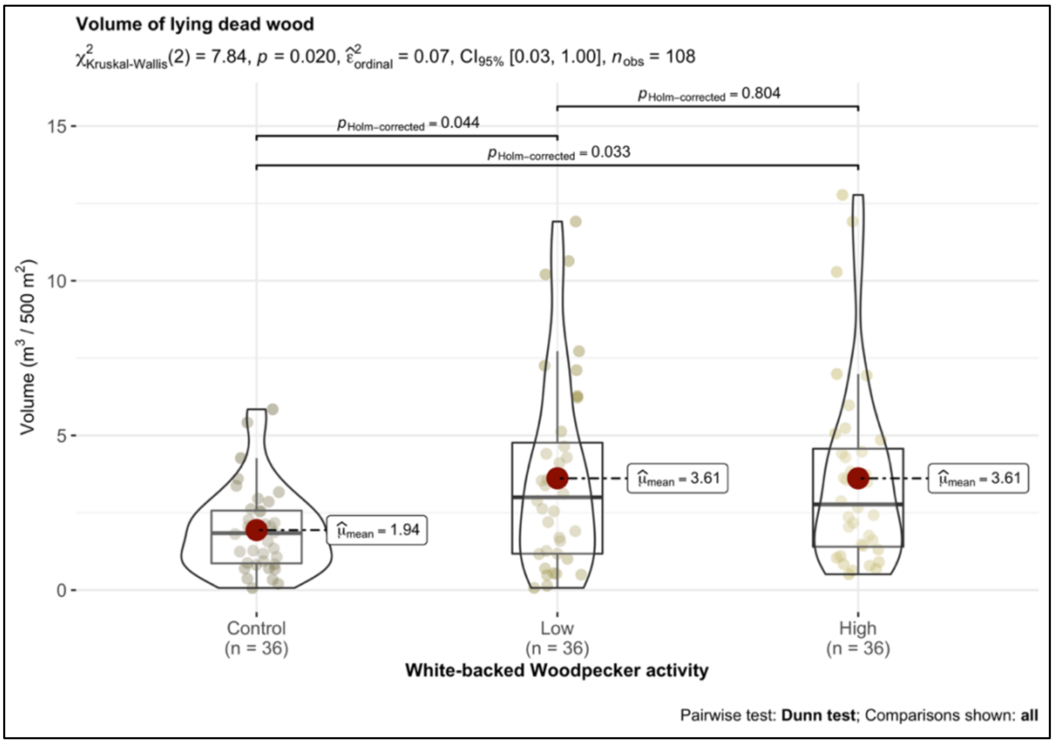
Supplementary materials



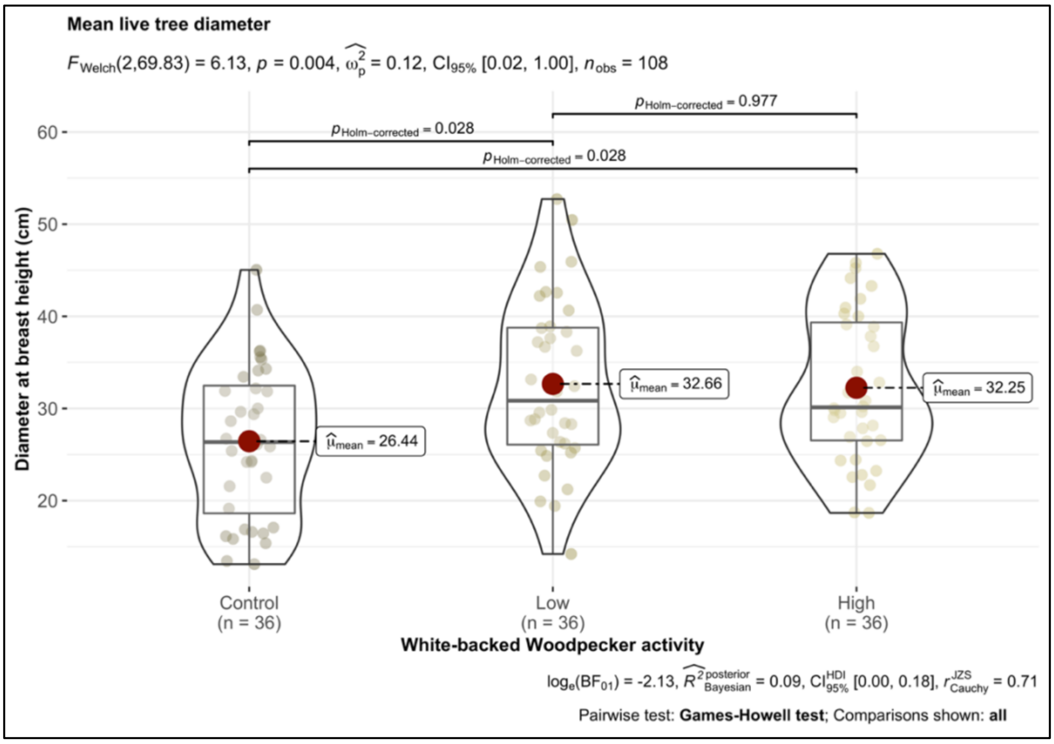
S1. Pairwise comparison of the explanatory variables selected to assess the effect of the White-backed Woodpecker activity and the habitat parameters on the saproxylic beetle communities; VHF telemetry observation density.



S2. Pairwise comparison of the explanatory variables selected to assess the effect of the White-backed Woodpecker activity and the habitat parameters on the saproxylic beetle communities; Volume of standing dead wood.



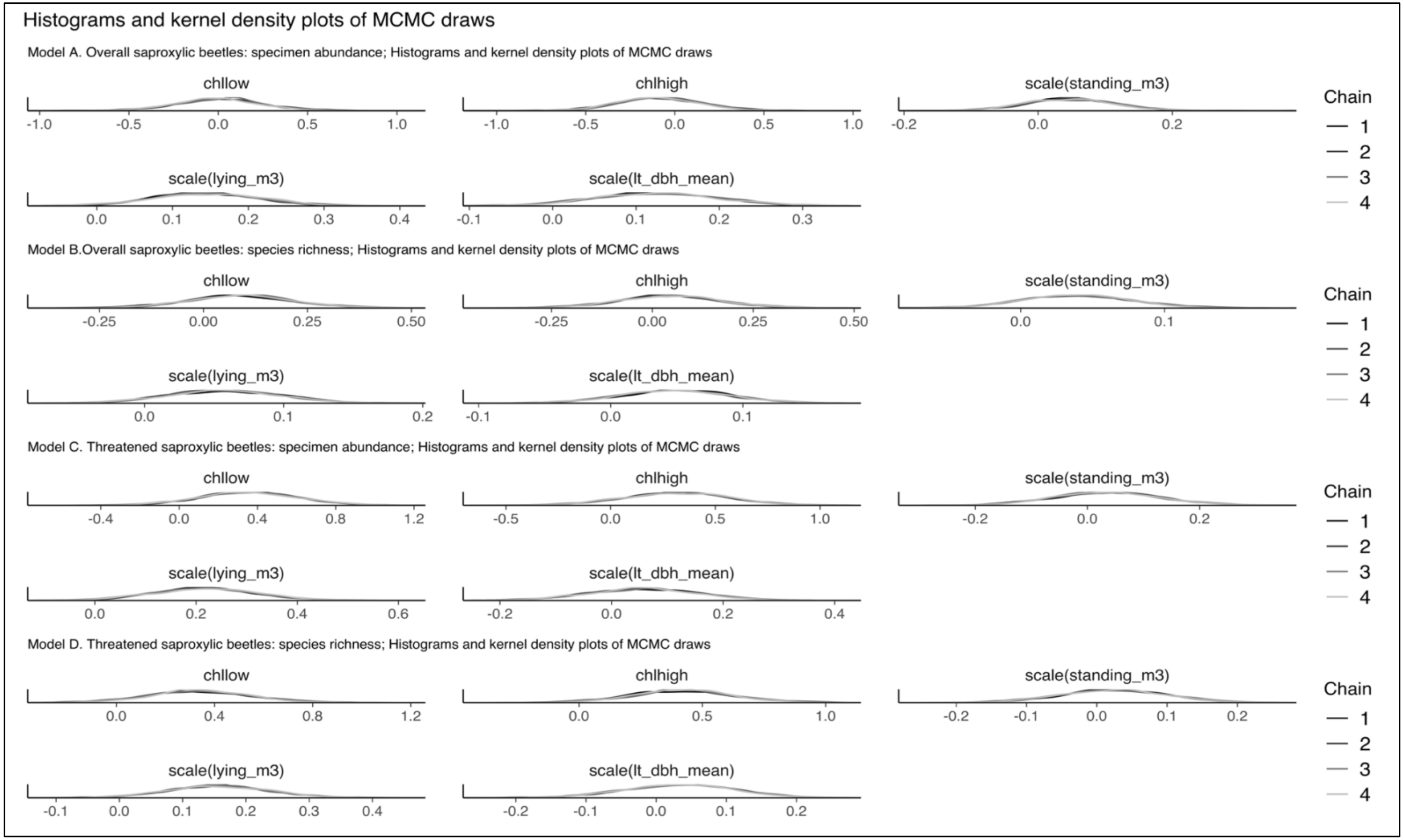
S3. Pairwise comparison of the explanatory variables selected to assess the effect of the White-backed Woodpecker activity and the habitat parameters on the saproxylic beetle communities; Volume of lying dead wood.



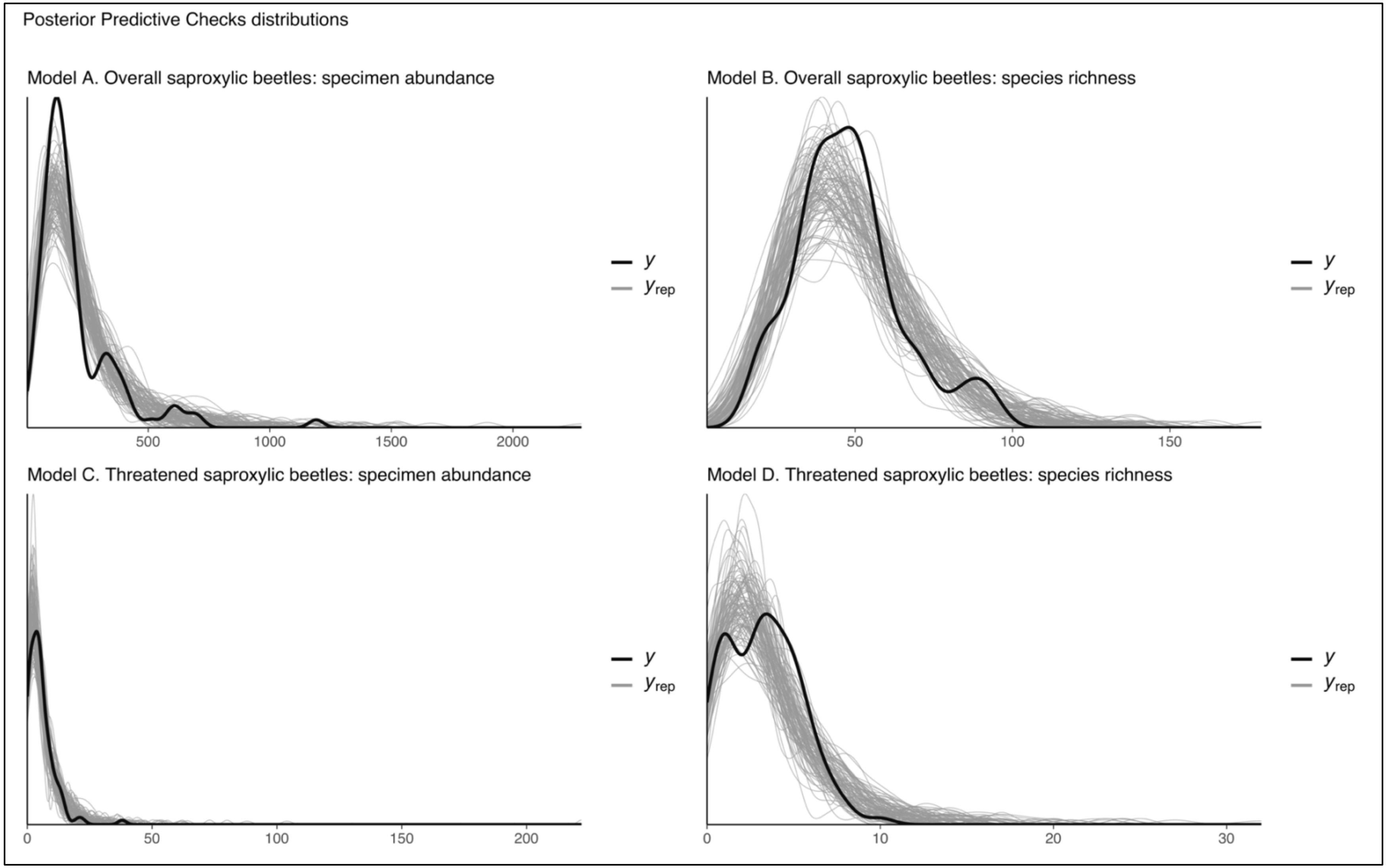
S4. Pairwise comparison of the explanatory variables selected to assess the effect of the White-backed Woodpecker activity and the habitat parameters on the saproxylic beetle communities; Mean live tree diameter at breast height.

S5. Summary table of the Bayesian generalized linear mixed models. Secondary model group with high treatment as the intercept. Explanatory variables with a predicted effect on saproxylic beetle’ s metrics are displayed in bold.

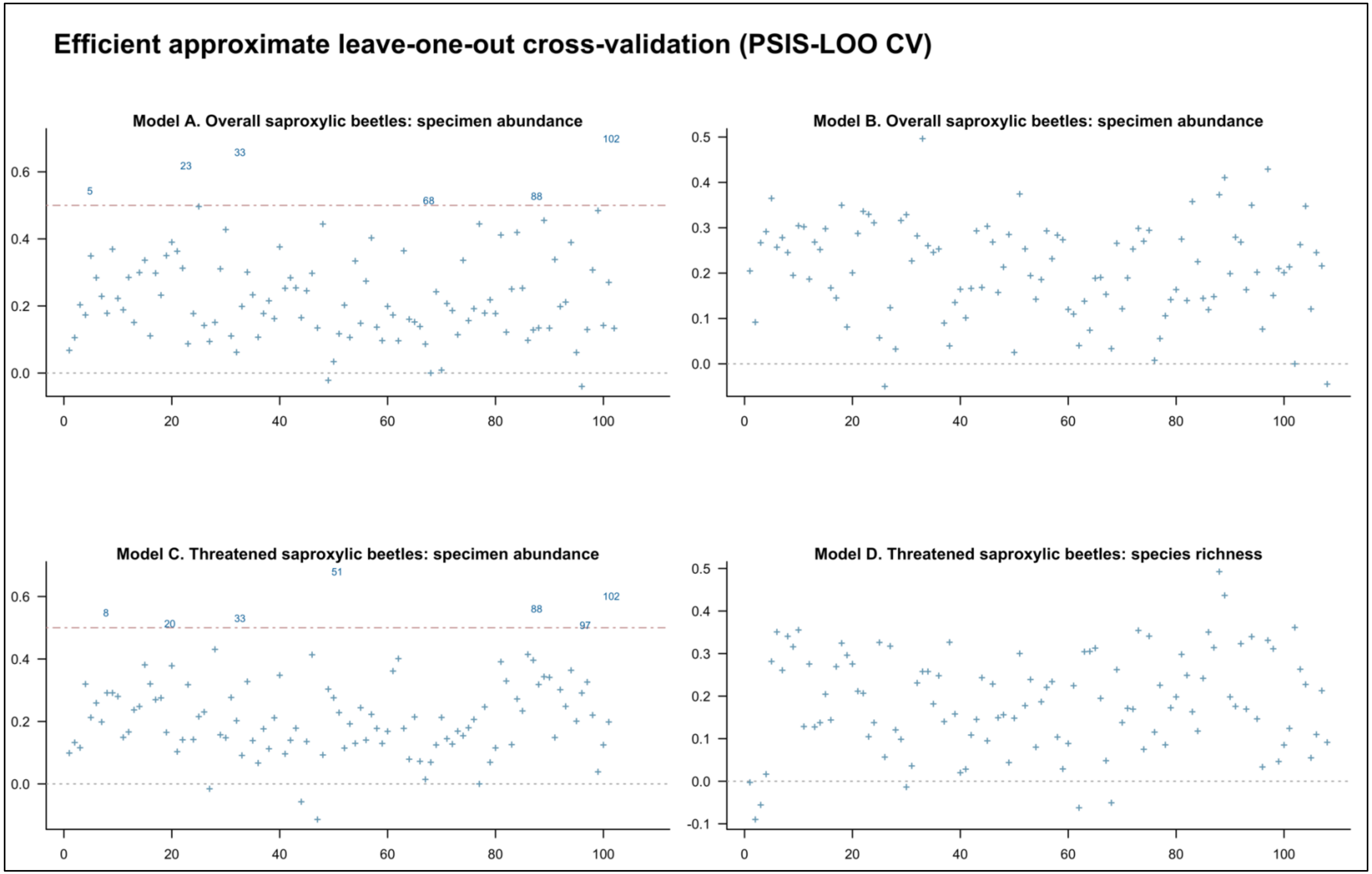
Model	Saproxylic beetles set	Response variable	Explanatory variable	Model output CrI 90% HDI posterior probability: median (min; max)	Effect size exponential(CrI 90% HDI posterior probability): median (min; max)
A	Overall	Specimen abundance	WBW activity: Control	0.063 (-0.358, 0.429)	1.065 (0.699, 1.536)
			WBW activity: Low	0.091 (-0.135, 0.325)	1.095 (0.874, 1.384)
			Volume of standing dead wood	0.047 (-0.064, 0.159)	1.048 (0.938, 1.172)
			Volume of lying dead wood	**0.145 (0.021, 0.26)**	**1.156 (1.021, 1.297)**
			Mean diameter of live tree	**0.123 (0.004, 0.253)**	**1.131 (1.004, 1.288)**
B	Overall	Species richness	WBW activity: Control	-0.048 (-0.254, 0.162)	0.953 (0.776, 1.176)
			WBW activity: Low	0.047 (-0.093, 0.179)	1.048 (0.911, 1.196)
			Volume of standing dead wood	0.038 (-0.025, 0.099)	1.039 (0.975, 1.104)
			Volume of lying dead wood	0.056 (-0.008, 0.125)	1.058 (0.992, 1.133)
			Mean diameter of live tree	0.047 (-0.016, 0.119)	1.048 (0.984, 1.126)
C	Threatened	Specimen abundance	WBW activity: Control	-0.328 (-0.769, 0.089)	0.72 (0.463, 1.093)
			WBW activity: Low	0.031 (-0.307, 0.392)	1.031 (0.736, 1.48)
			Volume of standing dead wood	0.04 (-0.123, 0.195)	1.041 (0.884, 1.215)
			Volume of lying dead wood	**0.214 (0.056, 0.397)**	**1.239 (1.058, 1.487)**
			Mean diameter of live tree	0.055 (-0.099, 0.229)	1.057 (0.906, 1.257)
D	Threatened	Species richness	WBW activity: Control	-0.415 (-0.759, -0.093)	0.66 (0.468, 0.911)
			WBW activity: Low	**-0.077 (-0.373, 0.194)**	**0.926 (0.689, 1.214)**
			Volume of standing dead wood	0.024 (-0.106, 0.145)	1.024 (0.899, 1.156)
			Volume of lying dead wood	**0.155 (0.027, 0.286)**	**1.168 (1.027, 1.331)**
			Mean diameter of live tree	0.034 (-0.098, 0.168)	1.035 (0.907, 1.183)



S6. Drivers of saproxylic beetle species richness and specimen abundance: Histograms and kernel density plots of MCMC draws; Main model group with Control level as intercept.



S7. Drivers of saproxylic beetle species richness and specimen abundance: Posterior predictive checks distribution; Main model group with Control level as intercept.



S8. Drivers of saproxylic beetle species richness and specimen abundance: Efficient approximate leave-one-out cross-validation for our main model group with Control level as intercept, using Pareto smoothed importance sampling (PSIS-LOO CV).

S9. Correlation table among selected set of explanatory variables.

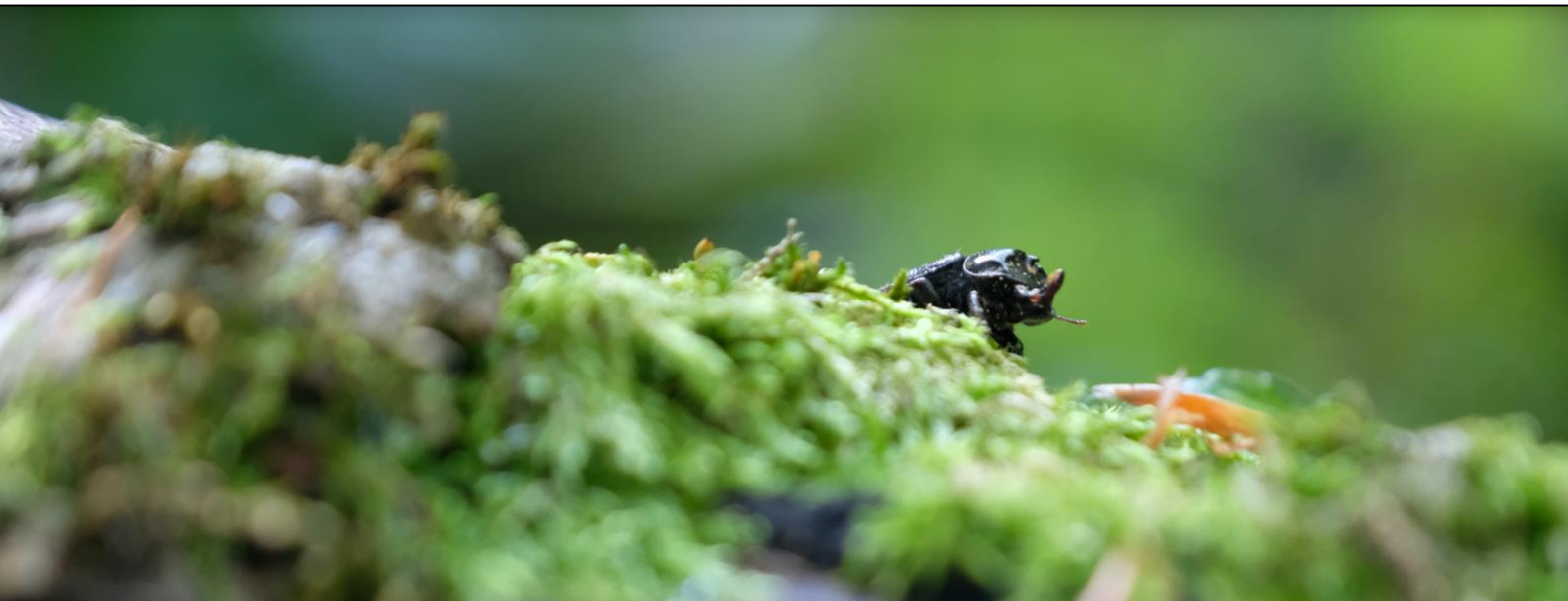
Correlation among predictors (FIT)

	obs57	standing_m3	lying_m3	lt_dbh_mean
obs57		0.178 (.066)	0.192 (.047)	0.159 (.101)
standing_m3			0.299 (.002)	0.118 (.223)
lying_m3				0.295 (.002)
lt_dbh_mean				

Computed correlation used pearson-method with listwise-deletion.

Chapter 2

Forest stands with large live and dead standing trees benefit both White-backed Woodpecker and saproxylic beetle communities



Forest stands with large live and dead standing trees benefit both White-backed Woodpecker and saproxylic beetle communities

Romain Angeleri [1,2,3], Nicolas Roth [1,3], Urs G. Kormann [4], Antonia Ettwein [4], Michael Lanz [4], Raphaël Arlettaz [2], Thibault Lachat [1,3]

[1] Bern University of Applied Sciences, School of Agricultural, Forest and Food Sciences HAFL, Zollikofen, Switzerland

[2] Conservation Biology, Institute of Ecology and Evolution IEE, University of Bern, Bern, Switzerland

[3] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[4] Swiss Ornithological Institute, Sempach, Switzerland

Chapter status: *Submitted to "Forest Ecology and Management" (Under review)*

Abstract

Effective forest management to promote biodiversity requires understanding the intricate relationship between forest characteristics and species occurrence. Dead wood structures have gained attention as key components of biodiversity-friendly forestry, given that more than 25% of forest taxa are associated with dead wood. The White-backed Woodpecker (*Dendrocopos leucotos*) is the rarest woodpecker in Central European deciduous forests, and observational studies often report the species preferentially foraging on dead standing trees. Despite lack of systematic assessment of the importance of dead wood structures for the woodpecker and its associated prey, conservation plans typically focus on dead standing tree enrichment when restoring forest patches for White-backed Woodpeckers. Here, we used confirmatory path analysis to compare the direct and indirect effect of structural characteristics of beech-dominated forest's on saproxylic beetle communities and White-backed Woodpecker activity, as measured with radiotelemetry. Using in situ emergence traps, we sampled saproxylic beetle communities emerging from 87 dead standing European beech trees over a period of two years, yielding 6519 specimens representing 156 saproxylic beetle species. We found White-backed Woodpecker activity to be positively correlated with the diameter of live trees. Live tree diameter was also positively correlated with species richness of saproxylic beetle communities via an indirect positive effect on snag diameter. Taken together, our results emphasize the importance of (1) retaining snags in extensively managed forests, and (2) setting aside forest reserves which are allowed to reach late-successional stages including the senescence of large trees to form large-diameter dead wood resources.

Keywords

White-backed Woodpecker; Saproxylic beetles; Dead standing trees; radio-telemetry; In-situ emergence traps; Confirmatory path analysis

Introduction

More than 25% of all forest species, ranging from arthropods (e.g., beetles) to vertebrates (e.g., birds), are considered to be saproxylic and thus depend on dead wood (Lachat & Müller, 2018). Among them, saproxylic beetles are arguably the most speciose group of this guild, and are defined as "species [of invertebrates] that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight, 1989). While the majority of the saproxylic beetles can survive with dead wood quantities compatible with managed forests (Müller and Bütler, 2010), some of them have high requirements regarding the quantity and the diversity of dead wood (Brin et al., 2013; Gossner et al., 2013; Jonsell et al., 2004; Jonsell & Weslien, 2003; Seibold et al., 2016; Siitonen et al., 2000).

This diversity of dead wood resource can be described in terms of taxonomy (i.e., tree category: broadleaved or coniferous; tree species), size (i.e., fine to coarse woody debris), position (i.e., lying, standing, attached), elevation above ground (i.e., from the forest floor to the canopy), origin (i.e., man-made or natural), as well as decay stage and decomposition rate (Niemelä et al., 2002; Onodera & Tokuda, 2015). While logs are a common element of European forests, the quantity of standing dead wood found in a forest stand is much more variable (Brändli et al., 2020; Guby & Dobbertin, 1996; Karjalainen & Kuuluvainen, 2002; Meyer & Schmidt, 2011; Sippola et al., 2001). This variability can be driven by many factors, either increasing its availability (e.g., windthrows (Thorn et al., 2014) and insect outbreaks (Müller et al., 2008)) or by removing it from the landscape (e.g., intensive logging and bioenergy (Ranius et al., 2018) or public safety (Carpaneto et al., 2010)). Due to their limited contact with the ground, snags are less humid than logs and offer specific habitat conditions for the development of dead wood dependent invertebrates (Ranius et al., 2019). They also remain out of snow during winter and might play an important role in providing food items for insectivorous birds such as woodpeckers.

The White-backed Woodpecker (*Dendrocopos leucotos*) for example, has previously been shown to largely rely on saproxylic beetles, both for adults (Aulén, 1988) and nestlings (Aulén, 1988; Hogstad & Stenberg, 1997), with large larvae (e.g., Cerambycidae) being the preferred prey. Because of this food specialization, the woodpecker requires habitat with high amounts of dead wood and its occurrence is thus restricted to stands with low to a total absence of management (Czeszczewik & Walankiewicz, 2006).

Although the White-backed Woodpecker has been suggested as an umbrella species for saproxylic beetles (Angeleri et al., under review), the link between saproxylic beetle communities and this bird species is still poorly understood. Nevertheless, Ettwein et al., (2020) found that the probability of White-backed Woodpecker occupancy was positively related to the density of saproxylic beetle emergence holes on both lying and standing dead wood. However, an increase in dead wood does not automatically benefit both saproxylic beetles and the White-backed Woodpecker. In a Swedish White-backed Woodpecker conservation project, which included measures to increase the volume and diversity of dead wood, saproxylic beetles but not the focal bird species reacted positively to habitat restoration (Bell et al., 2015). This shows that more research on the link between this insectivorous predator and its potential prey may be needed to effectively protect both White-backed Woodpeckers and saproxylic beetles. Snags have been shown to be used more often than logs by foraging White-backed Woodpeckers (Bühler, 2009; Czeszczewik, 2009; Hogstad & Stenberg, 2005) explaining habitat selection (Ettwein et al., 2020) and abundance (Czeszczewik et al., 2013). Thus, standing dead wood and its associated saproxylic beetle communities may be especially important for White-backed Woodpeckers.

In this study we explored the direct and indirect effects of local forest and snag characteristics, food resources, and temperature, on White-backed Woodpecker activity. We collected data on the birds' activity using repeated radiotelemetry and playback recording at 18 different sites. We also characterized the saproxylic beetle community emerging from dead standing trees, using a two-year eclector sampling method. We then combined the data in a confirmatory path analysis framework based on a three-step hypothesis: (1) we predicted that woodpecker activity would be positively correlated with saproxylic beetle species richness, abundance, and body size, as well as with the diameter of live trees, and the diameter and bark coverage of dead standing trees. (2) we predicted that beetle species richness, abundance and body size would be positively correlated with the diameter of live trees, and with the diameter and bark coverage of dead standing trees. (3) we predicted that the diameter of standing dead trees would be positively correlated with the diameter of live trees.

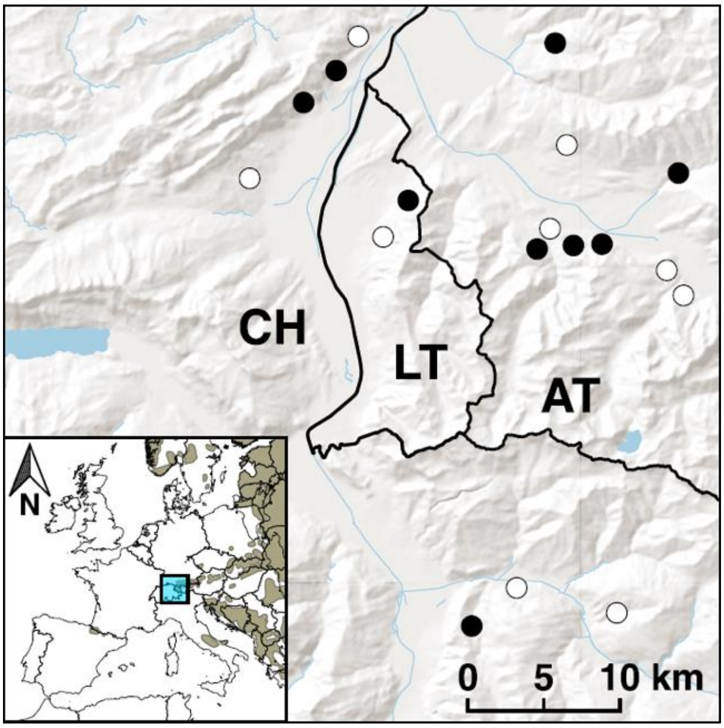


Figure 1. Map of the study region with the breeding home ranges of White-backed Woodpeckers (black dots) and the absence sites (white dots). The inset shows the White-backed Woodpecker distribution in Western European (khaki area) and the location of the study region (blue square) depicted in the main map. Source: BirdLife International and Handbook of the Birds of the World (2020): *Dendrocopos leucotos*. The IUCN Red List of Threatened Species. Version 2021-3. Downloaded on 09 March 2022.

