

Large live and dead trees promote saproxylic beetle diversity and White-backed Woodpecker breeding territories

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ABSTRACT

Effective forest management to promote biodiversity requires understanding the intricate relationship between forest characteristics and species occurrence. Given that more than 25% of forest taxa are associated with dead wood, this resource has gained attention as key component of closer-to-nature forest management. The White-backed Woodpecker (*Dendrocopos leucotos*) is one of Europe's rarest woodpeckers, and observational studies often report the species preferentially foraging on dead standing trees (i.e. snags) in deciduous forests. Despite the lack of systematic assessment of the importance of dead wood for the woodpecker and its associated saproxylic beetle community, conservation plans typically focus on snag enrichment when restoring forest patches for the target bird species. Here, we used confirmatory path analysis to compare the direct and indirect effects of structural characteristics of beech-dominated extensively managed forests on saproxylic beetle communities and on the White-backed Woodpecker activity. Using in situ electors, we sampled saproxylic beetle communities emerging from 87 European beech snags distributed in forests with and without the woodpecker, over a period of two years, yielding 6519 specimens represented by 156 saproxylic beetle species. While our study did not provide evidence that saproxylic beetle communities emerging from snags serve as a reliable predictor of White-backed Woodpecker activity, several habitat variables proved to be good predictors for saproxylic diversity. In addition to the positive effect of ambient temperature on saproxylic beetle richness, we identified that communities of saproxylic beetles were correlated with the diameter and the bark coverage of the snags, as well as indirectly with the diameter of the surrounding live trees. Taken together, our results emphasize the importance of promoting large live trees, benefiting subsequent late-successional dead wood resources to foster biodiversity in temperate deciduous forests. Independently of White-backed Woodpeckers known occurrence, practitioners and stakeholders should take on every opportunity of actively enhancing habitat quality where dead-wood dependent organisms occur. From retaining large live trees and snags in managed forests to focusing targeted conservation measures in forest stands where White-backed Woodpeckers occur, every measure increasing forest naturalness would ultimately benefit the fraction of biodiversity found in Central European forests.

1. Introduction

More than 25% of all forest-associated animal taxa are considered saproxylic species (i.e. "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)). Although many saproxylic beetles, particularly those occurring in later stages of wood decay, can

occur in managed forests, some of them have high requirements regarding the quantity and the quality of accessible dead wood (Siitonen et al., 2000; Jonsell and Weslien, 2003; Jonsell et al., 2004; Müller and Büttler, 2010; Brin et al., 2013; Gossner et al., 2013; Seibold et al., 2016; Haeler et al., 2024) and are thus predominantly found in forest with few to no human intervention and with great biodiversity conservation value (Eckelt et al., 2018; Ulyshen and Šobotník, 2018).

This diversity of dead wood can be described in terms of taxonomy,

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size (i.e. fine to coarse woody debris), height above ground (i.e. from the forest floor to the canopy), origin (i.e. anthropogenic or natural), decay stage (i.e. incipient to advanced) as well as position (i.e. lying, standing, attached) (Niemelä et al., 2002; Onodera and Tokuda, 2015). While logs are a common element of European forests, density of dead standing trees (hereafter snags) is much more variable (Brändli et al., 2020; Guby and Dobbertin, 1996; Karjalainen and Kuuluvainen, 2002; Meyer and Schmidt, 2011; Sippola et al., 2001). Variation in snag availability can be due to spatial variation in the processes creating them (e.g. wind-throws (Thorn et al., 2014), drought (Frei et al., 2022) and insect outbreaks (Müller et al., 2008)) or spatially variable processes of dead wood removal (e.g. removal for bioenergy harvesting (Ranius et al., 2018) or public safety constraints (Carpaneto et al., 2010)). Due to their limited contact with the ground, snags contain less moisture than logs on the ground and may offer specific habitat conditions for use by dead-wood dependent invertebrates (Ranius et al., 2019). Snags also remain out of snow during winter and might therefore play an important role in providing food resources for insectivorous birds such as woodpeckers (Czeszczewik and Walankiewicz 2006; Czeszczewik, 2009).

