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LiDAR metrics predict suitable forest foraging areas of endangered Mouse-eared bats (*Myotis myotis)*

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ABSTRACT

Habitat shift caused by human impact on vegetation structure poses a great threat to species which are specialized on unique habitats. Single layered beech forests, the main foraging habitat of Greater Mouse-eared Bats (*Myotis myotis*), are threatened by recent changes in forest structure. After this species suffered considerable population losses until the 1970s, their roosts in buildings are strictly protected. However, some populations are still declining. Thus, the spatial identification of suitable foraging habitat would be essential to ensure conservation policy. The aim of this study was (a) to verify the relevance of forest structural variables for the activity of *M. myotis* and (b) to evaluate the potential of LiDAR (Light Detection and Ranging) in predicting suitable foraging habitat of the species. We systematically sampled bat activity in forests close to 18 maternity roosts in Switzerland and applied a generalized linear mixed model (GLMM) to fit the activity data to forest structure variables recorded in the field and derived from LiDAR. We found that suitable forest foraging habitat is defined by single layered forest, dense canopy, no shrub layer and a free flight space. Most importantly, this key foraging habitat can be well predicted by airborne LiDAR data. This allows for the first time to create nationwide prediction maps of potential foraging habitats of this species to inform conservation management. This method has a special significance for endangered species with large spatial use, whose key resources are hard to identify and widely distributed across the landscape.

1. Introduction

The loss of biodiversity – irreversible and impalpable - is the most apprehensive process of environmental change (Wilson, 1989). Various global impacts like intensification in agriculture, climate change, urban sprawl or unsustainable forestry exert enormous pressure on biodiversity and are expected to further impact ecosystem conditions and habitat quality (Röschel et al., 2020). An important anthropogenic impact is the change in structure and composition of vegetation. Such interventions can significantly change the quality of habitats, as well as distribution and occurrence of species (Becker et al., 2017). Forests have been exploited and shaped by humans for many centuries and still are subject to constant change with major impacts on habitats. In the 19th century, coppice forests with originally broad-leaved species were intensively reforested with spruce (*Picea abies*), which is easy to establish. However, while this promoted the yield of timber it also led to dark, predominantly coniferous forests (Brockerhoff et al., 2008). Recently, the high nitrogen input from agriculture, industry and road traffic results in a decline of biodiversity (Braun et al., 2012). As a consequence, various strategies have been implemented to restore and maintain plenter and light forests with a diverse herbaceous layer (Bundesamt für Umwelt, 2013; Schweizerischer Bundesrat, 2017, 2012).

Bats (order Chiroptera) are particularly vulnerable to habitat changes, since most bat species have adapted their wing morphology, echolocation and foraging behaviour to a specific habitat structure (Norberg and Rayner, 1987; Schnitzler and Kalko, 2001; Froidevaux et al., 2016; Leidinger et al., 2021). Changes to such structures and the loss of essential habitats can result in population decline or extinction. Bat species that hunt close to or within vegetation like forests are generally more endangered than bats foraging in open space (Safi and

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Kerth, 2004). Thus, habitat change, fragmentation and intensification of the landscape are among the main reason why more than half (58%) of Swiss bat species are included on the Swiss Red List according to the criteria proposed by the IUCN (Bohnenstengel et al., 2014). Of the 30 bat species in Switzerland – all protected under Swiss federal law (Bohnenstengel et al., 2014) – 80% spend at least part of their lives in forests, either for roosting and rearing their young or foraging (Gebhard, 1997).

In Central Europe, Greater Mouse-eared Bats (*Myotis myotis*) forage in forests and over farmland and nurse their young in attics (Rudolph et al., 2009). Up to the 1970s, populations of *M. myotis* strongly decreased possibly due to pesticide use (DDT), toxic wood preservatives (Lindane), renovation of buildings, habitat loss, fragmentation and decreasing food supply induced by intensified agriculture. Since then, populations slowly recovered, however, *M. myotis* is still listed as vulnerable on the Swiss Red List today, of highest national priority because of its major conservation dependency and is included in Annex II of the Habitats Directive in Europe (Bundesamt für Umwelt, 2012; Bohnenstengel et al., 2014; Petrov et al., 2018). Even though roosts of *M. myotis* are strictly protected in Switzerland, some colonies are declining (Bohnenstengel et al., 2014). Thus, protecting roosts alone seem to be insufficient if parts of the habitat like foraging areas are missing. For the protection of these populations of *M. myotis*, it is of utmost importance that sufficient habitat availability is ensured. This is only possible if, firstly, the habitat requirements of the species are well known and, secondly, there are actionable ways to locate the specific areas; both questions we attempted to address in this research.

M. myotis mainly hunts in forests making use of a specialised foraging technique by passively tracking the rustling noises of flightless ground beetles (Carabidae) and catching them by gleaning them from the ground (Arlettaz et al., 2001; Audet, 1990). In previous studies, suitable foraging habitats have been shown to be characterized as forests with bare ground and free flight space that presumably simplifies search flight and the gleaning of prey (Arlettaz 1999; Güttinger, 1997; Zahn et al., 2005). Forests which typically fulfil these prerequisites are single-layered, old beech and mixed forests with a high amount of broad-leaved trees, a closed canopy that impedes ground vegetation and thus provides wide open flight space (Rudolph et al., 2009). However, beech forests are scarce and fragmented across vast parts of Switzerland (Begehold et al., 2015; Delarze et al., 2016). Nowadays, Swiss forest consists of 18% beech trees, whereby most of them occur in mixed forests (Abegg et al., 2014). Since the proclaimed aim of current and future forest management is to promote light forests with a diverse and rejuvenated shrub layer (Schweizerischer Bundesrat, 2012), the quality of *M. myotis'* foraging habitat is likely to deteriorate even more in the near future. It is therefore of major importance to identify, quantify and protect the remaining suitable foraging habitats of *M. myotis* in Switzerland.