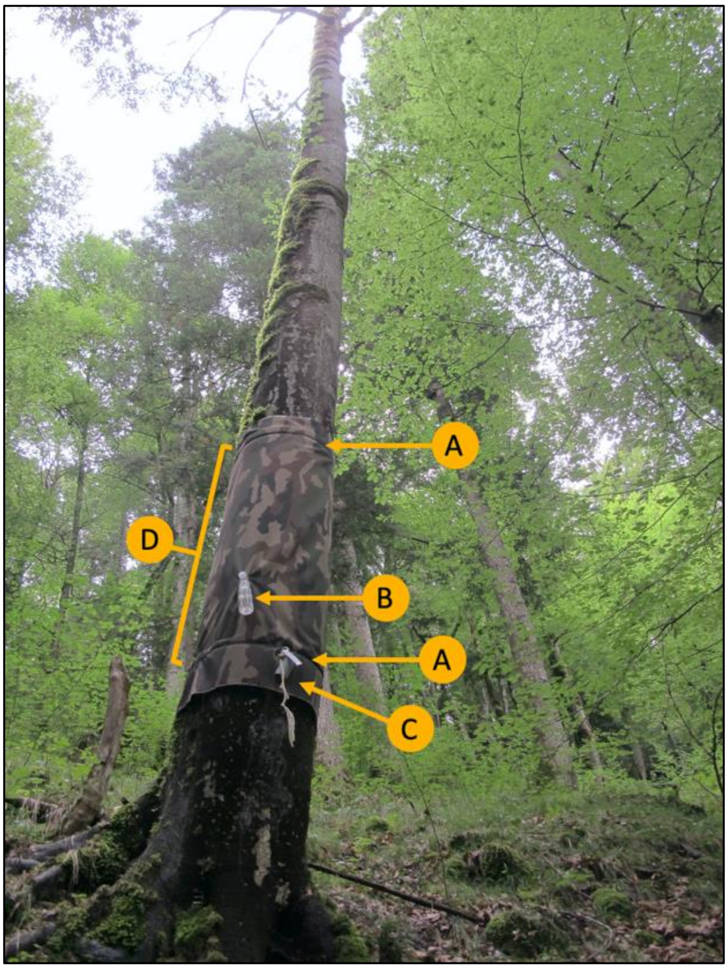


Figure 2. Eclector trap installed on a European beech snag to collect emerging saproxylic invertebrates.

A = Metallic wire closing the extremities of the trap;

B = Collecting device (plastic pipe + plastic bottle filled with 70% ethanol and water);

C = Temperature logger;

D = Sampling surface.

Material and method

Study area & site selection

The study took place in the Central European Alps, in Eastern Switzerland (cantons Grisons and St. Gallen), Western Austria (province Vorarlberg) and the Principality of Liechtenstein. (46.8 - 47.4°N, 9.2 - 10.2°E; Figure 1). The site selection was designed to represent a gradient of White-backed Woodpecker activity, from areas located within active breeding home ranges to areas where the species was absent. To identify these sites, we applied a two-step approach. (1) We used radiotelemetry data (hereafter "VHF") collected in 2016 and 2017 (Ettwein et al.– under review) to identify forest areas actively used by White-backed Woodpeckers. We identified White-backed Woodpecker activity plots by creating a heatmap layer based on the number of VHF observations using a hexagon approach of 500 m^2 in Quantum GIS (v.2.18) with the plugin QMarxan Toolbox (v.0.3.4). To avoid any potential confounding effects of visits to the nest on bird activity, we applied an exclusion buffer in a 150 m radius centered on the breeding cavity of the tracked bird individuals. We then selected two plots with the highest density of VHF observations and two additional plots with the lowest density per territory for a total of 36 plots in 9 breeding home ranges. (2) We then selected forests without known White-backed Woodpecker observations as absence sites, following the procedure described in Ettwein et al. (2020). The absence sites had a size of 550x550 m (= 30.25 ha), which approximately corresponds to the average breeding home range size of the tracked White-backed Woodpeckers (Ettwein et al. – under review). From February to March 2018, we confirmed the absence of White-backed Woodpeckers using playback recordings every 200 m. We then located two representative sampling plots around the center of each control site for a total of 18 plots at 9 absence sites. In both breeding home ranges and control sites, plots with overlapping rock cliffs and river streams were not selected for accessibility reasons. To avoid spatial autocorrelation, plots were installed 50 m apart within each site. Slope aspect and gradient of all plots were equally distributed across sites. All plots were situated in beech-dominated forest stands with an elevation ranging from 630 and 1230 m above sea level. Additional information can be found in Angeleri et al., (under review).

Beetle sampling

On each plot we sampled saproxylic beetles on all available dead standing European beech trees (hereafter "snags") with a diameter at breast height (DBH) > 10 cm, yielding a total of 87 snags (Control sites = 29 snags; Breeding home ranges = 58 snags). The number of snags per plot ranged from 0 to 5. A total of 10 plots could not be included in the analyses due to the absence of snags (Presence = 7; Absence = 3). Eclector traps were used to sample beetles, and snags were wrapped around the stem with a piece of camouflage patterned (160 cm length) polyester fabric to form a trap for emerging insects (Figure 2). To allow insects living in the snag to hatch and move around, we created a 4 cm gap between the fabric and the snag with foam strip at both ends on which the fabric was firmly attached with a metallic wire, resulting in as a closed cylindric trap of 150 cm long. The joint line was rolled on itself and stappled on the south-oriented side of the snag. To collect insects, a plastic bottle filled with 70% ethanol was attached to a 3 cm diameter plastic pipe which was in contact with the tree trunk. The bottle was attached to the north-oriented side of the snag to avoid excessive evaporation of the collecting and conservation fluid. Emerging insects were passively guided by the fabric to the collecting device as it was the only bright light source available in the sampled tree trunk section. Traps were emptied monthly from April 2018 to September 2019. Beetle specimens were then identified to species level in the lab and classified as threatened or least concern, following Schmidl and Bussler (2004). Samples were pooled across all months for every snag. Species without reliable information about their saproxylic habits were excluded from further analyses (*Pterostichus aethiops* = 1 specimen; *Halyzia sedecimguttata* = 1 specimen; *Batophila rubi* = 1 specimen; *Mniophila muscorum* = 3 specimens).

Trap and habitat characterization

In a 500 m^2 circular area centered on every sampled snag, we measured the diameter of all live and dead trees with a diameter at breast height ≥ 6 cm. For all sampled snags, we measured the diameter at breast height and the proportion of remaining bark was also estimated visually. Air temperature was measured every 2 hours throughout the sampling period on every plot, using a HOBO Pendant® temperature data logger (UA-001-08; Onset Computer Corporation). Temperature data loggers were attached at breast height on the northern side of a live or dead tree, as much as possible in the center of the plot. Temperature data loggers were shaded by a plastic tube to avoid direct sun radiation (Figure 2).

Statistical analysis

Using confirmatory path analysis in a piecewise structural equation modelling framework (hereafter "pSEM"; Lefcheck, 2016), we analyzed (1) how White-backed Woodpecker activity varied as a function of the different saproxylic beetle community metrics (species richness, abundance, community weighted means of body length), sampled snag characteristics (diameter at breast height and proportion of remaining bark) and habitat parameters (mean diameter at breast height of live trees and mean annual air temperature); (2) how saproxylic beetles communities (species richness, abundance, community weighted means of body length) varied as a function of sampled snags characteristics (diameter at breast height and proportion of remaining bark) and habitat parameters (mean diameter at breast height of live trees and mean annual air temperature); and (3) how the diameter of the sampled snags varied as a function of the mean live tree diameter (Table 1).

The analysis included the following steps. (1) The mean body length of the saproxylic beetle communities was computed, per snag, with the function ‘cwm’ in the R package ‘BAT’. (2) Abundance was log transformed to reduce the influence of outliers (Emery et al., 2021). (3) To account for plots with a White-backed Woodpecker activity equal to 0, yet encompassed within a breeding home range, as opposed to known White-backed Woodpecker absence sites, a theoretical VHF observation of a value equal to “1” was added to the White-backed Woodpecker activity-density variable (i.e., VHF count data). (4) All variables were normalized (mean = 0; sd = 1), allowing cross-comparison among variables. Because the mean diameter of the snag measured during the habitat inventories was correlated (Pearson’s correlation coefficient = 0.8) to the diameter of the sampled snags (also included in the habitat inventories), the latter was kept as explanatory variable as it was more relevant to our study question. Variables included in the final model showed little collinearity (Pearson’s correlation coefficient < 0.4). Snags were tested for non-spatial autocorrelation using Moran’s I test beforehand with the function ‘moran.test’ in the R package ‘spdep’.

Table 1. Description of the variable composing the confirmatory path analysis in the piecewise structural equation modelling framework.

Grouping	Variable name	Unit	Definition
White-backed Woodpecker	WBW activity	N	Sum of the very high frequency logs of the tracked White-backed Woodpeckers, per sampling plot.
Saproxylic beetle	Abundance	N	Number of emerged saproxylic beetle specimens, per sampled snag.
Saproxylic beetle	Richness	N	Number of different saproxylic beetle species, per sampled snag.
Saproxylic beetle	CWM body length	mm	Community weighted means of the body length of the emerged saproxylic beetles, per sampled snag.
Habitat	Live tree diameter	cm	Mean diameter at breast height of live tree in a centered circular surface of 500 m2, per sampled snag.
Habitat	Temperature	°C	Mean annual temperature measured, per sampling plot.
Sampled snag	Snag diameter	cm	Diameter at breast height of the sampled snag.
Sampled snag	Snag bark cover	%	Proportion of remaining bark, per sampled snag.

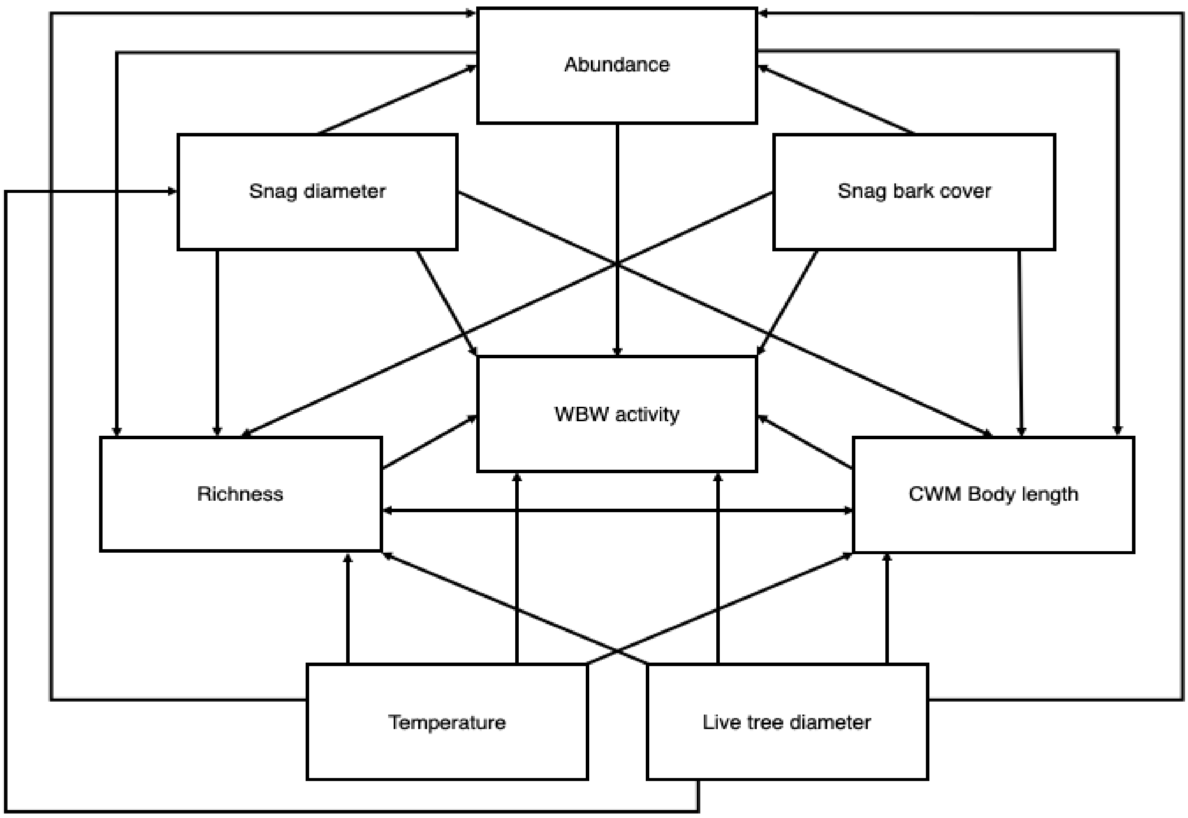


Figure 3. Complete path diagram of the hypothesized effects that were tested among the five models: White-backed Woodpecker activity (WBW activity), saproxylic beetle abundance (Abundance), saproxylic beetles' species richness (Richness), saproxylic beetles' community weighted mean of the body length (Body length), mean diameter at breast height of the sampled snag (Snag diameter).

Next, we built linear mixed models – without non-linear relationships du to computation limitations – for all response variables (Table 1), following a hypothesis testing approach (Tredennick et al., 2021),. Inclusion of random intercept was not possible due to computational limitations. Residuals of all models were checked for normality and heteroscedasticity.

Finally, we used pSEM to piece together, with direct and indirect effects, our set of linear models (Figure 2). In case of a missing path found to be both statistically significant and ecologically relevant, models were updated with the newly identified explanatory variable. Original and updated models were compared using Akaike Information Criterion (AIC). The model with the smallest AIC was selected as reference, and models were considered as equivalent if the delta-AIC was smaller than 2. Independence claims were defined as tying the snag diameter and the mean temperature, and as tying the snag diameter and the snag bark cover together, respectively. Missing paths in the initial pSEM were detected by the D-separation test and overall model fit was evaluated with Fischer's C statistic. If the p-value resulting from the evaluation of the model fit was greater than 5%, the model was considered to fit the data. Finally, the relative importance of the paths was determined using standardized path coefficients (Figure 3). All statistical analyses were performed using R Version 4.2.2 (R Core Team 2022).

Table 2. Direct standardized effect size of explanatory variables on the response variables for the 5-component models composing the final confirmatory path model (* = Significance ≤ 0.05; ° = Marginal significance; NS = non-Significant; - = Not considered). Abbreviations see Table 1.

Component model	Pseudo-R2	Abundance	Richness	CWM body length	Live tree diameter	Temperature	Snag diameter	Snag bark cover
WBW activity	0.19	NS	NS	NS	0.35 *	-0.23 *	NS	NS
Abundance	0.05	-	-	-	NS	NS	NS	NS
Richness	0.31	0.38 *	-	-	0.17 °	0.2 *	0.26 *	NS
CWM body length	0.06	-	-	-	NS	NS	NS	-0.23 *
Snag diameter	0.06	-	-	-	0.25 *	-	-	-

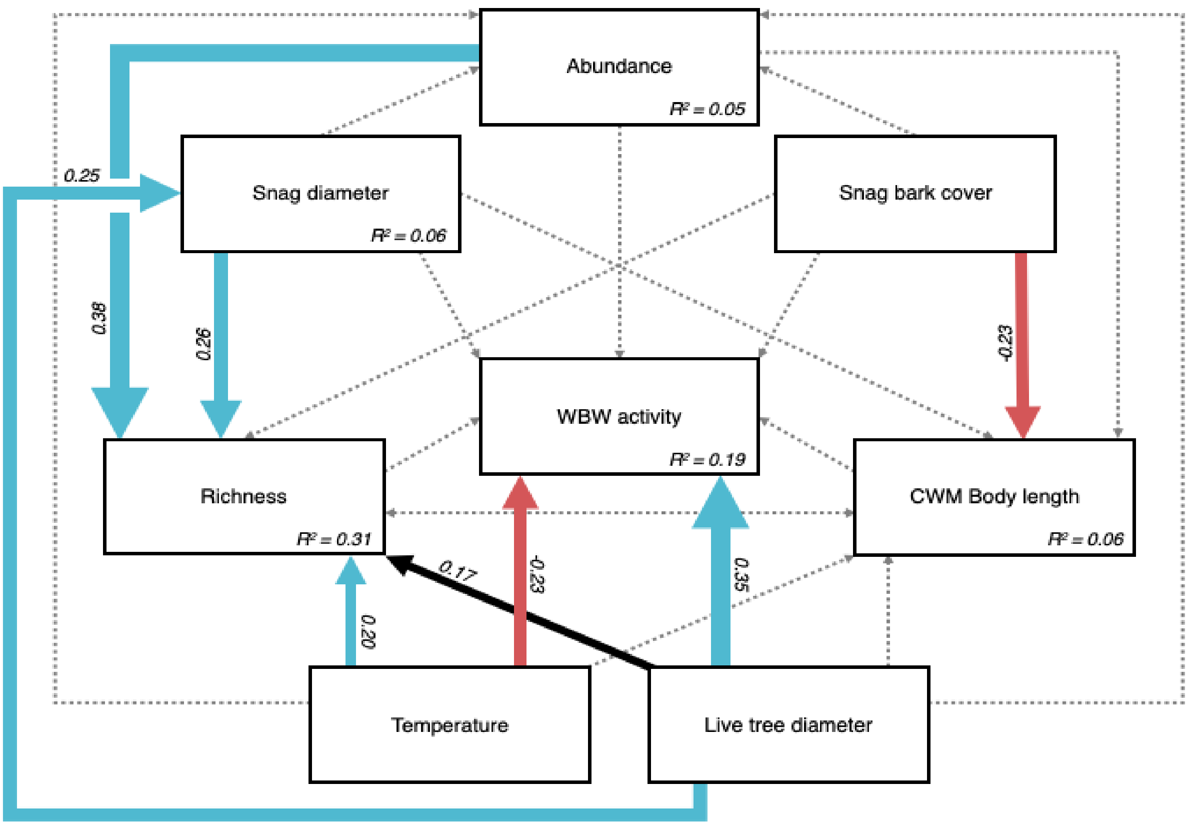


Figure 4. Direct and indirect effects of the five models composing the final confirmatory path analysis (AIC = 66.04, Fischer's C statistic = 4.04, p = 0.401, df = 4). Red arrows indicate a significantly negative effect, blue arrows indicate a significantly positive effect, black arrow indicates a marginal effect and dotted arrows indicates a non-significant effect. Arrows' width and associated value corresponds to the standardized effect of the path, for the significant and marginal correlations. R-squared values are associated to the response variable.

Results

Saproxylic beetle community

The 87 sampled snags yielded a total of 6519 specimens representing 156 species. From these, 6 species were identified as threatened (*Pteryngium crenatum* (Cryptophagidae) = 2 specimens in White-backed Woodpecker breeding home ranges; 1 in absence sites); *Hylis olexai* (Eucnemidae) = 1; 0); *Isorhipis melasoides* (Eucnemidae) = 5; 4); *Euconnus pragnesis* (Staphylinidae) = 0; 2); *Thymalus limbatus* (Trogossitidae) = 1; 0); *Colydium elongatum* (Zopheridae) = 1; 0) (See Supplementary materials).

White-backed Woodpecker model

White-backed Woodpecker activity was significantly positively correlated with the mean diameter of live trees ($p < 0.001$, Std. Estimate = 0.35), but significantly negatively correlated with the mean annual air temperature ($p = 0.037$, Std. Estimate = -0.23). Explained variance of this model was represented by a R-squared of 0.19 (Table 2; Figure 4, Figure 5).

Saproxylic beetle community models

No significant correlation was found between the abundance of saproxylic beetles and the set of selected explanatory variables. However, species richness of saproxylic beetles was significantly positively correlated with multiple explanatory variables: the abundance of saproxylic beetles ($p < 0.001$; Std. Eff. = 0.38), the diameter of the snag ($p = 0.008$; Std. Eff. = 0.26) and the mean annual temperature ($p = 0.037$; Std. Eff. = 0.20). Species richness of saproxylic beetles was marginally positively correlated to the mean diameter of live trees ($p = 0.082$; Std. Eff. = 0.17). Explained variance of this model was represented by a R-squared of 0.31. Finally, a significant negative correlation was found between the mean body length of the sampled saproxylic beetle communities and the proportion of remaining bark of the sampled snags ($p = 0.034$; Std. Eff. = -0.23). Explained variance of this model was represented by a R-squared of 0.06 (Table 2; Figure 4, Figure 5).

Dead standing tree model

We found a significant positive correlation between the diameter of the sampled snags and the mean diameter at breast height of live trees ($p = 0.0179$; Std. Eff. = 0.25). Explained variance of this model was represented by a R-squared of 0.06 (Table 2; Figure 4, Figure 5).

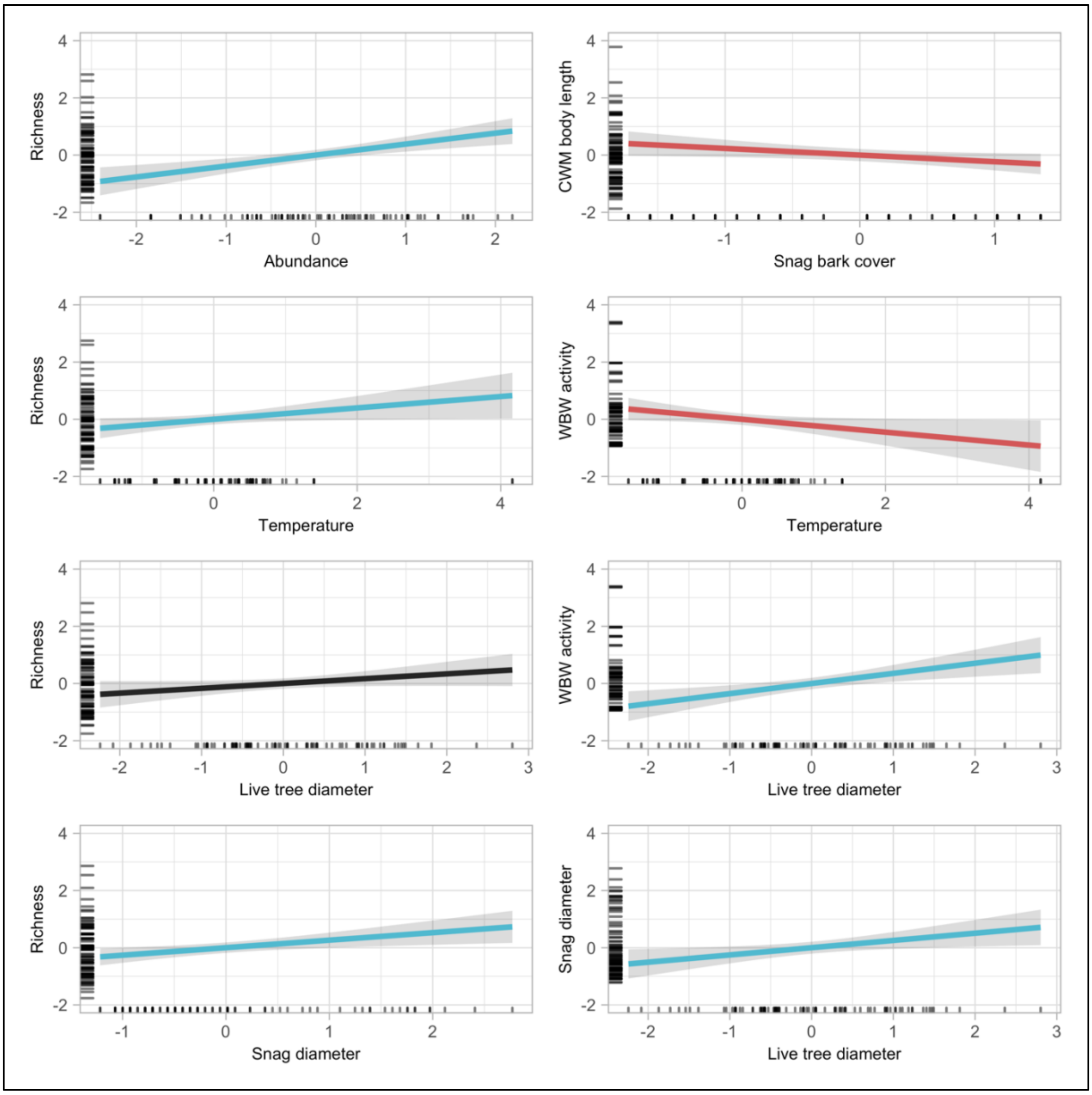


Figure 5. Standardized effect size for every significantly positive (blue), negative (red) and marginally significant (black) correlation identified within the final confirmatory path model. The grey area around the regression-function represents the 95% confidence interval.

Discussion

Our results show that the mean diameter of life trees directly and positively influences White-backed Woodpecker's activity and indirectly boosts species richness of saproxylic beetles. However, despite the often emphasized importance of dead standing trees for White-backed Woodpecker's foraging (Bühler, 2009; Virkkala et al., 1993), we could not establish a direct positive bottom-up effect (Campbell & Donato, 2014) of the saproxylic beetle community upon the feeding activity of the White-backed Woodpecker. From our understanding, predation or methodological biases could explain this apparent absence of link. (1) The snags that we sampled could have been partly depredated by insectivores prior to the installation of the emergence traps. If depleted, our samples may thus have hindered the demonstration of predator-prey relationships between the woodpecker and its staple food (Fayt et al., 2005). (2) While the diet of the White backed Woodpecker incorporates mostly large larvae (Aulén, 1988; Hogstad & Stenberg, 1997), saproxylic beetle communities with large species did not correlate with bird's presence, providing further support to our hypothesis that prey depletion may have taken place prior to our experiment. (3) Given that our traps were continuously active for a period of two years, we probably did not sample all potential prey occurring within a snag. More specifically, one could infer that species with longer life cycles (e.g., Cerambycidae) would have been underrepresented in our dataset. (4) Additionally, the probability of detection in visual bird surveys depends largely on vegetation clutter (Zwarts & Bijlsma, 2015), one could question whether former observations reporting snags to be the favored dead wood items by foraging White-backed Woodpeckers were not biased (Bühler, 2009). (5) White-backed Woodpeckers have been evidenced to use dead standing trees in wintertime, where lying dead wood items are covered by snow (Czeszczewik, 2009). As our sampling design assessed communities in standing dead wood items only, it is possible that the prey item stock found in lying dead wood would be the critical parameter influencing White backed Woodpecker's activity in a given forest patch.

Nonetheless, forest characteristics were identified as having both direct and indirect effects on both White-backed Woodpeckers and saproxylic beetle communities. Specifically, the mean diameter at breast height of live trees, selected as a proxy for forest maturity, was positively correlated with White-backed Woodpecker activity, Although forest maturity may not be properly assessed by a single variable (Roberge et al., 2008), this positive correlation is in line with previous studies conducted in identical (Ettwein et al., 2020) or other (Garmendia et al., 2006; Melletti & Penteriani, 2003; Virkkala et al., 1993) areas of the Eurasian distribution of the focal bird species. Due to their association with old forest stands (Corona, 2016; Gerdzhikov et al., 2018; Urkijo-Letona et al., 2020), White-backed Woodpeckers may therefore favour forest stands with live trees of large diameter, as a surrogate for potential old growth or primeval forests, when selecting breeding territories. In effect, compared to young stands, mature forests patches naturally host a higher number of large dead standing trees (Moroni & Harris, 2010) as well as large moribund trees offering a myriad of microhabitats such as large dead or decaying branches, i.e., suitable substrates for excavating breeding cavities (personal observation). Furthermore, mature forests also offer more dead wood resources notably fallen logs and branches lying on the ground, which promote saproxylic beetle communities and provide foraging hotspots for insectivorous predators. Our results reveal a cascading effect: live trees with a larger trunk diameter produce larger-sized dead standing trees that harbor richer saproxylic beetle communities. This positive interaction could be explained by multiple factors. Larger dead wood structures provide a diversity of substrates which may support more diverse saproxylic beetle communities. Furthermore, large diameter snags may persist longer (Onodera & Tokuda, 2015) and provide more stable environmental conditions for species sensitive to microclimatic fluctuation (Ranius et al., 2019). Snags with a large diameter will therefore provide greater resources for beetles that have long life cycles (Ranius et al., 2019) such as large body-sized species that are often red- listed (Hagge et al., 2021).

Finally, although it is well documented that species richness of saproxylic beetles is strongly correlated with thermal conditions (Lachat et al., 2014; Müller et al., 2015; Sanchez et al., 2016; Vogel et al., 2020), we found that White-backed Woodpecker activity was negatively correlated with air temperature. This contradicts the view of Hogstad and Stenberg's (1997) who showed that White-backed Woodpecker’s start of incubation and clutch size are positively influenced by temperature. However, geography may explain these differences as these two authors worked in boreal environments (Norway) while we operated next to the maximum western extension of its range (except Pyrenees). Yet, there might be some confounding factor. In our study area, forests that are easily accessible from the valley bottom are typically intensively managed, whereas stands situated on steep or inaccessible slopes, mostly at higher altitude (i.e., in colder environments) tend to be less used if at all for timber production (Ettwein et al., 2020; Sabatini et al., 2018). Consequently, forests at higher altitude tend to be more mature and more appropriate to harbor breeding White-backed Woodpeckers.

Conclusion

In conclusion, forests with large living trees promote the emblematic White-backed Woodpecker and provide the large dead standing trees that are key to a rich saproxylic beetle community. Saproxylic beetles seem to be able to colonize available standing dead wood resources across forest stands. Consequently, the cessation of management in mature forests, as well as the retention of large trees which are allowed to decay in managed forests, both benefit an entire ecological community, from wood decomposers to top predators, thus reinstating integral and functional food chains in woodland.

Acknowledgements

We are grateful to Alexander Szallies who participated in and supported the saproxylic beetle identification process. We also acknowledge the early involvement of Ueli Bühler in the development of this project within the Graubünden region and Gilberto Pasinelli for the management of the project "The White-backed Woodpecker in managed forests". The authors wish to express their thanks to Sarah Degenhart, David Hasler, Simon Niederbacher, Nicolaj Novikov and Silas Zurbuchen for their help, and especially to Pierre Cardineau, Valentin Sylvoz and Nina Marjanovic for their contributions to the fieldwork. Finally, Elena Haeler for stimulating discussions and insights, as well as Felicity Newell for significant comments on the manuscript. Financial support was provided by the Swiss Federal Office for the Environment, the Swiss Ornithological Institute and Inatura – Erlebnis Naturschau GmbH Dornbirn.

References

Aulén, G. (1988). Ecology and distribution history of the White-backed Woodpecker Dendrocopos leucotos in Sweden [Dissertation]. Swedish University of Agricultural Science.

Bell, D., Hjältén, J., Nilsson, C., Jørgensen, D., & Johansson, T. (2015). Forest restoration to attract a putative umbrella species, the White-backed Woodpecker, benefited saproxylic beetles. Ecosphere, 6(12), 1-14(278). https://doi.org/10.1890/ES14-00551.1

Brändli, Urs-Beat, Abegg, Meinrad, & Allgaier Leuch, Barbara. (2020). Inventaire forestier national suisse. Résultats du quatrième inventaire 2009-2017 (p. 341). Birmensdorf, Institut fédéral de recherches sur la forêt, la neige et le paysage WSL ; Berne, Office fédéral de l'environnement.