Literature suggests that the White-backed Woodpecker (*Dendrocopos leucotos*) largely relies on saproxylic beetles as food resource, both for adults and nestlings, with large larvae (e.g. Cerambycidae) being the preferred prey (Aulén, 1988; Hogstad and Stenberg, 1997). Because of this food specialization, White-backed Woodpecker's foraging habits requires forests with a high amount and diversity of dead wood (Bühler, 2008, 2009; Czeszczewik, 2009; Czeszczewik et al., 2013; Melletti and Penteriani, 2003). Although the occurrence of the White-backed Woodpecker has been shown to be positively correlated to the density of saproxylic beetle emergence holes on dead wood (Ettwein et al., 2020), an increase in dead wood does not automatically benefit both saproxylic beetles and the White-backed Woodpecker. For example, saproxylic beetles, but not the White-backed Woodpecker, positively reacted to measures aimed at increasing the volume and diversity of dead wood in Sweden (Bell et al., 2015; Mild and Stighäll, 2005, 2017). While the woodpecker is often referenced as an old growth forest stands specialist, its occurrence in central Europe spans from forest reserves to stands with extensive forest management regimes (Ettwein et al., 2020), demonstrating that more research on the link between this insectivorous predator, its potential prey, and its habitat is needed to efficiently protect both White-backed Woodpeckers and saproxylic beetles. In this study, we explored the direct and indirect effects of temperature, forest stand characteristics, saproxylic insect communities on White-backed Woodpeckers activity. To assess White-backed Woodpeckers' activity, we monitored the birds' activity through repeated radiotelemetry and playback recordings across known breeding home ranges and absence sites. In parallel, to characterize studied forest stands and snag-associated communities, we conducted a habitat inventory campaign and used emergence traps to characterize the saproxylic beetle communities emerging from snags over two subsequent years. Using confirmatory path analysis, we addressed the following three research questions: (1) Considering the recognized importance of snags and their associated saproxylic communities for White-backed Woodpeckers, is White-backed Woodpeckers activity 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 snags?; (2) Considering the ecological significance of large snags for saproxylic beetle communities, is saproxylic beetle species richness, abundance and body size positively correlated with the diameter of live trees, and with the diameter and bark coverage of snags?; (3) Given the importance of mature forest stands for dead wood resource supply, is the diameter of standing dead trees positively correlated with the diameter of live trees?

2. Materials and methods

2.1. Study area and site selection

This study took place in 18 sites within the Central European Alps in Eastern Switzerland (cantons of Grisons and St. Gallen), Western Austria (province Vorarlberg), and the Principality of Lichtenstein (46.8 – 47.4°N, 9.2 – 10.2°E; Fig. 1). All sites but one reserve were extensively managed for harvesting wood and/or protection of local infrastructure and human population. Nine of the sites (i.e. presence sites) corresponded to the breeding home range of nine adult White-Backed Woodpeckers radio-tracked during their breeding seasons. The additional nine sites (i.e. absence sites), without known White-Backed Woodpecker observations, had comparable characteristics to presence sites (altitude, forest surface, forest cover, forest mixture).

Presence sites were selected in 2018 using the following procedure. In 2016, 12 adult White-backed Woodpecker individuals were caught and tracked for at least two years. To do so, individuals were fitted with very high frequency (VHF) transmitters (PIP3, Biotrack/Lotek Ltd., Wareham, UK; weight = 3 g), which were either glued onto the base of the two central tail feathers or fixed on the back with a leg-loop harness. Each tagged individual was tracked with a portable receiver (R-1000, Communications Specialists, Orange, California) and a hand-held Yagi antenna (Advanced Telemetry Systems ATS, Isanti, Minnesota) twice a week during the two-year period. The start time of the tracking sessions was varied to cover the whole activity period of every individual, from sunrise to sunset. Within a tracking session, the individuals' locations were recorded every 15 min. While the birds were mostly located by triangulation, field operators tried to approach the bird as closely as possible despite the steep terrain and often inaccessible location, to improve the accuracy of the tracking campaign. Tagged White-backed Woodpeckers were usually tracked until the battery of the transmitters was drained or until individuals lost the transmitter. In early 2018, VHF data resulting from the tracking campaign was analyzed to identify the forested surface that corresponded to the breeding home ranges of radio-tracked White-backed Woodpeckers. Breeding home ranges were defined using kernel density estimation (KDE) based on the 95% utilization distribution including plug-in method for bandwidth selection, minimum convex polygons at 100% (MCPs) and autocorrelated kernel density estimation at 95% (AKDE). Prior to all home range analyses, we discarded locations with VHF accuracy > 200 m, locations recorded when a woodpecker was known to be in the breeding cavity and locations collected between egg-laying and fledging of the tracked White-backed Woodpeckers. Out of the 12 White-backed Woodpecker's breeding home ranges, nine were selected to host the saproxylic beetle sampling campaign due to accessibility issues and overlapping distances among breeding home ranges.