Since a comprehensive search for suitable forest areas in situ is very time-consuming, alternative ways like LiDAR (Light detection and ranging) are a promising approach to map forest structure (Davies and Asner, 2014). LiDAR has been used in Switzerland (Graf et al., 2009) and globally (Simard et al., 2011) to map forest structures, but rarely with reference to bats (Ashrafi et al., 2013; Froidevaux et al., 2016) and never to predict foraging habitat of *M. myotis*. Furthermore, controlled conservation measures have so far mainly focused on roosts or caves but never on the foraging habitats (see Berthinussen et al. 2021). As only the conservation of the complete habitat ensures the protection of the species in the long term, the knowledge of the availability and location of potential foraging patches is paramount to target conservation measures.

The aim of this study was to (a) verify the relevance of proposed structural forest variables on the activity of *M. myotis* in the field and (b) to investigate the potential of 3-dimensional LiDAR data to predict suitable foraging habitat of this species. We sampled bat activity in the forested vicinity of known maternity roosts and used a generalized linear mixed model (GLMM) to fit the activity data to different forest structure variables recorded in the field and derived from LiDAR vertical data point distribution. Airborne LiDAR data is recently available for whole Switzerland, and is increasingly used throughout Europe, thus possibly enabling us to create for the first time a nationwide predictive map of potential foraging habitat of *M. myotis* in forests.

2. Material and methods

2.1. Selection of roosts and study sites

Currently, 106 maternity roosts of *M. myotis* are known in Switzerland (Bohnenstengel et al., 2014). Out of these, 18 roosts, each accommodating>100 individuals (count 2018) were selected (Appendix S1, Table S1). The 18 study roosts were mainly located in the Swiss Central Plateau, representing the majority of the natural distribution of *M. myotis* in Switzerland (InfoFauna, 2020) (Fig. 1).

Within a radius of 5 km around each roost, we searched for four triplets of sampling sites, consisting of a habitat patch predicted as (a) suitable, (b) intermediate and (c) unsuitable as foraging habitat for *M. myotis* (Fig. 2; Appendix S2, Fig S2). The three suitability types ensured an even coverage of different forest types, with the forest variables of each site being specifically and quantitatively recorded. Suitability of selected sites was graded by experienced chiropterologists based on their knowledge about the foraging behaviour of *M. myotis* (Arlettaz, 1999; Güttinger, 1997; Zahn et al., 2005). Site selection was driven by rating habitat quality in the field.

Suitable: Single-layered forests with a bare ground or only low ground vegetation, no shrub layer, free flight space and a dense canopy were anticipated as suitable sampling sites and expected to be preferred foraging habitat of *M.myotis.*

Intermediate: Forests composed of vegetated ground, light and heterogeneous shrub layer, free flight space and a patchy canopy were expected to be intermediately preferred.

Unsuitable: Forests with open canopy, densely vegetated ground and/or dense shrub layer were expected to be unsuitable foraging places.

A sampling site consisted of the respective type of forest (either suitable, intermediate or unsuitable) and covered a circular area with a minimum diameter of 25 m (≈500 m^2). If a suitable sampling site was found, we searched intermediate and unsuitable sampling sites within distances of 50 m to 200 m to assure comparable reachability and to minimize other possible location effects. If possible, each of the four triplets were located in different forest patches and evenly distributed within the 5 km radius around the roost. The forest structure of these study sites was then determined both in the field and through remote sensing data.

2.2. Forest variables

To describe the forest characteristics as exactly as possible, a habitat survey was performed at every sampling site. The recorded variables were based on the methodology of the fourth Swiss National Forest Inventory (LFI4, Düggelin, 2019) and are described in detail in the Appendix S3. An extract of the variables can be found below in Table 1.

2.3. Bat activity

The activity of *M. myotis* was measured by recording the bats' echolocation calls with ultrasound bat recorders (BATLOGGER M, A+ and C, Elekon AG, Lucerne, Switzerland). We used 24 devices, distributing them randomly across sites and habitat suitability. The microphones were mounted on poles about 1.5 m above ground in the centre of the selected sampling site. The recordings started automatically 15 min before sunset and stopped 15 min after sunrise. Within this time window, recordings were triggered by tonal ultrasound signals ('Period Trigger' of the Batlogger), thereby largely avoiding recordings of noise like wind, rain or orthopterans. Echolocation recordings of 1.5–10 sec in

