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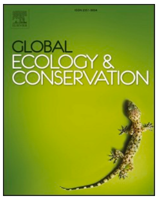

Environmental features around roost sites drive species-specific roost preferences for boreal bats

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ABSTRACT

Bats and their reproductive roost sites are strictly protected by legislation in Europe. Although knowledge on foraging habitats of boreal bats has increased vastly over the last decades, little is known on how habitat surrounding the roosts influences the selection of roost sites. We combined citizen science and molecular methods to determine the most critical environmental features within different radiuses around roost sites of bats inhabiting human settlements at the northernmost edge of their distribution range in Finland. We compared six different land-use types around the roost sites to randomly selected points for each species to determine at which radiuses around the roost are land-use types most critical. We found that for the northern bat (*Eptesicus nilssonii*), built environment, open areas, and water within the 200 m radius were the most important in roost site selection. The Brandt's myotis (*Myotis brandtii*) favored roost sites in landscape not affected by human disturbance within 5 km radius. Based on our results, the surrounding habitat around a roost plays a vital role for bat species, and it should be protected along with the roost and considered in land-use planning. Furthermore, species-specific variation in roost site selection should be considered in conservation planning.

1. Introduction

Human-inflicted habitat loss and degradation are the main causes of the present global biodiversity decline (e.g., Vitousek et al., 1997; Pimentel et al., 2007; Cardinale, 2012; Newbold et al., 2015; Wang and Dong, 2019). Slow-reproducing species with a long lifespan, such as bats (Barclay et al., 2004; Ancillotto et al., 2021), are especially vulnerable to habitat loss because their populations are slow to recover from sudden environmental changes (Southwood et al., 1974; Wilkinson and South, 2002; Heinrichs et al., 2016). Bats use several habitats and associated roosts during their annual cycle and even within the season (e.g., de Jong, 1994, Haupt et al.,

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2006; Vasko et al., 2020; Smirnov et al., 2021) These sites are used for swarming and hibernation during winter, temporary roosts for resting during foraging flight, maternity roosts for reproduction and bachelor roosts for males (Alston et al., 2019). This raises the need to identify these sites to effectively facilitate conservation.

Environmental and geographical features have an impact on the habitats used by bats. For example, in temperate regions, bats utilize caves for breeding (Kunz, 1973; Mann, 1999; Mann et al., 2002), while in the boreal region caves are often too cold for reproduction but are used for swarming and hibernation during the wintertime (Randall and Broders, 2014). However, in Fennoscandia caves are rare, and bats use other natural formations such as rock screes (Michaelsen et al., 2013), ancient shores, rock outcrops, glacial erratic formations (Blomberg et al., 2021), and have also taken advantage of human modified structures, such as mines (Rydell et al., 2018), that provide relatively steady temperature and humidity for hibernating bats (Masing and Lutsar, 2007; Siivonen and Wermundsen, 2008; Belkin et al., 2015). Some species however, such as Nathusius' pipistrelle (*Pipistrellus nathusii*) and particoloured bat (*Vespertilio murinus*), migrate to Central Europe (Hutterer et al., 2005), because they prefer to hibernate in above ground sites that are too cold at northerly latitudes. In the summer, bats use buildings, tree crevices and snags (Fabianek et al., 2015; Michaelsen, 2016; Alston et al., 2019; Thomas et al., 2019, 2021) as diurnal roost sites in the boreal zone.

While many bat species globally rely on natural diurnal summer roost sites, such as tree crevices and cavities (e.g., Fabianek et al., 2015; Michaelsen, 2016; Alston et al., 2019; Thomas et al., 2019, 2021), caves (e.g., Tanalgo et al., 2022), and foliage (e.g., Kunz et al., 2003), some bat species have taken advantage of human built structures as diurnal roost sites (e.g., Marnell and Presetnik, 2010). Buildings provide relatively steady humidity and temperature conditions bats require at northerly latitudes. However, it is not yet fully understood which species use human-built structures in the boreal zone, and how their roosts are allocated latitudinally and within the landscape.