Absence sites were selected in early 2018 using the following procedure. We first created a 550 × 550 m grid to obtain potential absence sites (=30.25 ha) corresponding in size to a White-backed Woodpecker breeding home range (mean breeding home range size of 12 individuals tracked in 2016 and 2017 was 29 ha). Next, we calculated the proportions of deciduous or mixed forest area and of total forest area from CORINE Land Cover data (European Environment Agency 2019, CORINE Land Cover (CLC) 2018, Version 20, Copenhagen, Denmark) for the breeding home ranges of birds tracked in 2016 and 2017 and for all potential absence sites. We then calculated the 25% quantiles of the proportions of deciduous or mixed forest and of total forest area, respectively, in the breeding home ranges and omitted all potential absence sites in which the proportion of deciduous or mixed forest area and of total forest area was below these 25% quantiles. Moreover, we omitted potential absence sites that were closer than 1000 m to a previous White-backed Woodpecker observation. Finally, we visually assessed whether the nine selected absence sites were accessible for fieldwork using topographic maps. We checked whether White-backed Woodpeckers were present in the nine absence sites in two surveys

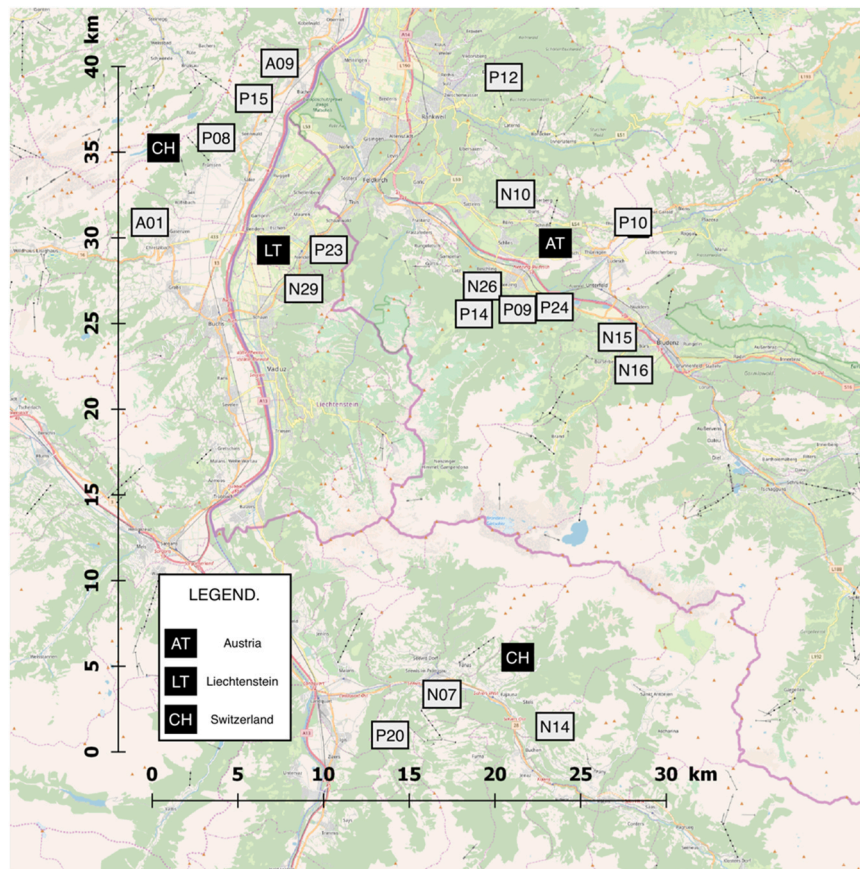


Fig. 1. Map of the study region with the repartition of the breeding home ranges of tracked White-backed Woodpeckers (letter P followed by the site's number) and the repartition of the pseudo-absence sites (letter N or A followed by the site's number). Map data copyrighted OpenStreetMap contributors and available from <https://www.openstreetmap.org>.

between February and April 2018 and 2019. During each survey, an operator used playbacks of drumming and calls (1 min of drumming, 1 min of calls and 1 min of drumming; 1 min of waiting after playing each sound) every 200 m, on a 200 × 200 m grid. In every of the nine absence sites, no White-backed Woodpeckers were detected during the surveys. More details can be found in [Ettwein et al. \(2024\)](#).

