

RESEARCH ARTICLE

Disentangling direct and indirect effects of forest structure on biodiversity: Bottom-up and top-down effects between forestry, bats and their insect prey

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Handling Editor: Marc-André Villard**Abstract**

1. Timber-oriented forest management profoundly alters forest structure and composition, with complex effects on associated biodiversity. However, while species' responses to forest management and resulting structural characteristics have been the subject of numerous studies, direct and indirect effects that cascade through trophic levels are rarely disentangled. As insectivorous bats are particularly sensitive to changes in forest structure, that shape their available flight space, we investigated how forest structure, composition and management also indirectly modify their habitats, for example, by affecting important insect prey groups.
2. We used structural equation models (SEMs) to test bat responses to forest composition, structure (forest heterogeneity, old-growth attributes) and management intensity, quantifying direct and indirect prey-mediated effects. For that, three bat guilds—short- (SRE), mid- (MRE) and long-range echolocating (LRE) bats—and their prey insects (moths and ground beetles) were analysed from 64 sites in the Black Forest, Germany.
3. We found guild-specific effects on bats: While the structural heterogeneity of forests directly influenced the activity of bat guilds, the main influence of forest management, composition and structure was mediated through their prey-groups.

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4. SRE activity responded to moths and LRE activity was associated with ground beetles, with positive effects of the insect groups' abundance, but negative effects of the same group's species richness. In addition, the SEM approach revealed a negative top-down relationship between MRE activities and moths, suggesting predation or avoidance behaviour of moths.
5. While forest management directly or indirectly increased prey insect abundance, it negatively affected the availability of roosting structures for bats.
6. *Synthesis and applications.* The results highlight the indirect and positive effects of forest management on bats and support the important role of bats in insect regulation within continuous cover forests. Although forest management created small gaps that improved foraging habitats for most bats, it compromised the roosting functionality for bats. The 'close-to-nature forestry' currently prevalent in Europe mainly promotes continuous-cover forests in mid-successional stages. Expanding the forest management portfolio towards open and old-growth forests would increase roosting opportunities and provide complementary foraging habitats for different bat species, while promoting high biodiversity in managed forest landscapes.

KEYWORDS

Chiroptera, foraging, forest biodiversity conservation, forest management, insect availability, structural complexity, structural equation models, trophic linkages

1 | INTRODUCTION

Forest management alters the composition and structure of forests, by creating structurally homogenized landscapes in which key resources for forest dwelling species, such as senescent trees and deadwood, have become scarce (Bauhus et al., 2013; Braunisch et al., 2019). As a result, today diverse biodiversity conservation measures aim to restore the compositional and structural diversity of forests (Aggestam et al., 2020; Gustafsson et al., 2020). Taxonomic responses are usually assumed to relate directly to the studied forest characteristics, or serve as proxies describing intermediate resources, for example, unmeasured food resources that are relevant for the studied taxa (Zeller et al., 2023). This way, the species-habitat associations are described, while the underlying mechanisms remain unexplored. Understanding and disentangling direct and indirect effects of forest characteristics on target taxa is thus important for making effective management recommendations.

Many bat species require special conservation measures and rely on forests as one of their most important habitats (Tuttle, 2007). In these, bats are highly sensitive to forest compositional and structural characteristics (Froidevaux et al., 2016; Jung et al., 2012) and are key predators of insects (Beilke & O'Keefe, 2022). To thrive, bats rely on suitable roosting and foraging sites within forests. Although forest characteristics affect foraging bats indirectly by modifying prey insect availability, they also directly influence the

site accessibility and consequently foraging efficiency (Adams et al., 2009; Blakey et al., 2016; Carr et al., 2020; Froidevaux et al., 2021). Bat foraging habitat preferences are related to their echolocation calls and morphology (Schnitzler et al., 2004). Based on those, bat species have been grouped into three different guilds (Frey-Ehrenbold et al., 2013): (1) short-range echolocating bats (SRE), which prefer denser forests; (2) mid-range echolocating bats (MRE), foraging predominantly in semi-open spaces; and (3) fast-flying, long-range echolocating bats (LRE) that forage over the canopy or in forest gaps.

European bat species prey on various arthropods, including flies (Diptera), moths (Lepidoptera), beetles (Coleoptera), caddisflies (Trichoptera) and spiders (Arachnida) (Froidevaux et al., 2023; Vaughan, 1997; Ware et al., 2020). Across habitats, prey availability not only influences habitat selection (Bartonicka & Zúkal, 2003; Mendes et al., 2016), but also within a habitat type, bat activity should increase with insect abundance, previously confirmed for open and edge habitats (Cel'uch & Kropil, 2008; Ciechanowski et al., 2007; de Jong & Ahlén, 1991; Froidevaux et al., 2021; Müller et al., 2012). In forests, dense vegetation could reduce prey capture, while providing reliable food resources for bats (Blakey et al., 2016; Carr et al., 2020; Müller et al., 2012). However, opposing evidence exists (Cel'uch & Kropil, 2008; Kusch et al., 2004) as many insect groups are associated with conditions of open forest canopies. Furthermore, the effects of insect species richness on foraging bats remain largely unexplored because they have not been

isolated from those of insect abundance (Mirts et al., 2022; Treitler et al., 2016), despite the known relationship between the two (e.g. more-individuals hypothesis, Storch et al., 2018). However, positive effects can occur as species-rich habitats provide stable feeding resources over time (i.e. diversity-stability hypothesis, as in Haddad et al., 2011). This highlights the uncertainty about the extent and nature of the relationships between forest characteristics, insects and bats, and whether these are direct or prey-mediated. Furthermore, to derive targeted management recommendations supporting bats, the combined direct and indirect effects of multiple compositional and structural characteristics need to be considered.

