



## Bat habitat selection reveals positive effects of retention forestry

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### ABSTRACT

Retention forestry, which retains small set-asides within forests managed for timber production and other services, is an important conservation instrument for enhancing structural complexity and biodiversity in multi-functional forests. However, in contrast to local scale effects, its large-scale effectiveness is largely unknown, as this requires area-wide and sufficiently precise information on key structural elements and associated species' habitats. Bats are particularly sensitive to forest structural characteristics and are target organisms of most retention programs. To assess their response to existing retention efforts, we here compared key habitat structures and overall habitat suitability for bats across forest areas with and without retention, using forest type and structure variables derived from remote sensing along with topographic, climatic and land-cover variables in a multi-scale modelling approach. Based on acoustic data from 135 1-hectare plots across the Black Forest, Germany, we calibrated region-wide species distribution models for 9 bat species or bat species groups thereby identifying the best-performing scale (50 – 1000 m radius) for each predictor and species(-group). Among predictors and species(-groups), forest cover and structural variables explained most (44.0 % and 38.3 %) of bat habitat selection, with forest height heterogeneity (16.4 %) and the percentage area with standing dead trees (11.7 %) performing best, mostly at small scales (50–100 m). Forests with retention showed higher values of these key structural variables, resulting in higher predicted habitat suitability for all species(-groups), highlighting positive effects of retention on structural complexity in forests and on species that benefit thereof.

### 1. Introduction

Covering >42 % of the European surface and harboring numerous species, forests play a key role in biodiversity conservation (European Environment Agency, 2016). Yet, even though forest cover has recently increased in most European countries (Winkler et al., 2021), forests qualitatively often lack important key resources for forest dwelling species (Bauhus et al., 2013; Braunisch et al., 2019). The majority of European forests are managed for timber production, with 'close to nature forestry' (CNF) as the predominant silvicultural regime that focuses on continuous forest cover, natural regeneration and selective cutting (Bauhus et al., 2013; Mason et al., 2022). CNF promotes uneven-aged forests with heterogeneous vertical structure at the stand scale. However, as harvesting takes place in the optimal phase when the timber stock is at its maximum, natural disturbances are largely

suppressed and old growth elements and natural gap dynamics have largely disappeared (Bauhus et al., 2013).

Most European forests are seminatural and only 15 % of the forest area is protected to conserve biodiversity (Forest Europe, 2020), while <1 % can still be considered primary forests (Sabatini et al., 2018). As this is insufficient for maintaining structural complexity and associated biodiversity in a forest landscape, the integrative approach of retention forestry (i.e. retaining groups of trees or parts of the stands from harvesting) is becoming a popular conservation strategy for enhancing old-growth elements in multifunctional managed forests (Lindenmayer et al., 2012). Retention forestry has initially been introduced in clearcutting systems, but is now also applied in continuous cover forestry (Gustafsson et al., 2020). Many retention programs focus on the retention of 'habitat trees' (ForstBW, 2016), i.e. trees that are particularly large, dead or characterized by 'tree-related microhabitats'

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(Larrieu et al., 2018), or small forest patches which are retained beyond harvesting cycles. A regular distribution of retention elements across the forest matrix aims at providing structures in sufficient quantity and connectivity to support forest-dwelling species with specific structural requirements. Whether retention forestry actually fulfils these expectations has been the subject of several recent studies (Asbeck et al., 2020; Basile et al., 2019, 2020; Großmann et al., 2018), most of them comparing local structural or biodiversity characteristics of retention elements (trees, tree-groups or small stands) with corresponding, but managed “reference”-elements (e.g. with tree-groups selected from the managed forest matrix, Großmann et al., 2018). Yet, studies addressing effects on mobile species across entire forest landscapes are lacking.

As bats respond sensitively to environmental changes (Jones et al., 2009; Russo et al., 2021) and are closely linked to forest structural characteristics (Basile et al., 2020; Meschede & Heller, 2000), they have been selected as target organisms for retention programs (Braunisch et al., 2020; ForstBW, 2016). Even though few European bat species are genuine woodland bats, most bat species depend on resources that are provided by forests (Gebhard, 1997). For forest-dwelling bats, roosts and insect-rich foraging habitats are scarce key resources (Russo et al., 2010), that are considered to be supported by retention forestry. The former are provided when the retained habitat trees develop cavities and cracks (Regnery et al., 2013). The latter, in contrast, are mainly related to gap dynamics that affect stand structure, light regime and microclimate for insect development (Burford et al., 1999; Ober & Hayes, 2008; Seibold et al., 2016; Topp et al., 2006) as well as the accessibility of this food resource to bats (Blakey et al., 2017; Froidevaux et al., 2021; Zahn et al., 2006). Accessibility to dense forests is often restricted, as many bat species are adapted to fly either in semi-open spaces or open spaces (Grindal & Brigham, 1999), and even bats with a high maneuverability have been found to concentrate in vertically less complex forests (Froidevaux et al., 2016).

The influence of forest structures on bat presence, activity and species richness has been analyzed using data representing those structures locally (Froidevaux et al., 2016; Jung et al., 2012). In addition, area-wide geodata has been used to model distributions and uncover large-scale effects of landscape structure, land use and topography on these highly mobile organisms (Jaberg & Guisan, 2001; Rebelo & Jones, 2010; Rutishauser et al., 2012). However, since high-resolution data on habitat structures are often not available across large spatial scales, local and landscape effects were often analyzed based on different types of data, with different information content, level of detail or spatial coverage (Bouvet et al., 2016; Erickson & West, 2003; Froidevaux et al., 2022; Kalda et al., 2015). The rapid advancement of remote sensing techniques and the consequential availability of area-wide, high-resolution data on habitat structures makes it now possible to explore bat responses along a continuum of spatial scales using the same type of information. This may be important since different species, including bats, may respond to the same resource or structure at different scales, depending on the species traits, the variable in question and its function (Bellamy et al., 2013; Gorresen et al., 2005; Kotliar & Wiens, 1990; Razgour et al., 2011; Wiens, 1989). In complex three-dimensional structured environments like forests, bat species' adaptations in echolocation and flight likely influence the scale at which they interact with the environment. Narrow space foraging bats maneuver through dense canopy, glean insects from trees, and often forage just a few kilometers away from their roost. Consequently, their habitat selection is expected to take place at smaller scales than that for fast flying bats, which forage in open spaces and travel much greater distance. Moreover, structural variables that reflect direct resources for roosting and foraging may be selected at smaller scales than land cover variables that determine overall habitat composition. Identifying the scales that are relevant to the focal species is thus crucial to designing and evaluating conservation programs for structural enhancement across large landscapes.