In early 2018, within the 18 sites selected for the saproxylic beetle campaign, we selected a total of 54 circular plots of 1 ha spanning over the gradient of White-backed Woodpecker activity. White-backed Woodpecker activity is characterized as the number of VHF observations per plot. Plots with a high White-backed Woodpecker activity are plots where White-backed Woodpeckers were often observed within their breeding home ranges ($n = 18$). Plots with a low White-backed Woodpecker activity are plots where White-backed Woodpeckers were rarely observed within their breeding home ranges ($n = 18$). Plots in absence sites are plots where White-backed Woodpeckers were never observed ($n = 18$). To obtain a measure of White-backed Woodpecker activity within the breeding home ranges, we used the previously acquired VFH data to extract White-backed Woodpecker observation density information. We first created a heatmap layer based on the number of VHF observations in QGIS (v.2.18) software and with the QMarxan Toolbox (v.0.3.4) plugin. To avoid any potential confounding effects of visits to the nest on bird activity, we applied an exclusion buffer in a 150 m radius (average VHF accuracy) centered on the breeding cavity of the tracked White-backed Woodpeckers. After in-situ visits of area of interest, we then selected, within every breeding home range, two sampling plots with the highest density of VHF observations and two additional plots with the lowest density of VHF observations, per breeding home range. Finally, we calculated the number of VHF observations per sampling plot as a measure representing White-Backed

Woodpecker activity. Within the absence sites, trained ornithologists helped in determining two sampling plots, around the center of each site, as being representative of potential White-backed Woodpecker habitat. In both breeding home ranges and absence sites, plots with overlapping rock cliffs and streams were not selected for accessibility reasons. Cardinal direction and slope inclination of all plots were comparable across sites. All plots were situated in beech-dominated forest stands with an elevation ranging from 630 to 1230 m above sea level.

2.2. Beetle sampling

On each plot, we sampled saproxylic beetles on all available dead-standing European beech trees (*Fagus sylvatica*) with a diameter at breast height (DBH) > 10 cm, for a total of 87 sampled snags (absence sites = 29 snags, high activity in breeding home ranges = 33 snags, high activity in breeding home ranges = 25 snags). Because incorporating in our analysis plots without snags, and thereof without snag-emerged beetles would bias the results, this study focuses on forest plots with snags (see [supplementary materials S1](#)). Emergence eclector traps were used to sample beetles hatching from the snag. Emergence eclector traps were positioned on the bole section that was between 100 and 250 cm above ground. To allow insects living in the bole to hatch and move around, we created a 4 cm gap between a piece of camouflage patterned polyester fabric (160 cm length) wrapping the bole, with a foam strip at both ends, on which the fabric was firmly tightened with a metallic wire. The joint line of the fabric rolled on itself and was then stapled on the south-oriented side of the snag. To collect insects, a plastic bottle filled with preservation fluid (70% ethanol), was attached to a 3 cm diameter plastic pipe that was in contact with the dead wood at breast height. The bottle was attached to the north-oriented side of the snag to avoid

excessive evaporation of the collecting and preservation fluid. Emerging insects were passively guided by the fabric to the collecting device as it was the only bright light source available in the wrapped bole section (Fig. 2). Traps were active from April 2018 to September 2019. Except during winter, traps were emptied monthly. During the dismantlement of the trap, no apparent damage to the fabric was observed, allowing the inference of a proper sampling coverage of dispersing invertebrates. Then, samples were pooled across all months for every trap. Beetle specimens were then identified to species level and their categorized as saproxylic or not following an enhanced list of Schmidl and Bussler (2004). Species without reliable information about their saproxylic habits were excluded from further analyses (*Pterostichus aethiops* = 1 individual; *Halyzia sedecimguttata* = 1 individual; *Batophila rubi* = 1 individual, *Mniophila muscorum* = 3 individuals; see S3 for additional information on included species).