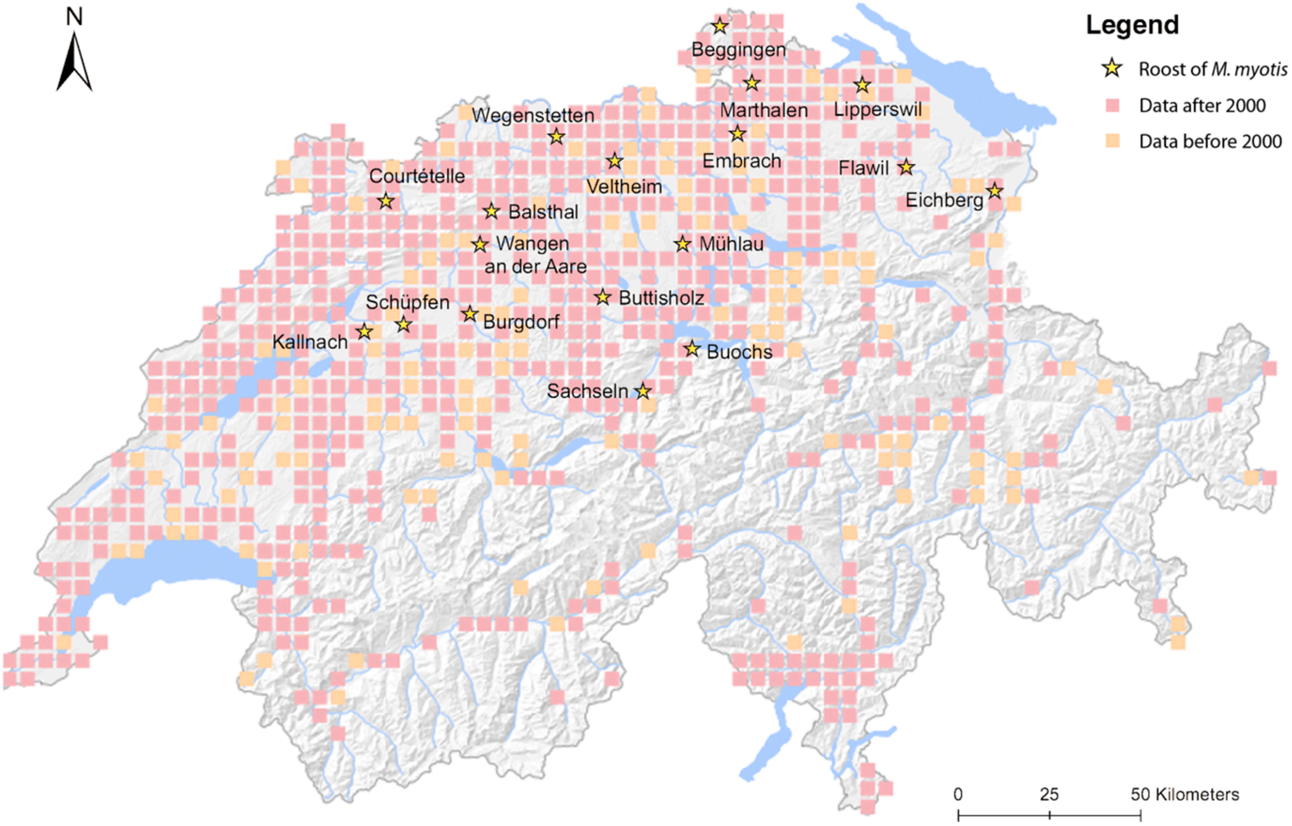

Fig. 1. The distribution of the 18 selected study locations (maternity roosts of *M. myotis*) overlaid on the known distribution of *M. myotis* shown as red (data from 2001 to 2020) and orange (data from 1903 to 2000) 5x5 km squares (InfoFauna, 2020).

length (pre-trigger 0.5 s, post-trigger 1 s) were stored on SD memory cards as WAV files and are hereafter termed as sequences. The acoustic signals were recorded at a sampling rate of 312.5 kHz (16-bit).

The data collection took place from mid-May to the end of July 2019 during ten consecutive weeks. Forests around two roosts were examined in the same week for preferably three nights with good weather conditions. In case of rain, strong wind or cold temperatures below 7° Celsius the devices were left to record longer to achieve at least two nights of recordings under favourable conditions.

2.4. *Analysis of the recordings*

The sequences were first analysed with the software BatScope4 (Obrist and Boesch, 2018) - a software that cuts recorded sequences into single calls, measures their temporal and spectral characteristics, and statistically classifies them to species according to an integrated call library. Automated classifications were all manually verified and, in case of unclear outcome (e.g. few calls detected, diverging call classifications), assigned to species groups. This process ascertains high identification accuracy, thereby avoiding errors that can occur in automated identification (Russo and Voigt, 2016). We could not acoustically differentiate between the two sibling species *M. myotis* and *M. blythii.* However, based on known trophic and foraging niche separation of the two species (Arlettaz and Perrin, 1995; Arlettaz, 1996) and considering the fact, that in none of the sampled roosts mixed colonies were recorded, we savely assumed all *M. myotis* type calls to emanate from this species.

After extracting all *M. myotis'* calls, the other recorded bat calls were categorized into three groups to test the validity of the models for these groups. Bat species with echolocation calls of bandwidths > 50 kHz and durations ≤ 6 ms were grouped in a guild of short-range echolocators (SRE) whereby *M. myotis* belongs to this group (containing the genera *Myotis*, *Barbastella*, and *Plecotus*). A second group termed long-range echolocators (LRE) was uniting species which call with bandwidths < 30 kHz and durations > 9 ms (containing the genera *Eptesicus*, *Nyctalus*, *Vespertilio*). All remaining species with intermediate bandwidths and call durations were assigned to mid-range echolocators (MRE) guild (containing the genera *Hypsugo*, *Miniopterus*, *Pipistrellus*). These groups based on the classification of Frey-Ehrenbold et al. (2013) and Obrist et al. (2004) and follow a concept similar to the guilds for 'narrow space', 'edge space' and 'open space' used by Denzinger and Schnitzler (2013). Using the guild concept, it simplified the statistical comparison of *M. myotis* with other bat species (SRE without *M. myotis*, MRE, LRE). The final output of the acoustics analyses consisted of the number of echolocation sequences comprising calls of *M. myotis*, of the SRE guild (without calls of *M. myotis)*, the MRE guild and the LRE guild per night and sampling site, representing the activity of the bats.

2.5. *Remote sensing data*

To predict the distribution of potential foraging habitats of *M. myotis* in forests nationwide, remote sensing data displaying the structural information on the vegetation were used (Table 2). LiDAR data is available for most of Switzerland, with average densities of 15 – 20 points per m^2, a horizontal accuracy of 20 cm and a height accuracy of 10 cm (Swisstopo, 2017). For those areas which are not covered yet by the new nationwide campaign of swisstopo, LiDAR data from the cantons were used.

The LiDAR data was normalized by subtracting the elevation from the digital terrain model (DTM) SwissAlti3D from swisstopo (resolution 2 m × 2 m) and points on buildings were removed. Because the DTM is created from different input sources and the rather coarse resolution in comparison to the point density, negative values in the normalized point clouds were possible. The remaining vegetation height data was