We used forest structural information derived from remote sensing to model bat habitat selection inside forests. We also compared key

structures and the overall suitability of forests with and without retention forestry. Focusing on 9 different bat species or bat species(-groups) across the Black Forest, Germany, our objectives were fourfold: (I) to identify key forest structural variables that define bat forest habitats and assess their relative importance compared to land cover, topography and climate variables, (II) to describe at which scale these variables are selected, and (III) to quantify species-specific habitat suitability based on the amounts of key structural elements in the forest landscape. Finally, we (IV) compared key forest structures and predicted habitat suitability for bats in forests with and without retention forestry to evaluate whether this conservation tool can enhance structural complexity and therefore improve the suitability of forests for structural indicator species.

## 2. Methods

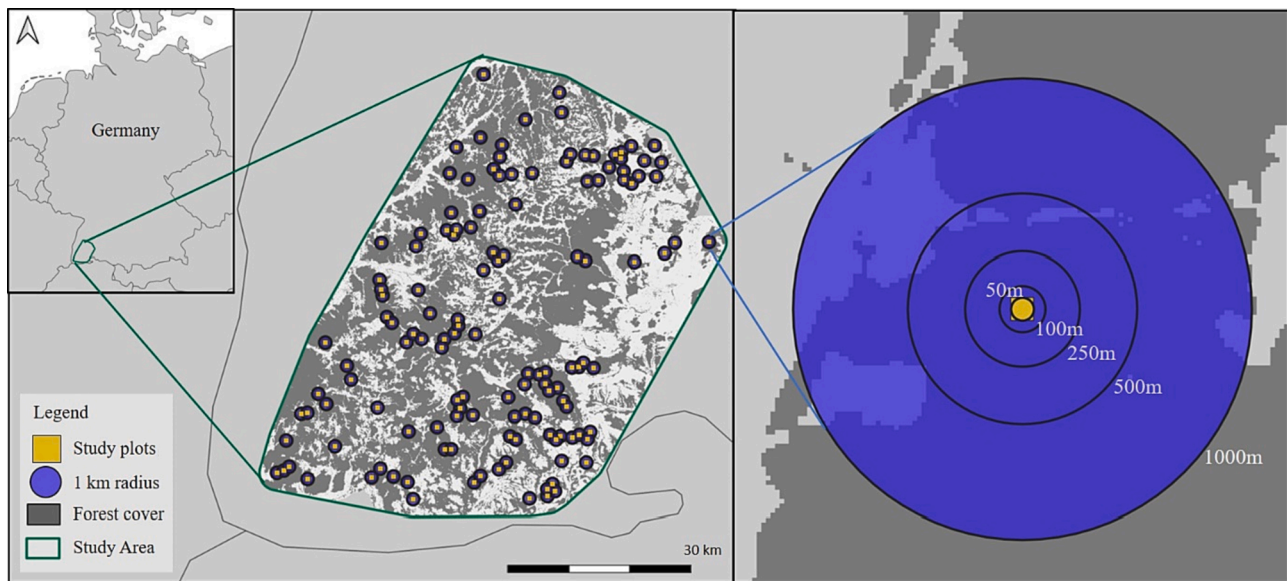
The study was conducted in the southern Black Forest, a forest-dominated lower mountain range in Baden-Württemberg, southwestern Germany (Fig. 1). The region has a long history of human use, so that human settlements and agricultural areas intersperse the forested landscape, which is dominated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). In 2010, a retention program was introduced (ForstBW, 2016) and made obligatory in the state's forest and optional in communal and private forests. The program promotes two retention elements: first, the ‘habitat tree group’ (HTG) consisting of about 15 trees that are selected every 3 ha and retained until their natural decay; second, the establishment of permanently protected forest refuges with a size of 1–3 ha on 3 % of the forest area (ForstBW, 2016). Within our study area, 135 1-hectare plots were selected along two environmental gradients, each classified in 3 categories: percent forest cover within a 25 km<sup>2</sup> circular area around the plot center (50 %, 50–75 % and > 75 %) and number of standing dead trees per hectare (0, 1–9 and > 10). Plots were arranged so that each combination of the 3 × 3 categories was replicated 15 times across the landscape to yield a stratified design. All plots were located at altitudes between 500 and 1400 m and in a minimum distance of 750 m from each other.

### 2.1. Bat acoustic data

To obtain presence information for each bat species(-group), we deployed ultra-sound detectors (Batloggers; Elekon AG) to record bat echolocation calls on all plots in 2016 and 2017 (details in Supplementary data S1). Two detectors were simultaneously installed per plot, one with the microphone pointing towards the most open space and the second one pointing towards a space with plot characteristic vegetation following the recommendations of Froidevaux et al. (2014). Each plot was repeatedly sampled, once during May - July and once during August - October in either 2016 only (22 plots), 2016 and 2017 (68 plots) or 2017 only (45 plots). As the recorders were running for at least two consecutive nights during each sampling period, we aimed at a minimum number of four full-night recordings per logger, i.e. eight logger-nights per plot, which resulted in 7.2 (SD = 3.2) logger-nights after excluding nights with weather conditions unfavorable to bats. Those were defined as nights with minimum temperatures below 5 °C or as nights with >3 h of rain (>0.2 mm/h) or strong winds (>8 m/s), for which weather station data of the 5 closest weather stations was aggregated. The weather data was obtained from the climate data center of the German Weather Service (<https://opendata.dwd.de/>).

#### 2.1.1. Echolocation analysis

To identify bat echolocation calls to species(-groups), we used the software ‘BatScope’ Version 3 (Obrist & Boesch, 2018). To improve the quality of the automatic identification of the recordings, we complemented it with a manual verification process (for details see Supplementary data S1). As echolocation calls of related bat species are



**Fig. 1.** Left: The study area (green) in south-western Germany (inlet), with the forested area (grey) and the location of the 135 1-hectare sampling plots. Right: Representation of one sampling plot and the radii, in which each variable was calculated to assess scale-effects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Bat species(-groups) included in the analysis, their allocation to foraging habitats (according to [Denzinger & Schnitzler \(2013\)](#)), their foraging distances from the roost (as determined from literature) as well as the number of sampling plots with presence detected (n).