In this study, we investigate the relationships between forest composition, structure and management, the abundance and richness of nocturnal insects and the activity of bats in a temperate mountain forest, using structural equation models (SEMs). Our research questions were: (1) What are the (direct) effects of forest management, composition, heterogeneity and the availability of old-growth structures on different bat guilds? (2) How does forest management, different forest characteristics and the understorey vegetation influence the abundance and richness of insect prey groups for bats? (3) How do bat guild activities respond to insect groups and what are the resulting indirect effects of forest

characteristics on bat guild activities? and (4) Is there evidence for top-down effects of bats on insects?

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area is located in the Black Forest, Southwest Germany (516–1334 m a.s.l.; Figure 1), a temperate mixed montane forest dominated by Norway spruce (*Picea abies* L.), beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill). Large parts of the study area are forested, with approximately 25% of the forest being state-owned and managed under 'close-to-nature forestry' (CNF). Data were used from 64 one-hectare plots (see Appendix S1.1). All plots had an average stand age over 60 years and represented gradients of coniferous tree shares, canopy openness, vertical complexity and dead wood volumes. Plots were located on base-poor bedrock types and excluded waterbodies and human infrastructure. Plot access was provided by ForstBW, and the conservation authorities of the State of Baden-Württemberg issued a permit for insect collection (RPF55-56-8852-133/1/10). No further ethical approvals were required.

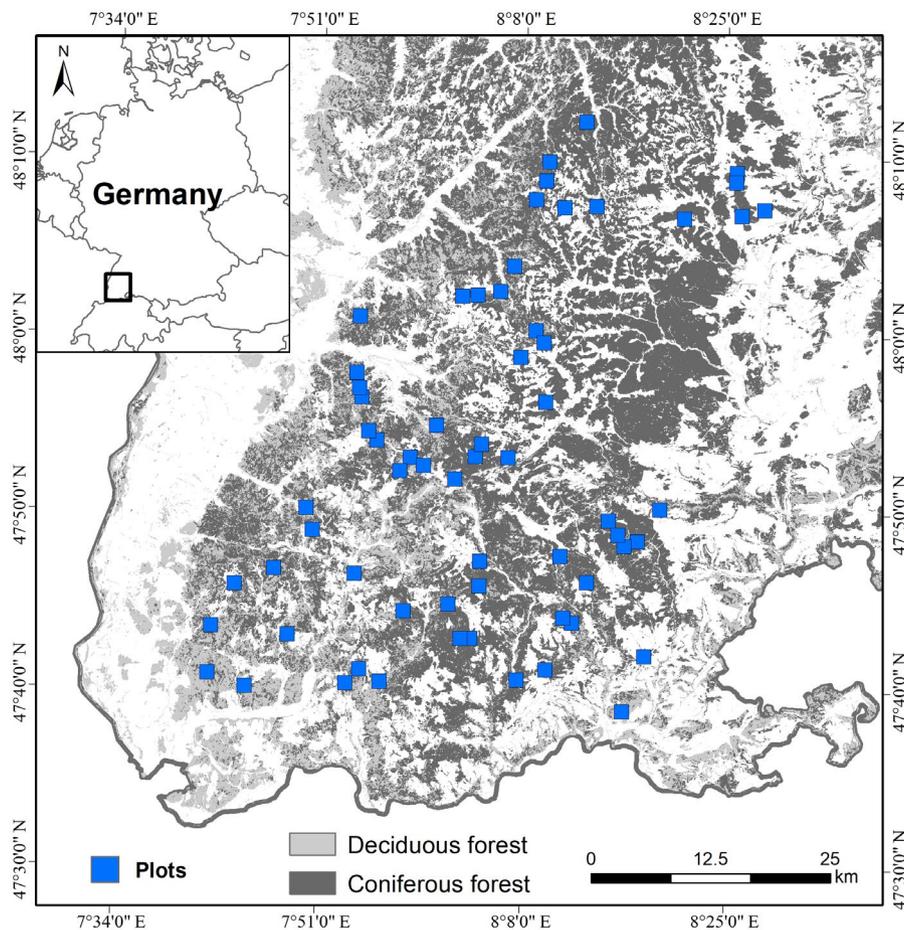


FIGURE 1 Overview of the study area and the plot locations ($N=64$). The plot sizes are 1 ha in size but were enlarged to increase visibility. Minimum distances between the plots were 750 m.

2.2 | Variable descriptions

2.2.1 | Forest management

We used the Management Intensity Index 'ForMI' to quantify past management on each plot (Kahl & Bauhus, 2014). The index integrates (1) proportions of harvested tree volume, (2) proportions of non-native tree species and (3) proportions of dead wood showing signs of saw cuts. ForMI values increase with management intensity (Table 1). Data for the first two ForMI components came from a full inventory in 2016/2017 (Storch et al., 2020), that included all trees with a diameter at breast height (1.3 m, DBH) above 7 cm. Deadwood data were collected in 2020 (Asbeck & Frey, 2021).

2.2.2 | Forest composition

The forest composition was described by the 'tree species richness' and 'coniferous share' and was assessed during the full inventory (Storch et al., 2020). The coniferous share was calculated as the proportion of the total basal area occupied by coniferous trees.

