



Research article

What do tree-related microhabitats tell us about the abundance of forest-dwelling bats, birds, and insects?

Marco Basile^{a,*}, Thomas Asbeck^b, Marlotte Jonker^{a,c}, Anna K. Knuff^d, Jürgen Bauhus^b,
Veronika Braunisch^{c,e}, Grzegorz Mikusiński^{a,f}, Ilse Storch^a

^a Chair of Wildlife Ecology and Management, University of Freiburg, Tennenbacher Str. 4, D-79106, Freiburg, Germany

^b Chair of Silviculture, Institute of Forest Sciences, University of Freiburg, Tennenbacher Str. 4, D-79106, Freiburg, Germany

^c Forest Research Institute of Baden-Württemberg (FVA), Wonnhaldestr. 4, D-79100, Freiburg, Germany

^d Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Tennenbacher Str. 4, D-79106, Freiburg, Germany

^e Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstr. 6, CH-3012, Bern, Switzerland

^f Department of Ecology, Swedish University of Agricultural Sciences SLU, Grimsö Wildlife Research Station, SE 730 91, Riddarhyttan, Sweden



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ABSTRACT

Retaining trees during harvesting to conserve biodiversity is becoming increasingly common in forestry. To assess, select and monitor these habitat trees, ecologists and practitioners often use Tree-related Microhabitats (TreMs), which are assumed to represent the abundance and diversity of environmental resources for a wide range of forest-dwelling taxa. However, the relationship between TreMs and forest organisms is not fully understood. In this context, we attempted to identify and quantify the links between TreMs and three groups of forest organisms: insects, bats, and birds. Specifically, we tested whether species abundance is influenced by TreM abundance, either as direct predictor or as mediator of environmental predictors.

We collected data in 86 temperate, 1-ha mixed forest plots and employed a hierarchical generalized mixed model to assess the influence of seven environmental predictors (aspect, number and height of standing dead trees, cover of herb and shrub layer, volume of lying deadwood, and terrain ruggedness index (TRI)) on the abundance of TreMs (15 groups) on potential habitat trees, insects (10 orders), bats (5 acoustic groups) and birds (29 species) as a function of seven environmental predictors: aspect, number and height of standing dead trees, cover of herb and shrub layer, volume of lying deadwood, and terrain ruggedness index (TRI). This allowed us to generate a correlation matrix with potential links between abundances of TreMs and co-occurring forest organisms. These correlations and the environmental predictors were tested in a structural equation model (SEM) to disentangle and quantify the effects of the environment from direct effects of TreMs on forest organisms.

Four TreM groups showed correlations $> |0.30|$ with forest organisms, in particular with insects and bats. Rot holes and concavities were directly linked with three insect groups and two bat groups. Their effect was smaller than effects of environmental predictors, except for the pairs “rot holes – Sternorrhyncha” and “rot holes – bats” of the *Pipistrellus* group. In addition, TreMs had indirect effects on forest organisms through mediating the effects of environmental predictors.

We found significant associations between two out of fifteen TreM groups and five out of 44 forest organism groups. These results indicate that TreM abundance on potential habitat trees is not suited as a general indicator of the species abundance across broad taxonomic groups but possibly for specific target groups with proven links.

1. Introduction

Forest biodiversity plays an increasingly important role in forest management, but it is challenging to measure and monitor (Paillet et al., 2010), for example to demonstrate the effectiveness of different

management approaches to support biodiversity. Numerous forest indicators have been proposed and tested to offer efficient biodiversity monitoring schemes. Taxon-based indicators consist of biological entities that can reflect processes and patterns of larger arrays of biological entities (Lindenmayer et al., 2000). Examples of taxon-based

* Corresponding author.

E-mail address: marcob.nat@gmail.com (M. Basile).

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biodiversity indicators include woodpeckers (Drever et al., 2008; Roberge et al., 2008), fungal fruiting bodies (Komonen, 2003) and bird species occurrence (Pakkala et al., 2014). Taxon-based indicators have also been proposed to predict phylogenetically-distant biological assemblages, though their use is debated (Lindenmayer et al., 2000). Examples of taxon-based indicators include the density of polypore fungi to predict cavity-nesting bird occurrence (Löhmus, 2016) or species richness of epiphytes to predict the occurrence of Red List species (Norden et al., 2007). In general terms, however, it has been found that single taxonomic groups are poor indicators of overall biodiversity in forest ecosystems (Jokela et al., 2018; Smith et al., 2008).

Forest structure indicators of biodiversity use the relationship between habitat features and the occurrence of forest dwelling taxa instead (Lindenmayer et al., 2000; McElhinny et al., 2006). Examples of such structural indicators include the frequency of uprooted trees (Angelstam and Dönnz-Breuss, 2004), the quantity, quality, and diversity of deadwood (Lassaue et al., 2011). In addition, indices have been developed that include a comprehensive set of forest attributes to define structural diversity at the stand scale (e.g. Storch et al., 2018).

In addition, the approach to link structural elements with habitat requirements of forest-dwelling species has been applied to so-called microhabitats that are found on individual trees (Larrieu et al., 2018; Michel and Winter 2009; Winter and Möller, 2008). This approach is based on the recognition of the 'ecological value' of single trees, which may be retained during harvesting to preserve valuable microhabitats for biodiversity (Lindenmayer, 2017). Often, these 'ecologically valuable' trees are large and/or old trees that function as 'habitat trees' (Bütler et al., 2013; Loyn and Kennedy, 2009; Mazurek and Zielinski, 2004).