Guild	Species (-group)	n	Species	Foraging distance	Reference
Narrow space	Plecotus	39	Plecotus auritus	0.5–2.8 km	( <a href="#">Entwistle et al., 1996</a> )
			Plecotus austriacus	1–5 km	( <a href="#">Ancillotto et al., 2022</a> ; <a href="#">Razgour et al., 2011</a> )
	M. nattereri	53	Myotis nattereri	3–4 km	( <a href="#">Siemers et al., 1999</a> )
	M. myotis	114	Myotis	2.5–10.8 km up to 25 km	( <a href="#">Rudolph et al., 2009</a> ) ( <a href="#">Arlettaz, 1999</a> )
Edge space	P. pygmaeus	31	Pipistrellus pygmaeus	1–2 km	( <a href="#">Davidson-Watts et al., 2006</a> )
	P. kuhlii / P. nathusii	127	Pipistrellus nathusius	1–5 km	( <a href="#">Flaquer et al., 2009</a> ; <a href="#">Schorcht et al., 2002</a> )
			Pipistrellus kuhlii	up to 5 km	( <a href="#">Maxinová et al., 2016</a> ; <a href="#">Serangeli et al., 2012</a> )
B. barbastellus	21	Barbastella barbastellus	3–4.5 km	( <a href="#">Steinhauser et al., 2002</a> )	
Open space	Eptesicus	63	Eptesicus serotinus	6–11 km	( <a href="#">Catto et al., 1996</a> ; <a href="#">Robinson &amp; Stebbings, 1997</a> )
			Eptesicus nilsonii	10–15 km	( <a href="#">De Jong, 1994</a> )
	V. murinus	16	Vespertilio murinus	6–20 km	( <a href="#">Safi et al., 2007</a> )
	Nyctalus	90	Nyctalus leisleri	20 km	( <a href="#">Kronwittter, 1988</a> )
Nyctalus noctula			25 km	( <a href="#">Kronwittter, 1988</a> )	

often very similar, they were identified to species(-groups) ([Table 1](#)). Calls of *Nyctalus*, *Eptesicus* and *Vespertilio* that could not be identified to the genus were excluded from the analysis. Additionally, we excluded *Pipistrellus pipistrellus* as it occurred in all of the plots. As identifying bats of the genus *Myotis* to the species levels is often not possible, we only included *M. myotis* and *M. nattereri* in the study. In total, we modelled the habitat selection of 9 species(-groups), which differ with regard to their foraging habitat characteristics, echolocation range and mobility and are thus often grouped to guilds ([Denzinger & Schnitzler, 2013](#)).

## 2.2. Environmental variables

We used environmental variables that were identified as relevant for bats in previous studies, and that represent forest structural attributes, forest type, topography and climate ([Table 2](#)).

### 2.2.1. Forest structure

Forest structure variables included forest height ([Ganz et al., 2020](#); [Schumacher et al., 2019](#)), forest height heterogeneity, tree volume ([Schumacher et al., 2019](#)), the percentage with standing deadwood (according to [Zielewska-Büttner et al. \(2020\)](#), see details in [Supplementary data S2](#)) as well as the percentage area with gaps and open forest ([Zielewska-Büttner et al., 2016](#)) ([Table 2](#)). To derive the forest structure variables, digital stereo aerial imagery products: orthophotos and vegetation height models or a combination thereof with optical satellite imagery were used (see details in [Supplementary data S2](#)). 3D photogrammetric point clouds and digital orthophotos were produced using the image-matching software SURE of nFrames ([nFRAMES, 2020](#)) and vegetation height models ( $1 \times 1$  m resolution) were calculated as described in [Schumacher et al. \(2019\)](#) and [Ganz et al. \(2020\)](#). Forest structure variables were originally developed at a  $1 \times 1$  m resolution and were provided in an aggregated format with a resolution of  $10 \times 10$  m through the project MoBiTools at the Forest Research Institute (FVA) of Baden-Württemberg ([FVA, 2020](#)).

### 2.2.2. Forest cover and forest type

We calculated the percentage cover with forest and of different forest types by using a forest type classification map ([FVA, 2020](#)) with original resolution of  $10 \times 10$  m. For the forest classification support vector

**Table 2**

The environmental variables used for modelling bat habitat selection. Variables of different variable groups came with different spatial resolutions and were all processed to represent different spatial scales (see chapter 2.2.5).

Variable Group	Variable	Short Description	Unit
Forest Cover	Forest	Percentage forest cover including all forest types.	%
Forest Structure	Forest Height	Forest height calculated as the median of a normalized digital surface model (nDSM).	m
	Forest Height Heterogeneity	The forest height heterogeneity calculated as the standard deviation of the forest height with a 3 × 3 pixel moving window.	m
	Tree Volume	Modelled tree volume after Schumacher et al. (2019).	m <sup>3</sup> /ha
	Standing Deadwood	Percentage area with standing dead trees (Zielewska-Büttner et al., 2020)	%
	Gaps	Percentage area with gaps defined as canopy openings of at least 10 m <sup>2</sup> in dense forests (Zielewska-Büttner et al., 2016).	%
	Open Forest	Percentage area with open forests (<60 % canopy cover) and gaps (as defined above) (Zielewska-Büttner et al., 2016).	%
Forest Type	Deciduous Forest	Percentage cover with deciduous forests.	%
	Coniferous Forest	Percentage cover with coniferous forests.	%
	Mixed Forest	Percentage cover with mixed forests.	%
Climate	Temperature	Average annual air temperature minima.	°C
	Precipitation	Average annual precipitation sum.	mm
	Windspeed	Average annual windspeed.	km/h
	Saturation Deficit	Average annual saturation deficit.	0.01 hPa
	Sun Duration	Average annual global radiation sum on inclined surfaces.	0.01 MJ / m <sup>2</sup>
Topography	Slope	Slope describes the terrain steepness.	°
	Roughness	Terrain Roughness is the difference between the maximum and the minimum altitude of the focal cell and its 8 surrounding cells (Wilson et al., 2007).	m
	Curvature	Terrain total curvature displays the profile and horizontal curvature of the terrain (Zevenbergen & Thorne, 1987).	Index
	Northness	Cosine of aspect in degrees. Values range from 1 (north) to -1 (south), with zero representing east- or west.	°
	Eastness	Sine of aspect in degrees. Values range from 1 (east) to -1 (west), with zero representing north- or south.	°

machine (SVM) regression models were applied to optical remote sensing data (see details in Supplementary data S2) according to Schumacher et al. (2019). The estimated proportion of deciduous trees per pixel was divided into the following classes: Coniferous forests (deciduous trees < 20 %), mixed forests (20–80 % deciduous trees) and deciduous forests (>80 % deciduous trees).

### 2.2.3. Climate

The climatic data is based on regionalization with a resolution of 250 × 250 m by the Department of Physical Geography at the University of Hamburg (Dietrich et al., 2019). To represent multiyear climatic influences, the original daily raster time series was provided in an aggregated temporal format for each year, which we summarized for the years 1991 to 2018. The climatic variables were: the average yearly minimum temperatures, the precipitation sums, the mean windspeed, the mean saturation deficit and the average yearly radiation sums (Table 2).

### 2.2.4. Topography

Topographic variables included slope, topographic roughness, total curvature as well as northness and eastness (Table 2). All variables were derived from a digital elevation model (DEM) with an original horizontal resolution of 1 × 1 m provided by the State Office for Geoinformation and Land Development Baden-Württemberg (LGL, 2018). The total curvature was calculated according to Zevenbergen & Thorne, (1987) using the R package 'spatialEco' (Evans, 2021).