2.3. Trap and habitat characterization

In a 500 m² circular area centered on every trap, we characterized and recorded an array of parameters on every live, dead standing and lying trees. The variables used in this study to characterize sampling plots represent a fraction of the complete set. The diameter of all live and dead standing trees (i.e. snags with a height greater than 130 cm) with a DBH ≥ 6 cm. For all sampled snags, we measured the DBH and visually estimated the proportion of remaining bark. If a sampled snag was occurring within the 500 m² perimeter of the habitat inventory of another, the former was counted as a regular snag, and vice versa. Additionally, air temperature was measured to identify potential general differences among habitats (i.e. semi-open to closed canopy) and sampling years (i.e. 2018 and 2019). To control temperature variability across years, air temperature was measured every 2 h, for the duration of the sampling campaign, 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 the traps. Temperature data loggers were shaded by a plastic tube to avoid direct sun radiation (Fig. 2).



Fig. 2. Emergence eclector installed on a dead standing European beech tree 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). C = Sampling surface. D = Temperature logger. Snags were sampled in the bole section from 100 cm to 250 cm from the ground.

2.4. Statistical analysis

Using confirmatory path analysis in a Bayesian latent variable analysis framework (Merkle et al., 2021), we analyzed how (1) White-backed Woodpecker activity varied as a function of different saproxylic beetle community metrics (species richness, abundance, community weighted means of body length), snag characteristics (DBH and proportion of remaining bark) and habitat parameters (mean DBH of live trees and mean annual air temperature); how (2) species richness, (3) abundance, and (4) community weighted means of body size of saproxylic beetles communities varied as a function of snags characteristics (DBH and proportion of remaining bark) and habitat parameters (mean DBH of live trees and mean annual ambient temperature); and how (5) the DBH of snags varied as a function of the mean live tree DBH within a 500 m² radius (Table 1).

Data preparation, control, and modeling included the following steps: (1) Based on an extended list from Hagge et al. (2021), the mean body length of saproxylic beetle communities was calculated per trap using the cwm function from the R package BAT (Cardoso et al., 2015). (2) All 18 plots within the absence sites were assigned a White-backed Woodpecker activity level of zero. In White-backed Woodpecker breeding home ranges, some plots (i.e. in low activity areas) showed no VHF detections throughout the telemetry study period. To statistically distinguish these plots from those in absence sites, we incremented the total VHF detection count of plots located in White-backed Woodpecker presence sites by one. (3) Since the mean diameter of snags measured during habitat inventories was strongly correlated with the diameter of the sampled snags (Pearson’s correlation coefficient > 0.8), the latter was retained as the explanatory variable due to its greater relevance to the research question. All variables included in the model exhibited low collinearity (Pearson’s correlation coefficient ≤ 0.5). (4) Generalized linear mixed models were built for our five response variables (Table 1). Continuous response variables were modelled using normal distribution whereas discrete response variables were modelled using negative binomial distribution (see CDF visualization in supplementary materials S4). Ecologically irrelevant interactions were defined as tying together the snag diameter with the mean temperature and the snag diameter with the snag bark cover. Non-linear relationships were representative of the study design (i.e. traps nested within plots nested within sites). This set of five generalized linear models was then combined into a Bayesian structural equation model (Merkle et al., 2021) within a Stan framework (Goodrich et al., 2024) using the R package rstan (Stan Development Team, 2025). Our model used weakly informative priors. Regression coefficients used Normal(0,2) priors. Intercepts used Normal(0,5) priors. Random effect raw terms used Normal(0,1) priors. Site hyper-mean used Normal(0,5) priors. Standard deviations and

Table 1
Description of the variables composing the structural equation model.