2.2.3 | Forest structure

2.2.3.1 | Forest heterogeneity

We described forest structure heterogeneity using the 'openness' and the tree 'height heterogeneity'. Openness was measured using Solariscope SOL300 (Ing.-Büro Behling, Wedemark) at the top of the understorey vegetation and describes the openness of the mid- and canopy-forest layers. In each plot, we took measurements between May and September 2020 at 18 systematically arranged locations. Values were averaged per plot. The variable 'height heterogeneity' represents the standard deviation (SD) in canopy heights, which were obtained from UAV imagery in 2019/2020 using a structure-from-motion workflow (Frey et al., 2018).

2.2.3.2 | Old-growth structure

The average tree 'DBH' and the number of standing 'dead trees' per plot were used to describe old-growth forest structure. Data were collected during the inventory (Storch et al., 2020).

2.2.4 | Tree-related microhabitats

Tree-related microhabitats (hereafter microhabitats) were inventoried in 2019, 2020 from the ground using binoculars. Surveys of the 15 largest living trees and, where present, up to 15 dead trees were conducted in the winter, when crown visibility was enhanced. As bats use particular microhabitat types for roosting, we used the abundance of cavities, branch-holes, exposed heartwood, cracks and scars, and bark shelters or pockets (from the classification of Larrieu et al., 2018, see Appendix S2.2).

2.2.5 | Taxonomic groups

2.2.5.1 | Understorey surveys

Understorey vegetation included all vascular plants in the herb layer (lower than 1.50 m) and surveys were conducted between May and September 2020. Species identity and overall understorey cover were determined at 18 subplots of 1 m². The mean understorey plant cover and the total understorey plant richness were calculated per plot. For 12 plots with missing data, we estimated the data through regression (see Appendix S1.3).

2.2.5.2 | Insect surveys

We sampled insects with three pitfall traps, targeting ground beetles, and one ultra-violet (UV) light-trap per plot, targeting moths. The latter were flight interception traps (Knuff et al., 2019) equipped with UV fluorescence actinic tubes (15 W, Bioform, Article No.: A32b) in the middle. Light-traps were installed at 1.4 m height at the plot centre and were active once per plot for 6 h after sunset between May and August 2020 (Appendix S1.2).

TABLE 1 Untransformed value ranges for the variables describing forest management, forest characteristics (forest composition, forest heterogeneity and old-growth structures) and the availability of microhabitats in the study plots ($n = 64$).

Groups	Variables	Unit	Mean	Std	Min	Max
Forest management	ForMI	Index	1.2	0.5	0.0	2.4
Forest composition	Tree richness	Richness	5.1	1.6	2	10
	Coniferous share	%	77	23.6	8	100
Forest heterogeneity	Openness	Index	28.7	18.0	4	95
	Height heterogeneity	m	9.8	2.3	3.0	14.5
Old-growth structures	DBH	mm	304	79.1	141.6	526.2
	Dead trees	Count	48	74.2	0.0	394.0
Microhabitats	Microhabitats	Abundance	7.1	8.6	0	40

Light-trapping was synchronized with the bat survey and was performed during the second of three consecutive sampling nights. Insects were caught in 50% propylene glycol. Moth samples were counted in the laboratory and identified to species-level using metabarcoding (Appendix S1.4). Although 59% of the insects caught (body length > 2 mm) were moths, the samples also included bycatch consisting of 13% beetles, 11% flies, 9% caddisflies (Trichoptera) and 8% other orders (Hymenoptera, Neuroptera and Hemiptera). Due to the low numbers of individuals from these bycatch orders, and because light-trapping targets phototactic insects, they were excluded from our study. Pitfall traps targeting ground beetles (Coleoptera: Carabidae) were installed separately, between April and May 2020, following the elevational gradient, and were retrieved after approximately 36 days (Pereira et al., 2024). One pitfall trap was set at the plot centre and two at the opposing plot corners. The traps included a rain cover and were filled with 250 mL of 50% propylene glycol. All ground beetles were identified to species-level. Due to missing data from several traps, ground beetle abundance and species richness were averaged across traps per plot.

2.2.5.3 | Acoustic bat surveys

Acoustic bat surveys were conducted for three consecutive full nights between May and September 2020 (details in Appendix S1.2), by placing bat loggers (Elekon A+) near the centre of each plot with the microphone facing horizontally to the least vegetated space in the surrounding at a height of 1.8 m. The logger sampling rate was 312.5 kHz, and the recordings were triggered by bats. The maximum length of one sequence was set to 15 s, with pre- and post-trigger times of 0.5 and 1 s, respectively. We analysed the recordings using BatScope version 4 (Obrist & Boesch, 2018). Bat recordings except for the Common pipistrelle (*Pipistrellus pipistrellus*, Schreb.) were manually verified to the genus-level and then grouped into three bat guilds, namely short-range echolocators (SRE; *Myotis* spp., *Barbastella barbastellus* and *Plecotus* spp.), mid-range echolocators (MRE; *Pipistrellus* spp. and *Hypsugo savii*) and long-range echolocators (LRE; *Eptesicus* spp., *Nyctalus* spp. and *Vespertilio murinus*) (see Frey-Ehrenbold et al., 2013, details in Appendix S2.5). *P. pipistrellus* was analysed separately from MRE-bats. Although grouping *Myotis* species into one guild is inaccurate, similarities in their call characteristics did not permit a more precise classification. Bat activity was expressed as the number of 1-min intervals containing echolocation calls of each bat guild per night (Müller et al., 2012). As light-traps modify bat behaviour (Froidevaux et al., 2018), we used bat activity data from the first and third night, when UV-light-traps were inactive. We avoided nights with forecasted rain and around full moon (Perks & Goodenough, 2020). Weather data were collected in the subcanopy using data loggers (HOBO H21-USB) and sensors (temperature: HOBO S-THB_M002; wind: onset-S-WSB-M003) at each plot. The average minimum night temperature (20:00 to 07:00) was included in the models.