### 2.2.5. Environmental data preparation

All the environmental variables were prepared as raster maps in the geographic reference system ETRS89 / UTM zone 32 N (EPSG:25832) and resampled to 20 × 20 m resolution, using bilinear interpolation for continuous values and the nearest neighbor method for discrete raster values. To explore scale effects, all but the climate variables were calculated for circular moving windows with radii of 50, 100, 250, 500 and 1000 m. Finally, all variables at all scales were restricted to forested areas using an ecological forest mask, which also includes temporarily treeless forest areas, e.g. windthrow areas and gaps (Ganz et al., 2020). Geodata preparation was performed in R (Version 1.4.1106).

## 2.3. Modelling habitat selection

Habitat suitability models were calibrated and tuned separately for each bat species(-group) using the widely applied Maxent algorithm (Phillips et al., 2006) as integrated in the package SDMtune (Vignali et al., 2020). Maxent is a presence-only approach that estimates habitat suitability (defined as relative probability of species presence) by contrasting the environmental information at the species presence locations with the information extracted at background locations that are usually randomly sampled from the study area. In this study, background locations were restricted to the forested part of the study area. Moreover, since our bat sampling locations were selected following a stratified design, (i.e. considering the amount of deadwood and the forest cover gradient (i.e. the percentage cover within 25 km<sup>2</sup>) and overrepresented different environmental conditions, background locations were selected to have the same multivariate distributions of environmental conditions as the sampling locations (Kramer-Schadt et al., 2013). To exactly mirror the multivariate distributions of the presence points with the selection of background points, we ran a maxent model for all plot locations, using all environmental layers (described in Table 2) at the 50 m scale, the two design variables (the number of standing dead trees at a 50 m scale and the percentage forest cover in the surrounding 25 km) and two additional layers representing the distance to the outer forest edge and the distance to water as predictors (details in Supplementary data S3). The resulting prediction was then used as a bias file, from which background locations were sampled according to their likelihood.

### 2.3.1. Univariate models for scale selection

For model calibration, each species(-group) data set was split into 70 % training and 30 % test data. For identifying the 'best scale' for each variable, we first ran univariate models for each scale (i.e., 50, 100, 250, 500 and 1000 m) and compared their explanatory power using an ensemble metric approach to account for the advantages and disadvantages of the different metrics (Shabani et al., 2018). First, we



calculated four evaluation metrics: the true skill statistic (TSS, [Allouche et al., \(2006\)](#)) and the area under the receiver-operating characteristics curve (AUC, [Fielding & Bell, \(1997\)](#)), both on the test and on the training data. For the ensemble metric, the values for each variable and metric were then scaled between their minimum and maximum and then averaged across the metrics. For each variable the scale at which the ensemble metric of the univariate model was closest to 1 was selected as the best scale and tested in a global model ([Supplementary data S4](#)).

### 2.3.2. Variable selection and optimization

Besides the included variables at the selected scales, the global model also contained the climatic variables. A data-driven variable selection was performed using the 'varSel' function, retaining the best set of uncorrelated variables based on a spearman correlation threshold of  $r_s < 0.7$ . Subsequently, variables with a permutation importance of  $< 5\%$  were iteratively removed from the variable set if this did not decrease the model accuracy measured as the AUC (using the 'reduceVar' function). Hyperparameters were then tuned for the final set of variables: Regularization values were tested between 0.1 and 4.88 with an increment of 0.0002. Feature class combinations were used based on the number of presence locations: For 14 presence locations or less in the training dataset only linear and quadratic features were allowed, between 15 and 80 locations product features were added, and above 80 locations also hinge features. Finally, for achieving the highest predictive power possible, the training and test dataset were merged to build a final model applying the optimized hyperparameters. Whenever a variable's importance dropped below 5%, it was removed from the final model. In addition, to further avoid overfitting, variables with the least importance were removed until the number of variables did not exceed the rounded tenth of the number of presence points. The final models for each species were used to predict habitat suitability across the forested

part of the study area ([Supplementary data S6](#)).

### 2.4. Comparison of forests with and without retention measures

In order to compare forest structures and habitat suitability in forest stands with and without retention forestry, 900 random points were drawn from stands of each category all over the study area. Based on the digital forestry map of the federal state of Baden-Württemberg ([State Forestry Administration, 2022](#)), retention stands were defined as managed forest stands with at least 1 habitat tree group or forest refuge, while stands without retention had none of these elements. To exclude edge effects, forests stands bordering to the respective other forest management categories were buffered 50 m inwards before selecting random points. Moreover, a minimum distance of 500 m was applied between random points of the same forest management category to ensure their spatial independence.

## 3. Results

All models performed well in predicting bat species(-group) presences (according to [Swets, 1988](#)), with model AUCs ranging from 0.78 for the habitat prediction of the Eptesicus group to 0.91 for *V. murinus* ([Table 3](#)). Of all variables, the forest cover and forest structure variables explained bat presences best, contributing on average 44.0% and 38.3% to the overall model variable importance across all species(-groups). Models strongly leaned towards a high availability of forest cover while forest type variables did not influence habitat predictions of most species(-groups). Topographic variables explained on average 13.6%. Climatic variables were often excluded from the final models and hence only reached an overall variable importance of 1.8%.

**Table 3**

Percent importance of the predictor variables included in the final model of each bat species(-group), as well as their average importance across all species (total average) and the importance of each variable group per species(-group) (summed importance). Note that the number of variables allowed in each model was restricted for species with few presence locations. For the species(-groups) and sample size see [Table 1](#), for the response curves see [Supplementary data S7](#).

	Plecotus	P. pygmaeus	M. nattereri	P. nathusii/P. kuhlii	B. barbastellus	Eptesicus	V. murinus	Nyctalus	M. myotis	Total average
Forest Cover	62.2	39.8	47.1	53.1	45.0	73.8		34.5	40.1	44.0
Forest Height				10.3				7.7		2.0
Forest Height Heterogeneity		25.4		11.0	26.6	7.6	70.2	6.7		16.4
Tree Volume	22.3	11.2	23.0						11.5	7.6
Standing Deadwood	15.5	23.6	6.5			6.9	29.8	15.4	7.8	11.7
Gaps										0.0
Open Forest						5.9				0.7
<b>Sum Forest Structure</b>	37.8	60.2	29.5	21.4	26.6	20.4	100.0	29.8	19.2	38.3
Deciduous Forest				6.4					7.2	1.5
Coniferous Forest										0.0
Mixed Forest				3.2					4.5	0.9
<b>Sum Forest Type</b>	0.0	0.0	0.0	9.6	0.0	0.0	0.0	0.0	11.3	2.3
Temperature								6.4		0.7
Precipitation										0.0
Windspeed				3.6		5.8				1.0
Saturation deficit										0.0
Sun duration										0.0
<b>Sum Climate</b>	0.0	0.0	0.0	3.6	0.0	5.8	0.0	6.4	0.0	1.8
Slope								8.3		0.9
Roughness			10.6	12.3					9.2	3.6
Curvature			12.8					11.9	10.9	4.0
Northness										0.0
Eastness					28.5			9.1	8.8	5.2
<b>Sum Topography</b>	0.0	0.0	0.0	12.3	28.5	0.0	0.0	29.3	28.9	13.6
AUC	0.80	0.90	0.83	0.82	0.88	0.78	0.91	0.86	0.84	

### 3.1. Importance of forest structure variables

The most influential forest structure variable across all models was forest height heterogeneity, which was included in 6 out of the 9 models with a variable importance of on average 16.4 % across all species (Table 3). The percentage of standing deadwood was included in 7 species(-group) models but showed a lower average importance (11.7 %). The two highly correlated variables tree volume and forest height (Supplementary data S2) were included in 6 and 5 of the 9 models where they accounted for on average 7.6 % and 2.0 % of the total variable importance. The percentage area with open forest was only contained in the final model of the Eptesicus group, while the area with gaps did not affect species(-group) presences, but was highly correlated with the presence of open forests (Supplementary data S2).