Important habitat characteristics can drive the selection and use by bats and may vary at different scales around the roost (Ford et al., 2006; Thomas et al., 2021; Neubaum and Aagaard, 2022). For synanthropic boreal bats in the Nearctic, the surrounding forest cover is important (Shively and Barboza, 2017; Thomas et al., 2019, 2021). In Sweden, the distribution of bat activity between habitats was explained by the occurrence of swarming insects (de Jong and Ahlén, 1991). For a boreal bat species, the little brown myotis (*Myotis lucifugus*), that roosts in buildings (Shively and Barboza, 2017; Thomas et al., 2021), the foraging grounds in the forests determined the occurrence of the species if roosts were available (Thomas et al., 2021). Moreover, the selection of roost sites may be affected by the previous use of the area by humans (Monarchino et al., 2020). It is possible that boreal bat species also have similar requirements; hence understanding the essential landscape features in the north help targeting conservation actions at local scale.

In Europe, roost sites of bats are protected by national legislations and an agreement of European countries belonging to the EUROBATS organization (Agreement on the conservation of bats in Europe, EUROBATS, 1991). However, the protection is often strictly targeted to the roost itself or its immediate surroundings while the habitat surrounding the roost is often prone to anthropogenic exploitation (Bosso et al., 2018). This may lead to bats abandoning a roost altogether (Kunz, 1982) if the changes in the surrounding habitat do not meet the requirements of the bat species. International collaborations have taken several steps towards conserving habitats, such as protecting important foraging areas and commute routes to these areas (Kyheröinen et al., 2019); however, these are recommendations rather than legally binding documents. To further incorporate important habitats near the roosts into policy, identifying species-specific important landscape variables around the roosts are essential for the successful implementation of conservation measures.

Gaining information on roosts at the northern edge of the ranges of bat species is crucial for conservation measures, particularly as climate change is driving species distributions northwards (Chen et al., 2011); hence possibly making the boreal zone an important refugium for many species in the future (Berteaux et al., 2018). Thirteen species of bats have been recorded in Finland, yet most of our knowledge on the roosting habits of these species is from the temperate zone and only the southern parts of the boreal zone (e.g., Haupt et al., 2006; Marnell and Presetnik, 2010; Ciechanowski, 2015). However, several bat species are regularly found in northern Fennoscandia (Tidenberg et al., 2019; Kotila et al., 2023), and even breed above the Arctic Circle (Rydell et al., 1994). Species-specific roosting habitat requirements can vary latitudinally because of biotic and abiotic factors such as temperature or light. For example, in North America the critical temperature of summer roosts of *M. lucifugus* is only 36 °C at the northern limit of its range in Alaska (Shively and Barboza, 2017) but can exceed 40 °C in Wisconsin and Kentucky, USA (Davis et al., 1965; Burnett and August, 1981).

Roosts can be found in underground sites, tree crevices or in foliage, but they are also often located in privately owned buildings, and thus difficult for researchers to locate. Radio transmitters are sometimes used to find roosting bats (e.g., Mitchell-Jones and McLeish, 2003; Hillen et al., 2010; Dietz et al., 2018), but the method is time-consuming, expensive, and, to find several roosts, requires a huge capturing effort at multiple sites. Engaging property owners to assist in research can help locate new roost sites. Because bats produce fecal pellets within the roosts, property owners can be engaged to collect these droppings and deliver them to researchers to gain a variety of information, such as species identification by molecular genetic methods. (Walker et al., 2016). The use of a citizen science approach also enables the collection of data at multiple sites simultaneously (Heigl et al., 2019).

Our aim was to determine which bat species use human-built structures in Finland and the distribution of their roosts in the country. We hypothesized that use of human-built structures will vary by species and that an increase in latitude would decrease the number of the roost sites located. We predicted to find generalist species and species that are not prone to disturbance in the vicinity of the roosts utilizing buildings in Finland. As the distribution of the known diurnal summer roosts in Fennoscandia is biased towards the south (Tidenberg et al., 2019), with currently only one known *Eptesicus nilssonii* maternity roost above the Arctic Circle in Troms, Norway (Rydell et al., 1994), we predicted to find roosts distributed across the country, although the density of the roosts and number of species will decrease with increasing latitude. In addition, we investigated 1) land-use classes within various radiuses from the diurnal summer roosts of the boreal bat species that would influence the selection of the roost site and 2) species-specific habitat characteristics within these distances around the diurnal summer roost sites of boreal bat species. We hypothesized that there are differences between species in the radius around the roost at which land-use variables influence roost-site selection most, as seen in other geographic areas (Oakeley and Jones, 1998; Nicholls and Racey, 2006; Clergeau and Quenot, 2007; Grider et al., 2021). We predict that aerial hawking bats favoring open areas as their foraging habitat, such as northern bat (*E. nilssonii)* would have a smaller surrounding area around the roost where the land use types would affect the roost selection than species that require a more sheltered habitat, such as the brown long-eared bat (*Plecotus auritus*), Brandt's myotis (*M. brandtii*) and the whiskered bat (*M. mystacinus*). We predicted that generalist species, such as *E. nilssonii* would have more heterogenic environmental characteristics around their roost sites while specialist species, such as *P. auritus*, would require a specific habitat (e.g., Ancillotto et al., 2022; Gaulke et al., 2023). It is known that the important habitat characteristics can vary at different radiuses around the roost (Ford et al., 2006; Thomas et al., 2021; Neubaum and Aagaard, 2022). For example, mature boreal forest is an important foraging habitat for *M. lucifugus* in North America (Thomas et al., 2019, 2021; Slough et al., 2023), but the species exploits rural areas for roosting (Thomas et al., 2019). Addressing important landscape parameters for each species on different distances around the diurnal summer roosts would enhance the conservation actions for the species.