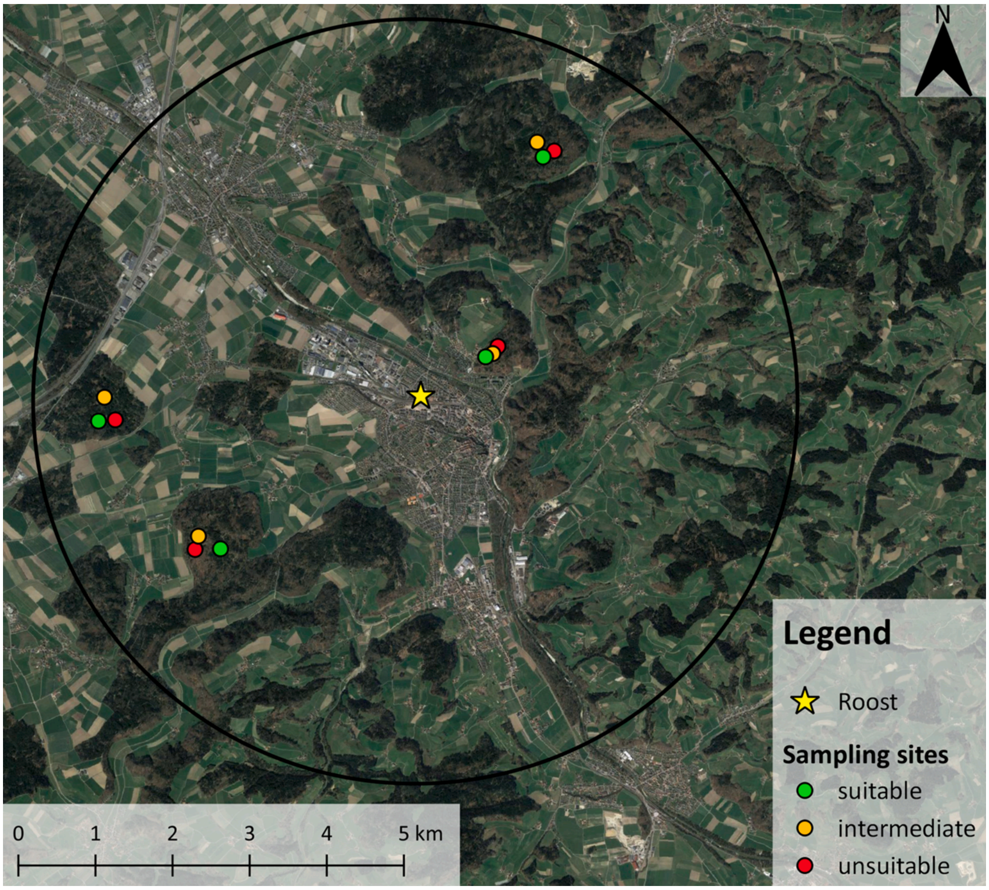

Fig. 2. Sampling design with four triplets of sampling sites (predicted as suitable, intermediate and unsuitable, respectively) in the forests around the maternity roost of *M. myotis* in Burgdorf. The circle defines the sampling area of 5 km around the roost. The design was repeated around 18 different maternity roosts.

Table 1
A selection of the most important forest variables recorded at sampling sites and retained in the final model. For more details see Appendix S3.

Variable	Details	Appendix S3 paragraph
Topographic slope	Average slope [degree] of sampling site	4
Free flight space	Height [m] from 0.5 m to first tree layer inhibiting flight	6
Stand structure	Single-layered, Multi-layered, All-sized, Clustered	8
Degree of mixture	Pure coniferous (91–100% conifers), Mixed coniferous (51–90% conifers), Mixed deciduous (11–50% conifers), Pure deciduous (0–10% conifers)	9
Stage of stand development	Young growth, Pole wood, Young timber, Medium timber, Old timber, Mixed trees	10
Coverage of herbaceous layer	Coverage of plants [%] up to 0.5 *m*	13
Coverage of shrub layer	Coverage of plants [%] between 0.5 and 3 m	15
Coverage of tree canopy	Ratio [%] between total area and area covered by canopy	16
Humidity	Average of humidity per night	18
Distance to roost	Straight line distance from roost to sampling site [km]	21

classified into different forest metrics and gridded on a raster of 12.5 × 12.5 m by using lascanopy metrics from LAStools (Isenburg, 2019). The classifications were fitted manually on variables of the Swiss National Forest Inventory to optimally reproduce the forest characteristics found to be suitable for *M. myotis*. Negative numbers in the height range resulted from normalizing the LiDAR data and were included by choosing a range starting at −3 m. In order to distinguish between field variables and remote sensing variables, the latter are marked with RS.

2.6. *Statistical analysis*

The two datasets contained different variables, describing the sampling site either as recorded in the field or by remote sensing data. Bat activity as the response variable comprised Poisson distributed count data.

Numerical analyses were performed with the statistical software R (R Core Team, 2019). The explanatory variables were standardized and checked for correlation with the non-parametric Spearman's (rho) rank correlation coefficient.

Kruskal-Wallis test and a post hoc test (Dunn's test for pairwise comparisons) were used to examine univariate differences in the effects of categorical variables on bat activity (Dunn, 1964). Both datasets (field data and remote sensing data) were then analysed by a Poisson generalized linear mixed model (GLMM) with the activity of *M. myotis* as response variable, the environmental predictors as explanatory variables and 'sampling location', 'recording hours per night' (due to partially irregular recording durations because of device failures) and 'batlogger ID' as random variables. Automatic stepwise variable selection implies the risk of omitting important biological variables for pure computational reasons. Since we were interested in ecological models of high interpretability, we built for both data sets an initial model based on knowledge from literature (Field data: Arlettaz, 1999; Güttinger, 1997; Zahn et al., 2005. Remote sensing data: Davies and Asner, 2014; Froidevaux et al., 2016; Jung et al., 2012; Müller et al., 2013) to test the hypotheses. They were then stepwise improved by variable selection based on their significance (Field et al., 2012) and were ranked by the

Table 2
Remotely sensed variables, their calculation and structural meaning, and the respective data sources and resolution of the layers used in this study. All remote sensing variables are marked with RS.