### 3.2. Scale selection

Forest structural variables influenced bat habitat selection inside forest most often within a surrounding of 50 and 100 m, but scales of 250 and 500 m were also selected (Table 4). Species(-groups) that selected habitats according to the forest height heterogeneity, selected them at scales of 100 and 250 m. All other forest structural variables generally performed best at a scale of 50 m with the following exceptions: P. nathusii/ P. kuhlii responded best to the tree volume at a scale of 500 m and M. nattereri, P. pygmaeus and V. murinus selected standing deadwood at a scale of 100 m. Eptesicus additionally selected open forests within a radius of 100 m. The scale selection for forest type variables and

topography was more heterogeneous. Across all species(-groups), the mean selected scale was lowest for forest structure variables, followed by forest type and topography variables. There was no pattern suggesting that species(-groups) with larger foraging distances responded to environmental conditions at larger spatial scales (Table 4).

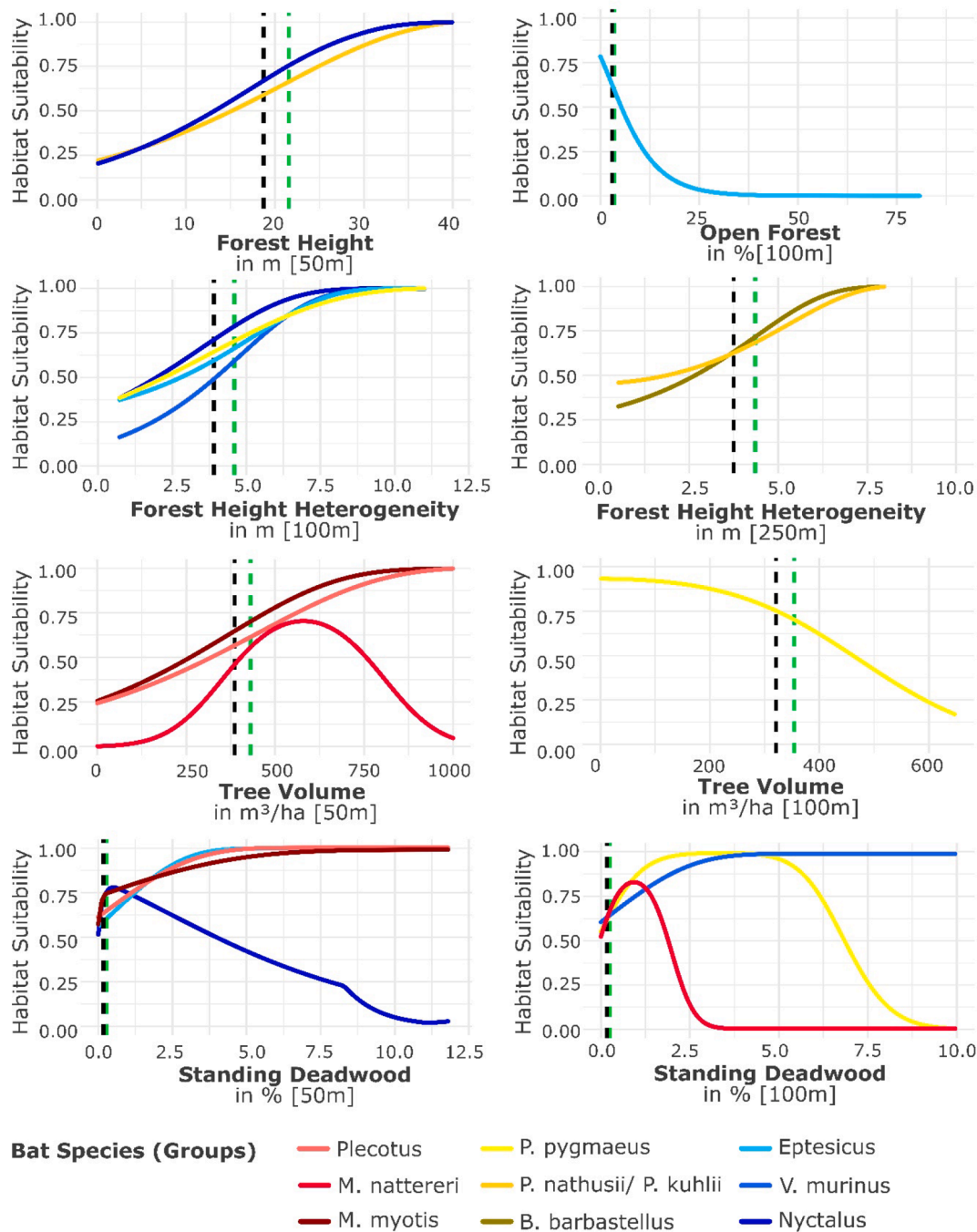
### 3.3. Species responses to forest structure

The marginal response curves (Fig. 2) showing the relationship between forest structural variables and the predicted habitat suitability demonstrate a positive effect of forest height [scale: 50 m] for the species (-groups) P. nathusii / P. kuhlii and Nyctalus. Also, forest height heterogeneity [100 m and 250 m] was strongly positively associated with all bat species(-groups) that were influenced by that variable. Tree volume positively affected the habitat suitability of the two narrow-space foraging bats Plecotus and M. myotis [both 50 m] while M. nattereri showed a unimodal response [50 m] and P. pygmaeus responded negatively to increasing tree volumes [100 m] (Fig. 2). Standing deadwood [50 m and 100 m] had a positive effect on Plecotus, M. myotis, Eptesicus and Nyctalus. The response curves show a steep increase in habitat suitability at low area-percentages of standing deadwood that asymptotically approach the maximum at values that far exceed the average deadwood values in the study area. The model for P. pygmaeus, Nyctalus and M. nattereri showed a unimodal effect of deadwood, yet with optima also located above the average deadwood amounts present. The percentage area with open forest [100 m] was negatively associated with the probability of presence of Eptesicus.

**Table 4**

Predictor variables included in the final models explaining habitat selection of the bat species(-groups) with the “best scale” at which there were selected. Median and Mean of the selected scales are shown for each species and variable type as well as and across all species and variable types. Bat species(-groups) are ordered according to their mobility, with increasingly mobile species from left to the right.