Tree-related microhabitats, short TreMs, are "distinct, well delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrate or life site for species or communities during at least a part of their life cycle to develop, feed, shelter or breed" (Larrieu et al., 2018). Owing to their different origins, substrates, and positions on trees, TreMs represent an array of resources available for forest organisms, and are of conservation relevance. Hence, TreMs are used in forest management to identify habitat trees for retention (e.g. Forst, 2016; Santopuoli et al., 2019). They are considered structure-based indicators, though some TreMs are actually living organisms, such as epiphytes (Larrieu et al., 2018). The abundance of TreMs, i.e. the number of TreMs per tree, may be predicted from both common stand level forest attributes such as tree species composition or tree level attributes such as species or diameter (e.g. Asbeck et al., 2019; Winter and Möller, 2008). Some specific interactions between forest-dwelling species and TreMs are well known. For example, relationships between living TreMs such as wood-decaying fungi and woodpeckers (Cockle et al., 2012) or between invertebrates and lichens (Pettersson et al., 1995) have been documented. Non-living TreMs, such as rot holes and cavities, are often used by forest species including lichens, bryophytes bats and birds (Fritz and Heilmann-Clausen, 2010; Tillon and Aulagnier, 2014; Wesolowski, 2012). However, whether TreMs, being undoubtedly a keystone structures, can be used as unique indicators of the abundance and diversity of forest-dwelling species in forest monitoring schemes, has not been fully understood. So far, there have been rather few studies on the relationships between a whole set of TreMs and the abundance and diversity of forest-dwelling species. For example, birds' and bats' species richness was positively related to TreM diversity (Paillet et al., 2018; Regnery et al., 2013), while invertebrates showed positive associations with specific TreMs, like fruiting bodies of fungi or cavities (Friess et al., 2019; Paillet et al., 2018). Therefore, a better understanding of the links between a comprehensive set of TreMs and forest dwelling taxa may help to identify valuable habitat trees and provide a foundation for monitoring of some aspects of forest biodiversity.

We hypothesise that the abundance of selected groups of forest organisms in managed forests, is explained by the abundance of TreMs on

potential habitat trees at the plot scale. In contrast to previous studies, where TreMs were considered as independent variables, we modelled TreM abundance together with the abundance of forest organism groups, namely birds, bats and insects, as a function of the local forest structure and topography. This allowed us to search for the strongest associations between specific TreMs and forest organisms and to disentangle direct effects of TreMs on these organism groups from effects of environmental conditions mediated by TreMs. By identifying abundance patterns of TreMs and co-occurring forest organism groups in managed forests, we aimed to assess whether the abundance of specific TreMs can influence the abundance of forest organisms and, if so, to quantify the strength of this relationship.

2. Methods

2.1. Study area

The empirical data for forest structure, TreMs, insects, bats and birds were obtained from 86 1-ha plots in the Black Forest, southwest Germany (Latitude: 47.6°–48.3° N, Longitude: 7.7°–8.6° E; WGS 84). Plots were selected within the framework of the ConFoBi project (Storch et al., 2020), following two gradients: forest cover and the number of standing dead trees, which served as a surrogate for structural diversity. At the landscape scale, plots were selected to equally include three forest cover categories (<50%, 50–75% and >75% forest cover within 25 km² around the plot centers). At the plot scale, the selection criterion was the number of standing dead trees identified by photo stereo viewer technique representing a gradient from 0 to more than 20 dead trees per hectare. The plots, located at altitudes between 500 and 1400 m a.s.l., represent a typical temperate mixed montane forest, dominated by Norway spruce (*Picea abies* (L.) Karst.), European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.). All plots were selected in state owned forest managed in a continuous cover forestry system, following a close-to-nature management paradigm (Bauhus et al., 2013).

3. Environmental predictors

Forest inventory data comprised tree species identity and diameter at breast height (DBH) of all living trees (with DBH > 7 cm). In addition, DBH and height of all standing dead trees (snags) (with DBH > 7 cm and height > 1.3 m) on the plots were measured and these were classified as conifer or broadleaf. Other variables included the volume of lying deadwood, altitude, slope, aspect, understory vegetation cover and terrain ruggedness index (TRI) (Table 1). Details on the sampling methods are available in the supporting information, appendix S1.

TreM abundance was recorded at each plot on a selection of living trees, in order to reproduce forest managers' 'habitat tree' selection process, which is focused solely on living trees. First, the 15 individuals with the largest crown radius in each plot were selected. Since density

Table 1

Environmental predictors included in the hierarchical generalized linear mixed model with their mean \pm standard deviation (sd) and range (minimum - maximum). The full array of environmental predictors is available in the supporting information.

Structural variable	Mean \pm sd	Range
Aspect (rad)	170.3 \pm 109.6	4–360
Height of the standing dead trees (m)	12.1 \pm 4.3	5.1–26.0
Herb layer cover (m ²)	35.2 \pm 19.3	0.14–73.8
Lying deadwood (m ³)	47.9 \pm 48.8	2.68–282.9
Shrub layer cover (m ²)	14.3 \pm 13.4	0–55
Standing dead trees (n)	66.2 \pm 105.9	2–788
Terrain ruggedness index (TRI)	0.54 \pm 0.13	0.36–1.21

¹ Measured for eight 25 m²-subplots within the 1-ha plot.

² Measured with the line intersect method within the 1-ha plot, crossing ~ 223.6 m.

and diversity of TreMs typically increase with tree dimensions (Asbeck et al., 2019), these trees carry a large proportion of the TreMs to be found at the plot. We refer to them as potential habitat trees. Then, 6 trees with smaller crown sizes, inventoried on a random subset of 49 plots were added to the selection, to obtain a representation of all diameter size classes. We used a detailed catalogue for TreM classification by Kraus et al. (2016), and grouped TreMs in 15 groups (Larrieu et al., 2018). Details on the sampling methods are available in the supporting information, appendix S1.

3.1. Animal data collection

As forest-dwelling organisms, we sampled three taxonomic groups: insects, bats, and birds. To sample flying insects in the forest understory, we used window traps with collectors at the bottom and at the top of transparent plastic panes that served as flight barrier (Knuff et al., 2019). Catches were removed on a four-weekly interval. Data on catches from mid-March to mid-July in 2017 were used for analysis. The collected material was stored in 75% ethanol, sorted to order level (with Hemiptera being further separated into Auchenorrhyncha, Sternorrhyncha & Heteroptera) and counted. Details on the sampling methods are available in the supporting information, appendix S1.

Bat data were collected during four nights between May and October in 2016 and 2017 with two ultrasonic sound recorders per night and plot (Batloggers, Elekon AG, Lucerne, Switzerland). Bat calls were automatically classified using Batscope 3.2.0 (Obriest and Boesch, 2018), with a subsequent, visual verification of ambiguous calls using Raven Pro 1.5.0 (Bioacoustic Research Program, 2014). Acoustically similar bats species were grouped to avoid the problem of misidentification. As a proxy of bat abundance, we used the maximum number of bat calls per species or species groups respectively, recorded during the sampling period (in the following referred to as “bat abundance” for simplicity reasons). Details on sampling methods are available in the supporting information, appendix S1.