2.3 | Statistical analysis

2.3.1 | Modelling process

We used structural equation models (SEMs) (Shipley, 2016) to test for effects of different forest characteristics on bat guild activity, as well as their indirect effects through the understorey vegetation and different insect groups. The added value of SEMs lies in the reporting of dependencies between residual variable variances that were not specified to be in relationship (independence claims), therefore uncovering correlations and indirect effects that can be overlooked using traditional mixed models. The hypothesized causal structure is shown in Figure 2. The SEM was built in a piecewise manner (Lefcheck (2016); developer version 2.2.1), by combining several generalized additive models (gams). The causal model, consistent with the data, was built as follows: (1) We fitted individual gams for each dependent variable, including the full set of hypothesized variables (full gams). (2) Automated variable selection was used to reduce the number of variables (selected gams). (3) We combined the selected gams into the SEM and tested the model fit. (4) As the SEM suggested few modifications of the causal structure (independence claims), we modified the concerned selected gams accordingly (modified gams). (5) We rebuilt the SEM including the modified gams and evaluated its overall fit. Individual gams were fitted using mgcv library (Wood, 2017) and model residuals were checked for the correct distribution, dispersion and outliers using the DhARMA package (Hartig, 2007). We tested for spatial autocorrelation using Moran's I (Hartig, 2007), which indicated no significant spatial structure at the 0.05 level. Responses of the SEM-supported gams were visualized with ggeffects (Lüdtke, 2018). All statistical analyses were conducted in R (version 4.2.1.) using RStudio 2023.03.0.

2.3.2 | Individual generalized additive models

Gams were specified for each dependent (response) variable according to the hypothesized SEM structure (Figure 2; or Appendix S3.1). Based on their value distributions, we fitted models using negative binomial distributions, but the understorey- and insect-richness models were specified with Gaussian distributions. For microhabitat availability and understorey vegetation, we expected links with the ForMI and all forest characteristics (forest composition, forest heterogeneity and the old-growth variables). We additionally expected understorey cover to affect the understorey richness. Furthermore, we expected the ForMI, the forest characteristics and the understorey to influence the abundance and species richness of ground beetles and moths, while we linked insect species richness to their abundance. Bat activity models included all forest characteristics and the ForMI as direct influences. In addition, we included the microhabitat availability and the insect group abundance and richness. However, due to differences in prey selection, we specified relationships between insect groups and SRE- and LRE-bats only, as