	Plecotus	P. pygmaeus	M. nattereri	P. nathusii / P. kuhlii	B. barbastellus	Eptesicus	V. murinus	Nyctalus	M. myotis	Total scale average
Forest Cover	100	250	100	100	250	100		100	100	150
Forest Height				50				50		
Forest Height Heterogeneity		100		250	250	100	100	100		
Tree Volume	50	500	50						50	
Standing Deadwood	50	100	100			50	100	50	50	
Gaps										
Open Forest						100				
<b>Median scale Forest Structure</b>	50	100	75	150	250	100	100	50	50	100
<b>Mean scale Forest Structure</b>	50	233	75	150	250	83	100	67	50	118
Deciduous Forest				1000					1000	
Coniferous Forest										
Mixed Forest				250					50	
<b>Median scale Forest Type</b>				625					525	575
<b>Mean scale Forest Type</b>				625					525	575
Slope								500		
Roughness			100	500					1000	
Curvature			100					50	50	
Northness										
Eastness					1000			50	50	
<b>Median scale Topography</b>			100	500	1000			50	50	100
<b>Mean scale Topography</b>			100	500	1000			200	367	433
<b>Median scale (all variables)</b>	50	175	100	250	250	100	100	50	50	
<b>Mean scale (all variables)</b>	67	238	90	358	500	88	100	129	294	



**Fig. 2.** Marginal response curves representing the relationships between the selected forest structural variables (Table 3) at their selected scales (Table 4) and the predicted habitat suitability of the investigated bat species(-groups). The vertical dashed lines represent the mean values calculated for forest stands with (green) and without (black) retention measures. Statistics are provided in Supplementary data S5, variable descriptions in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 3.4. Species response to other environmental variables

The detailed effects of all selected environmental variables per species(-group) are represented in Supplementary data S7. The effect of forest cover [100 and 250 m] dominated the habitat suitability predictions of all species(-groups) but *V. murinus*. For all of them, habitat suitability predictions increased strongly as forest cover approached the maximum. *P. nathusii/ P. kuhlii* and *M. myotis* additionally responded positively to the cover of mixed forests [250 and 50 m, respectively] and *M. myotis* also to an increasing share of deciduous forest. Among the remaining variable groups, topographic variables were important

predictors for bat presence in forests (Table 3, Supplementary data S7). *Nyctalus* showed a slight preference for shallow slopes [50 m]. Topographic roughness affected the habitat suitability predictions negatively for *P. nathusii/ P. kuhlii* [1000 m], while *M. myotis* [500 m], *M. nattereri* [100 m] showed an unimodal response. *M. myotis*, *M. nattereri* and *Nyctalus* predictions also responded to the local curvature [50 m] and were more often observed in terrain with slightly positive curvatures. Aspect was an important predictor for the habitat suitability of *B. barbastellus*, *M. myotis* and *Nyctalus*. While the latter two species (-groups) responded negative to eastern expositions, *B. barbastellus* showed a preference for south-exposed slopes in the study area. Climate

variables were rarely included into the final models and only temperature and windspeed were retained, but they contributed only little to the overall variable importance.

### 3.5. Effects of retention forestry

#### 3.5.1. Forest structure

When comparing the bat-relevant forest structures in stands with and without retention measures across the study area (Fig. 2, for values see Supplementary data S5), forest height [50 m] and forest height heterogeneity [100 m] show slightly higher mean values of 21.6 m and 4.6 m compared to 17.7 m and 3.9 m, respectively. Retention stands were also characterized by a higher average tree volume [50 m] of 431 m<sup>3</sup>/ha (SD:  $\pm 152.6$  m<sup>3</sup>/ha) compared to 386 m<sup>3</sup>/ha ( $\pm 164.53$  m<sup>3</sup>/ha). Overall, most of the forest stands in the study area had very low percentages of standing deadwood. In retention stands the average percentage area with standing deadwood [50 m] was 0.27 % ( $\pm 0.62$  %), while the average value for stands without retention measures was even lower (0.17 %  $\pm 0.34$  %). Almost as equally scarce was the availability of forest areas with gaps and open forests. Across retention forests, the percentage area with gaps [50 m] was 2.92 % ( $\pm 4.21$  %) and of open forests [100 m] 3.52 % ( $\pm 4.58$  %), while in forest without retention measures the availability of these two structural elements was slightly lower with 2.68 % ( $\pm 4.21$  %) and 2.97 % ( $\pm 5.37$  %) respectively.

#### 3.5.2. Habitat suitability for bats

Based on the the species(-group)-specific habitat models, retention forests offered higher predicted habitat suitability for all bat species (-groups) compared to non-retention forests (Fig. 3, values in Table S5b). Differences were especially pronounced for *P. nathusii* /*P. kuhlii* and *Eptesicus* and lowest for *M. nattereri* und *V. murinus* (Supplementary data S5).

## 4. Discussion

Using area-wide remote sensing data, we demonstrate the strong relative importance of forest structures influencing the habitat selection of European bat species(-groups) inside temperate mountain forests. Forest height heterogeneity and standing deadwood were of particular relevance, but also forest height, a proxy for old trees, and the tree volume influenced bat habitat selection. The selected structures are all targeted by retention programs that aim at enhancing forest structural complexity. In fact, forests with retention measures showed on average higher values in these variables and, as a consequence, bat habitat suitability was higher in forest stands managed under retention forestry, even after a relatively short time after implementation. As previously demonstrated (Bellamy et al., 2013; Fuentes-Montemayor et al., 2017; Razgour et al., 2011), bats responded to variables at different spatial scales, however, contrary to our expectations, scale selection was not related to mobility and echolocation traits, but more to the variable type with forest structure variables being selected at smaller scales throughout. As forest habitat suitability for bats is strongly tied to the availability of local forest structures, we emphasize the importance of old-and deadwood retention programs for bat conservation.