Birds were sampled by employing standardized point counts with limited distance of 50 m, repeated three times during spring 2017, starting half an hour after sunrise with the latest ending at 12:00 CET. A single count lasted 20 min and consisted of four 5-min-blocks, during which every bird heard or seen was recorded. Details on the sampling methods are available in the supporting information, appendix S1.

3.2. Community model

The data on TreMs, insects, bats and birds were fed into a hierarchical generalized linear-mixed model (GLMM), built using the Hierarchical Modelling of Species Communities (HMSC) approach, a type of joint species distribution models (Ovaskainen et al., 2017). This approach allows to model abundance data as a function of environmental predictors and species ecological traits. In addition, it included the possibility to incorporate the spatial structure of the data in the random effect. We first checked our environmental predictors for collinearity, excluding all the variables that showed a Spearman rank correlation coefficient $R_s > |0.6|$, and performed a variance inflation analysis to exclude all the variables that can inflate the variance inflation factor > 3 . As response variable, we included the abundance data for TreMs, insects, bats and birds. A dummy categorical variable was included in the model grouping together all TreMs, insects, bats and birds, respectively. Finally, we ran the model in Bayesian language, using Markov chain Monte Carlo (MCMC) resampling with a thinning interval of 100 over 2000 samples, resulting in 205 000 iterations, from which the first 50 000 were discarded as transient. These settings were used to run 3 chains. We considered that chains reached convergence when the Gelman-Rubin statistic was ≤ 1.1 for all parameters (Gelman and Hill, 2007). The analysis was conducted in R environment, using the package ‘HMSC’ (Ovaskainen et al., 2017).

3.3. Associations between forest organisms and TreMs

We built a model combining four structural and compositional elements of the forest ecosystem: a) TreMs ($N = 15$); b) insect orders ($N = 10$); c) bat acoustic groups ($N = 5$); d) bird species ($N = 29$) (Table 1). We refer to these four as forest components. In our model, the associations between forest components co-vary as a function of the environmental predictors (Tikhonov et al., 2017). This allowed us to derive an association matrix (Ω), including correlations between forest components. This matrix was computed by transforming the variance-covariance matrix into a correlation matrix, using the posterior probabilities (Tikhonov et al., 2017). In this matrix, values close to 0 represent no associations and values close to either 1 or -1 indicate positive or negative associations, respectively. We considered only the associations included in more than half of the posterior probability distributions, resulting in a supporting level > 0.5 . As our aim was to test if TreMs directly influence the abundance of forest components or just mediate the effect of the environment, our next step was to understand if causal links could be inferred from our correlation matrix, i.e. if the correlations emerged as a consequence of similar responses to the environment or if there are potential underlying links. We selected all the correlated TreM – organism pairs scoring a correlation $\Omega > 0.3$ and built a structural equation model (SEM). For each forest component, we built a model including all environmental predictors and the correlated forest components as response variables. Taking into account overdispersion, each component was modelled assuming a Poisson or a negative binomial distribution. For each model, we performed a model selection procedure based on AIC scores, retaining only models scoring a $\Delta AIC < 2$ (Burnham and Anderson, 2002). For each forest component, the model with the lowest AIC and only significant response variables was chosen. These final models were then included in the SEM. We hypothesised the following paths, i.e. directional links between predictors and response variables: Environmental predictors - \rightarrow Forest components; TreMs - \rightarrow Organisms; Insects - \rightarrow Bats/Birds; Bats/Birds - \rightarrow Bats/Birds (Fig. 1). Correlated components within the same group were modelled assuming a correlated error. We tested for missing paths using the test for direct separation (Shipley, 2000) and the Fisher’s C statistic. We considered the model valid where no missing path was significant, the C statistic was not significant and all the response variables were significant. Furthermore, we looked at pseudo- R^2 as a measure of explained variance. Model selection was performed with the R package ‘glmulti’ (Caccagno and Mazancourt, 2010) and SEM were built with the package ‘piecewiseSEM’ (Lefcheck, 2016).

4. Results

The sampling returned data on 59 forest components including 15 TreM groups, 10 insect groups, 5 bat groups and 29 bird species (Table 2). All the variables in the model reached convergence showing an average Gelman-Rubin statistic of 1.06. Nonetheless, the effect estimates of many predictors on the forest components had standard deviations crossing 0, indicating potential null effects (Fig. 2). The estimated effects for each predictor can be found in the supplementary information (appendix S2).

Among the 59 forest components included in the model, 10 comprised association $\Omega > 0.30$, for a total of 25 associated pairs (see detailed correlation matrix in appendix S3). The TreMs rot holes, concavities, crown deadwood and exudates were related to other forest components (Fig. 3). In particular, abundance of four orders of insects, Auchenorrhyncha, Heteroptera, Psocoptera, Sternorrhyncha, and two bat groups, *Pipistrellus* group and *Nyctaloid* group, scored the highest correlations with TreM abundance, while the abundance of bird species was generally weakly correlated with them (Fig. 3). The 10 forest components that scored a correlation $\Omega > 0.30$ were included in the SEM. Following our theoretical path diagram (Fig. 1) and our correlation matrix (appendix S3), we included the seven environmental predictors