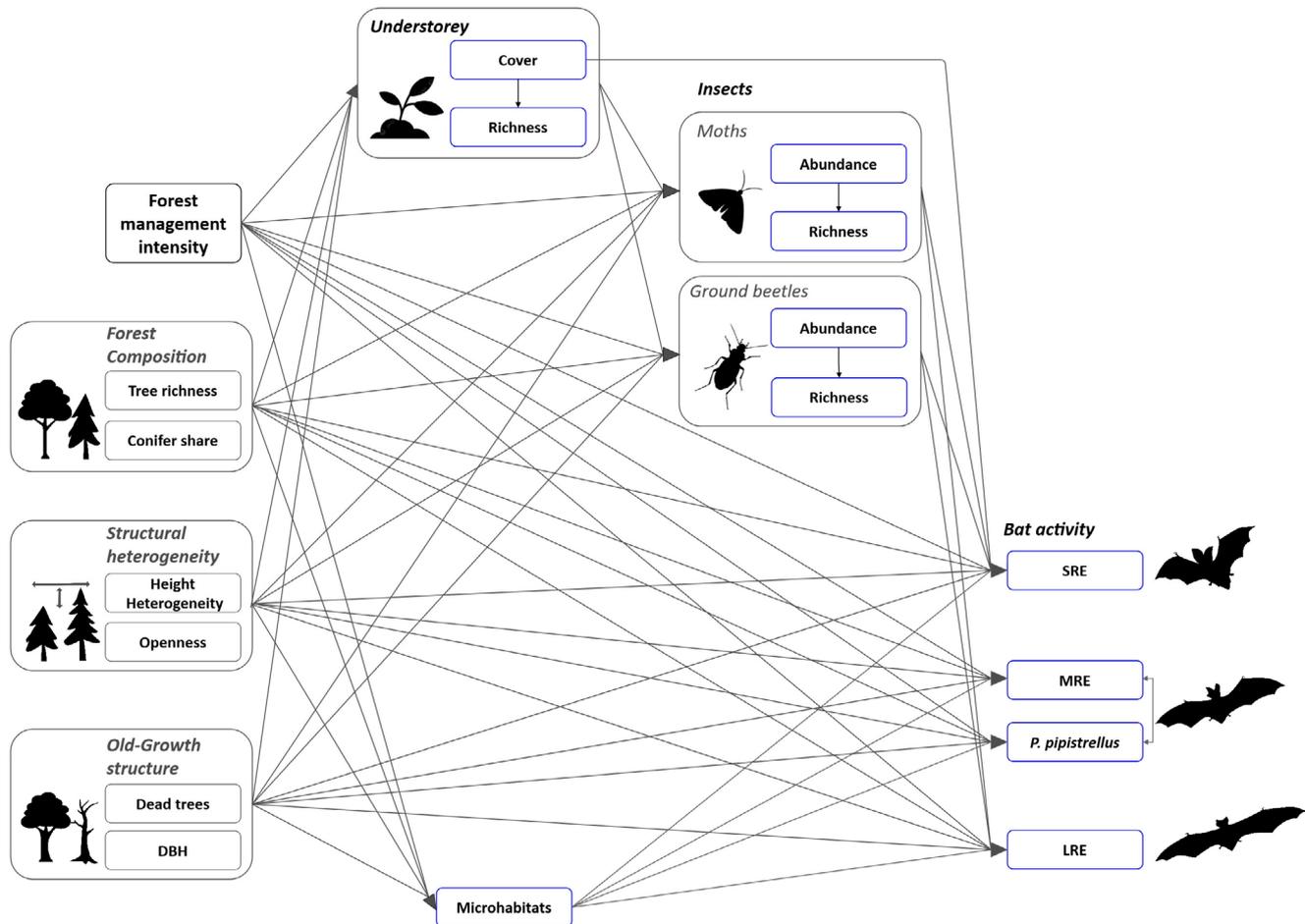


FIGURE 2 Hypothesized causal relationships between forest characteristics (forest composition, structural heterogeneity and old-growth structure), forest management intensity, microhabitats, understory vegetation and taxonomic (insect and bat) groups. The hypothesized causal relationships are represented by arrows. Dependent variables, for which generalized additive models were fitted, are highlighted with blue boxes. The relationships of variables of the same forest characteristic are visualized together. Note that relationships with elevation, date and temperature were also tested.

MRE-bats and *P. pipistrellus* primarily feed on flies (Vaughan, 1997; Ware et al., 2020). For SRE-bats, which include ground foraging species, we also used the understory cover as a predictor variable. In addition to the relationships visualized in Figure 2, all response variables were also expected to change with elevation (Appendix S3.1). Bat and moth models also included the sampling date and minimum temperature. Ground beetle models included the dates of trap installation. To allow simple non-linear relationships, all predictor variables (except for elevation and temperature for which we anticipated linear effects) were specified using smooth terms with three basis-functions.

2.3.3 | Variable selection

To simplify the causal structure, while avoiding a priori decisions, we performed automatic variable selection for the understory, insect and bat models using the MuMIn library (Barton, 2009). We selected the most parsimonious model based on the second-order Akaike

information criterion (AICc), limiting the models to a maximum of six predictor variables. When multiple models performed equally ($\Delta AICc < 2$), we included the six variables that occurred most often in the top-ranked candidate models ($\Delta AICc < 2$). When two variables appeared equally often, the variable appearing in the model with the lower AICc was chosen (Appendix S3.2).

2.3.4 | SEM evaluation

The selected gams were combined to resemble the hypothesized causal structure. Furthermore, we added a free correlation between the MRE and the *P. pipistrellus* activity. Shipley's test of directed separation (Fisher's C) was used to evaluate the SEM fit (Shipley, 2016; Shipley & Douma, 2021) and independence claims in the basis-set were derived according to Shipley and Douma (2021). Based on those, additional relationships were included in some of the selected gams. As Fisher's C test (Fisher's C-value = 321.6, $df = 216$, p -value < 0.05) rejected our hypothesized causal model and independence claims

suggested additional relationships between moth abundance and bats (MRE, *P. pipistrellus* and LRE activity). Thus, we included these top-down effects by adding *P. pipistrellus* and MRE (but not the rarer LRE) activities as predictors of moth abundance (Appendix S3.3). We also found statistical dependence between the ground beetle abundance and the microhabitat availability (negative) and between SRE/LRE activities and the date the ground beetle trap was set (positive). As a common unmeasured ancestor variable could have caused these relationships, we specified them as free correlations. The SEM with the modified gamms was re-evaluated. As we included non-linear relationships and untransformed variables into the SEM, we did not calculate total effects of forest structural components on bats.

3 | RESULTS

The SEM, which incorporated top-down effects from bats on moths, was consistent with our data (Fisher's C -value=208; $df=206$, p -value=0.44). Significant relationships between forest structural characteristics, forest management, insect groups and bats, which are supported by SEM, are presented in Figure 3 and described in the following sections. Based on the independence claims of the modified SEM, additional significant dependencies, for example, between further insect groups and microhabitats, were excluded.