Subject	Variable name	Unit	Definition
White-backed Woodpecker	WBW activity	count	Standardized sum of the very high frequency (VHF) records of the tracked White-backed Woodpeckers on 500 m ² plots.
Saproxylic beetles	Specimen abundance	count	Sum of emerging saproxylic beetle specimens per sampled snag.
Saproxylic beetles	Species richness	count	Sum of emerging saproxylic beetle species per sampled snag.
Saproxylic beetles	CWM body length	mm	Community weighted means of the body length of emerging saproxylic beetle specimens per sampled snag.
Habitat	Live tree diameter	cm	Mean diameter at breast height of live trees on the plot.
Habitat	Temperature	°C	Mean annual temperature.
Sampled dead standing tree	Snag diameter	cm	Diameter at breast height of the sampled snag.
Sampled dead standing tree	Snag bark cover	%	Proportion of remaining bark of the sampled snag.

dispersion parameters used Normal(0,2) T(0,) priors. All models used 4 mixing chains parameterized as 9999 iterations with a thinning of 1 iteration and warmup of 4999 iterations each. Then, the relative importance of the paths was determined using standardized path coefficients with the highest density of the credibility interval set at 0.9. All effective samples resulting from the four Markov Chains Monte Carlo were greater than 12000 and all Rhat were smaller or equal to 1, suggesting a good convergence of the mixing chains. Alternative R2 values (median and standard deviation) were computed following Gelman et al. (2019). All statistical analyses were performed using R Version 4.5.0 (R Core Team, 2022).

3. Results

3.1. Abundance and Richness of saproxylic beetles

The 87 sampled snags yielded a total of 6519 saproxylic beetle specimens representing 156 species (see [supplementary materials S2 and S3](#)). Two species dominated, representing 62% of the emerging saproxylic beetle specimens (*Ptilinus pectinicornis* = 2457 individuals, *Trypodendron domesticum* = 1609 individuals).

3.2. Bayesian latent variable analysis

First, our analysis did not identify a correlation between the selected predictors and the activity of the White-backed Woodpecker. Second, saproxylic beetle specimen abundance was negatively correlated with diameter of snags ($-0.031 - -0.002$ CrI, $R^2 = 0.90 \pm 0.10$). Third, saproxylic beetle species richness was positively correlated with saproxylic beetle specimen abundance ($1.30 \text{ e-}05 - 0.002$ CrI, $R^2 = 0.79 \pm 0.10$), diameter of snags ($0.001 - 0.016$ CrI, $R^2 = 0.79 \pm 0.10$) and temperature ($0.031 - 0.202$ CrI, $R^2 = 0.79 \pm 0.10$). Fourth, saproxylic beetle body length was negatively correlated with bark coverage of snags ($-0.017 - -0.002$ CrI, $R^2 = 0.08 \pm 0.05$). Finally, diameter of snags was positively correlated with diameter of live trees ($0.005 - 0.030$ CrI, $R^2 = 0.25 \pm 0.11$) (Table 2; Fig. 3).

4. Discussion

We conducted a confirmatory path analysis combining community metrics of saproxylic beetles sampled from dead standing beech trees with habitat characteristics from sites with and without White-backed

Woodpeckers. Our analysis showed that the average body size of the saproxylic beetle communities was negatively correlated with the proportion of remaining bark on snags, and the abundance of saproxylic beetles was negatively correlated with snag diameter. In addition, richness of saproxylic beetles was positively correlated with specimen abundance of saproxylic beetles, temperature and snag diameter. Finally, snag diameter was positively correlated with live tree diameter.

Generally, species richness of saproxylic beetles emerging from snags increased with warmer ambient temperature. It is well established that insect communities are more active in warm temperature (Lachat et al., 2014; Müller et al., 2015; Sanchez et al., 2016; Vogel et al., 2020). With the traps enclosing snags, some saproxylic beetle individuals may try to disperse from the dead wood piece they are developing from, at every generation. Others may develop within the same dead wood piece for multiple generations. Based on our interpretation, it is possible that saproxylic beetle communities at warmer location had an increased dispersing rate. Ultimately, a higher number of dispersing individuals would lead to a higher diversity of species captured, as evidenced by our structural model.

In addition, species richness of saproxylic beetles increased with the diameter of snags, and large snags tended to occur where live trees were also larger. These findings support the ecological significance of forest patches exhibiting mature structural attributes, such as large live trees and, consequently, large snags, in supporting saproxylic beetle communities (Grove, 2002; Moroni and Harris, 2010; Bouget et al., 2012; Lachat et al., 2013; Lachat and Müller, 2018; Rothacher et al., 2023; Angeleri et al., 2024; Ozaki et al., 2024).