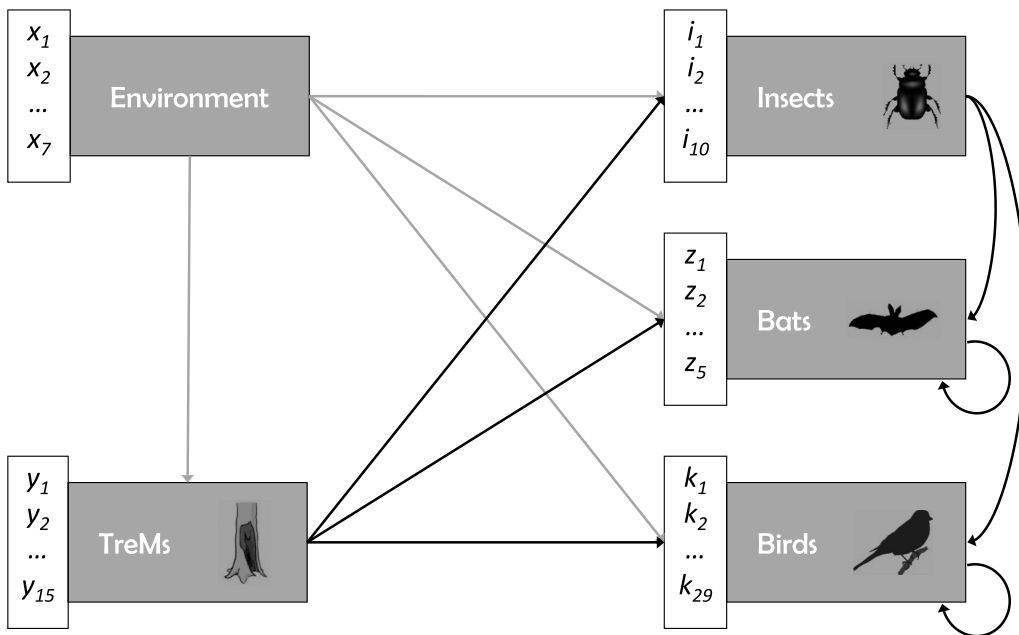


Fig. 1. Path diagram showing the theoretical paths hypothesised in this study. Other potential paths, not shown here, are tested for independence or modelled as correlated errors. Black arrows show the potential paths that constitute the objective of the present study. Letters indicate that each forest component is constituted of several components, each modelled separately (e.g. 'Birds' includes 29 species, i.e. k_{1-29}). Circular arrows indicate potential links between components within the same group.

in each model, and in addition: 1) TreMs as predictor variable for insects; 2) correlated insects as correlated errors; 3) TreMs and insects as predictor variables for bats; 4) *Pipistrellus* group as further explanatory variable for the *Nyctaloid* group. Crown deadwood and exudates were not significant predictors of any other forest component and Auchenorrhyncha were not significantly influenced by any other forest component. Therefore, they were excluded from the final SEM. The final SEM (after model selection) included two TreMs, rot holes and concavities, three insect orders, Heteroptera, Psocoptera and Sternorrhyncha, and bats from the *Pipistrellus* and *Nyctaloid* groups. All the other links between selected correlation pairs were not significant, and the Fisher's C test scored 73.4 ($p = 0.685$; $df = 80$). All the links included in the final SEM were significant ($p < 0.05$), including the correlation errors between rot holes – concavities and Heteroptera – Sternorrhyncha (appendix S4, table S4.1). We found direct links between the abundance of rot holes and Psocoptera, Sternorrhyncha and the *Pipistrellus* group and between concavities and Heteroptera and the *Nyctaloid* group (Fig. 4). In addition, rot holes had also an indirect effect on the *Nyctaloid* group, mediated by the *Pipistrellus* group and an indirect effect on both bat groups, mediated by Sternorrhyncha (Fig. 4). The total effect (direct + indirect effects) of rot holes on the *Pipistrellus* group was $0.116 + (0.1706 * 0.0103) = 0.118$. The total effect of rot holes on the *Nyctaloid* group was smaller: $(0.116 * -0.0011) + (0.1706 * 0.0446) = 0.008$. In most cases, the direct effect of TreMs on organisms was smaller than that of other environmental predictors (see example in Fig. 5, Psocoptera), except for the *Pipistrellus* group (Fig. 5). Nonetheless, TreMs contributed, via indirect links, to most of the paths (appendix S5, figure S5.1). Finally, pseudo- R^2 indicates that our SEM explained on average 51% of the variation in the data (appendix S4).

5. Discussion

5.1. Direct and indirect effects of TreMs on forest-dwelling animals

Our investigation of direct and indirect effects of TreM abundance on the abundance of forest-dwelling organisms indicated that other elements of forest composition and structure (e.g. lying deadwood) likely mediated the greatest effects. Yet, direct effects were also found between specific pairs of TreMs and organism groups. Our model provided evidence for the strongest associations with TreMs for invertebrates and bats. Birds showed overall weaker associations, which may be explained

by the wider spectrum of resources used by birds. Tree cavities, for example, are used by not more than 50% of the species in the assemblages of forest birds (Wesolowski and Martin, 2018), and this proportion is usually much lower in managed forests. Other TreMs present in studied forests are probably only of inferior importance for birds.

The strongest relationships were found with rot holes. Positive effects of rot holes on threatened epiphytes and saproxylic insects have also been demonstrated for beech forests (Fritz and Heilmann-Clausen, 2010; Müller et al., 2014). Rot holes, together with woodpecker cavities, play also an important role as roosting sites by bats (Boonman, 2000; Ruczyński and Bogdanowicz, 2005). All of the mentioned studies shared the use of TreM-related variables to model the abundance or occurrence of forest organisms or adopted an experimental design (e.g. in Müller et al., 2014, the authors placed insect traps in front of the rot holes; in Ruczyński et al., 2005, the authors radio-tracked bats and directly observed the roosting trees). In contrast, direct functional relationships between particular TreMs and certain taxa were not analysed in our design. Instead we modelled TreM abundance, as well as abundance of other forest organism, as a function of forest structure and other environmental variables and then investigated the relationships between abundances of TreM groups and co-occurring forest organisms. This approach allowed us to disentangle the direct effects of TreM groups on the other organism groups from the effects of forest structure, eventually mediated by TreMs. The identified correlations between TreMs and organisms along environmental gradients do not necessarily indicate causal links since other underlying factors may influence response variables. However, after testing the correlations in a structured equation model (SEM), we were able to identify direct effects between TreMs and organisms. An important qualification is that our study made use of count data only and we therefore consider the direct links indicated by the SEM as potential interactions. Further research could clarify the types of links we found, and potentially assess causal relationships. We did not find correlations in every case where these were expected. For instance, we did not find correlations between abundance of cavity-nesting birds and abundance of cavities, either woodpecker-made cavities or natural ones, even though such relationships are well known (Cockle et al., 2010; Newton, 1994). This may be attributable to our focus on management practices i.e. selection of live habitat trees (Forst, 2016). Therefore, TreMs on snags were not included in our study. It is likely that cavities on snags together with cavities in living trees could have higher level of association with cavity nesters at

Table 2

Forest components considered in the present study. Raw counts (mean ± sd) of components per plot (see appendix 1 for the definition of ‘counts’). Rarity expresses the % of plot in which the component has been found in. The sum of the means for each group of forest component is shown in bold (±sd).