3.1 | Effects of forest characteristics and management on bat guild activities

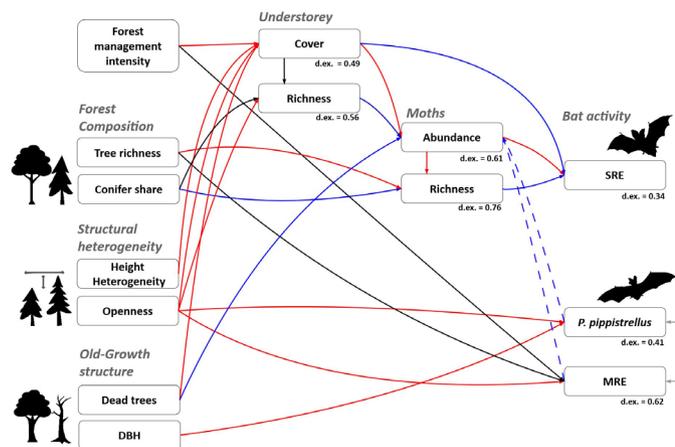
The average bat activity in the forest was 11.2 (SD=18.6) min for SRE-bats, 101.2 (SD=121.9) and 2.3 (SD=6.6) min for *P.*

pipistrellus- and MRE-bats, and only 1.2 (SD=2.0) min for LRE-bats per night. SRE-bat activity did not show significant direct responses to any of the forest structural variables. Instead, their activity decreased with understory cover, indicating preferences for closed and homogenous forest canopies with a low forest management intensity. Both *P. pipistrellus* and MRE activities increased with the canopy openness. In addition, a direct positive effect of tree size (DBH) was found for *P. pipistrellus*, while MRE activities showed unimodal responses to management intensity and tree species richness. LRE-bat activity increased strongly towards open and heterogeneous canopies. Overall, bat activities were most sensitive to forest management and aspects describing structural heterogeneity. The availability of microhabitats did not influence their activities (Figure 3), but was significantly reduced by the forest management intensity and high coniferous tree shares, and increased with the mean stand DBH.

3.2 | Influence of forest characteristics, management and understory characteristics on insect groups

Using the light-traps, we recorded on average 211.0 (SD=157.7) moths and 25.0 (SD=12.4) moth species per plot (Appendix S2.3). Mean ground beetle abundance per trap was 29.0 (SD=19.4), with an average of 5.4 (SD=1.8) ground beetle species (Appendix S2.4). Moth abundance increased with the understory cover, which was on average 38.7% (SD=25.4) and positively affected by forest height heterogeneity, forest management intensity and the number of standing dead trees. Despite its indirect positive effect through the understory cover, standing deadwood had a direct negative

(a) Short- and mid-range echolocating (SRE- and MRE-) bats



(b) Long-range echolocating (LRE-) bats

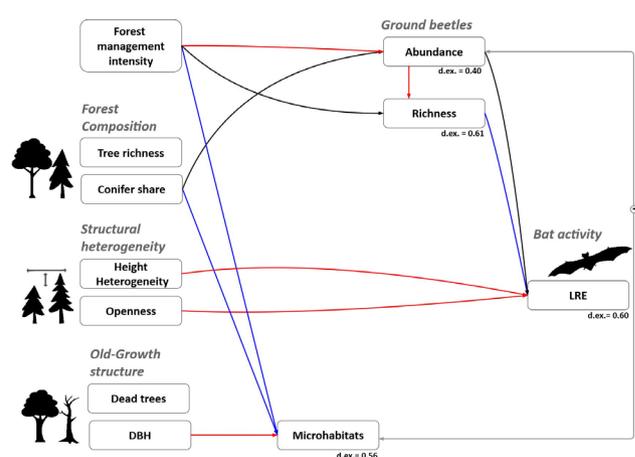


FIGURE 3 Structural equation model that presents significant relationships (p -value < 0.05) between forest characteristics, forest management, understory vegetation, insect groups and bat activity. Results for short- and mid-range echolocating (SRE- and MRE-) bats (a) are presented separately from those for long-range echolocating LRE-bats (b). Dashed lines highlight top-down relationships. Red lines indicate overall positive, blue lines negative relationships (linear or asymptotic). Black lines indicate unimodal relationships, while grey lines specify free correlations. For response variables, the deviance explained (d.ex.) is reported. Relationships with date, temperature and elevation are not shown (see Appendix S3.3). All significant relationships are visualized in S4.

relationship on moth abundance. Additionally, moth abundance decreased with the understorey vegetation richness. The latter increased with canopy openness and showed a unimodal relationship with understorey cover and the share of coniferous trees. Moth richness showed a positive relationship with moth abundance and was mediated by forest composition, with the tree species richness showing a positive effect, while the coniferous tree share had a negative effect. Ground beetle abundance showed a positive relationship with management intensity and a unimodal response to the share of coniferous trees. Ground beetle richness increased with the abundance and showed a peak in forests with an intermediate ForMI. Overall, forest management, forest composition and understorey characteristics predominantly influenced insect group abundance and richness.

3.3 | Insect–bat and bat–insect relationships

SRE- and LRE-bat activities were related to both insect group abundance and richness (Figures 3 and 4). SRE activity increased with moth abundance but decreased with moth richness. Although open forests with a heterogeneous canopy had an indirect negative effect on SRE activity by promoting understorey vegetation, they also promoted the occurrence of moths, which had a positive effect on SRE-bats (Figure 3). LRE-bat activity not only peaked at an intermediate ground beetle abundance but also decreased with the ground beetle richness. Indirectly, LRE activities were thus positively affected by forest management and a mixed forest composition (Figure 3). Moreover, the use of the SEM highlighted a negative influence of *P. pipistrellus* and MRE-bats on moth abundance. Although the variation in moth abundance was large where their respective activity was low, forest plots with high activity of these groups showed reduced moth abundance (Figure 4). However, the results for MRE bats should be interpreted with caution, as there were few forest plots with higher activity levels.