### 4.1. Bat habitat selection

In agreement with previous studies (Froidevaux et al., 2016; Jung et al., 2012; Müller et al., 2013) we found that forest height heterogeneity had a strong positive influence on most bat species(-groups), as heterogenous canopies protect bats from predators, shelter from wind (Verboom & Spoelstra, 1999) and serve as landmarks (Schaub & Schnitzler, 2007). Moreover, heterogeneity in canopy heights may create microclimatic conditions that can promote insect abundance and diversity (Haddad et al., 2009; Müller & Brandl, 2009; Ulyshen, 2011) attracting bats. Forest height positively influenced the habitat suitability

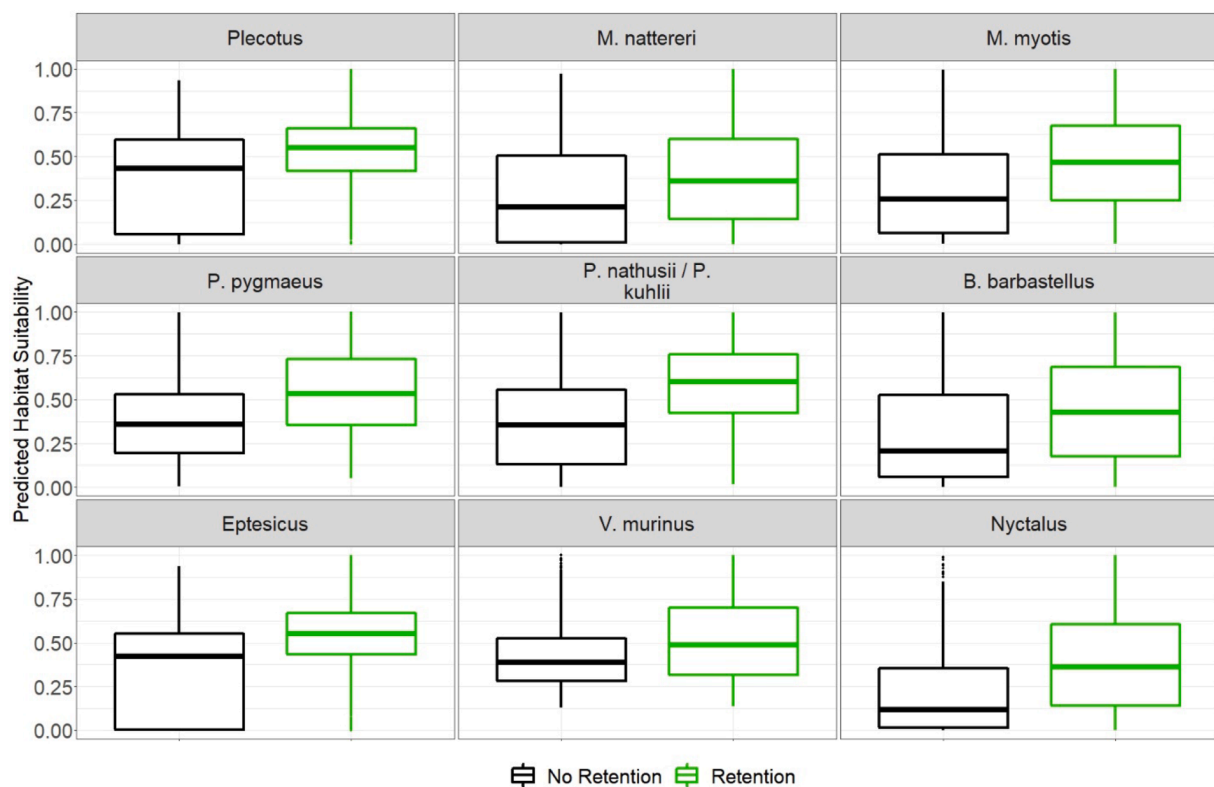


Fig. 3. Predicted habitat suitability for all bat species(-groups) measured at random locations drawn from forests with (n = 894) and without (n = 900) retention measures. Detailed values are provided in Supplementary data S5.



for *Nyctalus* and *P. nathusii* / *P. kuhlii*. In managed forests, forest height can be an indicator of forest age (Maltamo et al., 2020) and as older forests typically host more abundant and diverse tree-related microhabitats (Asbeck et al., 2019; Larrieu & Cabanettes, 2012) bat activity tends to increase with forest height or age (Jung et al., 2012; Ruczyński et al., 2010; Wegiel et al., 2019). The narrow space foraging bat species in our study were associated with higher tree volumes, reflecting their preference for mature forests with a high volume of foliage (Mehrer et al., 2012). In contrast, *P. pygmaeus* showed a negative response reflecting the species' adaptation to edge habitats (Nicholls & Racey, 2006). Our results are in line with previous studies showing that most bat species respond positively to the availability of standing deadwood (Bouvet et al., 2016; Tillon et al., 2016). While the predicted habitat suitability for most species showed a continuous increase, *M. nattereri*, *P. pygmaeus* and *Nyctalus* showed a unimodal response with a decrease in suitability at high percentages of standing deadwood. Their optimum, however, was still higher than the average amount of standing deadwood found in the study area, both in stand types with and without retention. While all bats should benefit, at least opportunistically, from a higher prey availability or roosting opportunities that deadwood provides (Tillon et al., 2016), the negative response of *Nyctalus* and *P. pygmaeus* to very high amounts of deadwood may reflect the fact that the species prefer riparian forests for foraging and migration (Davidson-Watts et al., 2006; Furmankiewicz & Kucharska, 2009), while very large amounts of standing dead trees in our study area occurred mainly in disturbed spruce-dominated forests in higher altitudes. Finally, bats are known to explore the open spaces in forest gaps and open forests (Denzinger & Schnitzler, 2013; Dodd et al., 2012; Grindal & Brigham, 1998). However, in our study only *Eptesicus* responded to open forests, but in the opposite way than expected for an open-space foraging bat. The comparison of the availability of forest structures in retention and non-retention stands in this study (Fig. 2, for details see Supplementary data S5) clearly showed a lack of open structures and gaps in the study area. Although this could be partly due to methodological limitations in the detection of smaller gaps (Zielewska-Büttner et al., 2016), we assume that the overall rarity of these structures was the main reason for not being able to detect the responses of bats to these habitats.

A main caveat of studies based solely on acoustic bat data is the need to form acoustic groups of acoustically indistinguishable species. This aggregation may have diluted some species-specific differences suggesting that bat species within a group respond to forest structures in a similar way. Moreover, some forest-specialist species, e.g. of the genus *Myotis*, could not be represented at all in this study, meaning that studies on the requirements of individual species should additionally be considered when deriving precise structural target values for forest management. Additionally, probably because of the small sample size and the narrow spatial range in which the species occurs in the study area, we were not able to fully capture the known structural demands of the forest specialist *B. barbastellus* (Langridge et al., 2019), so the model results for this species should be taken with caution. To better understand the multi-scale effects of retention forestry on *B. barbastellus* a model involving more presence locations in a larger study area while testing fine scale structural forest variables is required.