Forest component	Description	Raw counts	Rarity
Woodpecker cavities	Cavities excavated by woodpecker for breeding	0.14 ± 0.53	8.14
Rot holes	Cavities containing moulds, including trunk holes, chimneys and hollow branches	1.41 ± 1.89	52.33
Insect galleries	Hole network excavated by xylophagus insects	0.13 ± 0.98	3.49
Concavities	Dendrotelms, woodpecker foraging holes and root-buttress concavities	7.69 ± 8.64	89.53
Sapwood	Bark openings and fire scars	5.01 ± 15.58	88.37
Heartwood	Stem breakages, cracks and lightning scars	0.41 ± 1.18	22.09
Crown deadwood	Dead ends	3.51 ± 4.55	74.42
Tangles	Witch brooms and epicormics shoots	0.50 ± 1.14	26.74
Cankers	Burrs and cankers	0.35 ± 0.63	27.91
Perennial fungi	Perennial polypore	0.01 ± 0.11	1.16
Annual fungi	Annual polypore, pulpy agarics, pyrenomycetes and myxomycetes	0.08 ± 0.41	4.65
Epiphytes	Bryophytes, lichens, ivy, lianas, ferns and mistletoe	8.33 ± 9.93	88.37
Nests	Nests made by vertebrates and invertebrates	0.29 ± 0.65	20.93
Microsoils	Soil deposits on bark and crown	0.20 ± 0.50	15.12
Exudates	Sap run and resinosis	4.42 ± 6.28	69.67
TreMs (total)		32.47 ± 22.2	100
Auchenorrhyncha	Suborder of Hemiptera, Insecta	2.51 ± 3.05	98.84
Coleoptera	Order of Insecta	43.70 ± 27.67	100
Diptera	Order of Insecta	65.31 ± 47.22	100
Heteroptera	Order of Insecta	2.13 ± 1.96	91.86
Hymenoptera	Order of Insecta	12.83 ± 8.97	100
Lepidoptera	Order of Insecta	0.50 ± 0.65	43.02
Neuroptera	Order of Insecta	0.62 ± 0.58	56.98
Psocoptera	Order of Insecta	8.56 ± 6.85	100
Sternorrhyncha	Suborder of Hemiptera, Insecta	27.52 ± 22.18	100
Thysanoptera	Order of Insecta	2.67 ± 2.60	94.19
Insects (total)		540.0 ± 60.3	100
<i>Myotis</i> group	Alcathoe bat, Bechstein’s bat, Brandt’s bat, Daubenton’s bat, Geoffroy’s bat, Greater mouse-eared bat, Whiskered bat, Natterer’s bat	74.98 ± 181.6	100
<i>Pipistrellus</i> group	Kuhl’s Pipistrelle, Nathusius’ Pipistrelle, Common Pipistrelle, Soprano Pipistrelle, Savi’s Pipistrelle	306.5 ± 361.8	100
<i>Nyctaloid</i> group	Northern bat, Serotine bat, Noctule bat, Leisler’s bat, Parti-coloured bat	6.42 ± 18.36	77.91
<i>Barbastella barbastellus</i>	Barbastelle bat	0.50 ± 1.84	15.12
<i>Plecotus</i> group	Brown Long-eared bat, Grey Long-eared bat	0.27 ± 0.50	24.42
Bats (total)		388.6 ± 405.3	100

Table 2 (continued)

Forest component	Description	Raw counts	Rarity
<i>Aegithalos caudatus</i>	Long-tailed tit	0.22 ± 0.58	17.44
<i>Buteo buteo</i>	Common buzzard	0.16 ± 0.40	15.12
<i>Certhia brachydactyla</i>	Short-toed treecreeper	0.07 ± 0.26	6.98
<i>Certhia familiaris</i>	Eurasian treecreeper	0.94 ± 0.64	77.91
<i>Columba palumbus</i>	Wood pigeon	1.17 ± 2.52	61.63
<i>Corvus corone</i>	Carrion crow	0.43 ± 0.78	30.23
<i>Cyanistes caeruleus</i>	Blue tit	0.33 ± 0.69	22.09
<i>Dendrocopos major</i>	Great-spotted woodpecker	0.79 ± 0.81	59.30
<i>Dryocopus martius</i>	Black woodpecker	0.21 ± 0.44	19.77
<i>Erithacus rubecula</i>	Eurasian robin	1.44 ± 0.70	95.35
<i>Fringilla coelebs</i>	Chaffinch	2.12 ± 0.86	98.84
<i>Garrulus glandarius</i>	Eurasian jay	0.70 ± 0.91	52.33
<i>Lophophanes cristatus</i>	Crested tit	0.70 ± 0.67	58.14
<i>Loxia curvirostra</i>	Crossbill	0.29 ± 0.91	15.12
<i>Milvus milvus</i>	Red kite	0.15 ± 0.45	11.63
<i>Parus major</i>	Great tit	0.91 ± 0.76	67.44
<i>Periparus ater</i>	Coal tit	1.74 ± 0.77	96.51
<i>Phylloscopus collybita</i>	Chiffchaff	0.88 ± 0.90	63.95
<i>Poecile palustris</i>	Marsh tit	0.27 ± 0.56	20.93
<i>Prunella modularis</i>	Dunnock	0.52 ± 0.65	44.19
<i>Pyrrhula pyrrhula</i>	Bullfinch	0.31 ± 0.56	26.74
<i>Regulus ignicapilla</i>	Firecrest	0.80 ± 0.59	70.93
<i>Regulus regulus</i>	Goldcrest	1.22 ± 0.58	91.86
<i>Sitta europaea</i>	Eurasian nuthatch	0.73 ± 0.71	59.30
<i>Sylvia atricapilla</i>	Blackcap	1.00 ± 0.91	70.93
<i>Troglodytes troglodytes</i>	Eurasian wren	0.98 ± 0.67	77.91
<i>Turdus merula</i>	Eurasian blackbird	1.19 ± 0.80	82.56
<i>Turdus philomelos</i>	Song thrush	0.93 ± 0.82	68.60
<i>Turdus viscivorus</i>	Mistle thrush	0.41 ± 0.66	32.56
Birds (total)		21.62 ± 4.47	100

the plot level.