Brin, A., Bouget, C., Valladares, L., & Brustel, H. (2013). Are stumps important for the conservation of saproxylic beetles in managed forests? - Insights from a comparison of assemblages on logs and stumps in oak-dominated forests and pine plantations: Stumps and saproxylic beetle conservation. Insect Conservation and Diversity, 6(3), 255–264. https://doi.org/10.1111/j.1752-4598.2012.00209.x

Bühler, U. (2009). Totholz – existenziell für den Weissrückenspecht in Nordbünden | Dead wood – a vital necessity for the White-backed Woodpecker in the Grisons. Schweizerische Zeitschrift für Forstwesen, 160(7), 210–217. https://doi.org/10.3188/szf.2009.0210

Campbell, J. L., & Donato, D. C. (2014). Trait-based approaches to linking vegetation and food webs in early-seral forests of the Pacific Northwest. Forest Ecology and Management, 324, 172–178. https://doi.org/10.1016/j.foreco.2013.11.020

Carpaneto, G. M., Mazziotta, A., Coletti, G., Luiselli, L., & Audisio, P. (2010). Conflict between insect conservation and public safety: The case study of a saproxylic beetle (Osmoderma eremita) in urban parks. Journal of Insect Conservation, 14(5), 555–565. https://doi.org/10.1007/s10841-010-9283-5

Corona, P. (2016). Boschi vetusti del Parco Nazionale del Gran Sasso e Monti della Laga. Arezzo: Compagnia delle foreste.

Czeszczewik, D. (2009). Foraging behaviour of White-backed Woodpeckers Dendrocopos leucotos in a primeval forest (Białowieża National Park, NE Poland): Dependence on habitat resources and season. Acta Ornithologica, 44(2), 109–118. https://doi.org/10.3161/000164509X482687

Czeszczewik, D., & Walankiewicz, W. (2006). Logging affects the White-backed Woodpecker Dendrocopos leucotos distribution in the Białowieża Forest. Ann. Zool. Fennici, 43, 221–227.

Czeszczewik, D., Walankiewicz, W., Mitrus, C., Tumiel, T., Stański, T., Sahel, M., & Bednarczyk, G. (2013). Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. Bird Conservation International, 23(4), 414–425. https://doi.org/10.1017/S0959270912000354

Emery, S. E., Jonsson, M., Silva, H., Ribeiro, A., & Mills, N. J. (2021). High agricultural intensity at the landscape scale benefits pests, but low intensity practices at the local scale can mitigate these effects. Agriculture, Ecosystems & Environment, 306, 107199. https://doi.org/10.1016/j.agee.2020.107199

Ettwein, A., Korner, P., Lanz, M., Lachat, T., Kokko, H., & Pasinelli, G. (2020). Habitat selection of an old-growth forest specialist in managed forests. Animal Conservation, 23(5), 547–560. https://doi.org/10.1111/acv.12567

Fayt, P., Machmer, M. M., & Steeger, C. (2005). Regulation of spruce bark beetles by woodpeckers—A literature review. Forest Ecology and Management, 206, 1–14. https://doi.org/10.1016/j.foreco.2004.10.054

Garmendia, A., Cárcamo, S., & Schwendtner, O. (2006). Forest management considerations for conservation of Black Woodpecker Dryocopus martius and White-backed Woodpecker Dendrocopos leucotos populations in Quinto Real (Spanish Western Pyrenees). Biodiversity and Conservation, 15(4), 1399–1415. https://doi.org/10.1007/s10531-005-5410-0

Gerdzhikov, G. P., Georgiev, K. B., Plachiyski, D. G., Zlatanov, T., & Shurulinkov, P. S. (2018). Habitat Requirements of the White-backed Woodpecker Dendrocopos leucotos lilfordi (Sharpe & Dresser, 1871) (Piciformes: Picidae) in Strandzha Mountain, Bulgaria. Acta Zoologica Bulgarica, 70(4), 527–534.

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W., & Müller, J. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology, 27(3), 605–614. https://doi.org/10.1111/cobi.12023

Guby, N. A. B., & Dobbertin, M. (1996). Quantitative Estimates of Coarse Woody Debris and Standing Dead Trees in Selected Swiss Forests. Global Ecology and Biogeography Letters, 5(6), 327. https://doi.org/10.2307/2997588

Hagge, J., Müller, J., Birkemoe, T., Buse, J., Christensen, R. H. B., Gossner, M. M., Gruppe, A., Heibl, C., Jarzabek-Müller, A., Seibold, S., Siitonen, J., Soutinho, J. G., Sverdrup-Thygeson, A., Thorn, S., & Drag, L. (2021). What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. Journal of Animal Ecology, 90(8), 1934–1947. https://doi.org/10.1111/1365-2656.13512

Hogstad, O., & Stenberg, I. (2005). Sexual differences in physical condition in the White-backed Woodpecker Dendrocopos leucotos in relation to habitat type and across seasons. Ornis Fennica, 82, 26-31.

Jonsell, M., Nittérus, K., & Stighäll, K. (2004). Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation, 118(2), 163–173. https://doi.org/10.1016/j.biocon.2003.08.017

Jonsell, M., & Weslien, J. (2003). Felled or standing retained wood — It makes a difference for saproxylic beetles. Forest Ecology and Management, 175, 425–435. https://doi.org/10.1016/S0378-1127(02)00143-3

Karjalainen, L., & Kuuluvainen, T. (2002). Amount and diversity of coarse woody debris within a boreal forest landscape dominated by Pinus sylvestris in

Vienansalo wilderness, eastern Fennoscandia. Silva Fennica, 36(1), 147-167. https://doi.org/10.14214/sf.555

Lachat, T., Brang, P., Bollmann, K., Brändli, U.-B., Bütler, R., Herrmann, S., Olivier, S., & Wermelinger, B. 2014: Bois mort en forêt. Formation, importance et conservation. Not. prat. 52: 12 p.

Lachat, T., & Müller, J. (2018). Importance of Primary Forests for the Conservation of Saproxylic Insects. In Ulyshen, M. D., (Ed.), Saproxylic Insects (Vol. 1, pp. 581–605). Springer International Publishing. https://doi.org/10.1007/978-3-319-75937-1_17

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution, 7(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Melletti, M., & Penteriani, V. (2003). Nesting and feeding tree selection in the endangered White-backed Woodpecker, Dendrocopos leucotos lilfordi. The Wilson Bulletin, 115(3), 299–306. https://doi.org/10.1676/03-022

Meyer, P., & Schmidt, M. (2011). Accumulation of dead wood in abandoned beech (Fagus sylvatica L.) forests in northwestern Germany. Forest Ecology and Management, 261(3), 342–352. https://doi.org/10.1016/j.foreco.2010.08.037

Moroni, M. T., & Harris, D. D. (2010). Snag frequency, diameter and species distribution and input rate in Newfoundland boreal forests. Forestry, 83(3), 229–244. https://doi.org/10.1093/forestry/cpp027

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I. M. M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., & Gossner, M. M. (2015). Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography, 38(5), 499–509. https://doi.org/10.1111/ecog.00908

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., & Duelli, P. (2008). The European spruce bark beetle Ips typographus in a national park: From pest to keystone species. Biodiversity and Conservation, 17(12), 2979–3001. https://doi.org/10.1007/s10531-008-9409-1

Niemelä, T., Wallenius, T., & Kotiranta, H. (2002). The Kelo tree, a vanishing substrate of specified wood-inhabiting fungi. Polish Botanical Journal, 47(2), 91–101.

Olav Hogstad & Ingvar Stenberg. (1997). Breeding Success, Nestling Diet and Parental Care in the White-backed Woodpecker Dendrocopos leucotos. Journal Für Ornithologie, 138, 25–38.

Onodera, K., & Tokuda, S. (2015). Do larger snags stand longer? — Snag longevity in mixed conifer–hardwood forests in Hokkaido, Japan. Annals of Forest Science, 72(5), 621–629. https://doi.org/10.1007/s13595-015-0478-5

Ranius, T., Hämäläinen, A., Egnell, G., Olsson, B., Eklöf, K., Stendahl, J., Rudolphi, J., Sténs, A., & Felton, A. (2018). The effects of logging residue extraction for energy on ecosystem services and biodiversity: A synthesis. Journal of Environmental Management, 209, 409–425. https://doi.org/10.1016/j.jenvman.2017.12.048

Ranius, T., Hämäläinen, A., Sjögren, J., Hiron, M., Jonason, D., Kubart, A., Schroeder, M., Dahlberg, A., Thor, G., & Jonsell, M. (2019). The evolutionary species pool concept does not explain occurrence patterns of dead-wood-dependent organisms: Implications for logging residue extraction. Oecologia, 191(1), 241–252. https://doi.org/10.1007/s00442-019-04473-2

Roberge, J.-M., Angelstam, P., & Villard, M.-A. (2008). Specialised woodpeckers and naturalness in hemiboreal forests – Deriving quantitative targets for conservation planning. Biological Conservation, 141(4), 997–1012. https://doi.org/10.1016/j.biocon.2008.01.010

Sabatini, F. M., Burrascano, S., Keeton, W. S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P. J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Marques Duarte, I., Meyer, P., Midteng, R., Mikac, S., … Kuemmerle, T. (2018). Where are Europe's last primary forests? Diversity and Distributions, 24(10), 1426–1439. https://doi.org/10.1111/ddi.12778

Sanchez, A., Chittaro, Y., Monnerat, C., & Gonseth, Y. (2016). les coléoptères saproxyliques emblématiques de Suisse, indicateurs de la qualité de nos forêts et milieux boisés | List of saproxylic beetles with a high conservation value in Switzerland, providing indication of the quality of our woodland areas. Bulletin de la Société Entomologique Suisse, 89, 267-280. https://doi:10.5281/zenodo.192638

Schmidl, J., & Bußler, H. (2004). Ökologische Gilden xylobionter Käfer Deutschlands. Naturschutz Und Landschaftsplanung, 36, 202–218.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M. D., & Müller, J. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology, 53(3), 934–943. https://doi.org/10.1111/1365-2664.12607

Siitonen, J., Martikainen, P., Punttila, P., & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management, 128(3), 211–225. https://doi.org/10.1016/S0378-1127(99)00148-6

Sippola, A. L., Lehesvirta, T., & Renvall, P. (2001). Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. Ecological Bulletin, 49, 243–254.

Speight, M. C. D. (1989). Saproxylic invertebrates and their conservation (Nature and environment). Strasbourg, France: Council of Europe.

Thorn, S., Bässler, C., Gottschalk, T., Hothorn, T., Bussler, H., Raffa, K., & Müller, J. (2014). New Insights into the Consequences of Post-Windthrow Salvage Logging Revealed by Functional Structure of Saproxylic Beetles Assemblages. PLoS ONE, 9(7), e101757. https://doi.org/10.1371/journal.pone.0101757

Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology, 0(0), 1-16. https://doi.org/10.1002/ecy.3336

Urkijo-Letona, A., Cárcamo, S., Peña, L., Fernández de Manuel, B., Onaindia, M., & Ametzaga-Arregi, I. (2020). Key elements of the White-backed

Woodpecker's (Dendrocopos leucotos lilfordi) habitat in its European south-western limits. Forests, 11(8), 1–15. https://doi.org/10.3390/f11080831

Virkkala, R., Alanko, T., Laine, T., & Tiainen, J. (1993). Population contraction of the White-backed Woodpecker Dendrocopos leucotos in Finland as a consequence of habitat alteration. Biological Conservation, 66(1), 47–53. https://doi.org/10.1016/0006-3207(93)90133-L

Vogel, S., Gossner, M. M., Mergner, U., Müller, J., & Thorn, S. (2020). Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. Journal of Applied Ecology, 57(10), 2075–2085. https://doi.org/10.1111/1365-2664.13648

Zwarts, L., & Bijlsma, R. G. (2015). Detection Probabilities and Absolute Densities of Birds in Trees. Ardea, 103(2), 99–122. https://doi.org/10.5253/arde.v103i2.a1

R Packages

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Bivand, R. (2022) R Packages for Analyzing Spatial Data: A Comparative Case Study with Areal Data Geographical Analysis, 54(3), 488-518 URL Cardoso P, Mammola S, Rigal F, Carvalho J (2022). _BAT: Biodiversity Assessment Tools_. R package version 2.9.0, <https://CRAN.R-project.org/package=BAT>.

Lefcheck, Jonathan S. (2016) piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution. 7(5): 573-579. DOI: 10.1111/2041-210X.12512

Supplementary materials

S1. Forest stands with large live and dead standing trees benefit both White-backed Woodpecker and saproxylic beetle communities.

Family	Species	*D. leucotos* absence: Abundance (Incidence)	*D. leucotos* presence: Abundance (Incidence)	Total: Abundance (Incidence)
Anthribidae	*Choragus sheppardi*		1 (1)	1 (1)
Anthribidae	*Dissoleucas niveirostris*	1 (1)		1 (1)
Anthribidae	*Platystomos albinus*	2 (2)	4 (3)	6 (5)
Apionidae	*Eutrichapion punctiger*		1 (1)	1 (1)
Biphyllidae	*Diplocoelus fagi*	2 (2)	20 (3)	22 (5)
Cantharidae	*Malthodes crassicornis*		1 (1)	1 (1)
Cantharidae	*Malthodes fuscus*	3 (2)	1 (1)	4 (3)
Cantharidae	*Rhagonycha translucida*	1 (1)		1 (1)
Cerambycidae	*Anaglyptus mysticus*		2 (2)	2 (2)
Cerambycidae	*Leiopus nebulosus*	10 (5)	52 (10)	62 (15)
Cerambycidae	*Mesosa nebulosa*	1 (1)		1 (1)
Cerambycidae	*Phymatodes testaceus*		1 (1)	1 (1)
Cerambycidae	*Rhagium bifasciatum*		1 (1)	1 (1)
Cerambycidae	*Rhagium mordax*	2 (1)	4 (4)	6 (5)
Cerambycidae	*Rutpela maculata*	7 (6)	1 (1)	8 (7)
Cerambycidae	*Stictoleptura scutellata*	1 (1)		1 (1)
Cerylonidae	*Cerylon ferrugineum*	7 (3)	2 (2)	9 (5)
Ciidae	*Cis boleti*		3 (1)	3 (1)
Ciidae	*Cis dentatus*		2 (2)	2 (2)
Ciidae	*Cis fagi*	5 (3)	28 (4)	33 (7)
Ciidae	*Cis festivus*	1 (1)		1 (1)
Ciidae	*Ennearthron cornutum*	3 (2)	11 (4)	14 (6)
Ciidae	*Orthocis alni*		1 (1)	1 (1)
Cleridae	*Korynetes caeruleus*		1 (1)	1 (1)
Cleridae	*Thanasimus formicarius*	1 (1)	3 (3)	4 (4)
Cleridae	*Tillus elongatus*	175 (19)	223 (22)	398 (41)
Corylophidae	*Orthoperus atomus*	79 (1)	2 (1)	81 (2)
Cryptophagidae	*Atomaria pulchra*		3 (2)	3 (2)
Cryptophagidae	*Caenoscelis sibirica*		1 (1)	1 (1)
Cryptophagidae	*Cryptophagus dentatus*	12 (10)	39 (19)	51 (29)
Cryptophagidae	*Cryptophagus scanicus*	4 (2)		4 (2)
Cryptophagidae	*Pteryngium crenatum*	1 (1)	2 (1)	3 (2)
Cucujidae	*Pediacus dermestoides*		1 (1)	1 (1)
Curculionidae	*Dryocoetes autographus*		1 (1)	1 (1)
Curculionidae	*Echinodera hypocrita*	7 (4)	13 (6)	20 (10)
Curculionidae	*Ernoporicus fagi*	1 (1)	265 (5)	266 (6)
Curculionidae	*Otiorhynchus lepidopterus*		1 (1)	1 (1)
Curculionidae	*Otiorhynchus singularis*	1 (1)	1 (1)	2 (2)

Family	Species	*D. leucotos* absence: Abundance (Incidence)	*D. leucotos* presence: Abundance (Incidence)	Total: Abundance (Incidence)
Curculionidae	*Phyllobius argentatus*		1 (1)	1 (1)
Curculionidae	*Polydrusus aeratus*	3 (2)		3 (2)
Curculionidae	*Rhyncolus ater*		1 (1)	1 (1)
Curculionidae	*Stereocorynes truncorum*		1 (1)	1 (1)
Curculionidae	*Taphrorychus bicolor*	38 (3)	385 (14)	423 (17)
Curculionidae	*Trachodes hispidus*	1 (1)		1 (1)
Curculionidae	*Tropiphorus elevatus*		1 (1)	1 (1)
Curculionidae	*Trypodendron domesticum*	174 (10)	1435 (30)	1609 (40)
Curculionidae	*Xyleborinus saxesenii*	17 (7)	237 (19)	254 (26)
Curculionidae	*Xylosandrus germanus*	36 (7)	79 (20)	115 (27)
Dasytidae	*Dasytes plumbeus*	1 (1)	3 (3)	4 (4)
Dermestidae	*Anthrenus fuscus*	1 (1)		1 (1)
Dermestidae	*Attagenus smirnovi*	1 (1)		1 (1)
Dermestidae	*Megatoma undata*	1 (1)	1 (1)	2 (2)
Elateridae	*Ampedus erythrogonus*		1 (1)	1 (1)
Elateridae	*Ampedus pomorum*	1 (1)	3 (2)	4 (3)
Elateridae	*Ampedus sanguineus*	1 (1)		1 (1)
Elateridae	*Athous vittatus*		1 (1)	1 (1)
Elateridae	*Denticollis linearis*		3 (3)	3 (3)
Elateridae	*Denticollis rubens*	1 (1)	2 (1)	3 (2)
Elateridae	*Hypoganus inunctus*	1 (1)		1 (1)
Elateridae	*Melanotus villosus*	2 (1)	2 (2)	4 (3)
Endomychidae	*Endomychus coccineus*		2 (1)	2 (1)
Erotylidae	*Tritoma bipustulata*		4 (1)	4 (1)
Eucnemidae	*Dromaeolus barnabita*	14 (1)		14 (1)
Eucnemidae	*Hylis olexai*		1 (1)	1 (1)
Eucnemidae	*Isorhipis melasoides*	4 (1)	5 (2)	9 (3)
Eucnemidae	*Melasis buprestoides*	1 (1)		1 (1)
Eucnemidae	*Microrhagus pygmaeus*		2 (1)	2 (1)
Latridiidae	*Corticaria longicornis*		1 (1)	1 (1)
Latridiidae	*Corticarina minuta*		1 (1)	1 (1)
Latridiidae	*Corticarina similata*	1 (1)		1 (1)
Latridiidae	*Dienerella vincenti*	3 (3)	5 (4)	8 (7)
Latridiidae	*Enicmus fungicola*	1 (1)		1 (1)
Latridiidae	*Enicmus rugosus*	1 (1)	5 (5)	6 (6)
Latridiidae	*Latridius hirtus*	3 (2)	6 (5)	9 (7)
Latridiidae	*Stephostethus alternans*		6 (1)	6 (1)
Leiodidae	*Agathidium confusum*	1 (1)	1 (1)	2 (2)
Leiodidae	*Agathidium laevigatum*		1 (1)	1 (1)
Leiodidae	*Amphicyllis globus*		1 (1)	1 (1)
Leiodidae	*Leiodes oblonga*		1 (1)	1 (1)
Lucanidae	*Platycerus caraboides*		1 (1)	1 (1)
Lucanidae	*Sinodendron cylindricum*	8 (7)	39 (9)	47 (16)

Family	Species	*D. leucotos* absence: Abundance (Incidence)	*D. leucotos* presence: Abundance (Incidence)	Total: Abundance (Incidence)
Lymexylidae	*Elateroides dermestoides*		13 (2)	13 (2)
Malachiidae	*Ebaeus abietinus*	2 (1)		2 (1)
Malachiidae	*Hypebaeus flavipes*		3 (3)	3 (3)
Melandryidae	*Abdera flexuosa*	35 (1)	3 (2)	38 (3)
Melandryidae	*Conopalpus testaceus*	1 (1)		1 (1)
Melandryidae	*Melandrya caraboides*		8 (2)	8 (2)
Melandryidae	*Orchesia micans*	10 (2)	1 (1)	11 (3)
Melandryidae	*Orchesia minor*	1 (1)	1 (1)	2 (2)
Melandryidae	*Orchesia undulata*		1 (1)	1 (1)
Monotomidae	*Monotoma longicollis*		1 (1)	1 (1)
Monotomidae	*Rhizophagus bipustulatus*	4 (3)	14 (8)	18 (11)
Monotomidae	*Rhizophagus dispar*	2 (2)	26 (13)	28 (15)
Monotomidae	*Rhizophagus grandis*		1 (1)	1 (1)
Mordellidae	*Mordellochroa abdominalis*	1 (1)	3 (1)	4 (2)
Mordellidae	*Tomoxia bucephala*	18 (1)	7 (4)	25 (5)
Mycetophagidae	*Litargus connexus*	4 (3)	19 (7)	23 (10)
Mycetophagidae	*Mycetophagus multipunctatus*	6 (2)	2 (2)	8 (4)
Nitidulidae	*Epuraea unicolor*		6 (4)	6 (4)
Ptiliidae	*Acrotrichis rosskotheni*		9 (1)	9 (1)
Ptinidae	*Hemicoelus costatus*	5 (3)	12 (6)	17 (9)
Ptinidae	*Hyperisus plumbeum*		8 (2)	8 (2)
Ptinidae	*Microbregma emarginatum*	1 (1)		1 (1)
Ptinidae	*Ptilinus pectinicornis*	751 (23)	1706 (43)	2457 (66)
Ptinidae	*Ptinomorphus imperialis*	15 (6)	12 (8)	27 (14)
Ptinidae	*Ptinus fur*	5 (3)	6 (5)	11 (8)
Ptinidae	*Ptinus subpilosus*		1 (1)	1 (1)
Salpingidae	*Salpingus planirostris*		2 (2)	2 (2)
Salpingidae	*Salpingus ruficollis*	1 (1)	1 (1)	2 (2)
Salpingidae	*Sphaeriestes castaneus*		1 (1)	1 (1)
Salpingidae	*Vincenzellus ruficollis*	4 (2)	3 (2)	7 (4)
Scraptiidae	*Anaspis lurida*	2 (2)	5 (5)	7 (7)
Scraptiidae	*Anaspis ruficollis*	17 (9)	40 (14)	57 (23)
Scraptiidae	*Anaspis thoracica*	14 (7)	19 (13)	33 (20)
Silphidae	*Phosphuga atrata*		1 (1)	1 (1)
Silvanidae	*Uleiota planatus*		2 (1)	2 (1)
Staphylinidae	*Aleochara ruficornis*		1 (1)	1 (1)
Staphylinidae	*Aleochara sparsa*	2 (2)	9 (6)	11 (8)
Staphylinidae	*Anomognathus cuspidatus*		2 (2)	2 (2)
Staphylinidae	*Atheta vaga*		5 (2)	5 (2)
Staphylinidae	*Bibloporus bicolor*		2 (2)	2 (2)
Staphylinidae	*Bythinus macropalpus*		1 (1)	1 (1)
Staphylinidae	*Cypha longicornis*		1 (1)	1 (1)
Staphylinidae	*Euconnus pragensis*	2 (1)		2 (1)

Family	Species	*D. leucotos* absence: Abundance (Incidence)	*D. leucotos* presence: Abundance (Incidence)	Total: Abundance (Incidence)
Staphylinidae	*Euplectus brunneus*		1 (1)	1 (1)
Staphylinidae	*Eusphalerum rectangulum*	1 (1)	2 (2)	3 (3)
Staphylinidae	*Eusphalerum semicoleoptratum*		1 (1)	1 (1)
Staphylinidae	*Gabrius splendidulus*		1 (1)	1 (1)
Staphylinidae	*Leptusa fumida*	7 (5)	5 (5)	12 (10)
Staphylinidae	*Leptusa pulchella*	2 (1)	2 (2)	4 (3)
Staphylinidae	*Leptusa ruficollis*		3 (2)	3 (2)
Staphylinidae	*Neuraphes elongatulus*		5 (3)	5 (3)
Staphylinidae	*Ocypus nitens*	1 (1)		1 (1)
Staphylinidae	*Phyllodrepa melanocephala*	1 (1)	1 (1)	2 (2)
Staphylinidae	*Phyllodrepoidea crenata*		2 (1)	2 (1)
Staphylinidae	*Placusa tachyporoides*	2 (1)	5 (4)	7 (5)
Staphylinidae	*Plectophloeus nubigena*	2 (1)		2 (1)
Staphylinidae	*Proteinus ovalis*		7 (1)	7 (1)
Staphylinidae	*Quedius cruentus*	1 (1)		1 (1)
Staphylinidae	*Quedius invreae*		1 (1)	1 (1)
Staphylinidae	*Quedius mesomelinus*	1 (1)		1 (1)
Staphylinidae	*Quedius puncticollis*		1 (1)	1 (1)
Staphylinidae	*Quedius xanthopus*	1 (1)	5 (3)	6 (4)
Staphylinidae	*Stenichnus collaris*		2 (2)	2 (2)
Staphylinidae	*Stenichnus godarti*		1 (1)	1 (1)
Staphylinidae	*Trimium brevicorne*	1 (1)	1 (1)	2 (2)
Tenebrionidae	*Corticeus unicolor*	1 (1)	3 (2)	4 (3)
Tenebrionidae	*Mycetochara maura*		2 (2)	2 (2)
Tenebrionidae	*Nalassus convexus*	1 (1)		1 (1)
Trogossitidae	*Nemozoma caucasicum*	1 (1)		1 (1)
Trogossitidae	*Nemozoma elongatum*	1 (1)	1 (1)	2 (2)
Trogossitidae	*Peltis ferruginea*	1 (1)	1 (1)	2 (2)
Trogossitidae	*Thymalus limbatus*		1 (1)	1 (1)
Zopheridae	*Colydium elongatum*		1 (1)	1 (1)
Zopheridae	*Coxelus pictus*		1 (1)	1 (1)
Zopheridae	*Synchita humeralis*	3 (1)	1 (1)	4 (2)

Chapter 3

Exploring the vertical stratification of saproxylic beetle communities in the western Eurasian distribution front of a rare woodpecker

Exploring the vertical stratification of saproxylic beetle communities in the western Eurasian distribution front of a rare woodpecker

Romain Angeleri [1,2,3], Antonia Ettwein [4], Urs G. Kormann [1,4], Jörg Müller [5], Jiří Procházka [6,7], Nicolas Roth [1,3], Jiří Schlaghamerský[8], Raphaël Arlettaz [2], Thibault Lachat [1,3]

[1] Bern University of Applied Sciences – School of Agricultural, Forest and Food Sciences, Länggasse 85, 3052 Zollikofen, Switzerland

[2] University of Bern, Institute of Ecology and Evolution – Conservation Biology, Baltzerstrasse 6, 3012 Bern, Switzerland

[3] Swiss Federal Institute for Forest, Snow and Landscape Research – WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[4] Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

[5] National Park Bayerischer Wald, Freyungerstrasse 2, 94481 Grafenau, Germany

[6] Silva Tarouca Research Institute for Landscape and Horticulture – Department of Forest Ecology, Lidicka 25/27, 602 00 Brno, Czech Republic

[7] Moravian Museum, Zelny trh 6, 602 00 Brno, Czech Republic

[8] Masaryk University, Faculty of Science – Department of Botany and Zoology, Kotlářská 2, 611 37 Brno, Czech Republic

Chapter status: *In preparation*

Abstract

Efficiency of a conservation plan requires thorough knowledge of the selected focal species. The White-backed Woodpecker (*Dendrocopos leucotos*) was historically present in many European countries but has been facing a dramatic decline due to intensive forest management. While being often considered as an old-growth forest, the species now broadens its habitat to managed forest stands. To explore the potential of saproxylic beetles to colonize the dead wood resource in forests – inhabited or not – by the White-backed Woodpecker, we set up an experiment in 7 geographical regions using 408 standardized dead wood items exposed for two years in three different forest strata (forest floor, understory, canopy). Ex-situ rearing of the dead wood items demonstrated a higher species richness and abundance of saproxylic beetles emerging from dead wood items exposed in the understory and in the canopy, compared to the ones exposed on the forest floor. Community partitioning along the forest strata was strongly driven by species turnover and increased with above ground elevation. Generally, no differences were found between sites with presence or absence of the White-backed Woodpecker. Our experimental approach highlights the prime importance of a diversified position of the dead wood resource for saproxylic beetle communities, which may be predated by our focal bird species. Maintaining senescent and dead trees offering above-ground dead wood in managed forest stands would help in supporting the early colonizing communities, which are a fundamental component of the forest ecosystem and its associated diversity, including rare species with high habitat quality requirements such as the White-backed Woodpecker.

Keywords

Dendrocopos leucotos; Saproxylic beetles; Standardized dead wood exposition; Vertical stratification; Forest stratum; Community composition; Ex-situ emergence trap.

Introduction

Saproxylic beetles are defined as "species that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight, 1989). They are arguably the most speciose group of the saproxylic guild (Graf et al., 2022) fulfilling important functions in the forest cycle, such as dead wood decay (Hardersen et al., 2020; Seibold et al., 2021). Additionally, they – and especially their instar stages – play a critical role as the primary food source for many of their predators (Jennings et al., 2013; Pechacek & Kristin, 2004; Powell et al., 2002; Soto et al., 2017; Virkkala, 2006). Among them is the White-backed Woodpecker. This bird species has been observed extracting saproxylic invertebrates (Aulén, 1988; Hogstad & Stenberg, 1997) on a multitude of dead wood items (Bühler, 2009). While the White-backed Woodpecker was historically present in many European countries (Scherzinger, 1990), the number of individuals composing its western Eurasian population significantly dropped, as a result of intensive logging activities and dead wood removal (Carlson, 2000; Czeszczewik & Walankiewicz, 2006; Virkkala et al., 1993). Still being one of the rarest woodpeckers living in broadleaved forests, this old-growth forest specialist now broadens its habitat to managed stands, which could be attributed to the overall increase in dead wood amount over the last decade (Brändli & Abegg, 2009; FOREST EUROPE, 2020). In unmanaged forests, dead wood is mainly created by the natural senescence processes (Hilmers et al., 2018). However, natural disturbances such as bark beetle outbreaks (Müller et al., 2008) or extreme droughts (Senf et al., 2020) can greatly contribute to dead wood enrichment over large forest areas. Forest management can also play a role in increasing the amount of dead wood available in the forest. Either by leaving logging residues (Ranius et al., 2018), or by the implementation of active dead wood enrichment strategies (Doerfler et al., 2017; Floren et al., 2014; Roth et al., 2019; Vogel et al., 2020). Whereas dead wood volume is mainly driven by coarse woody debris lying on the ground (Siitonen et al., 2000), standing and suspended dead wood items are nonetheless fundamental in supporting the saproxylic guild, estimated to represent about one fourth of the species pool found in the forest ecosystem (Lachat & Müller, 2018). Saproxylic diversity encompasses many taxonomic groups, yet a much higher diversity in species can be observed in and for Coleoptera (Stokland et al., 2012).

While the influence of the forests stratum on saproxylic beetle's assemblages is well established (see Basset et al., 2003; Ulyshen, 2011), contrasting results emerge when focusing on species richness only (Maguire et al., 2014; Plewa et al., 2017; Ruchin & Egorov, 2021; Seibold et al., 2021; Weiss et al., 2016). It has been argued that, in temperate deciduous forests, stand characteristics along the vertical axis will tend to homogenize in wintertime (e.g., the loss of foliage, cold winter temperatures, light availability). Due to this seasonal homogenization of the habitat, fewer species would be restricted to a specific stratum, especially imagos moving closer to the ground to overwinter (Ulyshen, 2011).