Across species(-groups) forest cover played a dominant role in predicting bat occurrences in this study with predictions rapidly increasing towards high forest covers at the 100 and 250 m scale. As many of the investigated bat species(-groups) are well known to occur outside forests, we argue that this effect is stemming from our design, considering only within-forest habitat selection, and not from overall species preferences. Moreover, while we took great care to remove local biases resulting from the sampling locations by accounting for forest cover at local [50 m] and landscape [25 km<sup>2</sup>] scales, we did not account for the potential biases at all intermediate spatial scales, at which the forest cover was selected by bats. While we cannot rule out ecological reasons behind the selection pattern, the fact that our study plots were slightly biased towards a higher forest cover at these scales (for details see

Supplementary data S8) indicates that this result has to be taken with caution. Previous studies show forest type to play a subordinate role in bat habitat selection as bats utilize different forest types opportunistically once important key resources are available (Rachwald et al., 2022; Vasko et al., 2020) with interacting effects of stand and landscape context (Froidevaux et al., 2021). In our study, *P. nathusii* / *P. kuhlii* and *M. myotis*, for which clear preference for deciduous forests has been described (Rudolph et al., 2009), preferred forests with a higher share of deciduous trees in the surrounding landscape. Deciduous forests often support a higher number of insects (Kirby, 2013; Kirkpatrick et al., 2017), which increases their attractiveness as foraging habitats to bats. In addition, deciduous trees are also known to bear a greater number of different tree-related microhabitats (Asbeck et al., 2019; Großmann et al., 2018), so that bats may also be drawn by roost availability to deciduous forests.

After forest structure and type, bat habitat selection was influenced by topography. Convex surfaces increased the predicted habitat suitability for *M. nattereri*, *M. myotis* and *Nyctalus*. This effect may originate from convex surfaces being better drained and possibly more exposed to the sun, so that warmer microclimatic conditions may have promoted the activities of insects and bats. In contrast, concave surfaces as well as topographic roughness may reduce the acoustic detectability of bats as the terrain can affect the space in which bat sounds can be picked up by a microphone (Darras et al., 2016). Probably also due to more favorable microclimatic conditions, *B. barbastellus*, *Nyctalus* and *M. myotis* responded to the exposition, showing intermediate values for 'eastness' (Supplementary data S7) with the habitat maps indicating a preference for south-facing slopes (Supplementary data S6). The habitat suitability models contained few climatic variables, which is probably due to the restriction of our study area to a narrow altitudinal and thus climatic range (500–1400 m a.s.l.) of our study area. Consequently the responses to temperature and windspeed should be interpreted with caution as more favorable structural and topographical conditions in higher elevation of the study area may overrule climate effects (Braunisch et al., 2014).

Scale selection in this study appeared to be influenced by variable type. At this point we would like to point out that when variables were aggregated to represent larger scales, the absolute variable values became more similar and the variable gradient consequently smaller. This may have led to smaller effect sizes for variables representing larger spatial scales, so that the results of scale selection should be considered against this background. The effect of aggregation should be especially pronounced for variables or features that are common and regularly distributed in the landscape. As the different forest structure features showed different spatial distributions and occurred with varying frequencies in the landscape, while forest types showed small- and large-scale differences, we argue that the observed scale preferences are ecologically meaningful and that species may choose habitats at larger scales based on relative differences rather than absolute values.

#### 4.2. Remotely sensed forest structure data

The high predictive capabilities of forest structural attributes for the investigated bat species(-groups), highlight the value of large scale, detailed remote sensing data, obtained by combining optical remote sensing data with forest height information from digital aerial photogrammetry. Different studies have yet demonstrated the use of LiDAR data for habitat predictions of bats as this data can capture also subtle differences in forest strata lying below the canopy (Froidevaux et al., 2016; Rauchenstein et al., 2022), which is not possible using digital aerial photogrammetry only. However, the availability of landscape-wide LiDAR data is often limited so stereo aerial imagery provides a good alternative especially as the quality of the data is continuously improving. Although only the top layer of the forest can be characterized, stereo aerial imagery allows to capture conservation relevant forest structures such as standing deadwood at sufficient precision and across

multiple spatial scales. Besides, as the data is regularly updated by state surveys, it can also be useful for assessing structures and habitat conditions over time, in order to evaluate the effects of conservation instruments such as retention forestry.

#### 4.3. Effects of retention forestry

Although the structural differences between forests with and without retention were rather small in absolute terms, our finding that predicted habitat suitability was generally higher in retention forest stands suggests that most bat species already profit from structural changes induced by the new management concept, despite it was implemented less than a decade ago. This effect can be attributed to two aspects, which, however, can hardly be disentangled and operate in conjunction: First, based on the selection-guidelines (ForstBW 2016), retention sites are more likely to be established in areas that are older and more heterogeneous; second, since these areas are retained from logging, the natural development of these sites contribute to an increase in average age and heterogeneity of the forest stands with retention. Positive effects can be mainly attributed to an increase in heterogeneity in the canopy height, but also the forest height and tree volume. In contrast, the differences in standing deadwood, gaps or open forests between forest stands with and without retention were small. The higher habitat suitability in forests with retention may indirectly also be attributed to an increased abundance or richness of tree-related microhabitats (Basile et al. 2020). As the abundance of tree-related microhabitats was higher in retention trees compared to crop trees, and positively correlated with tree size (Großmann et al., 2018), we expect that the benefit of retention measures will increase and be more pronounced in the future, when higher amounts of deadwood provide resources and functions such as roosts and high-quality foraging areas.

#### 4.4. Conservation implications

Our findings show the importance of forest structure for bat habitat suitability inside forests. Even though bats are highly mobile animals which can exploit distant resources, forest structure influences bat species(-group) habitat selection mainly at small scales. As important structural features were enhanced in retention forests, we emphasize the importance of such integrative conservation approaches aiming at increasing structural complexity of forests locally, which effectively complements larger, segregative nature conservation instruments. Yet, the availability of key structures linked to old-growth forest such as open forest structures and deadwood are still scarce in the study area, and their contribution to the observed increase in bat habitat suitability in retention forest was negligible. As some bat species have high demands on old, structurally rich forests with a high availability of tree-related microhabitats, further measures may be needed locally to conserve them. In this context, the retention of 7–10 habitat trees per hectare forest providing 25–30 cavities per hectare was recommended (Meschede & Heller, 2000), i.e. retention levels that are 2–3 times higher than those currently implemented in the study area. However, as the abundance of tree-related microhabitats is not only related to the number of designated trees but also to their stage of development, a long-term monitoring of retention forestry effects is required to see if the current target values are high enough to provide sufficient amounts of structures for maintaining stable bat populations in the highly human-impacted forest environment. Moreover, as retention forestry enhanced old growth structures (tree volume, height, heterogeneity and deadwood) but did not affect open structures (gaps and open forest), this passive restoration tool may be complemented with other conservation instruments, that actively create forest structures by management, so as to provide the full range of structural complexity in the forest landscape and to meet the diverse demands of bats and other groups.

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#### Credit authorship contribution statement

**Anna-Lena Hendel:** Investigation, Data Analysis, Writing Original Draft. **Nathalie Winiger:** Data Analysis. **Marlotte Jonker:** Acoustic Data Collection and Acoustic Analysis. **Katarzyna Zielewska-Büttner, Selina Ganz and Petra Adler:** Methodology. **Veronika Braunisch:** Conceptualization, Methodology, Supervision. All authors contributed critically to the drafts and gave final approval for publication.

#### 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.

#### Data availability

Some parts of the data, including the forest structure data, are confidential and cannot be shared. The authors are willing to share e.g. the bat locations on request.

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#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.120783>.

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