5.2. Usefulness of TreMs as indicators of forest-dwelling animals

TreMs may be used to determine which trees to retain as habitat trees. In managed forests, this is relevant since many TreMs represent tree defects (Maxence and Raymond, 2019) that may decrease the current and future commercial value. Hence, if it was not for the habitat value of trees, the presence of TreMs could increase the probability that trees are harvested because they will likely not increase in value (Kenefic and Nyland, 2007). Assessment of TreMs may be incorporated

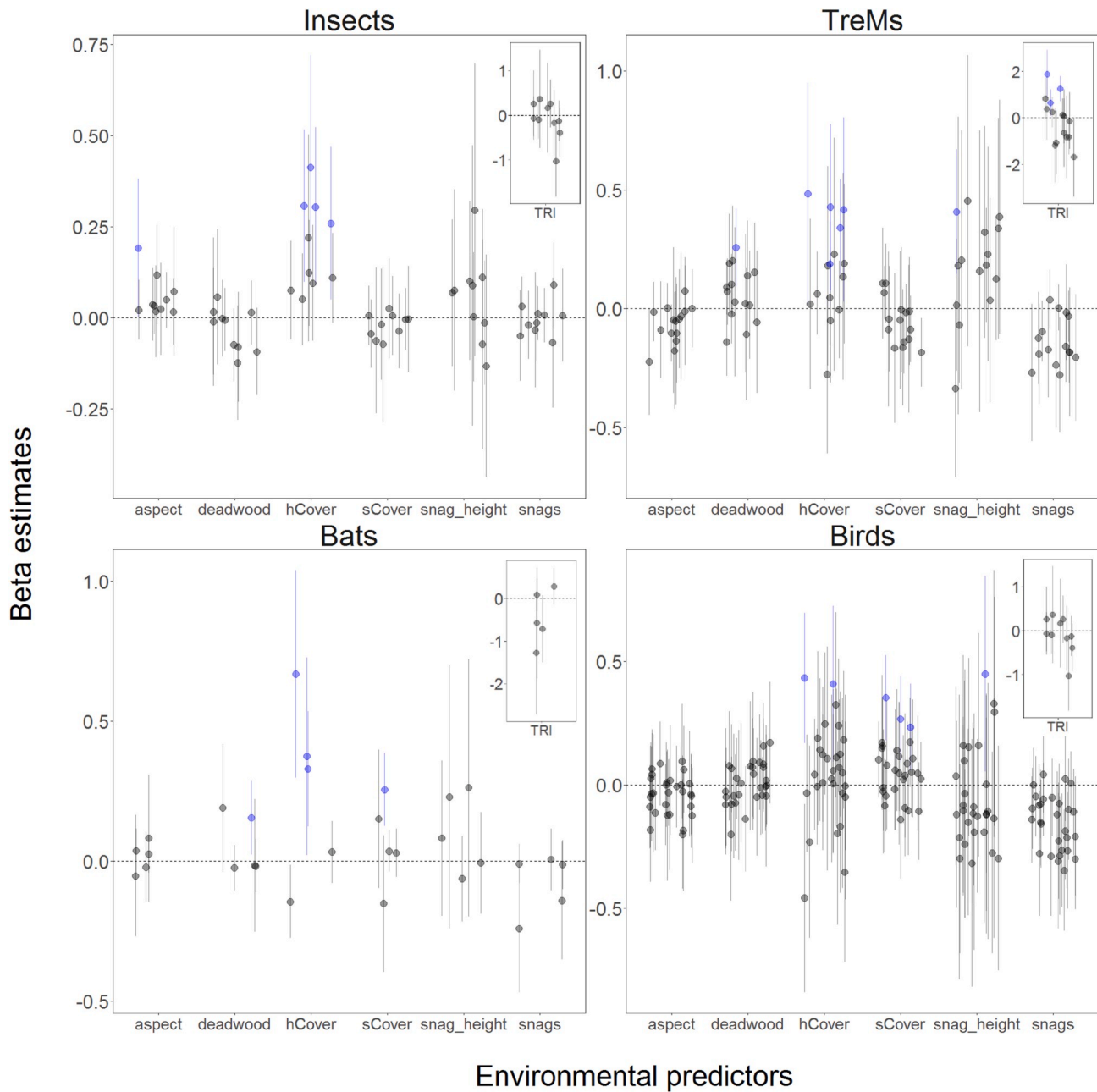


Fig. 2. Responses of the forest components considered in the present study to the environmental predictors. Beta estimates are the effect estimates of each environmental predictor on the abundance. Each dot represents a component belonging to one of the four groups. Blue dots indicate estimates which standard deviations do not cross 0. The response to TRI is shown in the top-right corner of each plot, due to the different scale of the effect (for graphic purpose only). Deadwood = lying deadwood volume; hCover = Herb layer cover; sCover = shrub layer cover; snag_height = height of the standing dead trees; snags = number of standing dead trees; TRI = terrain ruggedness index. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

into regular forest inventories since these tree attributes can be easily attached to other information on trees captured in the inventory (e.g. [Storch et al., 2018](#)). Even if TreM inventories are starting to be adopted in forest monitoring schemes ([Forst, 2016](#); [Santopuoli et al., 2019](#)), exhaustive knowledge on their direct links to biodiversity is still lacking (see [Larrieu et al. \(2018\)](#) for an overview of the direct links found in the literature). The weak evidence for many forest structural indicators as surrogates for elements of forest biodiversity has been highlighted in a recent systematic review ([Gao et al., 2015](#)). The evidence for TreMs points in the same direction, showing a weak but positive relationship with the species richness of saproxylic beetles, bats and birds ([Bouget et al., 2013](#); [Regnery et al., 2013](#); [Winter and Möller, 2008](#)). Furthermore, TreMs can mediate the effects of forest structure, such as

deadwood, on species richness and abundance of forest-dwelling taxa and may have a positive effect on bat species richness ([Paillet et al., 2018](#)). Our study is the first to test for direct links between all currently recognized tree-related microhabitats of temperate forests and a set of forest organisms, using sampling methods corresponding to common TreM monitoring schemes. Our results revealed several types of associations, which might indicate true biotic interactions hiding behind the co-occurrence patterns. In particular, we found that rot holes and concavities were the TreMs with strongest linkages to the studied organism groups. They can have positive or negative effects, depending on the group considered. However, except for the *Pipistrellus* bat group, the role of TreMs in predicting the abundance of dependent forest organisms is not as relevant as the role of other forest structures, like deadwood.