However, for species such as the White-backed Woodpecker, a top predator in the saproxylic food chain, having a sufficient continuous access to prey is fundamental. This might be even more important in wintertime when snow cover is preventing access to most of the dead wood items lying on the ground (Czeszczewik, 2009). Above-ground dead wood structures might therefore play an important role in providing year-round prey availability, represented by the larvae and pupae hidden under the bark or deeper in the wood. While the White-backed Woodpecker is a flagship species highly sensitive to logging activity, to our knowledge, conservation plans focusing on this bird species were only implemented in Fenno-Scandia. While the action plan targeting the Finnish White-backed Woodpecker population has been reported to be successful by setting aside forest surface used by the bird (Virkkala et al., 1993), the active restoration that took place in Sweden was not successful in bringing the bird back. Partially due to the lack of knowledge and data necessary for successful implementation of action plan (Blicharska et al., 2014). Nonetheless, the plan succeeded in attracting saproxylic species, especially threatened ones (Bell et al., 2015).

To better understand the structuration of the early colonizing saproxylic beetle communities associated with the White-backed Woodpecker habitat, we explored the colonization of fresh dead wood by saproxylic beetles occurring in and outside of the White-backed Woodpecker home range, in multiple sites across the western Eurasian distribution front of the focal woodpecker. Specifically, we exposed dead wood pieces of a standardized size along three forest strata of the studied forests, over a period of two years. The results of this experiment would ultimately help improve the efficiency of future conservation plans aiming at protecting the White-backed Woodpecker and the saproxylic communities it represents.

Methods

Site selection

The experiment was conducted in 7 geographical regions occurring in the western Eurasian range of the White-backed Woodpecker and spanning along a longitudinal and latitudinal gradient of ± 800 km and ± 350 km, respectively (Figure 1). Within each region, trained ornithologists identified sites where the White-backed Woodpecker was either present or absent. The White-backed Woodpecker was considered present at a site if a specimen had been observed within it, during its breeding period, at least once in the past 10 years. If no White-backed Woodpecker had been historically observed within a site, the species was considered absent. Once sites with presence and absence of the species had been identified, a subset of those was selected for the experiment based on the following criteria: (1) European beech (Fagus sylvatica) as the dominant tree species, (2) sites to be compared had to have similar elevations above sea level, and (3) absence sites had to be at least 2 km but not more than 5 km apart from the closest presence site. Two to four sampling plots, each of a circular area of 500 m^2, representative of the dead wood availability at the given site, were delimited at every site, resulting in a total of 68 sampling plots.

Wood exposition and beetle rearing

In winter 2018, we installed six pieces of wood per sampling plot. To mimic a fallen log, two pieces were installed lying on the forest floor. To mimic a dead standing tree, two pieces were attached at breast height (± 130 cm) on a healthy European beech tree. To mimic crown dead wood, two pieces were installed in the canopy (hereafter "canopy samples") of a large European beech tree found in the center of each plot. The 408 wood pieces had a mean diameter of 13 cm (± 2 cm) and a mean length of 82 cm (± 6 cm). All wood pieces were sourced from healthy European beech trees found in the surroundings of the plot, or from outside of the forest reserve when appropriate. Per sampling plot, all pieces of wood were placed with the same orientation as the canopy treatment. After the first year of exposure (winter 2019), one piece of wood from every stratum and every plot was retrieved and installed in ex-situ emergence traps. The remaining wood samples were retrieved after a second year of colonization (winter 2020) and installed in emergence traps as well. Each emergence trap consisted of a polyethylene tube (length = 1 m; diameter = 20 cm) with one end closed with a piece of black polyester fabric and the other with a polyethylene cap. This cap with a diameter of 8 cm, had an opening covered with a fine metal mesh (0.13 * 0.13 mm) improving air circulation through the tube while preventing the escape of emerged insects. To collect emerging insects, a plastic bottle filled with 70% ethanol was connected to a second hole in the cap, using a plastic pipe connecting the two (see Supplementary materials S5). Emergence traps were placed under climatic conditions comparable to the studied forests and were protected by a roof from direct solar radiation and rain. Samples from Austria, Germany, Liechtenstein, and Switzerland were pooled together in the Swiss rearing station. Samples from Czechia were reared on their own. Overall, the 408 wood pieces (204 with one year of colonization and 204 with two years of colonization) were placed in emergence traps for one year after being retrieved from the forest. Wood pieces were randomly distributed within their respective rearing stations. Emerging invertebrates were pooled per emergence trap and year of emergence. After sorting, beetles were identified to species level by trained entomologists.

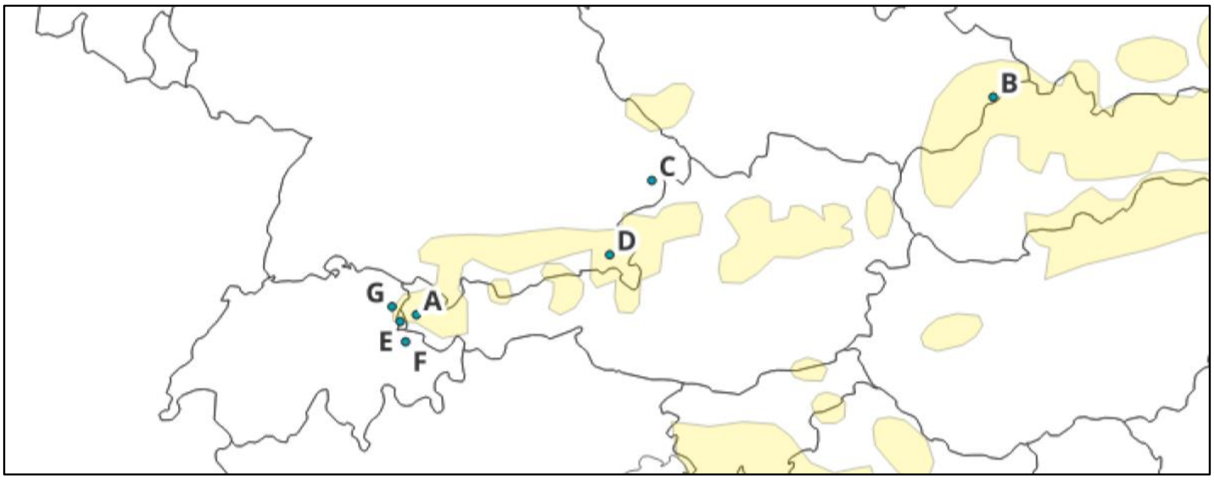


Figure 1. Map of the western Eurasian distribution front of the White-backed Woodpecker in yellow (source: BirdLife International and Handbook of the Birds of the World (2020). *Dendrocopos leucotos*. The IUCN Red List of Threatened Species. Version 2021-3. Downloaded on 09 March 2022) with the study regions marked by the blue dots: A. Vorarlberg (AT) = 28 sampling plots; B. Beskids (CZ) = 8; C. Bayerwald (DE) = 4; D. Traunstein (DE) = 2; E. Liechtenstein (LT) = 6; F. Grisons (CH) = 8; G. St Gallen (CH) = 12. Maps created in QGIS 3.28.0.

Statistical analysis

Linear regression

Using two Bayesian generalized linear models with group-specific terms via Stan (stan_glmer.nb {rstanarm}), we analyzed how species richness and specimen abundance of saproxylic beetles varied as a function of the White-backed Woodpecker activity levels (presence, absence), strata (forest floor, understory, canopy) and wood pieces characteristics (colonization time, sample diameter, sample length). The two models were run under a negative binomial distribution, implementing four chains with 4000 iterations each (warmup = 2000; sampling = 2000) and uninformed priors, for 408 observations. To account for potential regional effects, the region, site, and plot identities were used as random intercepts. Additionally, sampling units were controlled for absence of spatial autocorrelation using Moran's I test beforehand (moran.test {spdep}). All numerical explanatory variables were normalized (mu = 0; sd = 1) and controlled for absence of collinearity.

Community composition

We investigated compositional differences of the saproxylic beetle communities in relation to the group levels (i.e., the two White-backed Woodpecker occurrence levels, or the three forest strata and the colonization time of the wood sample, independently) using complementary multivariate analyses. First, we tested whether the group levels differed in species composition, using a permutational multivariate analysis of variance (adonis2 {vegan}) (Anderson, 2017). This method tests whether the group centroids (i.e., the average identity of saproxylic beetle species composing the community of a given group level, or average-group dispersion) in multivariate species space differ between groups, where overlapping group dispersions indicate a degree of community similarity across the groups. Second, we tested if groups differed in their β-diversity, that is, the degree of variation in species identities among groups, using a permutational test for homogeneity of multivariate dispersion with 9999 permutations (betadisper {vegan}) (Anderson et al., 2006, 2011). This method statistically assesses the degree of species homogenization among treatments, where large treatment-wise dispersion indicates a large variation in species identities within a group and thus a low species overlap between sampling plots representing a group (i.e., high β-diversity); as opposed to small group-wise dispersion (i.e., low β-diversity). Differences in β-diversity among groups were assessed using a pairwise Tukey Honest Significant Differences Test corrected for multiple comparisons (TukeyHSD {stats}). To account for potential regional effects, the region was used as the blocking factor for these two community analyses. Finally, based on species occurrence data, we assessed how the β-diversity relative to the group levels was partitioned into species turnover (i.e., replacement of some species by others) and nestedness (i.e., the biotas of sites with smaller numbers of species being subsets of the biotas at species-richer sites) components using the Jaccard dissimilarity index (beta {BAT}) (Baselga, 2010; Cardoso et al., 2014; Legendre, 2014). All statistical analyses were performed using R Version 4.1.1 (R Core Team 2021).

Results

Specimen abundance and species richness

In total, we obtained 48632 individuals belonging to 147 species. The absence sites yielded 82 species and 14528 individuals compared to 126 species and 34104 individuals obtained from the presence sites. Wood pieces laying on the forest floor yielded 83 species and 6971 individuals, those installed in the understory 91 species and 17904 individuals, and those installed in the canopy 84 species and 23757 individuals.

Table 1. Summary table of the Bayesian generalized linear mixed models. Explanatory variables with a non-null predicted effect (89% of the HDI posterior probability excluding 0) are displayed in bold.

Response	Parameter	HDI posterior probability median (CrI 89%)	exp[HDI posterior probability median (CrI 89%)]	Predicted direction
(a) Abundance	(Absence) Presence	0.222 (-0.265, 0.679)	1.249 (0.767, 1.972)	
	(Floor) Understory	**1.143 (0.859, 1.445)**	**3.136 (2.361, 4.242)**	**Positive**
	(Floor) Canopy	**1.376 (1.068, 1.669)**	**3.959 (2.91, 5.307)**	**Positive**
	Exposure time	**-0.528 (-0.647, -0.404)**	**0.59 (0.524, 0.668)**	**Negative**
	Wood diameter	**0.31 (0.174, 0.456)**	**1.363 (1.19, 1.578)**	**Positive**
	Wood length	0.08 (-0.058, 0.222)	1.083 (0.944, 1.249)	
(b) Species richness	(Absence) Presence	0.052 (-0.094, 0.193)	1.053 (0.91, 1.213)	
	(Floor) Understory	**0.286 (0.164, 0.418)**	**1.331 (1.178, 1.519)**	**Positive**
	(Floor) Canopy	**0.346 (0.218, 0.477)**	**1.413 (1.244, 1.611)**	**Positive**
	Exposure time	**0.102 (0.055, 0.152)**	**1.107 (1.057, 1.164)**	**Positive**
	Wood diameter	0.045 (-0.01, 0.103)	1.046 (0.99, 1.108)	
	Wood length	0.031 (-0.027, 0.096)	1.031 (0.973, 1.101)	

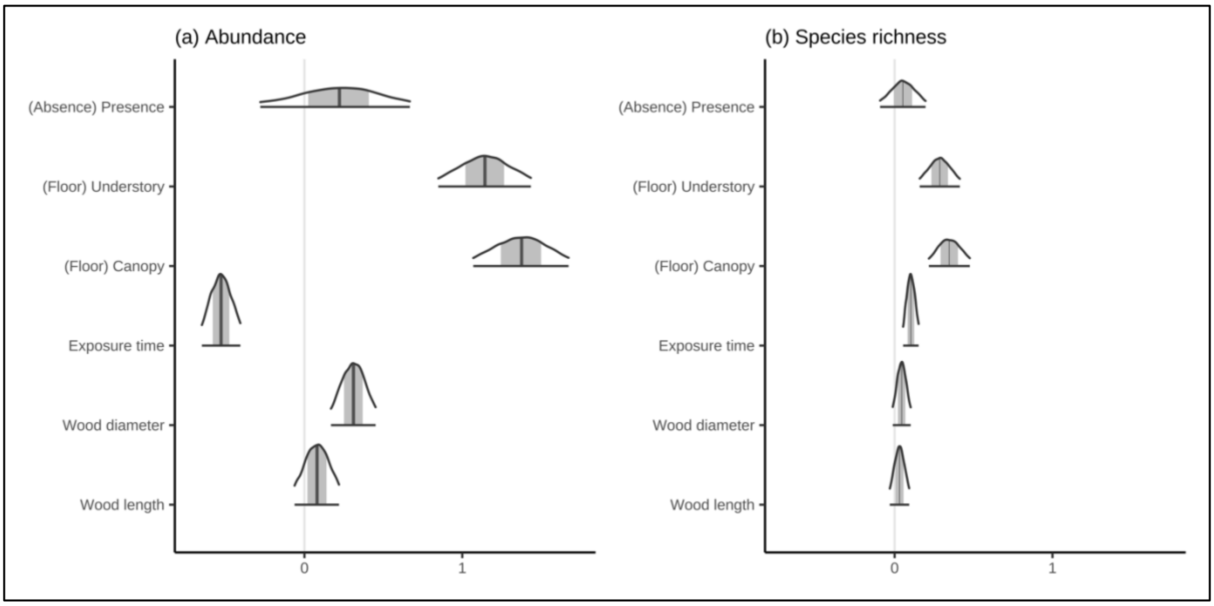


Figure 2. Summary of parameter estimates for the effects of the White-backed Woodpecker occurrence (presence, absence), the forest strata (forest floor, understory, canopy), colonization time (1, 2 years), diameter, and length of the exposed pieces of wood, respectively. Reference level of factorial explanatory variables is set in parentheses. Models are using the individual abundance (panels a) and species richness (panels b) as response variables. Vertical lines represent the parameter estimates. The grey area, total area, and the border of the area under curve represent the 50%, the 89%, and the distribution of the HDI posterior probability, respectively.

Drivers of saproxylic beetle species richness and abundance

Whereas the occurrence of the White-backed Woodpecker did not explain the abundance and species richness of saproxylic beetles (Figure 2, panel a and b), forest stratum, exposure time and wood pieces diameter did. First, wood pieces placed in the understory had 3.1 times more individuals (Posterior Probability Credible Interval median [lower and upper 5.5%] = 1.143 [0.859, 1.445]; Figure 2, panel a; Table 1) and 1.3 times more species (0.286 [0.164, 0.418]; Figure 2, panel b; Table 1) than wood pieces placed on the floor. The observed abundance and species richness increased with height, wood pieces exposed in the canopy having 3.9 (1.376 [1.068, 1.669]; Figure 2, panel a; Table 1) and 1.4 (0.346 [0.218, 0.477]; Figure 2, panel b; Table 1) times more individuals and species, respectively, than wood pieces exposed on the forest floor. Second, the exposure time had an opposite effect on the abundance and species richness. Abundance was responding negatively to the exposure time, with 0.59 (-0.528 [-0.647, -0.404]; Figure 2, panel a; Table 1) times less individuals emerging after two years of exposure. In contrast, species richness increased with exposure time, with 1.1 (0.102 [0.055, 0.152]; Figure 2, panel b; Table 1) times more species after two years of exposure. Third, we did not observe the diameter of the wood having an effect on the species richness. Yet, it had a positive effect on the abundance, with an increase of 40% (0.31 [0.174, 0.456]; Figure 2, panel b; Table 1) individuals per centimeter. Finally, our models did not detect an effect of wood sample length on the emerging saproxylic beetle communities. Exploratory analyses did not detected differences between the understory and the canopy.

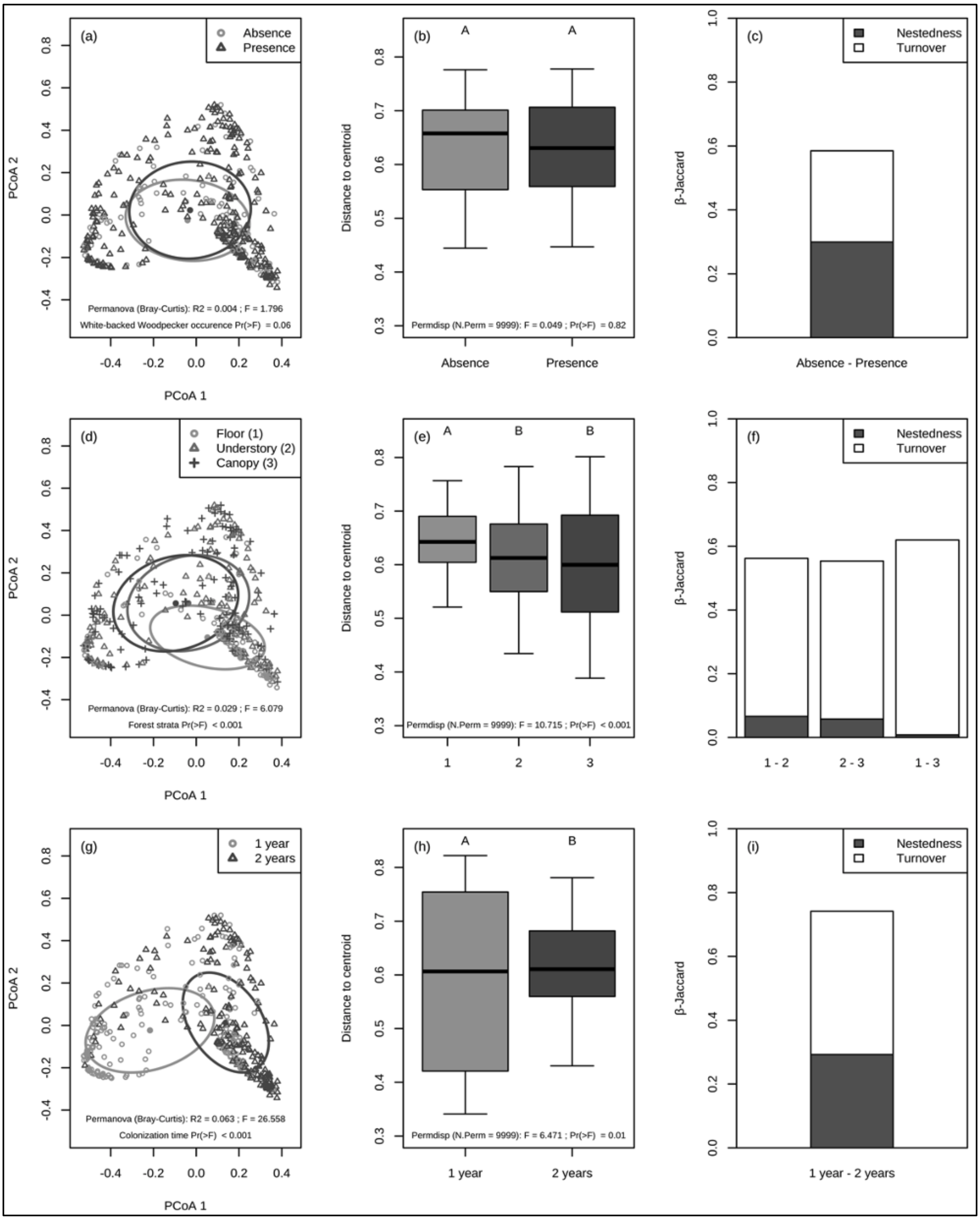


Figure 3. Summary of the community composition of the saproxylic beetles as a function of the presence/absence of the White-backed Woodpecker (panels a, b, c), of the forest strata (panels d, e, f) and of the colonization time (panels g, h, i). Group centroid position was tested with a permutational multivariate analysis of variance (panels a, d, g), average distance to group centroid was tested with a permutational test for homogeneity of multivariate dispersions and letters represent significant differences among groups resulting from a pairwise Tukey Honest Significant Difference test (panels b, e, h). Beta-diversity partitioning was assessed with the species turnover and nestedness components (panels c, f, i).

Community composition

Whereas the average community identity of saproxylic beetles was marginally different regarding the White-backed Woodpecker occurrence (PERMANOVA: Pr(>F) = 0.057; R^2 = 0.004; F = 1.796; Figure 3, panel a), no significant difference in average group dispersion was detected among sites with or without an occurrence of the target bird species (Figure 3, panel b). Additionally, beta-diversity partitioning revealed that differences in species composition were equally driven by turnover and nestedness in relation to the occurrence of the White-backed Woodpecker (Figure 3, panel c). Second, the assemblages found in the understory and in the canopy were significantly different from the ones found on the forest floor in terms of average community identity (Pr(>F) < 0.001; R^2 = 0.029; F = 6.079; Figure 3, panel d) and of community homogeneity (Pr(>F) < 0.001; F = 10.715; Figure 3, panel e). A pairwise comparison of the beta-diversity of the three forest strata revealed a community partitioning strongly driven by species turnover, which increased with height differences between the strata (Figure 3, panel f). Third, communities emerging from wood samples left in the forest for one year of colonization were significantly different from those emerging from samples left for two years of colonization, both in terms of average community identity (Pr(>F) < 0.001; R^2 = 0.063; F = 26.558; Figure 3, panel g) and of community homogeneity (Pr(>F) = 0.01; F =6.471; Figure 3, panel h). A pairwise comparison of the beta-diversity partitioning of the two decay stages revealed that the species-community shift was driven slightly more by species turnover than by nestedness (Figure 3, panel i).

Discussion

Influence of the dead wood characteristics

One of the goals of our experiment was to assess the colonization by saproxylic beetles of fresh dead wood pieces during the first two years of exposure in the forest. Our findings highlighted important community shifts from one year to another. Specifically, the abundance of emerging saproxylic beetles was higher after one year of exposure and lower after two years of exposure (i.e., colonization by the beetles). In contrast, the number of species showed an opposite pattern, with a more species emerging from a dead wood item being colonized for a period of two years. These opposite patterns as a function of decay rate could be explained by the specificity of the colonizing communities and their relative r/K-selection strategies (Macarthur & Wilson, 1967). Pioneer species, (e.g., *Taphrorychus bicolor* and *Ernoporicus fagi*) were represented by very high numbers of individuals after one year of exposure (see Supplementary material S6). Such early dead wood colonizers with high reproduction rates and several generations per year are predominantly found in short-lived habitats, such as recently felled or naturally died trees (Graf et al., 2022; Leather et al., 2014; Ramilo et al., 2017).

Additionally, we observed significant changes in average community composition as well as a homogenization of the saproxylic beetle beta-diversity after two years of exposure. These changes in species composition were mostly influenced by species turnover. While saproxylic beetle species colonizing fresh dead wood items would provide a pathway for many saproxylic species through the creation of galleries (Speight, 1989) and providing access to the fresh resource, saproxylic beetle assemblage will homogenize and/or specialize along dead wood decay process, with microclimatic conditions converging to a stable state.

Finally, the abundance of emerging saproxylic beetles was positively correlated with the diameter of the exposed wood pieces. Despite the effort to standardize the diameter of the exposed substrate and to randomly distribute it across the forest strata, the diameter of the wood pieces significantly decreased with altitude above ground (see Supplementary material S1). Yet, even if the diameter of a dead wood item and its decay stage played a role in shaping emerging saproxylic insect communities (Brin et al., 2011), the effect of the vertical stratification of the dead wood items along the forest was much more pronounced.

Importance of the vertical stratification of the dead wood resource

Saproxylic beetles emerging from wood pieces on the forest floor strongly diverged from the communities found in pieces exposed in the understory and in the canopy. Species richness was positively correlated with above ground elevation, putting our results in line with Seibold et al., (2018; to our knowledge the sole experiment rearing fresh dead wood exposed along the vertical axis of Central european forests). Yet, the peer study observed a higher abundance of saproxylic beetles emerging from dead wood items exposed near the ground, whereas we an opposite pattern was observe in our experiment. From our understanding, such discrepancies could be explained by both the experimental design and the dead wood characteristics. First, we collected beetles emerging from our wood pieces for one year, whereas the process of Seibold et al., (2018) took three years. As reported, their second year of emergence yielded 60% of the total abundance of emerging beetles. It is therefore possible that our data is not yet representative of the communities present in the colonized dead wood items.

Second, as Vogel et al., (2021) demonstrated, broadleaved trees tend to harbor a greater number of saproxylic beetle species than conifers. The type of tree species used in the respective experiments might therefore play an important role in colonization patterns. Whereas we exposed medium sized logs sourced from European Beech only, Seibold et al. (2018) exposed bundles of branches sourced from Norway Spruce, European Beech, and Silver Fir. One could infer the smaller species richness observed in the fresh dead wood samples exposed along several strata by Seibold et al., (2018) is due to the greater proportion of coniferous tree species composing the branch bundles as opposed to our logs, represented by a single tree species with a higher potential in harboring many saproxylic species (Vogel et al., 2021).

Finally, we observed a strong community partitioning along the forest strata, which was dominated by a gradual species turnover following the forest vertical plane, putting our result in line with peer studies rearing dead wood sourced from different strata in European forests (Bouget et al., 2011; Seibold et al., 2018). From a wider perspective, partitioning of saproxylic beetle communities along the vertical gradient of forests has been widely studied (Basset et al., 2003; Ulyshen, 2011). Yet, whereas activity-based sampling methods are more common (Floren et al., 2014; Procházka et al., 2018; Ruchin & Egorov, 2021; Ulyshen & Hanula, 2007; Weiss et al., 2016), rearing techniques remain more accurate when assessing the stratification of dead wood dependent invertebrate communities. For most of the species, imagines will move around the three-dimensional space of a forest stand. Traps intercepting flying or crawling invertebrates will therefore inevitably carry a background noise in their results. Even if the two sampling methods could yield similar results, their relevance will be strongly dependent of the study question. Here, by studying the potential prey-predator interaction between saproxylic beetles and White-backed Woodpeckers, colonization processes happening in the dead wood items would bring a more accurate representation of the expected trophic interactions.

Importance for conservation

As saproxylic beetle communities from our rearing experiment were not responding to the presence of the White-backed Woodpecker, we would argue that all sampled forests have the same potential for colonization of fresh dead wood. These findings underline the potential for foraging of the White-backed Woodpecker outside of its breeding habitat if above-ground fresh dead wood is integrated in management practices. Despite being considered as an old-growth forest specialist (Roberge & Angelstam, 2004; Urkijo-Letona et al., 2020), the White-backed Woodpecker is also able to successfully establish in managed forests offering large trees and higher amount of dead wood (Ettwein et al., 2020). Senescent trees, providing dead wood structures, will be colonized by saproxylic beetles, constituting potential prey for the White-backed Woodpecker. Especially in wintertime, when snow cover is blocking access to dead wood lying on the forest floor. Additionally, fresh dead wood is a fundamental component of the forest ecosystem, providing specific habitat conditions for specific species (e.g., *Poecilium pusilum*, *Nemozoma elongatum* and *Salpingus ruficollis*; see Supplementary materials S6) and during a shorter time frame compared to the following stages of decay.

Based on the present results, we propose to maintain standing senescent and dead trees, offering above-ground dead wood in managed forests within and in the surroundings of the breeding habitat of the White-backed Woodpecker. This measure should complement the setting aside of forest reserves to increase the stock of larvae being potentially accessible throughout the year as well as supporting saproxylic beetle species associated with recently dead wood items.

Acknowledgments

We are grateful to Vasyl and Maksym Chumak who have coordinated the saproxylic beetle identification process. We also acknowledge the work of Michael Lanz for the general coordination of the project "The White-backed Woodpecker in managed forests" and of Ueli Bühler for his early support in the development of the project in the Graubünden region (CH). We thank Sarah and Markus Degenhart, as well as Simon Niederbacher, for their help, and especially Nina Marjanovic, Justin Reymond, Valentin Sylvoz and Silas Zurbuchen for their enduring involvement in the fieldwork. We would like to specially thanks Joern Buse from the Black Forest National Park (DE) and Susana Cárcamo Bravo from the Bioma Forestal (ES) for their early involvement in this research project. Financial support was supported by Inatura – Erlebnis Naturschau GmbH Dornbirn; the Swiss Ornithological Institute; the Ministry of Culture Czech Republic (ref.MK000094862); Institutional subsidy (VUKOZ-IP-00027073); and the Swiss Federal Office for the Environment."

References

Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef: Statistics Reference Online, 1–15. https://doi.org/10.1002/9781118445112.stat07841

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. Ecology Letters, 14(1), 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9(6), 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Aulén, G. (1988). Ecology and distribution history of the White-backed Woodpecker Dendrocopos leucotos in Sweden [Dissertation]. Swedish University of Agricultural Science.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity: Partitioning beta diversity. Global Ecology and Biogeography, 19(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Basset, Y., Hammond, P. M., Barrios, H., Holloway, J. D., & Miller, S. E. (2003). Vertical stratification of arthropod assemblages. In Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. (Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), pp. 17–27). Cambridge University Press.

Bell, D., Hjältén, J., Nilsson, C., Jørgensen, D., & Johansson, T. (2015). Forest restoration to attract a putative umbrella species, the White-backed Woodpecker, benefited saproxylic beetles. Ecosphere, 6(12), 1-14(278). https://doi.org/10.1890/ES14-00551.1

Blicharska, M., Baxter, P. W. J., & Mikusiñski, G. (2014). Practical implementation of species' recovery plans—Lessons from the White-backed Woodpecker Action Plan in Sweden. Ornis Fennica, 91, 108–128.

Bouget, C., Brin, A., & Brustel, H. (2011). Exploring the "last biotic frontier": Are temperate forest canopies special for saproxylic beetles? Forest Ecology and Management, 261(2), 211–220. https://doi.org/10.1016/j.foreco.2010.10.007

Brändli, U.-B., & Abegg, M. (2009). Der Schweizer Wald wird immer natürlicher. Wald Und Holz, 90(7), 27–29.

Brin, A., Bouget, C., Brustel, H., & Jactel, H. (2011). Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. Journal of Insect Conservation, 15(5), 653–669. https://doi.org/10.1007/s10841-010-9364-5

Bühler, U. (2009). Totholz – existenziell für den Weissrückenspecht in Nordbünden | Dead wood – a vital necessity for the White-backed Woodpecker in the Grisons. Schweizerische Zeitschrift für Forstwesen, 160(7), 210–217. https://doi.org/10.3188/szf.2009.0210

Cardoso, P., Rigal, F., Carvalho, J. C., Fortelius, M., Borges, P. A. V., Podani, J., & Schmera, D. (2014). Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components. Journal of Biogeography, 41(4), 749–761. https://doi.org/10.1111/jbi.12239

Carlson, A. (2000). The effect of habitat loss on a deciduous forest specialist species: The White-backed Woodpecker (Dendrocopos leucotos). Forest Ecology and Management, 131(1–3), 215–221. https://doi.org/10.1016/S0378-1127(99)00215-7

Czeszczewik, D. (2009). Foraging behaviour of White-backed Woodpeckers Dendrocopos leucotos in a primeval forest (Białowieża National Park, NE Poland): Dependence on habitat resources and season. Acta Ornithologica, 44(2), 109–118. https://doi.org/10.3161/000164509X482687

Czeszczewik, D., & Walankiewicz, W. (2006). Logging affects the White-backed Woodpecker Dendrocopos leucotos distribution in the Białowieża Forest. Ann. Zool. Fennici, 43, 221–227.