Variable	Calculation	Structural meaning	Resolution	Data Source
Tree Canopy (RS)	percentage of first returns above 7 m	coverage of the tree canopy	12.5 m	LiDAR: Swisstopo, 2017
Shrub layer (RS)	percentage of points between 1 and 7 m	density of the shrub layer	12.5 m	LiDAR: Swisstopo, 2017
Herbaceous layer (RS)	percentage of points between −3 and 1 m	forest ground including the herbaceous layer	12.5 m	LiDAR: Swisstopo, 2017
Free flight space (RS)	skewness of points in the height range from −3 to 7 *m*	extent of free flight space in the understory (high skewness signifies high proportion of returns on the ground and strongly decreasing numbers aloft in the shrub layer)	12.5 m	LiDAR: Swisstopo, 2017
Degree of mixture (RS)	coniferous vs. deciduous in four levels (≥91%, 51–90%, 11–50%, ≤ 10% coniferous trees)		25 m	Waser and Ginzler, 2018
Slope (RS)	topographic slope		25 *m*	DTM25_L2, Swisstopo (Art. 30 GeoIV): 5704 000 000)

Akaike Information Criterion (AIC) whereby a model with a lower AIC was considered significantly better if ΔAIC was greater than two (Burnham and Anderson, 2004).

Further, both final models were tested against overdispersion and for both cross validation was calculated. Due to the setting of 18 test sites, we used a nine fold procedure with eight folds as training set and one fold as testing set, respectively.

To evaluate the fit of the models, a correlation between the logarithmized model predictions and the logarithmized observed bat activities was calculated with Pearson correlation coefficients (Becker et al., 1988). The correlation coefficients were compared by cocor package in R (Diedenhofen and Musch, 2015) with the Dunn and Clark's z test (1969). The same procedure was also used to control if the models specifically predict the activity of *M. myotis* better than that of the other defined bat guilds (SRE without *M. myotis*, MRE, LRE).

3. Results

At 18 different roosts across the Swiss Central Plateau, recordings were made during 810 sampling nights (12 sites per roost = 216 sites, 3–5 nights per site). The batloggers registered a total of 199′134 sequences during 6′639 recording hours. Thereof, 1′929 sequences (0.96%) were attributed to *M. myotis*.

3.1. Impact of forest structure derived from field data on M. Myotis activity

The incidence rate ratios (IRR) of the field variables are shown in Fig. 3 and listed in the Appendix S4, Table S4. A closed tree canopy had a positive effect on *M. myotis* activity (IRR: 1.18 > 1), whereby the shrub layer negatively affected *M. myotis* activity (IRR: 0.71 < 1). The herbaceous layer had a slightly negative (IRR: 0.97), the free flight space a slightly positive effect (IRR: 1.05) on *M. myotis* activity. A distinct impact on *M. myotis* activity showed the 'stand structure' where single layered forests had the strongest effect of all tested variables and were strongly preferred (IRR: 1.77), all-sized forest clearly avoided (IRR: 0.35) by the bats. Looking at the 'stage of stand structure' we see a clear preference: The bigger the trees, the more the *M. myotis* activity was positively affected. Pure coniferous forests affected *M. myotis* activity negatively (IRR: 0.45), but mixed coniferous and pure deciduous forests both had a positive effect. A larger distance from roost to foraging place (IRR: 0.87) and also humidity (IRR: 0.81) negatively affected *M. myotis* activity, whereas the topographic slope had a positive effect (IRR: 1.22). A selection of the most important field variables is presented in Fig. 4, which describe forest structure and show the preference of *M. myotis* concerning foraging habitat.

4. Impact of forest structure derived from remote sensing data on *M. myotis* activity

The incidence rate ratios (IRR) of the remote sensing variables are shown in Fig. 5 and listed in the Appendix S5, Table S5. By far the strongest positive effect of remote sensing data variables on *M. myotis* activity generated a closed tree canopy (RS, IRR: 10.06). Similar as in the field data model, the shrub layer (RS) negatively affected *M. myotis* activity with an IRR of 0.75. Variables integrated in the model as interactions must not be interpreted as individual variables. The interaction of tree canopy and free flight space (RS, IRR: 1.91) positively affected *M. myotis* activity. The highest positive effect of the 'degree of mixture' showed the interaction of herbaceous layer and pure deciduous forest (RS, IRR: 2.83).

4.1. Evaluation of field and remote sensing model predictions

To evaluate both, field and remote sensing model, they were compared with the total observed activity of *M. myotis,* resulting in a correlation coefficient of 0.710 (predicted activity by field model) and 0.687 (predicted activity from remote sensing model). Both coefficients indicate a strong correlation and do not differ significantly from each other (Dunn and Clark's z test (1969): z = 1.3853, $p = 0.166$, Table 5).

To test whether the models specifically predicted the activity of *M. myotis* rather than general bat foraging activity, the activity of the classified bat guilds (SRE without *M. myotis*, MRE, LRE) were compared against the predictions of the field data and the remote sensing data model. All the correlations between the activities of non *M. myotis* functional groups and the respective data model revealed correlation coefficients significantly lower than the correlations between *M. myotis* activity and the respective data models (Dunn and Clark's z test (1969): $p < 0.001$ in all cases, Table 3).

5. Discussion

In this study, we generated a model, predicting suitable foraging habitat for *M. myotis* in forests by first identifying suitable forest structures with 21 variables recorded in the field, and second, fitting remote sensing data (derived from LiDAR). The results revealed that *M. myotis* favoured single-layered forests with free above ground flight space, a dense canopy and forest stands of young timber age class and older, that are at least partially deciduous. In contrast, forests with an all-sized stand structure, a dense shrub layer and young trees were avoided by