4 | DISCUSSION

Forest characteristics and management directly and indirectly affected bat foraging activity by altering prey abundance and richness, influencing SRE- and LRE-bats. While SRE-bats responded to moths, LRE activity was related to ground beetles. Although the results for LRE-bats should be interpreted with caution, as their observed activity was low and because ground beetles were sampled during day and night over longer periods, activities for both bat guilds increased with insect group abundance, particularly where insect group richness was low. This supports earlier findings (Carr et al., 2021; Mirts et al., 2022) and suggests that bats are attracted to places with high abundance of few insect species, which may enhance hunting efficiency. However, insect species richness is essential for prey continuity, benefitting bats with high foraging site fidelity (Kerth et al., 2001). To the best of our knowledge, this is the first study to report that SRE activity increases with moth abundance in continuous cover forests. Missing relationships in previous studies (Adams et al., 2009; Charbonnier et al., 2014; Froidevaux et al., 2021; Müller et al., 2012) were attributed to the restricted accessibility of denser forests even for manoeuvrable SRE bats. Relationships between SRE-bats and insects in forests should be explored further.

The SEM approach revealed a negative relationship between *P. pipistrellus* activities and the abundance of moths. Although analogous observations were attributed to divergent habitat preferences of bats and moths (Müller et al., 2012), our approach suggests a top-down relationship. The same negative top-down influence on moths was also found for MRE bats at much lower activity levels than *P. pipistrellus*, but remains to be verified as the relationship was driven by few datapoints. As *P. pipistrellus* and MRE-bats only occasionally forage on moths (Vaughan, 1997; Ware et al., 2020), the observed relationship may be caused by moths perceiving echolocation (Miller & Surlykke, 2001), and reducing their activity in the vicinity of bats or avoiding areas frequently used by them. While predation by bats can regulate (pest) insect populations (Beilke & O'Keefe, 2022;

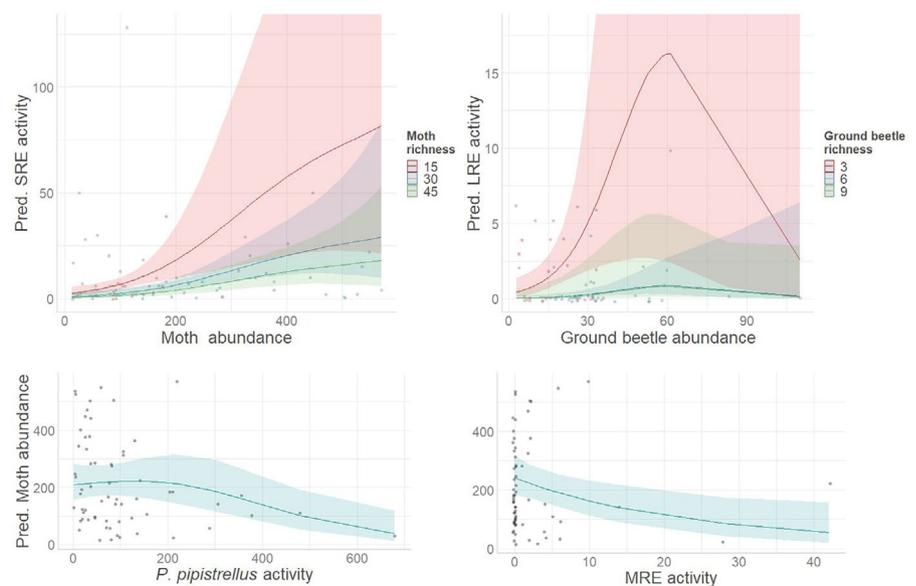


FIGURE 4 Predicted bottom-up responses of short- and long-range echolocating bats (SRE and LRE) to insect groups (top) and top-down responses of moth abundance to bat activity (bottom). Prediction ranges were reduced to the observed range for bat activity. Insect richness was categorized by dividing the gradients of insect richness in three equal-interval parts.

Böhm et al., 2011), this study suggests that bats' acoustic activity may suffice to lower local moth abundance. While the SEM indicated a similar influence of LRE-bats on moths, the influence of a bat guild likely scales with its observed activity. In our study, *P. pipistrellus* is expected to exert the greatest influence on moths. The specification of the bottom-up effect of moths on SRE-bats excludes testing the reverse relationship; however, since echolocation calls of SRE bats attenuate quickly, their influence on moths is likely locally restricted.

4.1 | Direct responses of bats to forest characteristics and management

Direct responses of bat guilds to forest structure corresponded to their eco-morphological adaptations (Denzinger & Schnitzler, 2013). MRE-bats also responded positively to intermediate forest management intensities, likely due to lower vegetation densities in those stands (Carr et al., 2020; Patriquin & Barclay, 2003). *P. pipistrellus* was most active in forests with larger tree diameters, supporting conservation strategies that promote old-growth elements. SRE-bat activity showed no direct response to forest characteristics but decreased with the understorey cover. This aligns with previous observations for ground-foraging SRE-bats (Carr et al., 2020; Rainho et al., 2010), but different responses to the understorey can be expected where aerial-foraging SRE-bats dominate the activity (Froidevaux et al., 2016). Unlike previous studies (Carr et al., 2020; Langridge et al., 2019), we found no direct effects of deadwood or microhabitats on bats. While microhabitats are of critical importance for tree-roosting bats (Meschede & Heller, 2000), bat activity in our study may be dominated by commuting or foraging bats. Optimal tree roosts such as large tree cavities were also scarce (see Appendix S2.2). Potential bat roost availability increased with stand age and tree species richness but decreased with the coniferous tree share and management intensity (Asbeck et al., 2019; Spínu et al., 2022).