Doerfler, I., Müller, J., Gossner, M. M., Hofner, B., & Weisser, W. W. (2017). Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. Forest Ecology and Management, 400, 607–620. https://doi.org/10.1016/j.foreco.2017.06.013

Ettwein, A., Korner, P., Lanz, M., Lachat, T., Kokko, H., & Pasinelli, G. (2020). Habitat selection of an old-growth forest specialist in managed forests. Animal Conservation, 23(5), 547–560. https://doi.org/10.1111/acv.12567

Floren, A., Müller, T., Dittrich, M., Weiss, M., & Linsenmair, K. E. (2014). The influence of tree species, stratum and forest management on beetle assemblages responding to deadwood enrichment. Forest Ecology and Management, 323, 57–64. https://doi.org/10.1016/j.foreco.2014.03.028

FOREST EUROPE. (2020). State of Europe's Forests 2020.

Graf, M., Lettenmaier, L., Müller, J., & Hagge, J. (2022). Saproxylic beetles trace deadwood and differentiate between deadwood niches before their arrival on potential hosts. Insect Conservation and Diversity, 15(1), 48–60. https://doi.org/10.1111/icad.12534

Graf, M., Seibold, S., Gossner, M. M., Hagge, J., Weiß, I., Bässler, C., & Müller, J. (2022). Coverage based diversity estimates of facultative saproxylic species highlight the importance of deadwood for biodiversity. Forest Ecology and Management, 517, 120275. https://doi.org/10.1016/j.foreco.2022.120275

Hardersen, S., Macagno, A. L. M., Chiari, S., Audisio, P., Gasparini, P., Lo Giudice, G., Nardi, G., & Mason, F. (2020). Forest management, canopy cover and geographical distance affect saproxylic beetle communities of small-diameter beech deadwood. Forest Ecology and Management, 467, 118152. https://doi.org/10.1016/j.foreco.2020.118152

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018). Biodiversity along temperate forest succession. Journal of Applied Ecology, 55(6), 2756–2766. https://doi.org/10.1111/1365-2664.13238

Jennings, D. E., Gould, J. R., Vandenberg, J. D., Duan, J. J., & Shrewsbury, P. M. (2013). Quantifying the Impact of Woodpecker Predation on Population Dynamics of the Emerald Ash Borer (Agrilus planipennis). PLoS ONE, 8(12), e83491. https://doi.org/10.1371/journal.pone.0083491

Lachat, T., & Müller, J. (2018). Importance of Primary Forests for the Conservation of Saproxylic Insects. In Ulyshen, M. D., (Ed.), Saproxylic Insects (Vol. 1, pp. 581–605). Springer International Publishing. https://doi.org/10.1007/978-3-319-75937-1_17

Leather, S. R., Baumgart, E. A., Evans, H. F., & Quicke, D. L. J. (2014). Seeing the trees for the wood—Beech (Fagus sylvatica) decay fungal volatiles influence the structure of saproxylic beetle communities. Insect Conservation and Diversity, 7(4), 314–326. https://doi.org/10.1111/icad.12055

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity: Replacement and richness difference components. Global Ecology and Biogeography, 23(11), 1324–1334. https://doi.org/10.1111/geb.12207

Macarthur, R. H., & Wilson, E. O. (1967). The Theory of Island Biogeography. Princeton University Press.

Maguire, D. Y., Robert, K., Brochu, K., Larrivée, M., Buddle, C. M., & Wheeler, T. A. (2014). Vertical Stratification of Beetles (Coleoptera) and Flies (Diptera) in Temperate Forest Canopies. Environmental Entomology, 43(1), 9–17. https://doi.org/10.1603/EN13056

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., & Duelli, P. (2008). The European spruce bark beetle Ips typographus in a national park: From pest to keystone species. Biodiversity and Conservation, 17(12), 2979–3001. https://doi.org/10.1007/s10531-008-9409-1

Olav Hogstad & Ingvar Stenberg. (1997). Breeding Success, Nestling Diet and Parental Care in the White-backed Woodpecker Dendrocopos leucotos. Journal Für Ornithologie, 138, 25–38.

Pechacek, P., & Kristin, A. (2004). Comparative Diets of Adult and Young Three-Toed Woodpeckers in a European Alpine Forest Community. The Journal of Wildlife Management, 68(3), 683–693.

Plewa, R., Jaworski, T., Hilszczański, J., & Horák, J. (2017). Investigating the biodiversity of the forest strata: The importance of vertical stratification to the activity and development of saproxylic beetles in managed temperate deciduous forests. Forest Ecology and Management, 402, 186–193. https://doi.org/10.1016/j.foreco.2017.07.052

Powell, H. D. W., Hejl, S. J., & Six, D. L. (2002). Measuring woodpecker food: A simple method for comparing wood-boring beetle abundance among fire-killed trees. Journal of Field Ornithology, 73(2), 130–140. https://doi.org/10.1648/0273-8570-73.2.130

Procházka, J., Cizek, L., & Schlaghamerský, J. (2018). Vertical stratification of scolytine beetles in temperate forests. Insect Conservation and Diversity, 11(6), 534–544. https://doi.org/10.1111/icad.12301

Ramilo, P., Guerrero, J. R., Micó, E., & Galante, E. (2017). Volatile organic compounds emitted by Quercus pyrenaica Willd. And its relationship with saproxylic beetle assemblages. Arthropod-Plant Interactions, 11(2), 221–234. https://doi.org/10.1007/s11829-016-9483-3

Ranius, T., Hämäläinen, A., Egnell, G., Olsson, B., Eklöf, K., Stendahl, J., Rudolphi, J., Sténs, A., & Felton, A. (2018). The effects of logging residue extraction for energy on ecosystem services and biodiversity: A synthesis. Journal of Environmental Management, 209, 409–425. https://doi.org/10.1016/j.jenvman.2017.12.048

Roberge, J.-M., & Angelstam, P. (2004). Usefulness of the Umbrella Species Concept as a Conservation Tool. Conservation Biology, 18(1), 76–85. https://doi.org/10.1111/j.1523-1739.2004.00450.x

Roth, N., Doerfler, I., Bässler, C., Blaschke, M., Bussler, H., Gossner, M. M., Heideroth, A., Thorn, S., Weisser, W. W., & Müller, J. (2019). Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity. Diversity and Distributions, 25(3), 430–441. https://doi.org/10.1111/ddi.12870

Ruchin, A. B., & Egorov, L. V. (2021). Vertical Stratification of Beetles in Deciduous Forest Communities in the Centre of European Russia. Diversity, 13(11), 508. https://doi.org/10.3390/d13110508

Scherzinger, W. (1990). Is competition by the Great-spotted Woodpecker the cause for White-backed Woodpecker rarity in Bavarian forest national park?

Seibold, S., Hagge, J., Müller, J., Gruppe, A., Brandl, R., Bässler, C., & Thorn, S. (2018). Experiments with dead wood reveal the importance of dead branches in the canopy for saproxylic beetle conservation. Forest Ecology and Management, 409, 564–570. https://doi.org/10.1016/j.foreco.2017.11.052

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M. D., Lorz, J., Cadotte, M. W., Lindenmayer, D. B., Adhikari, Y. P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R. S., Birkemoe, T., … Müller, J. (2021). The contribution of insects to global forest deadwood decomposition. Nature, 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8

Senf, C., Buras, A., Zang, C. S., Rammig, A., & Seidl, R. (2020). Excess forest mortality is consistently linked to drought across Europe. Nature Communications, 11(1), 6200. https://doi.org/10.1038/s41467-020-19924-1

Siitonen, J., Martikainen, P., Punttila, P., & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management, 128(3), 211–225. https://doi.org/10.1016/S0378-1127(99)00148-6

Soto, G. E., Pérez-Hernández, C. G., Hahn, I. J., Rodewald, A. D., & Vergara, P. M. (2017). Tree senescence as a direct measure of habitat quality: Linking red-edge Vegetation Indices to space use by Magellanic woodpeckers. Remote Sensing of Environment, 193, 1–10. https://doi.org/10.1016/j.rse.2017.02.018

Speight, M. C. D. (1989). Saproxylic invertebrates and their conservation (Nature and environment). Strasbourg, France: Council of Europe.

Stokland, J. N., Siitonen, J., & Jonsson, B. G. (2012). Biodiversity in dead wood. Cambridge: Cambridge University Press.

Ulyshen, M. D. (2011). Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. Forest Ecology and Management, 261(9), 1479–1489. https://doi.org/10.1016/j.foreco.2011.01.033

Ulyshen, M. D., & Hanula, J. L. (2007). A Comparison of the Beetle (Coleoptera) Fauna Captured at Two Heights Above the Ground in a North American Temperate Deciduous Forest. The American Midland Naturalist, 158(2), 260–278. https://doi.org/10.1674/0003-0031(2007)158[260:ACOTBC]2.0.CO;2

Urkijo-Letona, A., Cárcamo, S., Peña, L., Fernández de Manuel, B., Onaindia, M., & Ametzaga-Arregi, I. (2020). Key Elements of the White-backed Woodpecker's (Dendrocopos leucotos lilfordi) Habitat in Its European South-Western Limits. Forests, 11(8), 831. https://doi.org/10.3390/f11080831

Virkkala, R. (2006). Why study woodpeckers? The significance of woodpeckers in forest ecosystems. Annales Zoologici Fennici, 43, 82–85.

Virkkala, R., Alanko, T., Laine, T., & Tiainen, J. (1993). Population contraction of the White-backed Woodpecker Dendrocopos leucotos in Finland as a consequence of habitat alteration. Biological Conservation, 66, 47–53.

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E., & Thorn, S. (2021). Diversity and conservation of saproxylic beetles in 42 European tree species: An experimental approach using early successional stages of branches. Insect Conservation and Diversity, 14(1), 132–143. https://doi.org/10.1111/icad.12442

Vogel, S., Gossner, M. M., Mergner, U., Müller, J., & Thorn, S. (2020). Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. Journal of Applied Ecology, 57(10), 2075–2085. https://doi.org/10.1111/1365-2664.13648

Weiss, M., Procházka, J., Schlaghamerský, J., & Cizek, L. (2016). Fine-Scale Vertical Stratification and Guild Composition of Saproxylic Beetles in Lowland and Montane Forests: Similar Patterns despite Low Faunal Overlap. PLoS ONE, 11(3), e0149506. https://doi.org/10.1371/journal.pone.0149506

R packages

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Bivand, Roger S. and Wong, David W. S. (2018) Comparing implementations of global and local indicators of spatial association TEST, 27(3), 716-748. https://doi.org/10.1007/s11749-018-0599-x

Bivand, R. (2022) R Packages for Analyzing Spatial Data: A Comparative Case Study with Areal Data Geographical Analysis, 54(3), 488-518. https://doi.org/10.1111/gean.12319

Cardoso P, Mammola S, Rigal F, Carvalho J (2022). _BAT: Biodiversity Assessment Tools_. R package version 2.9.0. https://CRAN.R-project.org/package=BAT

Gabry J, Mahr T (2022). "bayesplot: Plotting for Bayesian Models." R package version 1.9.0. https://mc-stan.org/bayesplot

Goodrich B, Gabry J, Ali I & Brilleman S. (2022). rstanarm: Bayesian applied regression modeling via Stan. R package version 2.21.3. https://mc-stan.org/rstanarm

Pedersen T (2022). _patchwork: The Composer of Plots_. R package version 1.1.2. https://CRAN.R-project.org/package=patchwork

Roger S. Bivand, Edzer Pebesma, Virgilio Gomez-Rubio, 2013. Applied spatial data analysis with R, Second edition. Springer, NY. https://asdar-book.org/.

Gabry J, Mahr T (2022). "bayesplot: Plotting for Bayesian Models." R package version 1.9.0, https://mc-stan.org/bayesplot

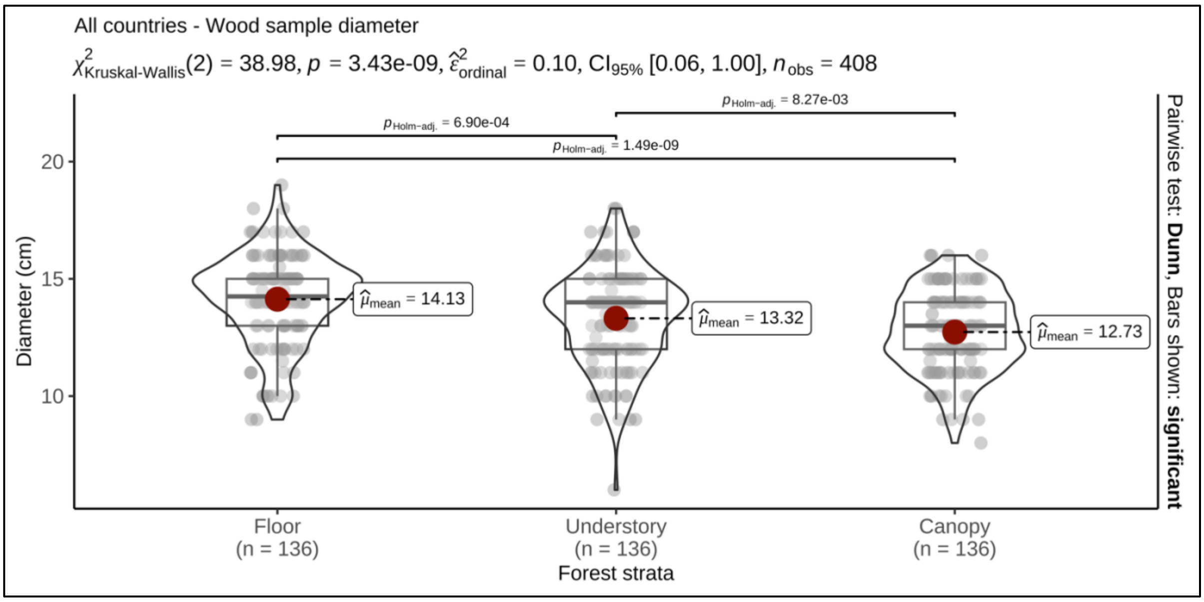
Patil, I. (2021). Visualizations with statistical details: The 'ggstatsplot' approach. Journal of Open Source Software, 6(61), 3167, doi:10.21105/joss.03167

Auguie B (2017). _gridExtra: Miscellaneous Functions for "Grid" Graphics_. R package version 2.3, https://CRAN.R-project.org/package=gridExtra

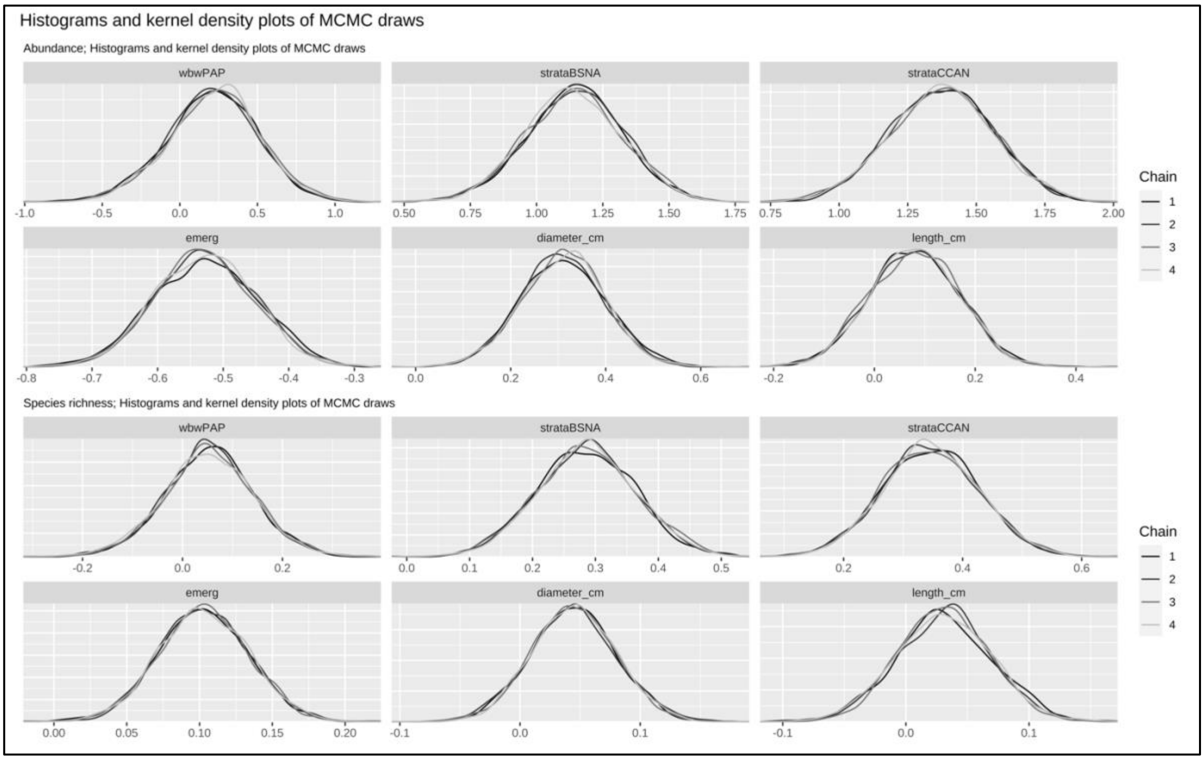
Pedersen T (2022). _patchwork: The Composer of Plots_. R package version 1.1.2, https://CRAN.R-project.org/package=patchwork

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019). "Welcome to the tidyverse." _Journal of Open Source Software_, *4*(43), 1686. doi:10.21105/joss.01686 https://doi.org/10.21105/joss.01686

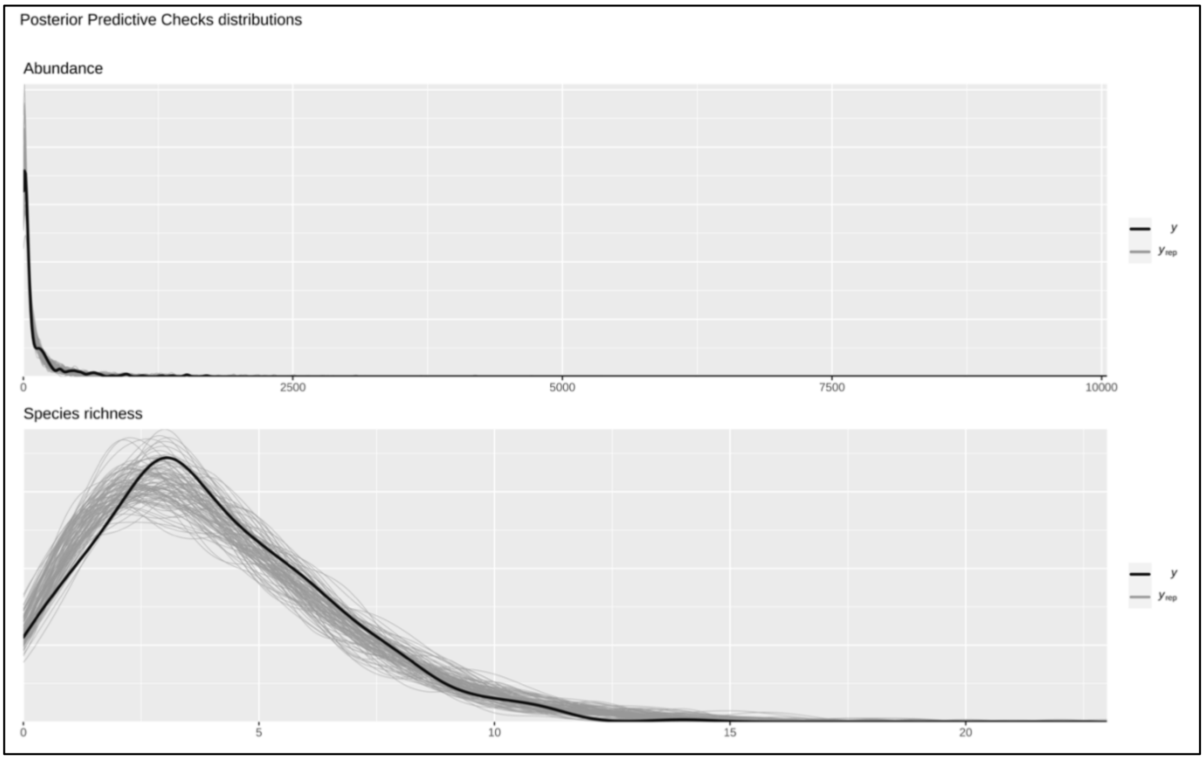
Supplementary materials



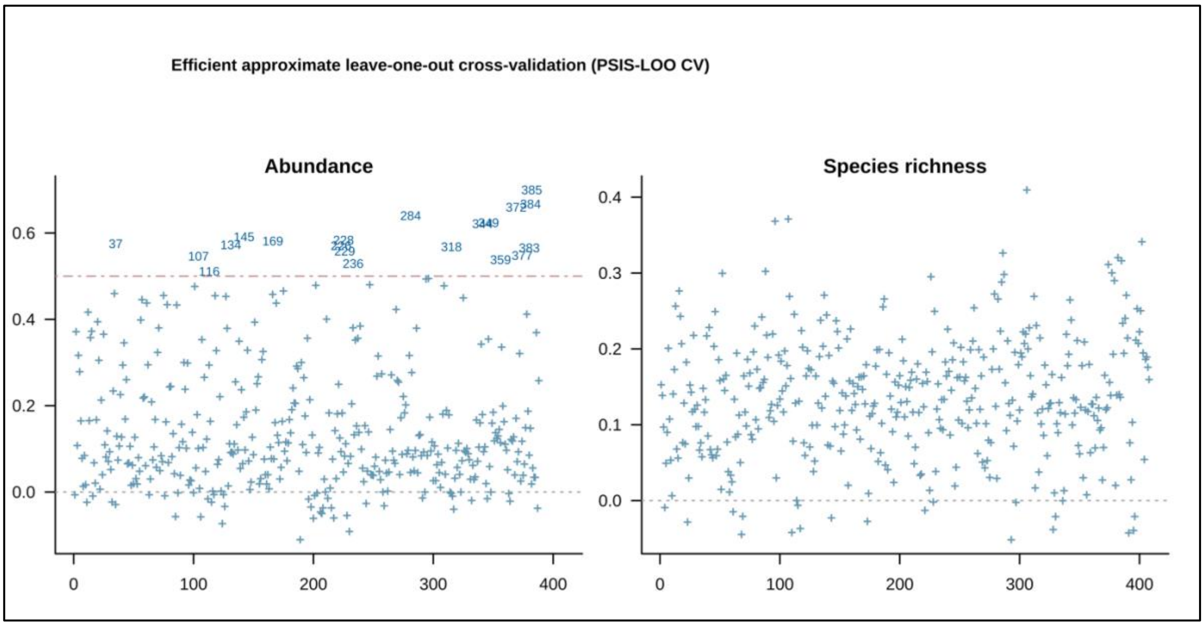
S1. Pairwise comparison of the diameter of the exposed piece of wood per forest strata.



S2. Drivers of saproxylic beetles' abundance and species richness: Histograms and kernel density plots of MCMC draws; Main model group with Control level as intercept. Woodpecker absence and Forest floor as intercept. wbwPAP = woodpecker presence. strataBSNA = understory. strataCCAN = canopy.



S3. Drivers of saproxylic beetles' abundance and richness: Posterior predictive checks distribution; Main model group with Control level as intercept.



S4. Drivers of saproxylic beetle's abundance and richness: Efficient approximate leave-one-out cross-validation for our main model group with Control level as intercept, using Pareto smoothed importance sampling (PSIS-LOO CV).

S5. Picture of the Swiss rearing installation.

S6. Abundance and proportion per exposition time of the trapped saproxylic beetle species.

Family	Species	Year 1		Year 2		Total	
		Abundance	Proportion	Abundance	Proportion	Abundance	Proportion
Curculionidae	*Taphrorychus bicolor*	31001	82.93%	3067	27.26%	34068	70.05%
Curculionidae	*Ernoporicus fagi*	4347	11.63%	5274	46.88%	9621	19.78%
Cerambycidae	*Leiopus nebulosus*	401	1.07%	474	4.21%	875	1.80%
Cryptophagidae	*Cryptophagus punctipennis*	24	0.06%	767	6.82%	791	1.63%
Curculionidae	*Anisandrus dispar*	435	1.16%			435	0.89%
Trogossitidae	*Nemozoma elongatum*	31	0.08%	373	3.32%	404	0.83%
Mycetophagidae	*Litargus connexus*	190	0.51%	166	1.48%	356	0.73%
Corylophidae	*Sericoderus lateralis*	209	0.56%	84	0.75%	293	0.60%
Cryptophagidae	*Cryptophagus pallidus*	254	0.68%	5	0.04%	259	0.53%
Latridiidae	*Enicmus histrio*	123	0.33%			123	0.25%
Corylophidae	*Orthoperus brunnipes*	17	0.05%	95	0.84%	112	0.23%
Latridiidae	*Latridius minutus*			105	0.93%	105	0.22%
Corylophidae	*Orthoperus atomus*			92	0.82%	92	0.19%
Salpingidae	*Salpingus ruficollis*	57	0.15%	26	0.23%	83	0.17%
Latridiidae	*Cartodere nodifer*	23	0.06%	50	0.44%	73	0.15%
Curculionidae	*Taphrorychus villifrons*			73	0.65%	73	0.15%
Mycetophagidae	*Mycetophagus atomarius*	11	0.03%	59	0.52%	70	0.14%
Corylophidae	*Arthrolips obscura*			62	0.55%	62	0.13%
Curculionidae	*Orchestes fagi*	6	0.02%	44	0.39%	50	0.10%

Family	Species	Year 1		Year 2		Total	
		Abundance	Proportion	Abundance	Proportion	Abundance	Proportion
Salpingidae	*Salpingus planirostris*	31	0.08%	13	0.12%	44	0.09%
Cryptophagidae	*Atomaria umbrina*			30	0.27%	30	0.06%
Curculionidae	*Xyleborinus saxesenii*	10	0.03%	20	0.18%	30	0.06%
Cryptophagidae	*Cryptophagus dentatus*	5	0.01%	22	0.20%	27	0.06%
Cryptophagidae	*Atomaria analis*	23	0.06%			23	0.05%
Latridiidae	*Dienerella vincenti*			21	0.19%	21	0.04%
Ptinidae	*Ptilinus pectinicornis*			21	0.19%	21	0.04%
Dasytidae	*Dasytes caeruleus*	20	0.05%			20	0.04%
Cerambycidae	*Pogonocherus hispidulus*	17	0.05%	3	0.03%	20	0.04%
Ciidae	*Orthocis alni*			18	0.16%	18	0.04%
Curculionidae	*Cryptorhynchus lapathi*			17	0.15%	17	0.03%
Dasytidae	*Dasytes plumbeus*	1	< 0.01%	15	0.13%	16	0.03%
Staphylinidae	*Holobus flavicornis*			14	0.12%	14	0.03%
Cryptophagidae	*Atomaria pusilla*			13	0.12%	13	0.03%
Endomychidae	*Endomychus coccineus*	12	0.03%	1	0.01%	13	0.03%
Curculionidae	*Trypodendron domesticum*	13	0.03%			13	0.03%
Monotomidae	*Rhizophagus bipustulatus*	7	0.02%	5	0.04%	12	0.02%
Staphylinidae	*Holobus apicatus*			11	0.10%	11	0.02%
Latridiidae	*Latridius consimilis*	8	0.02%	3	0.03%	11	0.02%
Curculionidae	*Xylosandrus germanus*			11	0.10%	11	0.02%
Staphylinidae	*Acrotona aterrima*			10	0.09%	10	0.02%
Scraptiidae	*Anaspis flava*	3	0.01%	7	0.06%	10	0.02%
Coccinellidae	*Aphidecta obliterata*			10	0.09%	10	0.02%
Staphylinidae	*Cypha longicornis*			10	0.09%	10	0.02%
Staphylinidae	*Mocyta fungi*			10	0.09%	10	0.02%
Monotomidae	*Rhizophagus dispar*	1	< 0.01%	9	0.08%	10	0.02%
Latridiidae	*Dienerella clathrata*	4	0.01%	5	0.04%	9	0.02%
Staphylinidae	*Phloeocharis subtilissima*			9	0.08%	9	0.02%
Cryptophagidae	*Cryptophagus badius*	8	0.02%			8	0.02%
Dasytidae	*Dasytes obscurus*			8	0.07%	8	0.02%
Curculionidae	*Kyklioacalles roboris*	5	0.01%	3	0.03%	8	0.02%
Cerambycidae	*Phymatodes testaceus*	8	0.02%			8	0.02%
Silvanidae	*Silvanus bidentatus*	6	0.02%	2	0.02%	8	0.02%
Endomychidae	*Symbiotes gibberosus*	5	0.01%	3	0.03%	8	0.02%
Curculionidae	*Dryocoetes autographus*	7	0.02%			7	0.01%
Monotomidae	*Rhizophagus nitidulus*			7	0.06%	7	0.01%
Curculionidae	*Trachodes hispidus*	3	0.01%	3	0.03%	6	0.01%
Cryptophagidae	*Atomaria fimetarius*	5	0.01%			5	0.01%
Staphylinidae	*Cypha discoidea*			5	0.04%	5	0.01%
Staphylinidae	*Liogluta longiuscula*			5	0.04%	5	0.01%
Staphylinidae	*Atheta crassicornis*			4	0.04%	4	0.01%
Latridiidae	*Corticaria impressa*	3	0.01%	1	0.01%	4	0.01%
Cryptophagidae	*Cryptophagus cellaris*			4	0.04%	4	0.01%