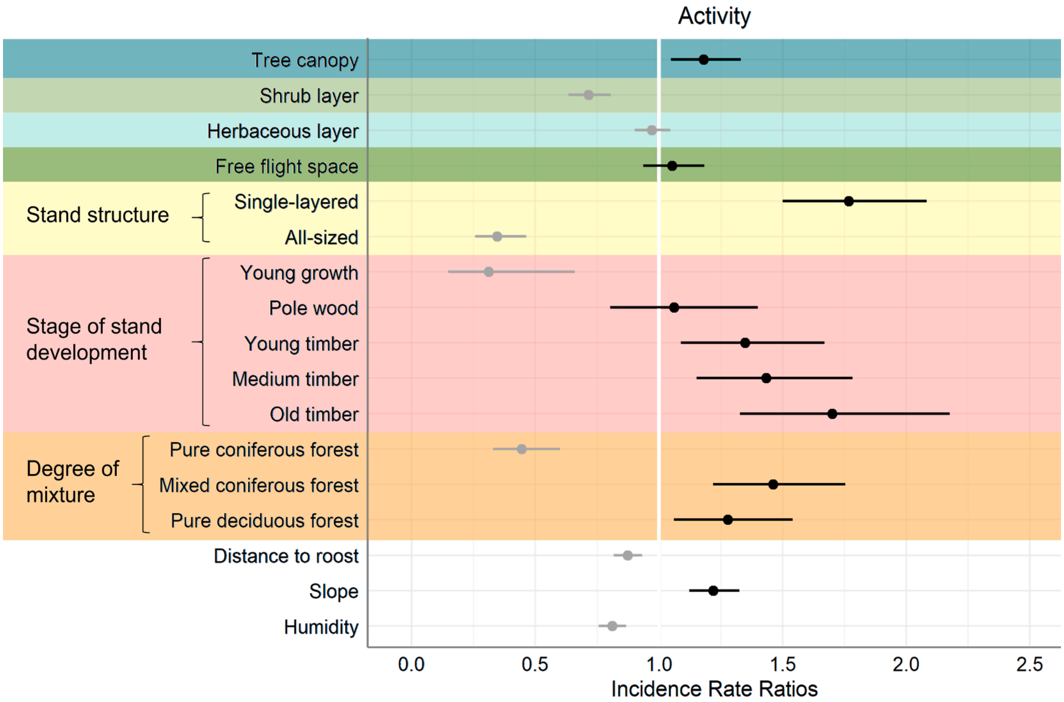

Fig. 3. GLMM of field data. Incidence rate ratio is the ratio between the activity of *M. myotis* per night attributable to the expressed variable and the total number of *M.myotis* activity. The higher the incidence rate ratio > 1, the more the activity of *M. myotis* is positively affected by this variable (black). The lower the incidence rate ratio < 1, the more the activity of *M. myotis* is negatively affected (grey).

M. myotis. For the first time, we could predict the activity of a bat species by forest indices derived from LiDAR data without significant difference to the field data model, which is therefore a close approximation to reality with promising potential for conservation.

5.1. *Interpretation of the field data modelling*

The main drivers of activity of *M. myotis* consisted of variables strongly influenced by the age, structure and mixture of the forest stands. With increasing forest age and homogeneity, the canopy cover becomes more closed and undergrowth more sparse. Indicative of old forests are trees with diameters of at least 30 cm ("young timber") or even>50 cm ("old timber"), both factors favouring the activity of *M. myotis*. With increasing forest age, biodiversity and insect biomass also rise, what leads to a better food supply for *M. myotis* (Moning and Müller, 2009). These older trees additionally offer tree holes for night-time resting (Broggi et al., 2011). Moreover, older trees exhibit more closed crowns and a larger free flight space, both again positively correlated with *M. myotis* activity (see below).

Forests structured as "single-layered" forests build a dense canopy with only little structure underneath (medium and lower layers coverage < 20%). The closed canopy prevents strong incidence of light, and therefore, a dense growth of the shrub layer (Härdtle et al., 2003). Free space in the shrub layer with shrub coverage<25% seemed to be preferred by *M. myotis.* Single layered forests also predicted a significantly higher activity than "multi-layered forests" and hardly any activity could be found at "all-sized forests" (continuous stratum of trees and shrubs). High coverage of shrub layer might hinder flying close to and gleaning from the ground. Consequently, the recorded variable 'free flight space' showed a higher bat activity at values of around 5 m to 20 m free vertical space.

The importance of the forest structure is also indicated by the 'degree of mixture', whereby *M. myotis* visited pure coniferous forests significantly rarer than forests with a certain proportion of deciduous trees: The pattern is most likely due to the spatial structure of pure spruce plantations rather than microclimatic changes (lower pH value, soil humidity, see Rudolph et al., 2009), since we see no graduation between forest types with different proportions of spruce.

Finally, dissimilar to previous studies, where *M. myotis* clearly preferred foraging habitats with no or only sparse ground vegetation (Güttinger, 1997; Zahn et al., 2005), the herbaceous layer influenced bat activity only slightly negatively. However, the majority of the study sites with activities in dense herbaceous coverage consisted of a homogeneous growth of small plants and a free flight space which did not seem to strongly hinder *M. myotis*.

5.2. *Interpretation of the remote sensing modelling*

Similar to the field model, a closed canopy (RS) affected *M. myotis* activity positively. The canopy is well represented by LiDAR measurement since it is the first vegetation layer the laser points are being reflected from. Conveniently, a dense canopy is a good basic assumption for suitable foraging habitats since it often implies several consequences like a low light incidence and thus reduced plant growth in the layers below. Also, the negative effect of the shrub layer (RS) on *M. myotis* activity corroborates the findings of the field data model. The herbaceous layer (RS) has a positive effect on *M. myotis* activity. However, since this variable was calculated by the laser points reflected from the ground, it can also symbolise a forest without many obstacles and thus a free flight space. The free flight space (RS) calculated as the skewness of points, in contrast, did not show a strong effect on *M. myotis* activity.

5.3. *Evaluation*

Both models showed a strong correlation to the observed *M. myotis* activity with a coefficient of 0.710 (field data model) and 0.687 (remote sensing data model). It was expected that the remote sensing model would correlate less with the activity of *M. myotis* than the field data model. However, there was no significant difference between these two correlation coefficients, which demonstrates a good model fit and a quite realistic representation of the forest structure through the remote sensing data.