Further, we observed that snags of large diameter tend to host fewer individuals and that saproxylic beetles tend to be larger in snags with reduced remaining bark. This seemingly counterintuitive pattern can be attributed to the composition of our emerging communities: two species, *Trypodendron domesticum* and *Ptilinus pectinicornis*, dominated these communities and emerged predominantly from small-diameter snags, thereby driving the negative correlation between saproxylic beetle abundance and snag diameter.

Moreover, snags with extensive bark coverage tend to harbor subcortical and pioneer species, which are typically represented by numerous small-bodied individuals. As decomposition progresses, only large and structurally stable snags, typically with fewer bark patches, are likely to persist for longer time (Onodera and Tokuda, 2015; Ranius et al., 2019). These snags will gradually be subject to a community shift in favor of larger-bodied saproxylic beetles, often occurring in little

Table 2

Direct standardized effect size of explanatory variables on the response variables for the five component models composing the final Bayesian structural equation model on the dataset including all beetle species. Abbreviations described in Table 1.

Component model	Parameter	Median	HDI 90% CrI lower	HDI 90% CrI higher	Probability of Direction	Region Of Practical Equivalence
WBW activity	Specimen abundance	9.2e-05	-0.001	0.002	0.54	1
WBW activity	Species richness	-0.016	-0.06	0.028	0.72	1
WBW activity	CWM body length	0.002	-0.136	0.143	0.51	0.79
WBW activity	Live tree diameter	-0.012	-0.047	0.024	0.72	1
WBW activity	Temperature	-0.195	-0.535	0.137	0.84	0.26
WBW activity	Snag diameter	0.009	-0.006	0.022	0.84	1
WBW activity	Snag bark cover	-0.003	-0.008	0.003	0.79	1
Specimen abundance	Snag diameter	-0.017	-0.031	-0.002	0.97	1
Specimen abundance	Snag bark cover	0.001	-0.004	0.007	0.65	1
Specimen abundance	Live tree diameter	-0.002	-0.032	0.025	0.55	1
Specimen abundance	Temperature	0.146	-0.028	0.321	0.92	0.33
Species richness	Specimen abundance	0.001	1.3E-05	0.002	0.95	1
Species richness	Snag diameter	0.008	0.001	0.016	0.97	1
Species richness	Snag bark cover	2.2e-05	-0.003	0.003	0.51	1
Species richness	Live tree diameter	0.012	-0.002	0.024	0.93	1
Species richness	Temperature	0.115	0.031	0.202	0.99	0.38
CWM body length	Snag diameter	-1.1e-04	-0.017	0.018	0.51	1
CWM body length	Snag bark cover	-0.01	-0.017	-0.002	0.98	1
CWM body length	Live tree diameter	0.007	-0.026	0.039	0.63	1
CWM body length	Temperature	0.075	-0.109	0.261	0.75	0.56
Snag diameter	Live tree diameter	0.017	0.005	0.03	0.98	1