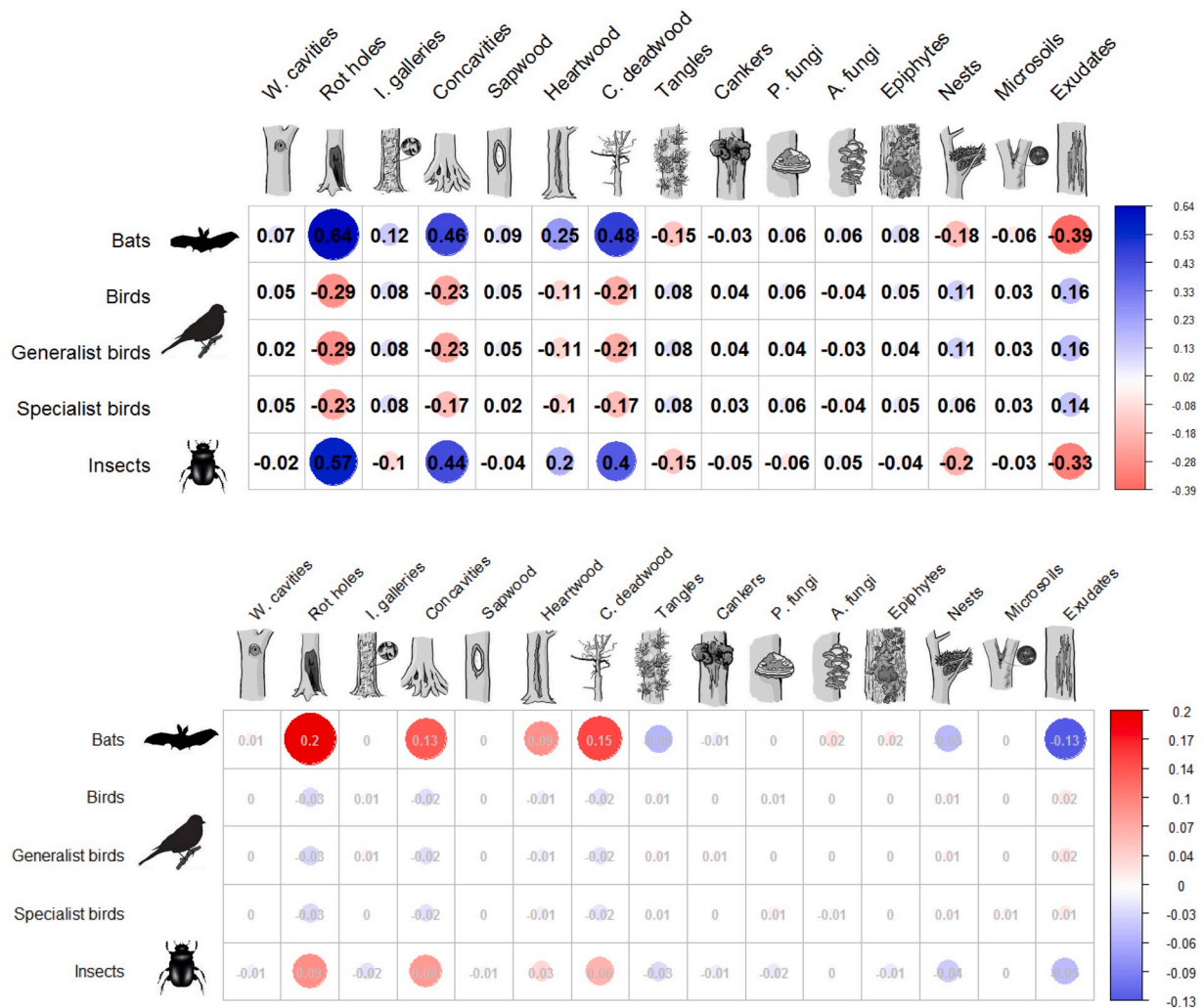


Fig. 3. Correlation matrix between bats, birds and insects with TreMs, showing the highest correlation found among the components in each group of organisms with TreMs. Red circles show positive correlations while blue circles show negative correlations. The number in the circles indicates the correlation score. Birds are classified as forest generalists or specialists, following Mikusiński et al. (2018). This correlation matrix is employed to hypothesise paths between TreMs and forest organisms. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Nevertheless, the ability of our model to predict links, as highlighted by the pseudo- R^2 , is generally good (and especially high for concavities and the *Nyctaloid* group). This indicates that it could be possible to predict the abundance of specific forest organisms from the abundance of specific TreMs. Yet, the weak correlation with forest organisms confirmed in this study and the minor role of TreMs as predictor variables do not provide a sound enough basis to suggest TreMs as general forest biodiversity indicators. Using TreMs instead of, or in addition to other indicators, includes the possibility to quantify the ecological value of trees in a more objective way.