Family	Species	Year 1		Year 2		Total	
		Abundance	Proportion	Abundance	Proportion	Abundance	Proportion
Cryptophagidae	*Cryptophagus subdepressus*	4	0.01%			4	0.01%
Latridiidae	*Stephostethus alternans*	4	0.01%			4	0.01%
Staphylinidae	*Atheta fungivora*			3	0.03%	3	0.01%
Cryptophagidae	*Atomaria apicalis*			3	0.03%	3	0.01%
Corylophidae	*Corylophus cassidoides*	1	< 0.01%	2	0.02%	3	0.01%
Staphylinidae	*Dinaraea angustula*			3	0.03%	3	0.01%
Latridiidae	*Latridius hirtus*	2	0.01%	1	0.01%	3	0.01%
Anthribidae	*Platyrhinus resinosus*			3	0.03%	3	0.01%
Anthribidae	*Platystomos albinus*	2	0.01%	1	0.01%	3	0.01%
Cerambycidae	*Poecilium pusillum*	3	0.01%			3	0.01%
Ptinidae	*Ptinomorphus imperialis*	3	0.01%			3	0.01%
Zopheridae	*Synchita humeralis*			3	0.03%	3	0.01%
Scraptiidae	*Anaspis brunnipes*			2	0.02%	2	< 0.01%
Zopheridae	*Coxelus pictus*			2	0.02%	2	< 0.01%
Laemophloeidae	*Cryptolestes duplicatus*	1	< 0.01%	1	0.01%	2	< 0.01%
Cryptophagidae	*Cryptophagus dorsalis*	2	0.01%			2	< 0.01%
Cryptophagidae	*Cryptophagus scanicus*			2	0.02%	2	< 0.01%
Cryptophagidae	*Cryptophagus subfumatus*			2	0.02%	2	< 0.01%
Staphylinidae	*Cypha punctum*			2	0.02%	2	< 0.01%
Latridiidae	*Dienerella filum*	1	< 0.01%	1	0.01%	2	< 0.01%
Biphyllidae	*Diplocoelus fagi*	1	< 0.01%	1	0.01%	2	< 0.01%
Latridiidae	*Enicmus transversus*	1	< 0.01%	1	0.01%	2	< 0.01%
Ptiliidae	*Nossidium pilosellum*	1	< 0.01%	1	0.01%	2	< 0.01%
Ptiliidae	*Ptenidium laevigatum*	1	< 0.01%	1	0.01%	2	< 0.01%
Cerambycidae	*Rhagium inquisitor*			2	0.02%	2	< 0.01%
Monotomidae	*Rhizophagus picipes*			2	0.02%	2	< 0.01%
Staphylinidae	*Rybaxis longicornis*			2	0.02%	2	< 0.01%
Curculionidae	*Trypodendron lineatum*			2	0.02%	2	< 0.01%
Silvanidae	*Uleiota planatus*	2	0.01%			2	< 0.01%
Salpingidae	*Vincenzellus ruficollis*			2	0.02%	2	< 0.01%
Curculionidae	*Acalles echinatus*			1	0.01%	1	< 0.01%
Elateridae	*Ampedus nigrinus*			1	0.01%	1	< 0.01%
Scraptiidae	*Anaspis thoracica*			1	0.01%	1	< 0.01%
Staphylinidae	*Anthobium atrocephalum*			1	0.01%	1	< 0.01%
Cryptophagidae	*Atomaria impressa*	1	< 0.01%			1	< 0.01%
Cryptophagidae	*Atomaria longicornis*			1	0.01%	1	< 0.01%
Cryptophagidae	*Atomaria turgida*	1	< 0.01%			1	< 0.01%
Staphylinidae	*Batrisodes venustus*			1	0.01%	1	< 0.01%
Staphylinidae	*Bolitochara obliqua*			1	0.01%	1	< 0.01%
Ciidae	*Cis castaneus*	1	< 0.01%			1	< 0.01%
Clambidae	*Clambus punctulum*			1	0.01%	1	< 0.01%
Clambidae	*Clambus simsoni*	1	< 0.01%			1	< 0.01%
Cerambycidae	*Clytus rhamni*			1	0.01%	1	< 0.01%

Family	Species	Year 1		Year 2		Total	
		Abundance	Proportion	Abundance	Proportion	Abundance	Proportion
Latridiidae	*Corticaria longicornis*			1	0.01%	1	< 0.01%
Latridiidae	*Corticarina curta*			1	0.01%	1	< 0.01%
Latridiidae	*Corticarina minuta*			1	0.01%	1	< 0.01%
Latridiidae	*Corticarina similata*			1	0.01%	1	< 0.01%
Laemophloeidae	*Cryptolestes corticinus*	1	< 0.01%			1	< 0.01%
Staphylinidae	*Cypha laeviuscula*			1	0.01%	1	< 0.01%
Dasytidae	*Dasytes niger*	1	< 0.01%			1	< 0.01%
Elateridae	*Denticollis linearis*			1	0.01%	1	< 0.01%
Anthribidae	*Dissoleucas niveirostris*	1	< 0.01%			1	< 0.01%
Carabidae	*Dromius quadrimaculatus*			1	0.01%	1	< 0.01%
Latridiidae	*Enicmus testaceus*			1	0.01%	1	< 0.01%
Nitidulidae	*Epuraea biguttata*			1	0.01%	1	< 0.01%
Nitidulidae	*Epuraea distincta*			1	0.01%	1	< 0.01%
Tetratomidae	*Hallomenus binotatus*			1	0.01%	1	< 0.01%
Ptinidae	*Hemicoelus canaliculatus*	1	< 0.01%			1	< 0.01%
Latridiidae	*Latridius porcatus*	1	< 0.01%			1	< 0.01%
Staphylinidae	*Leptusa ruficollis*			1	0.01%	1	< 0.01%
Curculionidae	*Liparus germanus*			1	0.01%	1	< 0.01%
Staphylinidae	*Microscydmus nanus*			1	0.01%	1	< 0.01%
Tenebrionidae	*Mycetochara maura*	1	< 0.01%			1	< 0.01%
Melandryidae	*Orchesia undulata*			1	0.01%	1	< 0.01%
Curculionidae	*Otiorhynchus tenebricosus*			1	0.01%	1	< 0.01%
Staphylinidae	*Oxypoda vittata*			1	0.01%	1	< 0.01%
Histeridae	*Paromalus flavicornis*			1	0.01%	1	< 0.01%
Cucujidae	*Pediacus dermestoides*			1	0.01%	1	< 0.01%
Laemophloeidae	*Placonotus testaceus*	1	< 0.01%			1	< 0.01%
Curculionidae	*Plinthus tischeri*			1	0.01%	1	< 0.01%
Ptiliidae	*Ptenidium pusillum*			1	0.01%	1	< 0.01%
Ptiliidae	*Pteryx suturalis*	1	< 0.01%			1	< 0.01%
Salpingidae	*Rabocerus foveolatus*	1	< 0.01%			1	< 0.01%
Cantharidae	*Rhagonycha lignosa*	1	< 0.01%			1	< 0.01%
Curculionidae	*Rhyncolus ater*	1	< 0.01%			1	< 0.01%
Staphylinidae	*Scydmaenus tarsatus*			1	0.01%	1	< 0.01%
Staphylinidae	*Sepedophilus bipustulatus*			1	0.01%	1	< 0.01%
Silvanidae	*Silvanus unidentatus*			1	0.01%	1	< 0.01%
Curculionidae	*Sitona hispidulus*	1	< 0.01%			1	< 0.01%
Staphylinidae	*Stenichnus godarti*	1	< 0.01%			1	< 0.01%
Latridiidae	*Stephostethus angusticollis*			1	0.01%	1	< 0.01%
Cleridae	*Thanasimus formicarius*			1	0.01%	1	< 0.01%
Latridiidae	*Thes bergrothi*			1	0.01%	1	< 0.01%
Mycetophagidae	*Triphyllus bicolor*	1	< 0.01%			1	< 0.01%
Mordellidae	*Variimorda villosa*			1	0.01%	1	< 0.01%
	Total	37381	76.87%	11251	23.13%	48632	100%

General Discussion

While several studies indirectly assessed the link between the White-backed Woodpecker and forest biodiversity (Bell et al., 2015; Roberge et al., 2008; Jonsell et al., 2004; Martikainen et al., 1998), evidence of the bird as an umbrella species for saproxylic beetles is still missing. In addition of finding that all studied sites had an equivalent potential for saproxylic beetle colonization (Chapter 2; Chapter 3), we evidenced saproxylic beetle species of conservation concern to be associated with the White-backed Woodpecker's breeding home range (Chapter 1). Informed by implemented past action plans targeting the White-backed Woodpecker in Fennoscandia (Mild & Stighäll, 2017; Virkkala et al., 1993), we propose forest management measures to enhance the quality of its central European habitat, using the White-backed Woodpecker as an indicator for forest naturalness supporting the array of rare saproxylic beetle species its occurrence may encompass.

Main findings

In Chapter 1, we evidenced the White-backed Woodpecker to be a suitable umbrella species for threatened saproxylic beetle communities. Species richness of threatened saproxylic beetles was higher in sites with high White-backed Woodpecker activity compared to absence sites. Community composition analyses showed threatened saproxylic beetle communities to be more homogeneous in presence of the bird compared to absence sites. Indicator species analysis showed that more saproxylic beetle species – including threatened ones – were positively associated with the breeding home range of the White-backed Woodpecker compared to absence sites. These results bring first-time evidence-based information on the role of the White-backed Woodpecker as an umbrella species for threatened saproxylic beetles. Besides the possibility to transfer our methodological approach to other potential surrogate species, our results should open new opportunities for action plans aiming at supporting the White-backed Woodpecker and saproxylic beetles in central European beech-dominated forests.

In Chapter 2, we confirmed the importance of mature forest attributes in supporting both saproxylic beetle and White-backed Woodpecker populations. The activity of the White-backed Woodpecker was positively correlated with the diameter of live trees. Live tree diameter was also positively correlated with the species richness of saproxylic beetles via an indirect positive effect of the diameter of the surrounding standing dead trees. However, we did not found evidence of a direct link between emerging saproxylic beetle communities and the White-backed Woodpecker's activity. Our results are calling for a reassessment of the dead standing trees’ importance in the woodpecker's foraging strategy. Nonetheless, we highlighted the equal contribution of dead standings trees in supporting saproxylic beetle communities associated with them. We believe our results could guide practitioners in integrating biodiversity-friendly actions in the development of their management strategies in extensively managed central European beech-dominated forests.

In Chapter 3, we highlighted an equivalent potential of forest sites in supporting communities of early colonizing saproxylic beetles, regardless of the White-backed Woodpecker’s occurrence. The forest stratum (ground, understory, canopy) was the most important variable driving the composition of saproxylic beetle assemblages emerging from fresh dead wood. Additionally, we evidenced a strong effect of the dead wood decay in structuring the communities of early colonizing saproxylic beetles. Our experimental approach shows the importance of a continuous and diversified dead wood resource in the three-dimensional space of the forest ecosystem for pioneer saproxylic beetle communities. Colonized standing and suspended dead wood could – hypothetically – support saproxylic predators by providing a year-round access to prey of utmost importance when the snow cover is blocking access to lying dead wood in wintertime.

Delayed recolonization

The White-backed Woodpecker can easily disperse over the landscape, eventually finding suitable forest patches for its survival. However, saproxylic species characterized by a reduced mobility might be enclosed in a large-scale ecological trap induced by former intensive logging regimes (following the "island theory"; see Macarthur & Wilson, 1967).

As shown in Chapter 1, sites inhabited by the White-backed Woodpecker harbored threatened (Bense, 2002) and primeval forest relict species (Eckelt et al., 2018). While the detection of these species of conservation concern attests to the presence of a rare community, this observation was only valid for flying species. However, most of threatened saproxylic beetles are characterized by a low dispersal ability and a reduced flying capacity (Carpaneto et al., 2010; Hagge et al., 2021). Considering the importance of dead standing trees for both White-backed Woodpeckers (Bühler, 2009; Czeszczewik, 2009; Ettwein et al., 2020; Melletti & Penteriani, 2003; Urkijo-Letona et al., 2020) and saproxylic invertebrates (Bouget et al., 2012; Brunet & Isacsson, 2009; Jonsell & Weslien, 2003; Onodera et al., 2017), and the presence of threatened saproxylic beetle taxa in presence of the bird, we hypothesized that snags found in the bird's breeding home range had greater value in supporting saproxylic beetles of conservation concern than the ones found in absence sites (Chapter 2). Yet, this could not be confirmed. Additionally, emerging saproxylic beetle communities were relatively similar among sites, regardless of the White-backed Woodpecker's occurrence.

In our opinion, this missing link between the White-backed Woodpecker occurrence and saproxylic beetles emerging from dead standing trees could be explained by the long-term pernicious effect of intensive forest management. After centuries of dead wood removal (Whitehouse, 2006), European forest management induced an interruption and a strong deficit in dead wood diversity (Speight, 1989), represented by tree species, decay stages, sizes and types (lying, standing, and suspended dead wood items). While the dead wood amount is generally increasing in European forests (FOREST EUROPE, 2020), the past massive dead wood depletion resulted in a long-term fragmentation of the ecosystem. As a result, many snag-dependent saproxylic species may have been subject to landscape-scale extinction. If no conservation measures are taken to sustain the increasing quality of European forest ecosystems (FOREST EUROPE, 2020), a valuable fraction of saproxylic diversity could struggle in recolonizing this valuable habitat.

Conservation action plans

To my knowledge, only two action plans have been implemented to preserve the European White-backed Woodpecker population. In Finland, Virkkala et al. (1993) proposed to set aside 199 forest sites of about 50 km^2 where White-backed Woodpeckers had been observed, including breeding sites. Additional measures were suggested to enhance the habitat quality of the selected sites by (1) reducing coniferous encroachment, (2) excluding 10% of the deciduous trees from harvesting and (3) stopping the extraction of dead wood (to provide foraging items for woodpeckers). While this action plan did not study saproxylic beetles, they observed a significant increase in the Finnish White-backed Woodpecker population (1993: 30 to 50 breeding pairs; 2015: ±200 breeding pairs; see Virkkala et al., 1993; Finnish Environment Institute (Web resource)). In Sweden, Mild & Stighäll (2017) proposed active restoration techniques (i.e., creation of nature reserves, habitat protection, conservation agreement, removal of spruce, prescribed burning, fencing and creation of dead wood) for over 10,000 ha of forested stands. Seven years after, only nine birds were identified as living permanently among restored sites (Bell et al., 2015). While the Swedish White-backed Woodpecker action plan was considered as a failure (Blicharska et al., 2014), red-listed flying (Bell et al., 2015) and snag-associated (Jonsell et al., 2004) saproxylic beetles communities benefited from it.

While the core area of our study is in beech-dominated managed forests of central Europe, past action plans promoting the White-backed Woodpecker focused their research in Fennoscandian woodlands (Bell et al., 2015; Jonsell et al., 2004; Martikainen et al., 1998; Mild & Stighäll, 2017; Virkkala et al., 1993). It is therefore legitimate to expect different biodiversity patterns emerging from such distinct ecozones, not to mention the diverging forest management history. Nonetheless, valuable information can be acquired from their experience. On the one hand, the Finnish approach enhanced the naturalness of current and potential White-backed Woodpecker habitats with biodiversity-friendly forest management measures. Thus, increasing the bird's population, but without assessing the potential beneficial effects of the measures on saproxylic beetle communities. On the other hand, the Swedish plan was to actively restore the habitat with heavy manipulations of the landscape, which attracted some red-listed saproxylic beetle species, but failed to bring the bird back. We believe that at the time the effectiveness of the Swedish plan was evaluated, the environmental conditions to attract the bird and its associated diversity were not yet met. As evidenced by our dead wood colonization experiment (Chapter 3), some saproxylic beetles can rapidly colonize a newly available habitat. However, the White-backed Woodpecker is primarily an old-growth deciduous forest specialist (Carlson, 2000). Ecological processes shaping primeval forests may take decades to centuries (Hilmers et al., 2018). Informed by studies observing the bird in its natural primeval habitat (Czeszczewik et al., 2013; Wesołowski, 1995), it is legitimate to hypothesize its occurrence to be governed by a strong connection to its biome. This hypothesis could be supported by the Finnish action plan, which sets aside forest stands deemed suitable and orienting its conservation strategy towards the improvement of the current habitat.

While habitat restoration will take many years before reaching the high level of naturalness the focal bird need, saproxylic beetle species of conservation concern can nonetheless be found in relatively young dead wood (Jonsell et al., 2004; Jonsell & Weslien, 2003), adding a conservation value to the ecosystem function of dead wood colonizers. In association with fungi, pioneer saproxylic beetle species are shaping the forest ecosystem as the future old-growth habitat the other members of their guild depend on (Jacobsen et al., 2017; Müller et al., 2008; Speight, 1989; Thorn et al., 2016). When developing conservation programs aiming at supporting forest biodiversity, members of the early colonizer guild should not be overlooked. To support forest biodiversity, while emphasizing its old-growth component, we believe that an ideal action plan should be inspired from both of the Fenno-Scandinavian initiatives.

Management recommendations

Considering the evidenced role of the White-backed Woodpecker as an umbrella species for threatened saproxylic beetles and its proxy role for forest naturalness, actions must be implemented to support its return. Political instances are now orienting forest management strategies towards a better integration of the biodiversity component (e.g., by reducing conifer encroachment (Hämäläinen, Junninen, Halme, & Kouki, 2020; Mild & Stighäll, 2017; Virkkala et al., 1993), diversifying stand's genetic pool and focusing on local tree variety (Ratnam et al., 2014), retaining dead and moribund trees (Carpaneto et al., 2010; Larrieu et al., 2018; Müller et al., 2022; Paillet et al., 2010) and more generally, the development of dead wood oriented management regimes (Doerfler et al., 2017; Gossner et al., 2013)). Even though being "biodiversity-friendly", modern forestry remains too conservative (Imesch et al., 2015). Studied sites harboring White-backed Woodpeckers were represented by large trees (around 32 cm DBH; see Chapter 1) and a dead wood volume was substantially higher than the European average (55 m^3 ha^{-1} compared to 11.5 m^3 ha^{-1}; see Ettwein et al., 2020 and FOREST EUROPE, 2020).

To protect and support the White-backed Woodpecker and its associated saproxylic community, informed public and private instances must therefore sit together to implement cost-effective and future-proof action plans (Blicharska et al., 2014; Verkerk et al., 2022). Due to the high value of the White-backed Woodpecker for forest biodiversity, political instances should take measures to preserve the species. Current breeding home ranges should benefit from the "strict nature reserve" status. This protection measure should be extended to all forest sites considered economically unsuitable for logging activity (e.g., situated on steep slopes or in remote locations) and with a surface of mixed forest suitable for hosting breeding individuals (c.a. 30-40 ha per White-backed Woodpecker couple; see Chapter 1); (Ettwein et al., 2020; Garmendia et al., 2006). In sites identified as potential White-backed Woodpecker breeding home ranges and yet being managed, practitioners could implement passive actions to create a sustainable and diversified dead wood resource over the landscape. Among them, the non-exportation of logging and natural disturbance residuals, the retention of dead and moribund trees, and the creation of senescence islands. Beside reducing habitat fragmentation, the persistence of these habitat quality enhancement efforts should provide the diversity of the habitats saproxylics depend on (i.e., tree species, decay stages, sizes, and types). The implementation of these long-term conservation measures should efficiently support the White-backed Woodpecker and the valuable diversity of saproxylic species that its presence encompasses, as well as bringing back primeval forests into the European landscape.

Study limitations and perspectives

We do believe that the results of this study can make a valuable contribution to our understanding of forest-dependent communities in a context of changing environment. This, in turn, can help in the development of efficient forest management strategies and conservation plans for dead wood-dependent biodiversity. However, we believe that some aspects have not been addressed and forest-dependent conservation plans would benefit from their investigation.

Little is known about the diet of the central European White-backed Woodpecker population. Few studies describe the bird as favoring Cerambycid larvae (Aulén, 1988; Hogstad & Stenberg, 1997). However, these observations – conducted in Fennoscandia – may not be valid in our geographical area. Although the bird was identified as foraging primarily on snags (Bühler, 2009), our exploration of standing dead trees did not allow us to confirm a prey-predator association. Methodologies relying on new technologies may help better understanding the specific trophic interactions occurring at the local scale, and improving management strategies if necessary (e.g., video recording of breeding cavities, sequencing of bird's fecal DNA).

A single species may not fully represent an ecosystem. Combining the White-backed Woodpecker with other highly specialized surrogate species for forest diversity could help develop holistic conservation programs (Roberge & Angelstam, 2004). Nevertheless, given that red-listed saproxylic beetles (Bell et al., 2015; Jonsell et al., 2004; Martikainen et al., 1998), woodland birds, and cryptogams (Roberge et al., 2008) are associated with the Fennoscandian White-backed Woodpecker habitat, testing the umbrella function of the central European White-backed Woodpecker population on a broader spectrum of organisms could increase the value of our surrogate bird species for saproxylic and forest-dependent diversity. With the data already available and the methodological framework we developed, assessing the response of several forest-dependent taxonomic groups would be a cost-effective approach to highlight biodiversity-rich forest patches that should be protected.

Long-term monitoring of the White-backed Woodpecker population and its associated saproxylic community is essential. Due to global warming and the increasing frequency of extreme climatic episodes (e.g., heatwaves and drought), central European beech forests have been subjected to significant stress in the past years (Klesse et al., 2022; Rohner et al., 2021). Moreover, the amplitude and direction of the ecosystems' response to this changing environment is not generalized but deeply linked to the geographic context they are embedded within (Frei et al., 2022; Hülsmann et al., 2016). In regard of the chaotic response of the forest ecosystem to human-induced stressors, and the uncertainty in the adaptive plasticity of the many species depending on this biome, it is our responsibility to be the custodians of their persistence and posterity.

References

Aulén, G. (1988). Ecology and distribution history of the White-backed Woodpecker Dendrocopos leucotos in Sweden [Dissertation]. Swedish University of Agricultural Science.

Bell, D., Hjältén, J., Nilsson, C., Jørgensen, D., & Johansson, T. (2015). Forest restoration to attract a putative umbrella species, the White-backed Woodpecker, benefited saproxylic beetles. Ecosphere, 6(12), 1-14(278). https://doi.org/10.1890/ES14-00551.1

Bense, U. (2002). Verzeichnis und Rote Liste der Totholzkäfer Baden-Württembergs. Landesanstalt für Umweltschutz Baden-Württemberg (LfU), 1–77.

Blicharska, M., Baxter, P. W. J., & Mikusiñski, G. (2014). Practical implementation of species' recovery plans—Lessons from the White-backed Woodpecker Action Plan in Sweden. Ornis Fennica, 91, 108–128.

Bouget, C., Nusillard, B., Pineau, X., & Ricou, C. (2012). Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags: Oak snags and saproxylic beetle conservation. Insect Conservation and Diversity, 5(4), 264–278. https://doi.org/10.1111/j.1752-4598.2011.00160.x

Brunet, J., & Isacsson, G. (2009). Influence of snag characteristics on saproxylic beetle assemblages in a south Swedish beech forest. Journal of Insect Conservation, 13(5), 515–528. https://doi.org/10.1007/s10841-008-9200-3

Bühler, U. (2009). Totholz – existenziell für den Weissrückenspecht in Nordbünden | Dead wood – a vital necessity for the White-backed Woodpecker in the Grisons. Schweizerische Zeitschrift für Forstwesen, 160(7), 210–217. https://doi.org/10.3188/szf.2009.0210

Carlson, A. (2000). The effect of habitat loss on a deciduous forest specialist species: The White-backed Woodpecker (Dendrocopos leucotos). Forest Ecology and Management, 131(1–3), 215–221. https://doi.org/10.1016/S0378-1127(99)00215-7

Carpaneto, G. M., Mazziotta, A., Coletti, G., Luiselli, L., & Audisio, P. (2010). Conflict between insect conservation and public safety: The case study of a saproxylic beetle (Osmoderma eremita) in urban parks. Journal of Insect Conservation, 14(5), 555–565. https://doi.org/10.1007/s10841-010-9283-5

Czeszczewik, D. (2009). Foraging behaviour of White-backed Woodpeckers Dendrocopos leucotos in a primeval forest (Białowieża National Park, NE Poland): Dependence on habitat resources and season. Acta Ornithologica, 44(2), 109–118. https://doi.org/10.3161/000164509X482687

Czeszczewik, D., Walankiewicz, W., Mitrus, C., Tumiel, T., Stański, T., Sahel, M., & Bednarczyk, G. (2013). Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. Bird Conservation International, 23(4), 414–425. https://doi.org/10.1017/S0959270912000354

Doerfler, I., Müller, J., Gossner, M. M., Hofner, B., & Weisser, W. W. (2017). Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. Forest Ecology and Management, 400, 607–620. https://doi.org/10.1016/j.foreco.2017.06.013

Eckelt, A., Müller, J., Bense, U., Brustel, H., Bußler, H., Chittaro, Y., Cizek, L., Frei, A., Holzer, E., Kadej, M., Kahlen, M., Köhler, F., Möller, G., Mühle, H., Sanchez, A., Schaffrath, U., Schmidl, J., Smolis, A., Szallies, A., … Seibold, S. (2018). "Primeval forest relict beetles" of Central Europe: A set of 168 umbrella species for the protection of primeval forest remnants. Journal of Insect Conservation, 22(1), 15–28. https://doi.org/10.1007/s10841-017-0028-6

Ettwein, A., Korner, P., Lanz, M., Lachat, T., Kokko, H., & Pasinelli, G. (2020). Habitat selection of an old-growth forest specialist in managed forests. Animal Conservation, 23(5), 547–560. https://doi.org/10.1111/acv.12567

FOREST EUROPE. (2020). State of Europe's Forests 2020.

Frei, E. R., Gossner, M. M., Vitasse, Y., Queloz, V., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Uitentuis, I., von Arx, G., & Wohlgemuth, T. (2022). European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. Plant Biology, 24(7), 1132–1145. https://doi.org/10.1111/plb.13467

Garmendia, A., Cárcamo, S., & Schwendtner, O. (2006). Forest management considerations for conservation of Black Woodpecker Dryocopus martius and White-backed Woodpecker Dendrocopos leucotos populations in Quinto Real (Spanish Western Pyrenees). Biodiversity and Conservation, 15(4), 1399–1415. https://doi.org/10.1007/s10531-005-5410-0

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W., & Müller, J. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. Conservation Biology, 27(3), 605–614. https://doi.org/10.1111/cobi.12023

Hagge, J., Müller, J., Birkemoe, T., Buse, J., Christensen, R. H. B., Gossner, M. M., Gruppe, A., Heibl, C., Jarzabek-Müller, A., Seibold, S., Siitonen, J., Soutinho, J. G., Sverdrup-Thygeson, A., Thorn, S., & Drag, L. (2021). What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. Journal of Animal Ecology, 90(8), 1934–1947. https://doi.org/10.1111/1365-2656.13512

Hämäläinen, K., Junninen, K., Halme, P., & Kouki, J. (2020). Managing conservation values of protected sites: How to maintain deciduous trees in White-backed Woodpecker territories. Forest Ecology and Management, 461, 117946. https://doi.org/10.1016/j.foreco.2020.117946

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018). Biodiversity along temperate forest succession. Journal of Applied Ecology, 55(6), 2756–2766. https://doi.org/10.1111/1365-2664.13238

Hülsmann, L., Bugmann, H. K. M., Commarmot, B., Meyer, P., Zimmermann, S., & Brang, P. (2016). Does one model fit all? Patterns of beech mortality in natural forests of three European regions. Ecological Applications, 26(8), 2465–2479. https://doi.org/10.1002/eap.1388

Imesch, N., Stadler, B., Bolliger, M., & Schneider, O. (2015). Biodiversité en forêt: Objectifs et mesures. Aide à l'exécution pour la conservation de la diversité biologique dans la forêt suisse (L'environnement pratique, Vol. 1–1503). Office fédéral de l'environnement OFEV.

Jacobsen, R. M., Kauserud, H., Sverdrup-Thygeson, A., Bjorbækmo, M. M., & Birkemoe, T. (2017). Wood-inhabiting insects can function as targeted vectors for decomposer fungi. Fungal Ecology, 29, 76–84. https://doi.org/10.1016/j.funeco.2017.06.006

Jonsell, M., Nittérus, K., & Stighäll, K. (2004). Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation, 118(2), 163–173. https://doi.org/10.1016/j.biocon.2003.08.017

Jonsell, M., & Weslien, J. (2003). Felled or standing retained wood—It makes a difference for saproxylic beetles. Forest Ecology and Management, 175, 425–435. https://doi.org/10.1016/S0378-1127(02)00143-3

Klesse, S., Wohlgemuth, T., Meusburger, K., Vitasse, Y., von Arx, G., Lévesque, M., Neycken, A., Braun, S., Dubach, V., Gessler, A., Ginzler, C., Gossner, M. M., Hagedorn, F., Queloz, V., Samblás Vives, E., Rigling, A., & Frei, E. R. (2022). Long-term soil water limitation and previous tree vigor drive local variability of drought-induced crown dieback in Fagus sylvatica. Science of The Total Environment, 851, 157926. https://doi.org/10.1016/j.scitotenv.2022.157926

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A. K., Regnery, B., & Vandekerkhove, K. (2018). Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecological Indicators, 84, 194–207. https://doi.org/10.1016/j.ecolind.2017.08.051

Macarthur, R. H., & Wilson, E. O. (1967). The Theory of Island Biogeography. Princeton University Press.

Martikainen, P., Kaila, L., & Haila, Y. (1998). Threatened Beetles in White-backed Woodpecker Habitats. Conservation Biology, 12(2), 293–301. https://doi.org/10.1111/j.1523-1739.1998.96484.x

Melletti, M., & Penteriani, V. (2003). Nesting and feeding tree selection in the endangered White-backed Woodpecker, Dendrocopos leucotos lilfordi. The Wilson Bulletin, 115(3), 299–306. https://doi.org/10.1676/03-022

Mild, K., & Stighäll, K. (2017). Action Plan for the Conservation of the Swedish Population of White-backed Woodpecker (Dendrocopos leucotos) (No. 5486). Swedish Environmental Protection Agency.

Müller, J., Bußler, H., Goßner, M., Rettelbach, T., & Duelli, P. (2008). The European spruce bark beetle Ips typographus in a national park: From pest to keystone species. Biodiversity and Conservation, 17(12), 2979–3001. https://doi.org/10.1007/s10531-008-9409-1

Müller, J., Mitesser, O., Cadotte, M. W., van der Plas, F., Mori, A. S., Ammer, C., Chao, A., Scherer-Lorenzen, M., Baldrian, P., Bässler, C., Biedermann, P., Cesarz, S., Claßen, A., Delory, B. M., Feldhaar, H., Fichtner, A., Hothorn, T., Kuenzer, C., Peters, M. K., … Eisenhauer, N. (2022). Enhancing the structural diversity between forest patches — A concept and real-world experiment to study biodiversity, multifunctionality and forest resilience across spatial scales. Global Change Biology, gcb.16564. https://doi.org/10.1111/gcb.16564

Olav Hogstad & Ingvar Stenberg. (1997). Breeding Success, Nestling Diet and Parental Care in the White-backed Woodpecker Dendrocopos leucotos. Journal Für Ornithologie, 138, 25–38.

Onodera, K., Tokuda, S., Hirano, Y., & Yamamoto, S. (2017). Vertical distribution of saproxylic beetles within snag trunks retained in plantation forests. Journal of Insect Conservation, 21(1), 7–14. https://doi.org/10.1007/s10841-016-9947-x

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., … Virtanen, R. (2010). Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. Conservation Biology, 24(1), 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x

Ratnam, W., Rajora, O. P., Finkeldey, R., Aravanopoulos, F., Bouvet, J.-M., Vaillancourt, R. E., Kanashiro, M., Fady, B., Tomita, M., & Vinson, C. (2014). Genetic effects of forest management practices: Global synthesis and perspectives. Forest Ecology and Management, 333, 52–65. https://doi.org/10.1016/j.foreco.2014.06.008

Roberge, J.-M., & Angelstam, P. (2004). Usefulness of the Umbrella Species Concept as a Conservation Tool. Conservation Biology, 18(1), 76–85. https://doi.org/10.1111/j.1523-1739.2004.00450.x

Roberge, J.-M., Mikusiński, G., & Svensson, S. (2008). The White-backed Woodpecker: Umbrella species for forest conservation planning? Biodiversity and Conservation, 17(10), 2479–2494. https://doi.org/10.1007/s10531-008-9394-4

Rohner, B., Kumar, S., Liechti, K., Gessler, A., & Ferretti, M. (2021). Tree vitality indicators revealed a rapid response of beech forests to the 2018 drought. Ecological Indicators, 120, 106903. https://doi.org/10.1016/j.ecolind.2020.106903

Speight, M. C. D. (1989). Saproxylic invertebrates and their conservation (Nature and environment). Strasbourg, France: Council of Europe.