4.2 | Bat prey availability inside forests

Moth abundance was indirectly affected by forest structural characteristics driving understorey vegetation and showed a negative response to standing dead trees. Moth abundance can increase with canopy cover and multilayered vegetation (Carr et al., 2020; Dodd et al., 2012; Shewring et al., 2022; Thorn et al., 2015). Overall, our findings highlight the importance of the understorey and living trees for providing habitat and shelter for forest moths. Although moth species developing on trees were dominant (Appendix S2.3), the understorey can provide cover and feeding resources for larvae and adult moths. Ground beetles showed positive responses to the forest management intensity. Their abundance peaked in forests with mixed tree compositions (Pereira et al., 2024), without positive effects of understorey cover or richness (Jouveau et al., 2020; Rainho et al., 2010), resulting from trophic cascades with herbivorous insects

(Castagneyrol & Jactel, 2012). In similar studies, flies were frequently sampled (Dodd et al., 2012; Fuentes-Montemayor et al., 2013; Knuff et al., 2020; Müller et al., 2012), which may be an available prey resource for (gleaning) SRE-bats.

4.3 | Importance of understanding indirect effects and insect-bat dynamics

In this study, insect group abundance and richness affected the activity of SRE- and LRE-bats. Insect groups were sensitive to forest management, forest characteristics and the understorey vegetation. Research should consider these relationships, as they indirectly modify bat activities. This was especially apparent for SRE-bats, as structurally rich forests promoted high moth abundance, while restricting foraging. Using an SEM approach allowed disentangling these complex relationships, while identifying relationship directionality. While hypothesizing bottom-up effects, we found negative responses of moth abundance to *P. pipistrellus*- and MRE-bat activity. Consequently, foraging SRE-bats may be disadvantaged, demonstrating indirect bat interactions beyond behavioural reactions towards the acoustic stimuli of other bat species (Lewanzik et al., 2019). Our study highlights the complex implications of forest management and resulting structures on bats.

While our focus was on local forest characteristics, future studies may consider larger spatial scales (Hendel et al., 2023) and variable interactions (Froidevaux et al., 2016, 2021; Jung et al., 2012). As we prioritized sample size over sampling repetitions, we did not consider seasonality in predator-prey relationships. By addressing the limitations above, including bat species-specific responses and conducting acoustic bat surveys in forest canopies (Müller et al., 2013), the understanding of bat forest habitats will be further advanced.

4.4 | Implications for forest management

Selective cutting under 'close-to-nature forestry' (CNF) management not only creates frequent small-scale disturbances important for foraging bats, but also reduces the availability of microhabitats for roosting. CNF, which replaced age-class forests in many European countries, still restricts the range of structural attributes compared to what is expected under natural forest dynamics (Bauhus et al., 2013; Braunisch et al., 2019; Kulakowski et al., 2017). While harvesting reduces late-successional elements required by many species (Bouvet et al., 2016; Carr et al., 2020), the promotion of multilayered canopies and the suppression of natural disturbances leads to a lack of open forest conditions. Although strictly protected forest reserves offer a broad structural gradient crucial for species conservation (Bouvet et al., 2016; Paillet et al., 2015) and retention programmes promote old-growth structures in managed forests with positive effects on various species (Hendel et al., 2023; Rappa et al., 2023), our results support the need for expanding the CNF management portfolio (Kuuluvainen et al., 2021). This portfolio

would mimic natural forest dynamics by allowing for more variable cutting treatments to conserve open forest communities (Eckerter et al., 2022; Viljur et al., 2022), including LRE bats, which we rarely recorded in our forests. Finally, as climate change increases the occurrence of natural disturbances, their potential should be used by retaining their structural legacies, which would improve roosting conditions for specialized bats (e.g. Kortmann et al., 2018) and benefit both photophilic and deadwood-dependent forest communities (Thorn et al., 2020; Viljur et al., 2022).

5 | CONCLUSIONS

Adapting forestry practices to improve bat habitat quality necessitates consideration of the habitat relationships of both insects and bats and their mutual relationships. While forest management intensity reduced the availability of roosting structures suitable for bats, it had several positive effects on foraging bats. Specifically, it (i) had a positive effect on ground beetles, (ii) enhanced the understorey cover, leading to higher moth abundance and (iii) increased forest accessibility for open- and edge-space foraging bats. To support roosting habitat functions for bat species in forests, retention programmes, as recently incorporated in the study area, can add an important component to secure old-growth forest elements in managed forest landscapes. As current management still restricts the range of structural elements in forests, the portfolio of silvicultural options should be expanded to provide complementary habitats that sustain the entire bat community and high biodiversity in managed forest landscapes.

AUTHOR CONTRIBUTIONS

Anna-Lena Hendel, Jacob C. Douma, Ilse Storch, Alexandra M. Klein and Veronika Braunisch conceived the ideas and designed methodology; Anna-Lena Hendel, Sara Klingenfuß, Joao M. C. Pereira, Laura Ruppert, Andreea P. Spînu, Julian Frey, Martin Denter and Xiang Liu collected and processed data for the study; Anna-Lena Hendel and Jacob C. Douma analysed the data; Anna-Lena Hendel and Veronika Braunisch led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

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.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: <https://doi.org/doi:10.5061/dryad.xksn02vr1> (Hendel et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Methodological details.

Appendix S2: Details for the collected data.

Appendix S3: Details on the model building.

Appendix S4: Visualization of the model responses.

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