Our results suggest that stand-level forest management should retain standing dead trees, as they showed strong positive correlation with some forest organisms, and develop or maintain a multi-layered and vertically complex structure, as suggested by the associations between some forest organisms and the terrain ruggedness index. At the same time, retention trees with rot holes and concavities and those with known association between microhabitats and certain forest species (e.g. woodpecker cavities) should be selected with priority. Further research may help to disentangle true biotic interactions from simple associations, leading to a better understanding of the role these tree features play and a better assessment of the ecological value of habitat trees. Our study was based on data originating predominantly from mature stands (>60 years) subjected to similar silvicultural

management regime. The stands are dominated by few tree species, with generally low variation in TreM abundance among stands (Asbeck et al., 2019), even if the sampling design covered the regional variation well. Possibly, in forest landscapes with wider-ranging conditions, from plantations with very few TreMs to old-growth stands with a high level of naturalness, a similar analysis might show a greater direct dependence of abundance of different taxa on these elements. In addition, we may also find stronger relationships, if we adapted the sampling design of TreMs to the habitat size of the analysed taxonomic groups. Here we had quantified TreMs on the largest 15 trees within a one ha plot, which may not be representative of the habitat patch of some of the analysed species such as bats and birds.

6. Conclusions

Positive associations between TreMs and species groups may be used to specify conservation goals (Santopuoli et al., 2019). If some TreMs were more relevant for the diversity of forest dwelling organisms of conservation interest, they may be given prominence for identifying or valuing of habitat trees. In our study, rot holes and concavities clearly played a greater role than other TreMs for the abundance of the selected taxa. For example, Fritz and Heilmann-Clausen (2010) studying epiphytic organisms proposed using the presence of rot holes in trees as

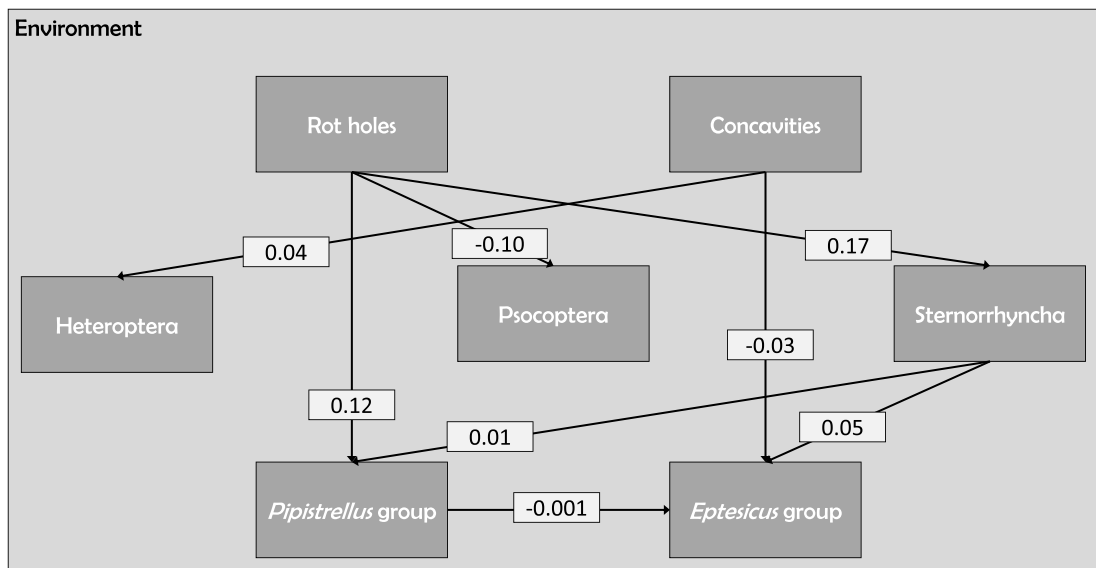


Fig. 4. Path diagram showing those forest components, for which significant relationships with other forest components considered in the present study were found. The effect of the background environment is not shown. The numbers in the white boxes indicate the effect estimate of the link. The arrows point at the response variables.

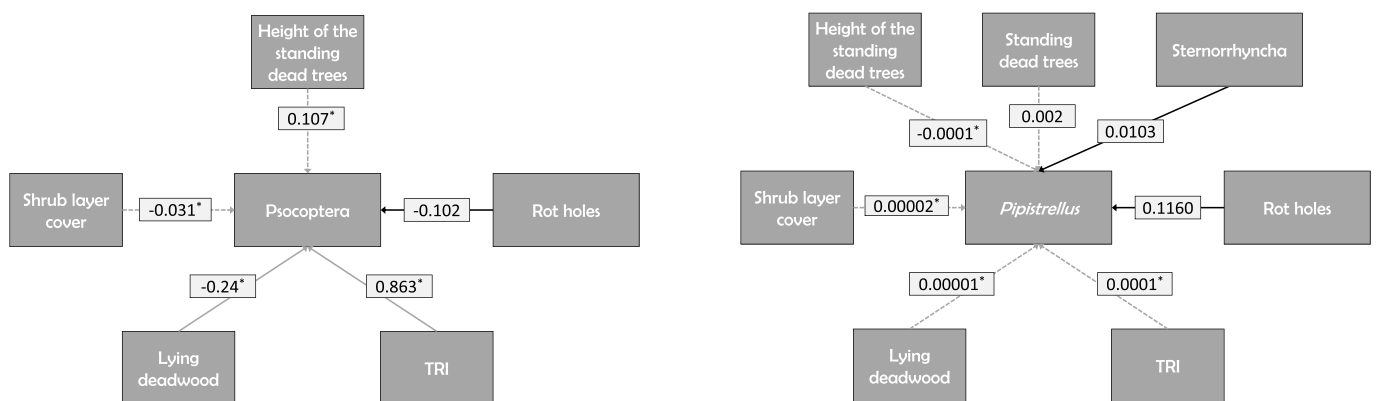


Fig. 5. Path diagrams showing all the significant independent variables influencing Psocoptera and the *Pipistrellus* group. The arrows point at the response variable. Grey-dashed arrows indicate only indirect effects; grey arrows indicate direct and indirect effects; black arrows indicate direct effects. The numbers in the boxes indicate the total effect estimate. A star next to the number indicates that the indirect effect is mediated by concavities.

a criterion for identifying retention trees. However, such decisions should be based on evidence for causal relationships between TreMs in a given forest ecosystem and a wider range of taxonomic groups.

Authors' contributions

MB conceived the idea for this analysis. All authors designed the data collection; IS, VB and JB co-designed the overall study. MB, TA, MJ, AKK and GM collected and managed the data. MB performed the analysis. MB and TA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interests

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. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2020.110401>.

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