Thorn, S., Bässler, C., Bußler, H., Lindenmayer, D. B., Schmidt, S., Seibold, S., Wende, B., & Müller, J. (2016). Bark-scratching of storm-felled trees preserves biodiversity at lower economic costs compared to debarking. Forest Ecology and Management, 364, 10–16. https://doi.org/10.1016/j.foreco.2015.12.044

Urkijo-Letona, A., Cárcamo, S., Peña, L., de Manuel, B. F., Onaindia, M., & Ametzaga-Arregi, I. (2020). Key elements of the White-backed Woodpecker's (Dendrocopos leucotos lilfordi) habitat in its European south-western limits. Forests, 11(8), 1–15. https://doi.org/10.3390/f11080831

Verkerk, P. J., Delacote, P., Hurmekoski, E., Kunttu, J., Matthews, R., Mäkipää, R., Mosley, F., Perugini, L., Reyer, C. P. O., Roe, S., Trømborg, E., European Forest Institute, & Colling, R. (2022). Forest-based climate change mitigation and adaptation in Europe. From Science to Policy. European Forest Institute. https://doi.org/10.36333/fs14

Virkkala, R., Alanko, T., Laine, T., & Tiainen, J. (1993). Population contraction of the White-backed Woodpecker Dendrocopos leucotos in Finland as a consequence of habitat alteration. Biological Conservation, 66, 47–53.

Wesołowski, T. (1995). Value of Białowieża Forest for the conservation of White-backed Woodpecker Dendrocopos leucotos in Poland. Biological Conservation, 71(1), 69–75. https://doi.org/10.1016/0006-3207(94)00022-I

Whitehouse, N. J. (2006). The Holocene British and Irish ancient forest fossil beetle fauna: Implications for forest history, biodiversity and faunal colonisation. Quaternary Science Reviews, 25(15–16), 1755–1789. https://doi.org/10.1016/j.quascirev.2006.01.010

Web resource

Finnish Environment Institute (published: 15.06.2015; accessed: 17.02.2023). The endangered White-backed Woodpecker can thrive in commercial forests. syke.fi. https://www.syke.fi/en-US/The_endangered_whitebacked_woodpecker_ca(31619)

Species list

Species list of all trapped beetles. Values are the summed abundance as a function of the sampling method. Saproxylic: O = Obligatory; F = Facultative (Bense, U. (2002). Verzeichnis und Rote Liste der Totholzkäfer Baden-Württembergs. Landesanstalt für Umweltschutz Baden-Württemberg (LfU), 1–77).

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Aderidae	*Anidorus nigrinus*	O	6				
Aderidae	*Anthicus oculatus*		4				
Aderidae	*Euglenes pygmaeus*	O	6				
Anthribidae	*Anthribus fasciatus*		1				
Anthribidae	*Anthribus nebulosus*	O	15				
Anthribidae	*Choragus sheppardi*	O		1			
Anthribidae	*Dissoleucas niveirostris*	O	4	1		1	
Anthribidae	*Platyrhinus resinosus*	O	8		1	2	1
Anthribidae	*Platystomos albinus*	O	9	6	2	2	3
Anthribidae	*Tropideres albirostris*	O	1				
Anthribidae	*Tropideres niveirostris*		17				
Apionidae	*Eutrichapion punctiger*			1			
Biphyllidae	*Biphyllus lunatus*	O	1				
Biphyllidae	*Diplocoelus fagi*	O	16	22		1	1
Buprestidae	*Agrilus angustulus*	O					1
Buprestidae	*Agrilus olivicolor*	O					1
Buprestidae	*Anthaxia helvetica*	O	2				
Buprestidae	*Anthaxia quadripunctata*	O	1				
Byrrhidae	*Cytilus sericeus*		1				
Byturidae	*Byturus ochraceus*		2				
Byturidae	*Byturus tomentosus*		15				
Cantharidae	*Ancistronycha abdominalis*		1				
Cantharidae	*Ancistronycha erichsonii*		4				
Cantharidae	*Cantharis decipiens*		1				
Cantharidae	*Cantharis fusca*		2				
Cantharidae	*Cantharis nigricans*		6				
Cantharidae	*Cantharis obscura*		3				
Cantharidae	*Cantharis pallida*		2				
Cantharidae	*Cantharis pellucida*		8				
Cantharidae	*Cantharis rufa*		2				
Cantharidae	*Cantharis rustica*		1				
Cantharidae	*Malthinus balteatus*	O	21				
Cantharidae	*Malthinus flaveolus*	O	18				
Cantharidae	*Malthinus frontalis*	O	2				
Cantharidae	*Malthodes crassicornis*	O		1			
Cantharidae	*Malthodes fuscus*	O		4			
Cantharidae	*Malthodes maurus*	O	1				
Cantharidae	*Malthodes mysticus*	O	2				
Cantharidae	*Malthodes spathifer*	O	11				
Cantharidae	*Metacantharis clypeata*		1				
Cantharidae	*Podabrus alpinus*		5				
Cantharidae	*Podistra prolixa*		1				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Cantharidae	*Podistra rufotestacea*		20				
Cantharidae	*Podistra schoenherri*		5				
Cantharidae	*Rhagonycha atra*		6				
Cantharidae	*Rhagonycha fulva*		10				
Cantharidae	*Rhagonycha lignosa*		17		1		
Cantharidae	*Rhagonycha lutea*		2				
Cantharidae	*Rhagonycha translucida*		24	1			
Carabidae	*Diachromus germanus*		1				
Carabidae	*Dromius fenestratus*	F	2				
Carabidae	*Dromius quadrimaculatus*	F	1			1	
Carabidae	*Pterostichus aethiops*			1			
Carabidae	*Sinechostictus doderoi*		1				
Carabidae	*Trichotichnus nitens*		12				
Cerambycidae	*Alosterna tabacicolor*	O	62				
Cerambycidae	*Anaglyptus mysticus*	O	5	2			
Cerambycidae	*Anastrangalia dubia*	O	8				
Cerambycidae	*Anisarthron barbipes*	O	2				
Cerambycidae	*Anoplodera sexguttata*	O	3				
Cerambycidae	*Arhopalus rusticus*	O	2				
Cerambycidae	*Axinopalpis gracilis*	O	3				
Cerambycidae	*Clytus arietis*	O	47				3
Cerambycidae	*Clytus lama*	O	2				
Cerambycidae	*Clytus rhamni*	O					1
Cerambycidae	*Cortodera holosericea*		3				
Cerambycidae	*Dinoptera collaris*	O	7				
Cerambycidae	*Evodinus clathratus*	O	1				
Cerambycidae	*Gaurotes virginea*	O	3				
Cerambycidae	*Grammoptera ruficornis*	O	4				
Cerambycidae	*Leiopus femoratus*	O	2				
Cerambycidae	*Leiopus linnei*	O	15				
Cerambycidae	*Leiopus nebulosus*	O	16	62	185	1153	569
Cerambycidae	*Mesosa nebulosa*	O	5	1			
Cerambycidae	*Molorchus minor*	O	27				
Cerambycidae	*Molorchus umbellatarum*	O	2				
Cerambycidae	*Oberea pupillata*	O	2				
Cerambycidae	*Obrium brunneum*	O	51				
Cerambycidae	*Oxymirus cursor*	O	8				
Cerambycidae	*Pachytodes cerambyciformis*	O	12				
Cerambycidae	*Phymatodes testaceus*	O	17	1		45	3
Cerambycidae	*Phytoecia cylindrica*		1				
Cerambycidae	*Pidonia lurida*	O	3				
Cerambycidae	*Poecilium pusillum*	O					3
Cerambycidae	*Pogonocherus hispidulus*	O	2		3	25	
Cerambycidae	*Pogonocherus hispidus*	O	2				
Cerambycidae	*Rhagium bifasciatum*	O	7	1			
Cerambycidae	*Rhagium inquisitor*	O	1			2	
Cerambycidae	*Rhagium mordax*	O	12	6			
Cerambycidae	*Rutpela maculata*	O	16	8			
Cerambycidae	*Spondylis buprestoides*	O	1				
Cerambycidae	*Stenostola dubia*	O	2				
Cerambycidae	*Stenurella melanura*	O	19				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Cerambycidae	*Stictoleptura rubra*	O	46				
Cerambycidae	*Stictoleptura scutellata*	O		1			
Cerambycidae	*Tetropium castaneum*	O	9				
Cerambycidae	*Tetropium fuscum*	O	6				
Cerylonidae	*Cerylon fagi*	O	17				
Cerylonidae	*Cerylon ferrugineum*	O	37	9			
Cerylonidae	*Cerylon histeroides*	O	43				
Cerylonidae	*Cerylon impressum*	O	2				
Chrysomelidae	*Batophila rubi*			1			
Chrysomelidae	*Calomicrus pinicola*		10				
Chrysomelidae	*Cassida denticollis*		1				
Chrysomelidae	*Chrysolina fastuosa*		1				
Chrysomelidae	*Chrysomela cuprea*		1				
Chrysomelidae	*Gonioctena quinquepunctata*		4				
Chrysomelidae	*Lilioceris merdigera*		1				
Chrysomelidae	*Mniophila muscorum*		1	3			
Chrysomelidae	*Oulema obscura*						1
Chrysomelidae	*Plagiosterna aenea*		2				
Ciidae	*Cis bidentatus*	O	23				
Ciidae	*Cis boleti*	O	112	3			
Ciidae	*Cis castaneus*	O	30		1		
Ciidae	*Cis dentatus*	O	47	2			
Ciidae	*Cis fagi*	O	163	33			
Ciidae	*Cis festivus*	O		1			
Ciidae	*Cis glabratus*	O	70				
Ciidae	*Cis jacquemartii*	O	34				
Ciidae	*Cis lineatocribratus*	O	9				
Ciidae	*Cis micans*	O	35				
Ciidae	*Cis quadridens*	O	23				
Ciidae	*Cis rugulosus*	O	105				
Ciidae	*Cis striatulus*	O	14				
Ciidae	*Ennearthron cornutum*	O	17	14			
Ciidae	*Octotemnus glabriculus*	O	341				
Ciidae	*Octotemnus mandibularis*	O	24				
Ciidae	*Orthocis alni*	O	17	1	1	10	7
Ciidae	*Orthocis pseudolinearis*	O	10				
Ciidae	*Ropalodontus perforatus*	O	19				
Ciidae	*Sulcacis bidentulus*	O	1				
Ciidae	*Sulcacis fronticornis*	O	4				
Ciidae	*Sulcacis nitidus*	O	13				
Ciidae	*Wagaicis wagae*	O	3				
Clambidae	*Calyptomerus alpestris*	O	11				
Clambidae	*Clambus armadillo*				1		
Clambidae	*Clambus minutus*		4				
Clambidae	*Clambus pubescens*		2				
Clambidae	*Clambus punctulum*						1
Clambidae	*Clambus simsoni*				1		
Cleridae	*Korynetes caeruleus*	O		1			
Cleridae	*Opilo mollis*	O	1				
Cleridae	*Thanasimus formicarius*	O	36	4		1	
Cleridae	*Tillus elongatus*	O	31	398			

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Coccinellidae	*Anatis ocellata*		1				
Coccinellidae	*Aphidecta obliterata*		4				10
Coccinellidae	*Bulaea lichatschovii*		1				
Coccinellidae	*Calvia decemguttata*		6				
Coccinellidae	*Chilocorus bipustulatus*		3				
Coccinellidae	*Chilocorus renipustulatus*		6				
Coccinellidae	*Coccinella septempunctata*		1				
Coccinellidae	*Exochomus quadripustulatus*		1				
Coccinellidae	*Halyzia sedecimguttata*		14	1			
Coccinellidae	*Nephus quadrimaculatus*		1				
Coccinellidae	*Scymnus abietis*		1				
Coccinellidae	*Scymnus impexus*		3				
Coccinellidae	*Scymnus schmidti*		2				
Corylophidae	*Arthrolips humilis*					1	
Corylophidae	*Arthrolips obscura*	O			32	36	39
Corylophidae	*Arthrolips picea*		1				
Corylophidae	*Corylophus cassidoides*				2	2	2
Corylophidae	*Orthoperus atomus*	O	6	81	73	37	61
Corylophidae	*Orthoperus brunnipes*	O	4		40	66	56
Corylophidae	*Sericoderus lateralis*		7		179	296	127
Cryptophagidae	*Antherophagus pallens*		9				
Cryptophagidae	*Antherophagus silaceus*		2				
Cryptophagidae	*Antherophagus similis*		4				
Cryptophagidae	*Atomaria analis*		3		8	11	4
Cryptophagidae	*Atomaria apicalis*				5	3	8
Cryptophagidae	*Atomaria diluta*	O	27				
Cryptophagidae	*Atomaria fimetarius*		1		2	1	2
Cryptophagidae	*Atomaria impressa*		5			1	
Cryptophagidae	*Atomaria longicornis*	O			1		
Cryptophagidae	*Atomaria nigripennis*					1	
Cryptophagidae	*Atomaria ornata*	O	4				
Cryptophagidae	*Atomaria pulchra*	O		3			
Cryptophagidae	*Atomaria pusilla*				6	2	8
Cryptophagidae	*Atomaria turgida*	O	860		1		
Cryptophagidae	*Atomaria umbrina*	O			10	11	25
Cryptophagidae	*Caenoscelis ferruginea*	O	3				
Cryptophagidae	*Caenoscelis sibirica*	O	3	1			
Cryptophagidae	*Cryptophagus badius*	O			4	4	
Cryptophagidae	*Cryptophagus cellaris*				2	3	11
Cryptophagidae	*Cryptophagus confusus*	O	8				
Cryptophagidae	*Cryptophagus corticinus*	O	1				
Cryptophagidae	*Cryptophagus cylindrellus*	O	2				
Cryptophagidae	*Cryptophagus dentatus*	F	2	51		6	21
Cryptophagidae	*Cryptophagus denticulatus*		3				
Cryptophagidae	*Cryptophagus distinguendus*		3				
Cryptophagidae	*Cryptophagus dorsalis*	O	1		2		
Cryptophagidae	*Cryptophagus fuscicornis*	O	3				
Cryptophagidae	*Cryptophagus labilis*	O	1				
Cryptophagidae	*Cryptophagus laticollis*		1		1		
Cryptophagidae	*Cryptophagus obsoletus*		2				
Cryptophagidae	*Cryptophagus pallidus*				126	70	85

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Cryptophagidae	*Cryptophagus parallelus*	O	2				
Cryptophagidae	*Cryptophagus populi*		1				
Cryptophagidae	*Cryptophagus puncticollis*		1				
Cryptophagidae	*Cryptophagus punctipennis*				742	686	454
Cryptophagidae	*Cryptophagus quercinus*	O	1				
Cryptophagidae	*Cryptophagus ruficornis*	O	2		10		1
Cryptophagidae	*Cryptophagus saginatus*		2				
Cryptophagidae	*Cryptophagus scanicus*		5	4	1	1	
Cryptophagidae	*Cryptophagus schmidtii*		1				
Cryptophagidae	*Cryptophagus setulosus*		2				
Cryptophagidae	*Cryptophagus subdepressus*	O	2				4
Cryptophagidae	*Cryptophagus subfumatus*		1		4		
Cryptophagidae	*Henoticus serratus*	O	4				
Cryptophagidae	*Hypocoprus lathridioides*		1				
Cryptophagidae	*Micrambe abietis*	O	4				
Cryptophagidae	*Micrambe bimaculata*	O	1				
Cryptophagidae	*Micrambe pilosula*		1				
Cryptophagidae	*Micrambe ulicis*		1				
Cryptophagidae	*Pteryngium crenatum*	O	57	3			
Cryptophagidae	*Sternodea baudii*		8				
Cucujidae	*Pediacus dermestoides*	O	85	1		1	
Curculionidae	*Acalles echinatus*	O	1		3		
Curculionidae	*Acalles fallax*	O			1		
Curculionidae	*Acalyptus carpini*		26				
Curculionidae	*Anisandrus dispar*	O	3678		183	218	34
Curculionidae	*Anthonomus rubi*		4				
Curculionidae	*Bradybatus fallax*					2	
Curculionidae	*Cryphalus intermedius*	O	27				
Curculionidae	*Cryphalus piceae*	O	259				
Curculionidae	*Cryptorhynchus lapathi*	O				3	16
Curculionidae	*Crypturgus cinereus*	O	125				
Curculionidae	*Crypturgus pusillus*	O	294				
Curculionidae	*Dendroctonus micans*	O	1				
Curculionidae	*Dryocoetes autographus*	O	391	1	4	3	
Curculionidae	*Dryocoetes hectographus*	O	4				
Curculionidae	*Dryocoetes villosus*	O	8				
Curculionidae	*Echinodera hypocrita*	O		20			
Curculionidae	*Ernoporicus fagi*	O	1208	266	1689	9024	10650
Curculionidae	*Hylastes ater*	O	512				
Curculionidae	*Hylastes cunicularius*	O	5				
Curculionidae	*Hylastinus obscurus*	F	2				
Curculionidae	*Hylesinus crenatus*	O	146				
Curculionidae	*Hylesinus fraxini*		6				
Curculionidae	*Hylesinus toranio*	O	140				
Curculionidae	*Hylesinus varius*	O	10				
Curculionidae	*Hylurgops glabratus*	O	2				
Curculionidae	*Hylurgops palliatus*	O	10				
Curculionidae	*Ips duplicatus*	O	1				
Curculionidae	*Ips sexdentatus*	O	1				
Curculionidae	*Ips typographus*	O	19				
Curculionidae	*Kyklioacalles roboris*	O			12	1	

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Curculionidae	*Liparus germanus*				1		
Curculionidae	*Lymantor coryli*	O	6				
Curculionidae	*Magdalis armigera*	O					1
Curculionidae	*Orchestes fagi*		13		2	9	43
Curculionidae	*Otiorhynchus lepidopterus*			1			
Curculionidae	*Otiorhynchus singularis*			2			
Curculionidae	*Otiorhynchus tenebricosus*						1
Curculionidae	*Phloeophagus lignarius*	O			1		
Curculionidae	*Phloeotribus spinulosus*	O	13				
Curculionidae	*Phyllobius argentatus*			1			
Curculionidae	*Pityogenes bidentatus*	O	13				
Curculionidae	*Pityogenes chalcographus*	O	36				
Curculionidae	*Pityogenes quadridens*	O	8				
Curculionidae	*Pityokteines curvidens*	O	2				
Curculionidae	*Pityophthorus micrographus*	O	2				
Curculionidae	*Pityophthorus pityographus*	O	206				
Curculionidae	*Plinthus tischeri*					1	
Curculionidae	*Polydrusus aeratus*			3			
Curculionidae	*Polydrusus formosus*		1				
Curculionidae	*Polygraphus poligraphus*	O	93				
Curculionidae	*Pteleobius vittatus*	O	12				
Curculionidae	*Rhyncolus ater*	O	2	1			1
Curculionidae	*Rhyncolus punctatulus*	O	35				
Curculionidae	*Scolytus intricatus*	O	26				
Curculionidae	*Scolytus laevis*	O	198				
Curculionidae	*Scolytus mali*	O	1				
Curculionidae	*Scolytus rugulosus*	O	3				
Curculionidae	*Sitona hispidulus*				1		
Curculionidae	*Stereocorynes truncorum*	O		1			
Curculionidae	*Taphrorychus bicolor*	O	286	423	5821	12873	19820
Curculionidae	*Taphrorychus villifrons*	O			240	97	370
Curculionidae	*Trachodes hispidus*	O		1	11	1	
Curculionidae	*Tropiphorus elevatus*			1			
Curculionidae	*Trypodendron domesticum*	O	40	1609	13		
Curculionidae	*Trypodendron lineatum*	O	27		1	2	1
Curculionidae	*Trypodendron signatum*	O	10				
Curculionidae	*Trypophloeus alni*		3				
Curculionidae	*Xyleborinus saxesenii*	O	348	254	9	13	22
Curculionidae	*Xylechinus pilosus*	O	18				
Curculionidae	*Xylocleptes bispinus*	O	4				
Curculionidae	*Xylosandrus germanus*	O		115	9		2
Dascillidae	*Dascillus cervinus*		13				
Dasytidae	*Aplocnemus nigricornis*	O	4				
Dasytidae	*Aplocnemus tarsalis*	O	1				
Dasytidae	*Danacea nigritarsis*		1				
Dasytidae	*Danacea pallipes*		1				
Dasytidae	*Dasytes caeruleus*	O	2		1	5	14
Dasytidae	*Dasytes niger*	O					1
Dasytidae	*Dasytes obscurus*	O			2	1	6
Dasytidae	*Dasytes plumbeus*	O	94	4		9	7
Dasytidae	*Dasytes subaeneus*	O	1				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Dasytidae	*Trichoceble memnonia*	O	2				
Dermestidae	*Anthrenus fuscus*		2	1			
Dermestidae	*Anthrenus museorum*		3				
Dermestidae	*Attagenus schaefferi*	O	2				
Dermestidae	*Attagenus smirnovi*			1			
Dermestidae	*Dermestes ater*		9				
Dermestidae	*Dermestes erichsoni*		1				
Dermestidae	*Dermestes frischii*		1				
Dermestidae	*Dermestes intermedius*		1				
Dermestidae	*Dermestes lardarius*		6				
Dermestidae	*Dermestes maculatus*		6				
Dermestidae	*Dermestes murinus*		361				
Dermestidae	*Dermestes undulatus*	F	284				
Dermestidae	*Globicornis emarginata*	O	2				
Dermestidae	*Globicornis nigripes*	O	1				
Dermestidae	*Megatoma undata*	O	3	2			
Drilidae	*Drilus concolor*		48				
Dryopidae	*Dryops rufipes*		1				
Dytiscidae	*Agabus bipustulatus*		1				
Elateridae	*Adrastus axillaris*		9				
Elateridae	*Adrastus limbatus*		1				
Elateridae	*Agriotes pilosellus*		102				
Elateridae	*Agrypnus murinus*		1				
Elateridae	*Ampedus balteatus*	O	4				
Elateridae	*Ampedus cinnabarinus*	O	7				
Elateridae	*Ampedus elongatulus*	O	21				
Elateridae	*Ampedus erythrogonus*	O	50	1			
Elateridae	*Ampedus nigerrimus*	O	63				
Elateridae	*Ampedus nigrinus*	O	4				1
Elateridae	*Ampedus nigrita*		1				
Elateridae	*Ampedus nigroflavus*	O	1				
Elateridae	*Ampedus pomonae*	O	71				
Elateridae	*Ampedus pomorum*	O	15	4			
Elateridae	*Ampedus quercicola*	O	1				
Elateridae	*Ampedus rufipennis*	O	4				
Elateridae	*Ampedus sanguineus*	O	6	1			
Elateridae	*Ampedus scrofa*	O	5				
Elateridae	*Ampedus triangulum*	O	1				
Elateridae	*Anostirus castaneus*	O	5				
Elateridae	*Anostirus purpureus*	O	8				
Elateridae	*Athous bicolor*		17				
Elateridae	*Athous campyloides*		1				
Elateridae	*Athous emaciatus*		6				
Elateridae	*Athous flavipennis*		3				
Elateridae	*Athous haemorrhoidalis*		1704				
Elateridae	*Athous subfuscus*		984				
Elateridae	*Athous vittatus*		705	1			
Elateridae	*Athous zebei*		105				
Elateridae	*Calambus bipustulatus*	O	3				
Elateridae	*Cardiophorus nigerrimus*		2				
Elateridae	*Cidnopus aeruginosus*		7				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Elateridae	*Ctenicera virens*		2				
Elateridae	*Dalopius marginatus*		337				
Elateridae	*Denticollis linearis*	O	225	3	1		
Elateridae	*Denticollis rubens*	O	27	3			
Elateridae	*Hemicrepidius hirtus*	F	21				
Elateridae	*Hemicrepidius niger*		7				
Elateridae	*Hypoganus inunctus*	O	31	1			
Elateridae	*Idolus picipennis*		2				
Elateridae	*Ischnodes sanguinicollis*	O	12				
Elateridae	*Limonius minutus*		1				
Elateridae	*Melanotus castanipes*	O	16				
Elateridae	*Melanotus crassicollis*	O	22				
Elateridae	*Melanotus villosus*	O	378	4			
Elateridae	*Nothodes parvulus*		21				
Elateridae	*Paraphotistus impressus*		180				
Elateridae	*Pheletes quercus*		1				
Elateridae	*Porthmidius austriacus*	F	4				
Elateridae	*Prosternon tessellatum*		2				
Elateridae	*Selatosomus aeneus*		2				
Elateridae	*Selatosomus latus*		16				
Elateridae	*Selatosomus melancholicus*		1				
Elateridae	*Sericus subaeneus*		8				
Elateridae	*Stenagostus rhombeus*	O	4				
Elmidae	*Riolus cupreus*		1				
Endomychidae	*Endomychus coccineus*	O	5	2	11	7	
Endomychidae	*Mycetina cruciata*	O	34				
Endomychidae	*Symbiotes armatus*	O	2				
Endomychidae	*Symbiotes gibberosus*	O	7		25	18	2
Endomychidae	*Symbiotes latus*	O			1		
Erotylidae	*Dacne bipustulata*	O	12				
Erotylidae	*Triplax elongata*	O	2				
Erotylidae	*Triplax lepida*	O	3				
Erotylidae	*Triplax rufipes*	O	1				
Erotylidae	*Triplax russica*	O	49				
Erotylidae	*Tritoma bipustulata*	O	30	4			
Eucnemidae	*Clypeorhagus clypeatus*		10				
Eucnemidae	*Dromaeolus barnabita*	O	10	14			
Eucnemidae	*Eucnemis capucina*	O	22				
Eucnemidae	*Hylis cariniceps*	O	70				
Eucnemidae	*Hylis foveicollis*	O	41				
Eucnemidae	*Hylis olexai*	O	111	1			
Eucnemidae	*Hylis procerulus*	O	87				
Eucnemidae	*Isorhipis melasoides*	O	2	9			
Eucnemidae	*Melasis buprestoides*	O	2	1		1	
Eucnemidae	*Microrhagus emyi*	O	19				
Eucnemidae	*Microrhagus lepidus*	O	47				
Eucnemidae	*Microrhagus pygmaeus*	O	87	2			
Eucnemidae	*Thambus frivaldskyi*		1				
Eucnemidae	*Xylophilus corticalis*	O	63				
Geotrupidae	*Anoplotrupes stercorosus*		63				
Histeridae	*Abraeus granulum*	O	61				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Histeridae	*Atholus duodecimstriatus*		3				
Histeridae	*Gnathoncus buyssoni*		12				
Histeridae	*Gnathoncus rotundatus*		11				
Histeridae	*Hister unicolor*		45				
Histeridae	*Margarinotus merdarius*		46				
Histeridae	*Margarinotus striola*	F	61				
Histeridae	*Paromalus flavicornis*	O	1		1		
Histeridae	*Paromalus parallelepipedus*	O	8				
Histeridae	*Plegaderus dissectus*	O	2				
Histeridae	*Plegaderus saucius*	O	1				
Histeridae	*Saprinus aeneus*		1				
Histeridae	*Teretrius fabricii*	O	1				
Hydraenidae	*Hydraena assimilis*		1				
Hydraenidae	*Hydraena lapidicola*		1				
Hydraenidae	*Hydraena truncata*		1				
Hydrophilidae	*Cercyon bifenestratus*		10				
Hydrophilidae	*Cercyon granarius*		17				
Hydrophilidae	*Cercyon haemorrhoidalis*		21				
Hydrophilidae	*Cercyon impressus*		19				
Hydrophilidae	*Cercyon lateralis*		11				
Hydrophilidae	*Cercyon pygmaeus*		2				
Hydrophilidae	*Cercyon quisquilius*		1				
Hydrophilidae	*Cercyon terminatus*		1				
Hydrophilidae	*Cercyon tristis*		91				
Hydrophilidae	*Cercyon unipunctatus*		9				
Hydrophilidae	*Cryptopleurum minutum*		14				
Hydrophilidae	*Megasternum concinnum*			1			
Hydrophilidae	*Sphaeridium lunatum*		1				
Hydrophilidae	*Sphaeridium scarabaeoides*		2				
Laemophloeidae	*Cryptolestes corticinus*	O				1	
Laemophloeidae	*Cryptolestes duplicatus*	O	4			1	3
Laemophloeidae	*Cryptolestes ferrugineus*		4		1		
Laemophloeidae	*Laemophloeus kraussi*	O	2				
Laemophloeidae	*Laemophloeus monilis*	O	1				
Laemophloeidae	*Leptophloeus alternans*	O	12				
Laemophloeidae	*Notolaemus castaneus*	O				1	
Laemophloeidae	*Placonotus testaceus*	O			2	1	
Laemophloidae	*Placonotus modestus*		1				
Lampyridae	*Lamprohiza splendidula*		5				
Lampyridae	*Lampyris noctiluca*		28				
Latridiidae	*Cartodere nodifer*	F	119		27	23	52
Latridiidae	*Corticaria crenicollis*		2				
Latridiidae	*Corticaria elongata*		5		1		
Latridiidae	*Corticaria impressa*		1		2	1	1
Latridiidae	*Corticaria longicollis*	O	1				
Latridiidae	*Corticaria longicornis*	O		1		1	
Latridiidae	*Corticaria obscura*		2				
Latridiidae	*Corticarina curta*				1		
Latridiidae	*Corticarina minuta*		9	1	1		1
Latridiidae	*Corticarina similata*			1		1	
Latridiidae	*Dienerella clathrata*				12	40	49