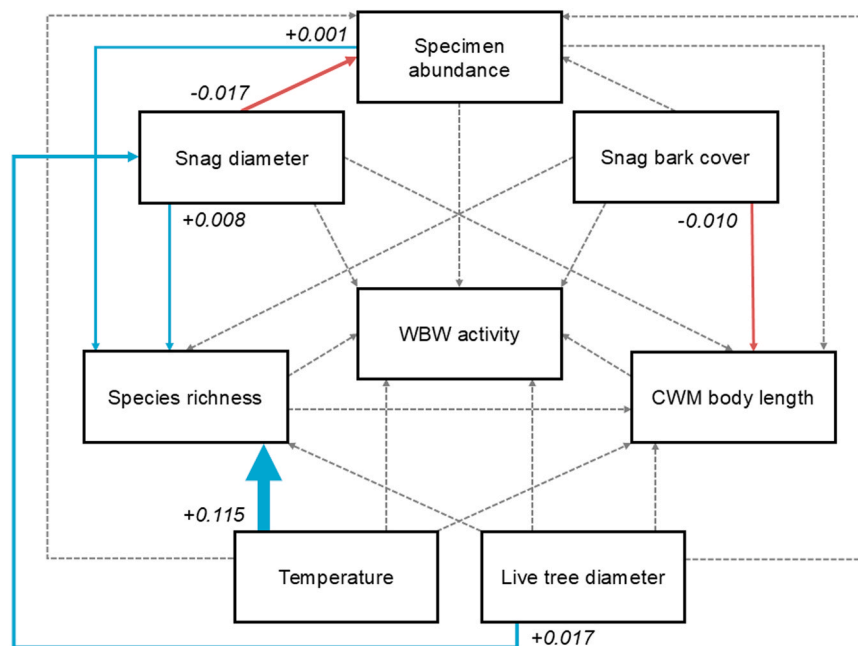


Fig. 3. Direct and indirect effects of the five component models. Red arrows indicate a negative correlation, blue arrows indicate a positive correlation, and dashed arrows indicate a correlation that was not identified as existing by the models. Associated values correspond to the standardized effect of the path.

abundance and requiring extended developmental periods (Procházka and Schlaghamerský, 2019; Hagge et al., 2021), which could be a possible interpretation of the negative relationship between bark coverage and beetle body size we observed.

However, our study did not provide evidence that saproxylic beetle communities emerging from snags serve as a reliable predictor of White-backed Woodpecker activity. Snags are often referred as of greater importance for White-backed Woodpecker's foraging strategy (Bühler, 2008, 2009; Czeszczewik, 2009). With no evident correlation between communities of saproxylic beetles emerging from snags located within White-backed Woodpecker breeding home ranges and absence sites, our findings challenge the preeminence of this dead wood resource in the habitat use of the bird. Interpreting these evidence-based results with caution, it is possible that former studies assessing White-backed Woodpecker's substrate's selection suffered from detection bias. Where observation on lying or attached dead wood are difficult to detect due to understory and tree crown's vegetation density (Zwarts and Bijlsma, 2015), former field observations assessing habitat features of prime importance for White-backed Woodpeckers may have over-emphasized snags. Equally, hypotheses on methodological biases could be raised to explain this apparent lack of association. While snags would have been colonized by saproxylic beetles at the same time as when our White-backed Woodpecker VHF observation campaign took place, they may have been partly depleted by insectivores prior to installing our emergence traps. It is also possible that, while being active for two complete years, not all emerging species have been captured by our passive sampling technique. Species with longer life cycles, such as Cerambycidae, a family often considered important prey (Gustaf, 1988; Hogstad and Stenberg, 1997), would likely have been underrepresented in our dataset. If so, the resulting altered saproxylic beetle communities in our samples would have a reduced power to expose relationships between the White-backed Woodpecker and emerging beetle communities (Fayt et al., 2005).

Nonetheless, similar studies conducted in the same geographical region demonstrated the importance of White-backed Woodpecker's habitat for conservation of overall forest-associated biodiversity in extensively managed forest stands (Ettwein et al., 2020; Angeleri et al., 2024). While it remains of high importance for conservation, further investigation into the diet of the White-backed Woodpecker could help

clarify which prey communities the species relies on, determine their association with lying, standing or attached dead wood and evaluate the relative contribution of each substrate type to the White-backed Woodpecker foraging ecology.

5. Conclusion

Our findings highlight the ecological benefits for saproxylic beetle communities arising from the retention of mature forest attributes, such as large live trees, which promotes the formation of large-diameter snags, a key structural element supporting deadwood-dependent diversity. These results align with previous studies emphasizing the role of mature forest structures in supporting forest-associated species, such as saproxylic beetles. Although the White-backed Woodpecker is often regarded as an old-growth forest specialist, our case study demonstrates that it can recolonize and breed successfully in extensively managed Central European forests. The presence of breeding White-backed Woodpeckers should thus guide forest managers and stakeholders in implementing saproxylic-oriented conservation strategies, such as retaining large trees throughout their full natural lifecycle, in managed Central European forests and surrounding areas. Doing so would ultimately help restore one of Central Europe's rarest woodpecker species and safeguard forest-associated communities that share its habitat.

CRediT authorship contribution statement

Nicolas Roth: Writing – review & editing, Methodology. **Urs G. Kormann:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Romain Angeleri:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Thibault Lachat:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Raphaël Arlettaz:** Writing – review & editing, Supervision. **Michael Lanz:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Antonia Ettwein:** Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123720](https://doi.org/10.1016/j.foreco.2026.123720).

Data availability

Data will be made available on request.

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