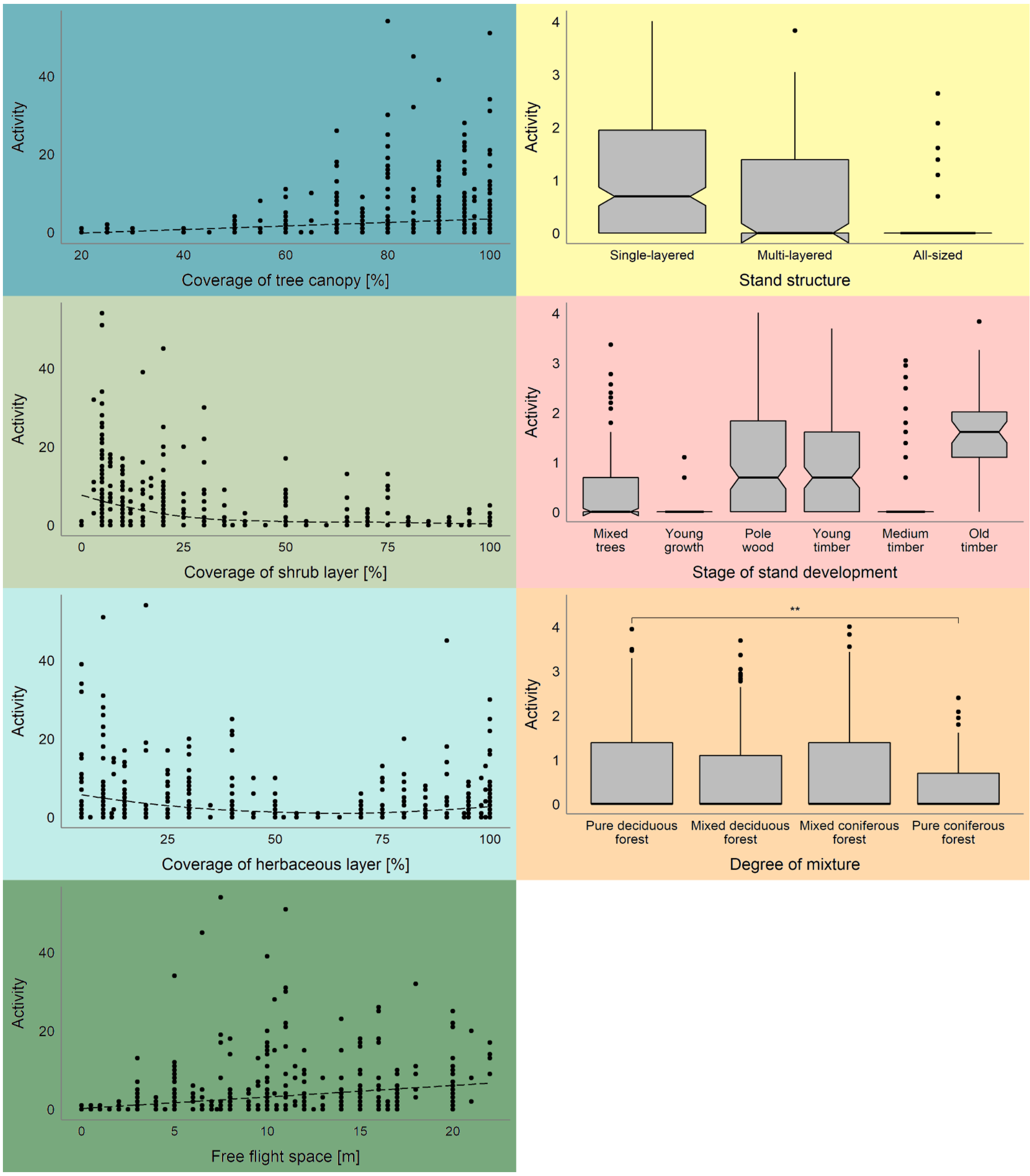

Fig. 4. A selection of field variables displaying forest structures on the x-axis and activity of *M. myotis* on the y-axis.Left side: Activity vs. continuous variables of coverages and flight space with a dashed smooth curve. Right side: Box plot of activity vs. categorical variables (with log transformed activity scales). Background colours match those in Fig. 3.

In contrast to field data, which has to be collected in a time-consuming manner, remote sensing data are available nationwide. Therefore, the reliable prediction of forest suitability for *M. myotis*' foraging through remote sensing data is a major achievement for forest conservation management.

According to our results, the comparison of both model predictions with the different bat guilds (*M. myotis*, SRE without *M. myotis*, MRE, LRE) resulted in a best prediction with the activity of *M. myotis*. All correlations with non *M. myotis* functional groups showed significantly lower correlation coefficients between 0.387 and 0.280. Therefore, it can sensibly be argued that the remote sensing model used herein specifically predicts *M. myotis* foraging habitat.

5.4. *Implications for management*

Open forests are often propagated by conservationists as key habitats when it comes to forest biodiversity (Imesch et al., 2021). Doubtlessly, this designation is legitimate for many species endangered today. For *M. myotis*, however, the currently widespread tendency to promote light forests in Switzerland is unfavourable, since thinning the stands on nutrient-rich grounds without regular removal of the young stands leads to open canopies and, consequently, dense shrub layers, indicators for unsuitable foraging habitat for *M. myotis*. To consider all species of conservation concern, conservation should promote a mosaic of different forms of forest management; with open areas for heliophilous and thermophilic species, but also with closed, single layered old-growth forests of sufficient size for *M. myotis* and other species e.g. *Phylloscopus sibilatrix* (Pasinelli et al., 2016) or *Myotis bechsteinii* and various woodpecker species (Singer et al., 2021). Finding and protecting forest patches that still fit the needs of *M. myotis* is thus a crucial step towards a better conservation of this, but also the other mentioned species.