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Latridiidae	*Dienerella filum*				1		1
Latridiidae	*Dienerella vincenti*	F		8	23		2
Latridiidae	*Enicmus fungicola*	O	11	1		1	
Latridiidae	*Enicmus histrio*		5		8	44	72
Latridiidae	*Enicmus rugosus*	O	1	6			
Latridiidae	*Enicmus testaceus*	O	26				1
Latridiidae	*Enicmus transversus*		1			1	1
Latridiidae	*Latridius consimilis*	O	158		5	9	9
Latridiidae	*Latridius hirtus*	O	8	9		2	1
Latridiidae	*Latridius minutus*				117	178	151
Latridiidae	*Latridius porcatus*		1				1
Latridiidae	*Stephostethus alternans*	O	1	6	1	3	
Latridiidae	*Stephostethus angusticollis*					1	
Latridiidae	*Thes bergrothi*		178				1
Leiodidae	*Agathidium atrum*		3				
Leiodidae	*Agathidium badium*		9				
Leiodidae	*Agathidium confusum*		25	2			
Leiodidae	*Agathidium discoideum*		5				
Leiodidae	*Agathidium laevigatum*		2	1			
Leiodidae	*Agathidium nigripenne*	O	20				
leiodidae	*Agathidium pilosum*		2				
Leiodidae	*Agathidium seminulum*		25				
Leiodidae	*Agathidium varians*		13				
Leiodidae	*Amphicyllis globiformis*		15				
Leiodidae	*Amphicyllis globus*	F	15	1			
Leiodidae	*Anisotoma axillaris*	O	1				
Leiodidae	*Anisotoma castanea*	O	4				
Leiodidae	*Anisotoma humeralis*	O	20				
Leiodidae	*Anisotoma orbicularis*	O	30				
Leiodidae	*Catops coracinus*		10				
Leiodidae	*Catops longulus*		12				
Leiodidae	*Catops subfuscus*		15				
Leiodidae	*Catops tristis*		15				
Leiodidae	*Choleva cisteloides*		1				
Leiodidae	*Choleva elongata*		1				
Leiodidae	*Choleva glauca*		4				
Leiodidae	*Choleva oblonga*		1				
Leiodidae	*Colenis immunda*		22				
Leiodidae	*Colon brunneum*		3				
Leiodidae	*Colon serripes*		2				
Leiodidae	*Hydnobius multistriatus*		2				
Leiodidae	*Leiodes cinnamomea*		8				
Leiodidae	*Leiodes fracta*		3				
Leiodidae	*Leiodes gyllenhalii*		12				
Leiodidae	*Leiodes hybrida*		1				
Leiodidae	*Leiodes obesa*		3				
Leiodidae	*Leiodes oblonga*		17	1			
Leiodidae	*Leiodes polita*		6				
Leiodidae	*Leiodes triepkei*		1				
Leiodidae	*Liodopria serricornis*	O	21				
Leiodidae	*Nargus velox*		3				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Leiodidae	*Nargus wilkini*		22				
Leiodidae	*Nemadus colonoides*	O	8				
Leiodidae	*Sciodrepoides fumatus*		156				
Leiodidae	*Sciodrepoides watsoni*		830				
Leiodidae	*Triarthron maerkelii*		1				
Lucanidae	*Ceruchus chrysomelinus*	O	7				
Lucanidae	*Platycerus caprea*	O	9				
Lucanidae	*Platycerus caraboides*	O	13	1			
Lucanidae	*Sinodendron cylindricum*	O	72	47			
Lycidae	*Dictyoptera aurora*	O	22				
Lycidae	*Erotides cosnardi*	O	2				
Lycidae	*Platycis minutus*	O	1				
Lycidae	*Pyropterus nigroruber*	O	9				
Lymexylidae	*Elateroides dermestoides*	O	76	13			
Malachiidae	*Ebaeus abietinus*			2			
Malachiidae	*Hypebaeus flavipes*	O		3			
Malachiidae	*Malachius aeneus*		3				
Melandryidae	*Abdera affinis*	O	21				
Melandryidae	*Abdera flexuosa*	O	4	38			
Melandryidae	*Abdera quadrifasciata*	O	1				
Melandryidae	*Anisoxya fuscula*	O	2				
Melandryidae	*Conopalpus testaceus*	O	7	1			
Melandryidae	*Dolotarsus lividus*	O	12				
Melandryidae	*Melandrya barbata*	O	1				
Melandryidae	*Melandrya caraboides*	O	14	8			
Melandryidae	*Melandrya dubia*	O	5				
Melandryidae	*Orchesia blandula*	F	3				
Melandryidae	*Orchesia fasciata*	O	1				
Melandryidae	*Orchesia luteipalpis*	O	2				
Melandryidae	*Orchesia micans*	O	1	11			
Melandryidae	*Orchesia minor*	O	5	2			
Melandryidae	*Orchesia undulata*	O	8	1	1		
Melandryidae	*Osphya bipunctata*	O	2				
Melandryidae	*Phloiotrya rufipes*	O	2				
Melandryidae	*Phloiotrya subtilis*		1				
Melandryidae	*Serropalpus barbatus*	O	18				
Melandryidae	*Xylita laevigata*	O	2				
Monotomidae	*Monotoma longicollis*	F	3	1			
Monotomidae	*Rhizophagus bipustulatus*	O	42	18	7	2	4
Monotomidae	*Rhizophagus cribratus*	O	16				
Monotomidae	*Rhizophagus depressus*	O	5		2		
Monotomidae	*Rhizophagus dispar*	O	17	28	5	3	3
Monotomidae	*Rhizophagus ferrugineus*	O	88				
Monotomidae	*Rhizophagus grandis*	O		1			
Monotomidae	*Rhizophagus nitidulus*	O	62		13	1	
Monotomidae	*Rhizophagus perforatus*	O	67				
Monotomidae	*Rhizophagus picipes*	O			2		
Mordellidae	*Curtimorda maculosa*	O	2				
Mordellidae	*Mordellaria aurofasciata*	O	1				
Mordellidae	*Mordellistena humeralis*	O	71				
Mordellidae	*Mordellistena neuwaldeggiana*	O	7				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Mordellidae	*Mordellochroa abdominalis*	O	156	4			
Mordellidae	*Mordellochroa tournieri*		47				
Mordellidae	*Tomoxia bucephala*	O	38	25			
Mordellidae	*Variimorda villosa*	O				1	
Mycetophagidae	*Litargus balteatus*	F	2				
Mycetophagidae	*Litargus connexus*	O	15	23	238	149	142
Mycetophagidae	*Mycetophagus atomarius*	O	31		115	26	1
Mycetophagidae	*Mycetophagus multipunctatus*	O	4	8			
Mycetophagidae	*Mycetophagus piceus*	O	2				
Mycetophagidae	*Mycetophagus populi*	O	3				
Mycetophagidae	*Mycetophagus quadripustulatus*	O	3				
Mycetophagidae	*Mycetophagus salicis*	O	1				
Mycetophagidae	*Triphyllus bicolor*	O				2	
Nitidulidae	*Amphotis marginata*	O	2				
Nitidulidae	*Carpophilus obsoletus*		1				
Nitidulidae	*Cryptarcha undata*	F	2				
Nitidulidae	*Cychramus luteus*	O	14				
Nitidulidae	*Cychramus variegatus*	O	10				
Nitidulidae	*Epuraea biguttata*	O	23				1
Nitidulidae	*Epuraea binotata*	O	7				
Nitidulidae	*Epuraea distincta*	O					1
Nitidulidae	*Epuraea limbata*	O	2				
Nitidulidae	*Epuraea longula*	O	1				
Nitidulidae	*Epuraea melanocephala*		45				
Nitidulidae	*Epuraea neglecta*	O	30				
Nitidulidae	*Epuraea pallescens*	O	113				
Nitidulidae	*Epuraea silacea*	O	1				
Nitidulidae	*Epuraea unicolor*		8	6			
Nitidulidae	*Glischrochilus quadriguttatus*	O	10				
Nitidulidae	*Ipidia binotata*	O	1				
Nitidulidae	*Omosita colon*		5				
Nitidulidae	*Omosita depressa*		4				
Nitidulidae	*Physoronia wajdelota*		1				
Nitidulidae	*Pityophagus ferrugineus*	O	51				
Nitidulidae	*Soronia grisea*	F	3				
Nitidulidae	*Soronia punctatissima*	F	3				
Nitidulidae	*Stelidota geminata*		15				
Nitidulidae	*Thalycra fervida*		2				
Oedemeridae	*Calopus serraticornis*	O	1				
Oedemeridae	*Ischnomera caerulea*	O	3				
Oedemeridae	*Ischnomera cyanea*	O	2				
Oedemeridae	*Ischnomera sanguinicollis*	O	3				
Oedemeridae	*Nacerdes carniolica*	O	4				
Oedemeridae	*Nacerdes melanura*	O	1				
Oedemeridae	*Oedemera croceicollis*		2				
Oedemeridae	*Oedemera femoralis*	O	1				
Oedemeridae	*Oedemera pthysica*		6				
Oedemeridae	*Oedemera tristis*		8				
Oedemeridae	*Oedemera virescens*		1				
Omalisidae	*Omalisus fontisbellaquaei*		7				
Orsodacnidae	*Orsodacne cerasi*		6				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Prostomidae	*Prostomis mandibularis*	O	2				
Ptiliidae	*Acrotrichis rosskotheni*			9			
Ptiliidae	*Nossidium pilosellum*	O	3		3		
Ptiliidae	*Ptenidium laevigatum*				2		
Ptiliidae	*Ptenidium pusillum*				1	1	
Ptiliidae	*Pteryx suturalis*	O			1		
Ptinidae	*Anobium punctatum*	O	100				
Ptinidae	*Dorcatoma chrysomelina*	O	3				
Ptinidae	*Dorcatoma dresdensis*	O	22				
Ptinidae	*Dorcatoma minor*	O	2				
Ptinidae	*Dorcatoma substriata*	O	1				
Ptinidae	*Episernus granulatus*	O	11				
Ptinidae	*Ernobius mollis*	O	12				
Ptinidae	*Hadrobregmus pertinax*	O	34				
Ptinidae	*Hemicoelus canaliculatus*	O				1	
Ptinidae	*Hemicoelus costatus*	O	448	17			
Ptinidae	*Hemicoelus fulvicornis*	O	15			2	
Ptinidae	*Hemicoelus rufipennis*		3				
Ptinidae	*Hyperisus plumbeum*	O	41	8			
Ptinidae	*Microbregma emarginatum*	O		1			
Ptinidae	*Ochina ptinoides*	O	2				
Ptinidae	*Priobium carpini*	O	1				
Ptinidae	*Ptilinus fuscus*	O	29				
Ptinidae	*Ptilinus pectinicornis*	O	4011	2457		66	6
Ptinidae	*Ptinomorphus imperialis*	O	106	27	2	2	10
Ptinidae	*Ptinus coarcticollis*	O	1				
Ptinidae	*Ptinus fur*	F		11			
Ptinidae	*Ptinus pilosus*					1	
Ptinidae	*Ptinus subpilosus*	O	5	1			
Ptinidae	*Ptinus villiger*		2				
Pyrochroidae	*Pyrochroa coccinea*	O	9				
Pyrochroidae	*Schizotus pectinicornis*	O	7				
Rhynchitidae	*Chonostropheus tristis*		1				
Salpingidae	*Cariderus aeneus*	O	6				
Salpingidae	*Lissodema cursor*	O	3				
Salpingidae	*Rabocerus foveolatus*	O	13			1	
Salpingidae	*Rabocerus gabrieli*	O	1				
Salpingidae	*Salpingus planirostris*	O	163	2	7	19	18
Salpingidae	*Salpingus ruficollis*	O	243	2	55	33	3
Salpingidae	*Sphaeriestes castaneus*	O		1			
Salpingidae	*Vincenzellus ruficollis*	O	103	7	1	2	
Scarabaeidae	*Aphodius corvinus*		108				
Scarabaeidae	*Aphodius depressus*		600				
Scarabaeidae	*Aphodius distinctus*		147				
Scarabaeidae	*Aphodius fimetarius*		16				
Scarabaeidae	*Aphodius foetidus*		3				
Scarabaeidae	*Aphodius rufipes*		27				
Scarabaeidae	*Aphodius rufus*		14				
Scarabaeidae	*Aphodius sticticus*		1				
Scarabaeidae	*Aphodius zenkeri*		20				
Scarabaeidae	*Gnorimus nobilis*	O	2				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Scarabaeidae	*Hoplia argentea*		2				
Scarabaeidae	*Onthophagus coenobita*		33				
Scarabaeidae	*Onthophagus fracticornis*		2				
Scarabaeidae	*Onthophagus ovatus*		109				
Scarabaeidae	*Onthophagus verticicornis*		7				
Scarabaeidae	*Serica brunnea*		10				
Scirtidae	*Contacyphon ochraceus*		1				
Scirtidae	*Contacyphon ruficeps*		5				
Scirtidae	*Microcara testacea*		2				
Scirtidae	*Odeles hausmanni*		4				
Scirtidae	*Prionocyphon serricornis*	O	1				
Scirtidae	*Scirtes haemisphaericus*		1				
Scirtidae	*Scirtes orbicularis*		2				
Scraptiidae	*Anaspis brunnipes*						2
Scraptiidae	*Anaspis costai*	O	15				
Scraptiidae	*Anaspis fasciata*	O	5				
Scraptiidae	*Anaspis flava*	O	32		4	5	10
Scraptiidae	*Anaspis frontalis*	O	142		1		
Scraptiidae	*Anaspis lurida*	O		7			
Scraptiidae	*Anaspis maculata*	O	7				
Scraptiidae	*Anaspis ruficollis*	O	17	57			
Scraptiidae	*Anaspis rufilabris*	O	127				
Scraptiidae	*Anaspis thoracica*	O	87	33	3		2
Scraptiidae	*Cyrtanaspis phalerata*	O	6				
Silphidae	*Nicrophorus humator*		2				
Silphidae	*Nicrophorus vespilloides*		182				
Silphidae	*Oiceoptoma thoracicum*		28				
Silphidae	*Phosphuga atrata*			1			
Silphidae	*Thanatophilus sinuatus*		6				
Silvanidae	*Silvanoprus fagi*	O	9				
Silvanidae	*Silvanus bidentatus*	O			17	4	1
Silvanidae	*Silvanus unidentatus*	O			1		1
Silvanidae	*Uleiota planatus*	O		2		1	1
Sphindidae	*Aspidiphorus orbiculatus*	O	69				
Sphindidae	*Sphindus dubius*	O	1				
Staphylinidae	*Acidota crenata*		1				
Staphylinidae	*Acrotona aterrima*				5	5	1
Staphylinidae	*Acrulia inflata*	O	1				
Staphylinidae	*Agaricochara latissima*	O	26				
Staphylinidae	*Aleochara bipustulata*		3				
Staphylinidae	*Aleochara brevipennis*		226				
Staphylinidae	*Aleochara curtula*		6849				
Staphylinidae	*Aleochara erythroptera*		23				
Staphylinidae	*Aleochara funebris*		4				
Staphylinidae	*Aleochara moerens*		1				
Staphylinidae	*Aleochara ruficornis*			1			
Staphylinidae	*Aleochara spadicea*		15				
Staphylinidae	*Aleochara sparsa*			11			
Staphylinidae	*Aleochara tristis*		1				
Staphylinidae	*Aloconota currax*		8				
Staphylinidae	*Aloconota planifrons*		5				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Staphylinidae	*Amischa analis*		1167				
Staphylinidae	*Amischa nigrofusca*		3				
Staphylinidae	*Anomognathus cuspidatus*	O	67	2			
Staphylinidae	*Anotylus politus*						1
Staphylinidae	*Anotylus rugosus*		93				
Staphylinidae	*Anotylus tetracarinatus*		1				
Staphylinidae	*Anthobium atrocephalum*		39		1		
Staphylinidae	*Anthophagus angusticollis*		1				
Staphylinidae	*Atheta aquatica*		2				
Staphylinidae	*Atheta basicornis*	O	6				
Staphylinidae	*Atheta crassicornis*		418		2		3
Staphylinidae	*Atheta diversa*		4				
Staphylinidae	*Atheta fungi*		71				
Staphylinidae	*Atheta fungicola*		7				
Staphylinidae	*Atheta fungivora*	O			2	4	1
Staphylinidae	*Atheta hygrotopora*		2				
Staphylinidae	*Atheta liliputana*		75				
Staphylinidae	*Atheta macrocera*		1				
Staphylinidae	*Atheta negligens*					1	
Staphylinidae	*Atheta nigritula*		11				
Staphylinidae	*Atheta sodalis*		2				
Staphylinidae	*Atheta vaga*		121	5			
Staphylinidae	*Atheta xanthopus*					2	
Staphylinidae	*Autalia rivularis*		5				
Staphylinidae	*Batrisodes venustus*	O	3			1	
Staphylinidae	*Batrisus formicarius*	O	2				
Staphylinidae	*Bibloporus bicolor*	O	2	2			
Staphylinidae	*Bisnius fimetarius*		745				
Staphylinidae	*Bolitochara bella*	O	16				
Staphylinidae	*Bolitochara obliqua*	O	25				1
Staphylinidae	*Bolitochara pulchra*	O	6				
Staphylinidae	*Brachygluta fossulata*						1
Staphylinidae	*Brachyusa concolor*		2				
Staphylinidae	*Bryaxis collaris*		11				
Staphylinidae	*Bythinus burrellii*		7				
Staphylinidae	*Bythinus macropalpus*		5	1			
Staphylinidae	*Carpelimus bilineatus*		81				
Staphylinidae	*Coprophilus striatulus*		13				
Staphylinidae	*Creophilus maxillosus*		15				
Staphylinidae	*Cypha discoidea*		5			3	4
Staphylinidae	*Cypha laeviuscula*					2	1
Staphylinidae	*Cypha longicornis*		90	1	3	17	12
Staphylinidae	*Cypha punctum*					2	
Staphylinidae	*Cyphea curtula*	O	1				
Staphylinidae	*Deleaster dichrous*		12				
Staphylinidae	*Dinaraea angustula*					3	
Staphylinidae	*Dinothenarus pubescens*		1				
Staphylinidae	*Emus hirtus*		1				
Staphylinidae	*Enalodroma hepatica*		2				
Staphylinidae	*Erichsonius subopacus*		1				
Staphylinidae	*Euconnus pragensis*	O		2			

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Staphylinidae	*Euplectus brunneus*	O		1			
Staphylinidae	*Euplectus monticola*		28				
Staphylinidae	*Eusphalerum luteum*		2				
Staphylinidae	*Eusphalerum macropterum*		2				
Staphylinidae	*Eusphalerum rectangulum*			3			
Staphylinidae	*Eusphalerum semicoleoptratum*			1			
Staphylinidae	*Falagria sulcatula*		2				
Staphylinidae	*Gabrius splendidulus*	O		1			
Staphylinidae	*Gauropterus fulgidus*		2				
Staphylinidae	*Geostiba circellaris*		1				
Staphylinidae	*Gymnusa brevicollis*		3				
Staphylinidae	*Gyrophaena affinis*		27				
Staphylinidae	*Gyrophaena boleti*	O	205				
Staphylinidae	*Gyrophaena gentilis*		328				
Staphylinidae	*Gyrophaena joyi*	O	9				
Staphylinidae	*Gyrophaena manca*	O	317				
Staphylinidae	*Gyrophaena pulchella*		3				
Staphylinidae	*Gyrophaena rugipennis*	O	8				
Staphylinidae	*Gyrophaena strictula*	O	25				
Staphylinidae	*Habrocerus capillaricornis*		19				
Staphylinidae	*Hapalaraea pygmaea*	O	1				
Staphylinidae	*Holobus apicatus*	O			3	8	1
Staphylinidae	*Holobus flavicornis*		2		3	6	5
Staphylinidae	*Homalota plana*	O	3				
Staphylinidae	*Ischnosoma splendidum*		1				
Staphylinidae	*Leptusa fumida*	O		12			
Staphylinidae	*Leptusa hoelzeli*		1				
Staphylinidae	*Leptusa pulchella*	O		4			
Staphylinidae	*Leptusa ruficollis*			3			1
Staphylinidae	*Lesteva monticola*		102				
Staphylinidae	*Liogluta alpestris*		64				
Staphylinidae	*Liogluta longiuscula*				1	4	3
Staphylinidae	*Liogluta microptera*		3				
Staphylinidae	*Lordithon exoletus*		8				
Staphylinidae	*Lordithon lunulatus*		218		1		
Staphylinidae	*Lordithon thoracicus*		8				
Staphylinidae	*Lordithon trinotatus*		2				
Staphylinidae	*Lypoglossa lateralis*		2				
Staphylinidae	*Medon apicalis*		4				
Staphylinidae	*Megarthrus denticollis*		7				
Staphylinidae	*Megarthrus depressus*		6				
Staphylinidae	*Microscydmus nanus*	F	31				1
Staphylinidae	*Mniusa incrassata*		449				
Staphylinidae	*Mocyta fungi*				10	5	3
Staphylinidae	*Nehemitropia lividipennis*		12				
Staphylinidae	*Neuraphes elongatulus*			5			
Staphylinidae	*Nudobius lentus*	O	1				
Staphylinidae	*Ocalea badia*		8				
Staphylinidae	*Ocalea concolor*		6				
Staphylinidae	*Ocypus biharicus*		1				
Staphylinidae	*Ocypus nitens*			1			

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Staphylinidae	*Oligota pumilio*		6				
Staphylinidae	*Oligota pusillima*		5				
Staphylinidae	*Olophrum assimile*		10				
Staphylinidae	*Omalium rivulare*		134				
Staphylinidae	*Ontholestes murinus*		3				
Staphylinidae	*Ontholestes tessellatus*		32				
Staphylinidae	*Othius lapidicola*		17				
Staphylinidae	*Oxypoda haemorrhoa*		1				
Staphylinidae	*Oxypoda mutata*		3				
Staphylinidae	*Oxypoda spectabilis*		1				
Staphylinidae	*Oxypoda vittata*		5		1		1
Staphylinidae	*Oxyporus mannerheimii*		1				
Staphylinidae	*Oxyporus maxillosus*	F	6				
Staphylinidae	*Oxytelus sculptus*		673				
Staphylinidae	*Pella limbata*		58				
Staphylinidae	*Philonthus carbonarius*		3				
Staphylinidae	*Philonthus chalceus*		1				
Staphylinidae	*Philonthus confinis*		4				
Staphylinidae	*Philonthus decorus*		450				
Staphylinidae	*Philonthus ebeninus*		6				
Staphylinidae	*Philonthus intermedius*		5				
Staphylinidae	*Philonthus nitidus*		1				
Staphylinidae	*Philonthus politus*		12				
Staphylinidae	*Philonthus punctus*		7				
Staphylinidae	*Philonthus splendens*		11				
Staphylinidae	*Phloeocharis subtilissima*	O			5	3	1
Staphylinidae	*Phloeopora concolor*	O	1				
Staphylinidae	*Phloeopora corticalis*	O	1				
Staphylinidae	*Phloeopora testacea*	O	4				
Staphylinidae	*Phyllodrepa melanocephala*	O		2			
Staphylinidae	*Phyllodrepoidea crenata*	O		2			
Staphylinidae	*Placusa atrata*	O	4				
Staphylinidae	*Placusa tachyporoides*	O		7			
Staphylinidae	*Plataraea brunnea*		2				
Staphylinidae	*Platystethus arenarius*		1				
Staphylinidae	*Platystethus nitens*		2				
Staphylinidae	*Platystethus nodifrons*		3				
Staphylinidae	*Plectophloeus nubigena*	O		2			
Staphylinidae	*Poromniusa procidua*		1				
Staphylinidae	*Proteinus brachypterus*		19				
Staphylinidae	*Proteinus ovalis*			7			
Staphylinidae	*Quedius boops*		64				
Staphylinidae	*Quedius cinctus*		4				
Staphylinidae	*Quedius cruentus*		2	1			
Staphylinidae	*Quedius curtipennis*		10				
Staphylinidae	*Quedius dilatatus*	O	3				
Staphylinidae	*Quedius fuliginosus*		13				
Staphylinidae	*Quedius fulvicollis*		1				
Staphylinidae	*Quedius invreae*	F		1			
Staphylinidae	*Quedius limbatus*		4				
Staphylinidae	*Quedius lucidulus*		1				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Staphylinidae	*Quedius mesomelinus*		197	1			
Staphylinidae	*Quedius minor*		1				
Staphylinidae	*Quedius puncticollis*			1			
Staphylinidae	*Quedius reitteri*		2				
Staphylinidae	*Quedius umbrinus*		5				
Staphylinidae	*Quedius xanthopus*	O	39	6			
Staphylinidae	*Rugilus erichsonii*		10				
Staphylinidae	*Rugilus rufipes*		4				
Staphylinidae	*Rybaxis longicornis*		4		1	2	
Staphylinidae	*Scaphidium quadrimaculatum*	O	30				
Staphylinidae	*Scaphisoma agaricinum*	O	6				
Staphylinidae	*Scaphisoma boleti*	O	24				
Staphylinidae	*Schistoglossa aubei*		1				
Staphylinidae	*Scydmaenus perrisi*	O	2				
Staphylinidae	*Scydmaenus tarsatus*						1
Staphylinidae	*Sepedophilus bipustulatus*	O	1			1	
Staphylinidae	*Sepedophilus immaculatus*		1				
Staphylinidae	*Sepedophilus littoreus*		2				
Staphylinidae	*Sepedophilus testaceus*	O				1	
Staphylinidae	*Stenichnus collaris*			2			
Staphylinidae	*Stenichnus godarti*	O		1			1
Staphylinidae	*Syntomium aeneum*		5				
Staphylinidae	*Tachinus basalis*		9				
Staphylinidae	*Tachinus humeralis*		24				
Staphylinidae	*Tachinus laticollis*		2				
Staphylinidae	*Tachinus pallipes*		10				
Staphylinidae	*Tachinus rufipes*		234				
Staphylinidae	*Tachinus sibiricus*		2				
Staphylinidae	*Tachinus subterraneus*		11				
Staphylinidae	*Tachyporus abdominalis*		5				
Staphylinidae	*Tachyporus chrysomelinus*		2				
Staphylinidae	*Tachyporus hypnorum*		13				
Staphylinidae	*Trimium brevicorne*		2	2			
Staphylinidae	*Xantholinus longiventris*		39				
Staphylinidae	*Xantholinus tricolor*		10				
Staphylinidae	*Xylodromus depressus*		3				
Staphylinidae	*Zoosetha inconspicua*		1				
Staphylinidae	*Zyras collaris*		5				
Staphylinidae	*Zyras haworthi*		14				
Tenebrionidae	*Corticeus bicolor*	O	1				
Tenebrionidae	*Corticeus linearis*	O	2				
Tenebrionidae	*Corticeus unicolor*	O	26	4			
Tenebrionidae	*Diaperis boleti*	O	2				
Tenebrionidae	*Gonodera luperus*	O	44				
Tenebrionidae	*Lagria hirta*		2				
Tenebrionidae	*Mycetochara axillaris*	O	5				
Tenebrionidae	*Mycetochara maura*	O	40	2		1	
Tenebrionidae	*Nalassus convexus*			1			
Tenebrionidae	*Prionychus melanarius*	O	1				
Tenebrionidae	*Pseudocistela ceramboides*	O	3				
Tenebrionidae	*Scaphidema metallica*	O	2				

Family	Species	S	Flight Interception traps	Snag Emergence Eclector	Dead Wood Rearing Forest Floor	Dead Wood Rearing Understory	Dead Wood Rearing Canopy
Tetratomidae	*Hallomenus binotatus*	O	17			1	
Tetratomidae	*Tetratoma ancora*	O	4				
Throscidae	*Aulonothroscus brevicollis*	O	284		1		
Throscidae	*Trixagus dermestoides*		1				
Trogossitidae	*Grynocharis oblonga*	O	9				
Trogossitidae	*Lophocateres pusillus*		1				
Trogossitidae	*Nemozoma caucasicum*	O	5	1			
Trogossitidae	*Nemozoma elongatum*	O	18	2	9	382	172
Trogossitidae	*Peltis ferruginea*	O	2	2			
Trogossitidae	*Thymalus limbatus*	O	8	1			
Zopheridae	*Bitoma crenata*	O	5				
Zopheridae	*Colydium elongatum*	O	2	1			
Zopheridae	*Coxelus pictus*	O	1	1	2		
Zopheridae	*Diodesma subterranea*	O	1				
Zopheridae	*Synchita humeralis*	O	3	4			3
Zopheridae	*Synchita variegata*	O	23				
	Grand Total		44530	6526	10223	25855	33275

Acknowledgements

I would like to thank ...

... Thibault Lachat. Without a doubt, you are one of the best supervisors a student can have. Thank you for your trust, your presence, and your attention. Giving me the opportunity to live this adventure and finally being a "real" entomologist is a childhood dream come true. Now let's build a beetle-collecting bicycle!

... Raphaël Arlettaz, even if we did not see each other often, I can say that our personal and professional interactions gave me the confidence and the maturity to go beyond the student, and let the scientist blossom. Thank you for your radiant inspiration and dedication in preserving biodiversity.

... Urs Kormann, you made statistics fun and interesting for me. Spending time on R is now a guilty pleasure. For this, you deserve the *"Nobel of my inner peace".*

... Lisa Hülsmann and Junior A. Tremblay, for agreeing to be my external reviewers, and contributing to the growth of the scientific community.

... Antonia Ettwein, Michael Lanz, Gilgerto Pasinelli and Ueli Bühler for the background work that made this study possible. *"By the way, do you have the DNA data?"*

... the and the many field biologists in the White-backed Woodpecker's research fleet who welcomed me with open arms. Especially Simon Niederbacher, Markus, and Sarah Degenhart, who provided me invaluable assistance.

... all the foresters composing the backbone of this study.

... Alexander Szallies who helped me in my saproxylic beetles' taxonomic education.

... Maksym and Vasyl Chumak. I will never forget the work you did under the stereomicroscopes, regardless of the circumstances, until the very end. Дякую.

... David Roy, David Häsler, and all the people who helped me in the field and in the lab. A special thanks to Pierre Cardineau who was a sleepless centerpiece in the seminal phase of the fieldwork; Nina Marjanovic who ran with me for 24 days to inventory the 6690 trees, 5096 logs, 1050 stumps, and 728 snags; Justin Reymond who is not only a great person but also a rare professional everyone should wish to work with when having to carry c.a. 3 tons of wood across the forest and in a middle of a pandemic crisis.

... Martin Gossner, for giving me the opportunity of being a guest scientist in the Forest Entomology group at the Swiss Federal Research Institute WSL.

… the Swiss Federal Office for the Environment OFEV, Swiss Ornithological Station of Sempach and Inatura Dornbirn for the financial and logistic support in this project.

... the Conservation Biology group at UniBern. There are too many names to mention, but I will never forget the incredible moment we shared in our (c)old CB building. A wonderful scientific community that makes this department feel like home. *"Aperooo?"*
... the too many people in the WWI group, and the HAFL in general. Being there with you is such an amazing working environment! I still can't figure out who does what, but I know I will always find someone to answer my questions, like Christian Rosset who gave me valuable advice in developing the *Management Recommendations* section. *"Who wants to have a break in the pool?"*
... the Forest Ecology team obviously! Chrisitian Willisch, Nelson Marreros, and Michael Grüter. Shout-out to Anke who has always taken care of our *"Alpen/Steinbock family"*.
... my colleagues and friends, Elena Haeler and Nicolas Roth, for their insightful and incredible support. *"Potato electronic music? You're gonna need a bigger banana."*
... Yukki, Karen, Fanny, Patou, Bubar, Bestah, Emi, Elisa, Ilenia, Niels, Vera, Julia, Patrick, Dora, Iva, Benno, Pierrot, and all my friends who were with me along the way and will recognize themselves... *"See, studying insects is a real thing!"*
... France, who was just there and kept me going. *"Hourra pour le Monodontomerus!"*
... Adrien von Virag, who deserves the title of *"best roommate ever"*, for the feeding me with healthy vegetables, and all the bike related memories. *"Rather be klunking?"*
... Valentin Sylvoz, who jumped on the opportunity to join me in the field. While the workload was crazy, you always had a smile on your face. It was simply wonderful to spend this month climbing trees with my brother. *"Mais dis-moi, tu es détendu?"*
... Justine Ackers, in a way, you are part of the reason I am writing this dissertation today. Whether it's with an iron or a surfboard, baking cookies or dancing like nobody is watching you, I know we'll always have a good time together. *"Ayé, j'ai finiiiiiii!"*
... all the pioneers of electronic music, allowing the exploration of the multiple meanings of the word *"frequency"* and pushing one's creativity further than ever.
... M. Chinery for "Les insectes d'Europe en couleurs" as a landmark in my childhood.
... all the invertebrates who gave their lives to hopefully help build a better future.
... ma famille, parce que je vous aime. Papa et Maman, pour toujours avoir été là pour nous, et nous avoir transmis un tel horizon de connaissances. Sans hésitation, vous êtes les parents les plus chouettes qu'un enfant puisse avoir. Nonno e Nonna, che mi ha insegnato tante cose fin da bambino. *"Se la vita no va ben, ciaparla come cheava".* And my sisters, for being there. But also, for Carla's linguistic revision of this dissertation, and Lucille's relentless medical support to keep me alive in the field. *"Bon, soirée chapeaux?"*

Declaration of consent

on the basis of Article 18 of the PromR Phil.-nat. 19

Name/First Name: Romain Angeleri

Registration Number: 17-144-718

Study program: Ecology & Evolution CUSO

Bachelor ☐ Master ☐ Dissertation ☑

Title of the thesis: Communities of saproxylic beetles associated with the White-backed Woodpecker (*Dendrocopos leucotos*) in temperate forests of central Europe.

Supervisors: Prof. Dr. Raphaël Arlettaz

Prof. Dr. Thibault Lachat

“I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 litera r of the University Act of September 5th, 1996 and Article 69 of the University Statute of June 7th, 2011 is authorized to revoke the doctoral degree awarded on the basis of this thesis. For the purposes of evaluation and verification of compliance with the declaration of originality and the regulations governing plagiarism, I hereby grant the University of Bern the right to process my personal data and to perform the acts of use this requires, in particular, to reproduce the written thesis and to store it permanently in a database, and to use said database, or to make said database available, to enable comparison with theses submitted by others.”

Place/Date:

Bern, le 20 Février 2023

Signature