Indications are strong that in recent years, suitable foraging habitat has become a key limiting factor for the further recovery of *M. myotis* populations in Switzerland (Güttinger and Beck, 2021), a species of

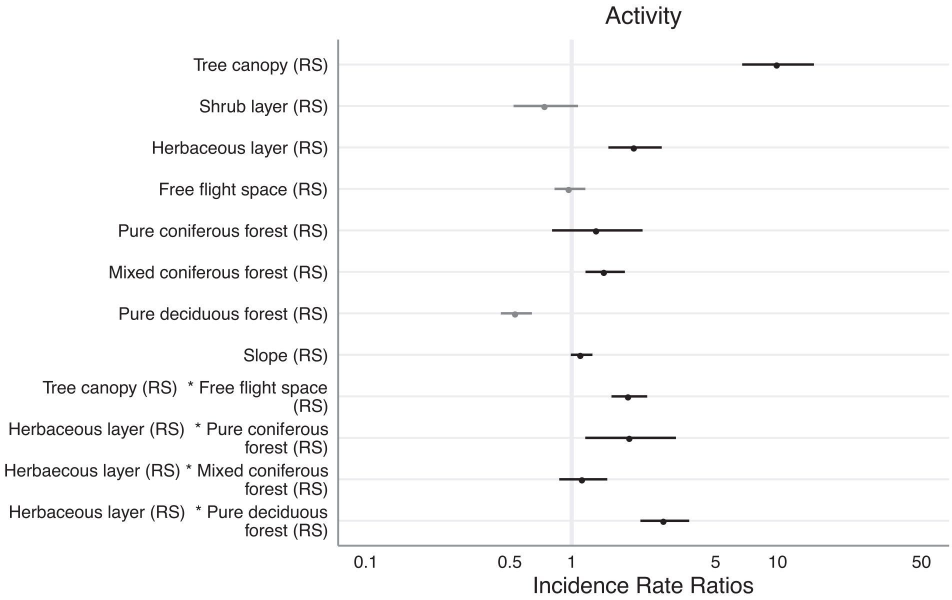

Fig. 5. GLMM of remote sensing data. All remote sensing variables are marked with RS. Incidence rate ratio is the ratio between the activity of *M. myotis* per night attributable to the expressed variable and the total number of *M. myotis* activity. The higher the incidence rate ratio > 1, the more the activity of *M. myotis* is positively affected by this variable (black). The lower the incidence rate ratio < 1, the more the activity of *M. myotis* is negatively affected (grey).

Table 3
Correlation of the field data model and the remote sensing data model with the activity of *M. myotis* and the other functional groups (SRE = short range echolocators, MRE = mid range echolocators, LRE = long range echolocators). Significance of difference against correlation of activity of *M. myotis* in the respective data model is given in brackets with *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

Activity of	Field data	Remote sensing data
M. myotis	0.710	0.687
SRE (without *M. myotis*)	0.387 (***)	0.344 (***)
MRE	0.370 (***)	0.355 (***)
LRE	0.291 (***)	0.280 (***)

highest national conservation priority (Bundesamt für Umwelt, 2019). Contrary to foraging habitats in agricultural areas, woodlands are important because prey insects are more diverse, available throughout the season and light pollution is limited (Máthé, 2006). However, to suit as foraging habitat for *M. myotis*, forests must contain considerable areas of unvegetated ground (Güttinger, 1997). The exclusive use of such forest structures suggests that *M. myotis* is an indicator species for these particular habitat requirements in forests. Because of the spatially extensive habitat requirements they may even act as an umbrella species for a species community that is adapted to mature, single layered deciduous or mixed-deciduous stands characterized by a dense canopy and sparse ground vegetation. This function should be used more broadly in the communication for the protection and management of these specific forest stands. The results of the latest National Forest Inventory (LFI4; Brändli et al. 2020, pp. 284ff and pp. 297ff) promise, that present forestry planning results in higher percentages of mature forests, also for future CO_2 storage, thus potentially better supporting *M. myotis*. However, this seems mainly the case in the Jura mountains, alpine regions and the southern part of the alps. Dense and closed forests, on the other hand are still decreasing in the central low-lands, the main distributional area of *M. myotis*. The rather small-scale forestry systems in Switzerland further complicate the generation of larger scale forests with closed canopy (Appendix S6, Fig. S6).

The remote sensing model based on airborne LiDAR data proves to be a powerful tool to identify forest stands with the requested forest structure. This major achievement allows for the first time to create nationwide prediction maps of potential foraging habitats in forests to inform conservation management (example in the Appendix S6, Fig. S6). To counteract the decrease of suitable foraging habitat, the model can help to identify (1) suitable forests which should be protected through longer harvesting intervals, and (2) unsuitable areas with revaluation potential. As a next step, we suggest to create overview maps of predicted suitable foraging sites of *M. myotis,* which are accessible to all stakeholders such as forest administrations, foresters and conservation organisations, clearing the way for in situ verification and definition of site-specific conservation measures. Further, such models might be adapted for other (bat) species with special needs in terms of forest structure.

6. Conclusions

To summarize, we were able to identify forest structures which predicted foraging habitat suitability for the endangered bat species *M. myotis*. Model predictions from both field and remote sensing data performed well in identifying areas that were frequently used by the targeted species. Specifically, forests structures like single-layered forests with a dense canopy, a free flight space and no shrub layer are relevant indicators for foraging habitats of *M. myotis*. A major achievement is the new model based on remote sensing data which predicts *M. myotis* activity in accordance with the field data. The practical implications of using such a model are far-reaching: a map of predicted suitable foraging habitats of *M. myotis* in Switzerland can serve as basis to identify important forest areas. This allows the focus for the conservation of endangered species to be extended to the major foraging grounds, even when they are scattered in the landscape. The method demonstrated has a special significance for endangered species with large spatial use, whose key resources are hard to identify and widely distributed across the landscape. There is growing acceptance that nature and species conservation is an enormously important, complex, large-scale, transnational issue. In order to achieve improvements on a large scale, modern technologies such as remote sensing data will be an important aid in the fight against species extinction.

Data Deposing.

All data of this study is available on EnviDat (https://www.doi.org/10.16904/envidat.306).

CRediT authorship contribution statement

Katja Rauchenstein: Conceptualization, Methodology, Data curation, Validation, Formal analysis, Writing – original draft. **Klaus Ecker:** Software. **Elias Bader:** Conceptualization, Methodology, Resources, Data curation. **Christian Ginzler:** Software. **Christoph Düggelin:** Data curation. **Fabio Bontadina:** Conceptualization, Resources, Writing – review & editing. **Martin K. Obrist:** Conceptualization, Methodology, Resources, Funding acquisition, Validation, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120210.

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