2. Material and methods

2.1. Sample collection

We used a combination of citizen science and efforts of professional bat specialists, molecular genetic analyses, and remote sensing, to gain knowledge from a breadth of roosts and their surrounding habitat. We compiled existing information on bat roosts in Finland and launched a citizen science project to locate new roost sites. In the spring of 2019 and 2020, we advertised our project in newspapers, radio and in social media to find citizens who knew they had bat colonies on their premises. We sent equipment for collecting a maximum of 160 single fecal droppings to these volunteers. The collection kit included eight pairs of disposable rubber gloves, eight single-wrapped disposable plastic forceps, 40 sheets of white printing paper, 8 times 20 single 2 ml tubes filled with RNAlater solution and 8 of the 15 ml Falcon tubes also filled with RNAlater to store the feacal droppings. In addition, we provided an information leaflet with detailed instructions on the collection of the droppings and in 2020, after the Covid 2019-outbreak, we also provided disposable facemasks. The participants placed blank paper sheets under the bat roost in the evening after bats had exited the building and gathered the fecal samples the following evening. During the day, bats defecated on the paper sheets. Participants collected the fecal samples with disposable forceps to a 2 ml tube each filled with 1 ml of RNAlater solution to restore the sample. If there were more than 20 feacal droppings, the remaining were pooled in one of the 15 ml tubes. The collection period started in the spring when the bats arrived at the roost and was repeated every second week throughout the season (eight times maximum). Specific dates varied, but all collections were conducted during paired weeks. After the collection period in the autumn, the participants sent the samples to the Finnish Museum of Natural History (FMNH) for laboratory analyses.

2.2. Laboratory analyses

From each sampling site, we chose five to ten pellets (as a representative subsample of the roost site) for species identification on laboratory methods (detailed laboratory protocol in Supplementary material). First, we removed the RNAlater solution from the sampling tubes and added phosphate-buffered saline solution (PBS) and homogenized the pellets in a Tissue Lyser. Subsequently, we used 250 μl of the homogenate for secondary homogenization with PowerBead Pro Plates (Qiagen) and DNeasy 96 PowerSoil Pro QIAcube HT Kit (Qiagen) and as an extra step, we added 20 μl of Proteinase K (Thermo Fisher Scientific) with 10 min incubation in room temperature (DNeasy® 96 PowerSoil® Pro QIAcube® HT Kit Handbook, August 2019: pp. 14–16).

We then transferred the S-Block to the QIAcube HT instrument for DNA isolation (DNeasy® 96 PowerSoil® Pro QIAcube® HT Kit Handbook, August 2019: pp. 17–20, steps 1–19) and followed the protocol until the final elution. To obtain more DNA, we stopped robot run before the elution step, added 75 μl of preheated (56 °C) C6-solution to columns, and incubated in 56 °C for 10 min. Then, we centrifuged at full speed (4000 rpm) with Centrifuge 5810 (Eppendorf) for 10 min to elute the purified DNA straight onto clean elution plates.

We measured DNA concentration and purity using NanoDrop ND-1000 Spectrophotometer (Thermo Fisher Scientific). DNA was aliquoted and stored at − 20 °C for later use.

To determine the species of bat from the DNA, we amplified a short fragment of *cytochrome oxidase subunit I* gene, the so-called animal DNA barcoding marker. We used "SFF" primers (Species From Feces; Walker et al., 2016) following our earlier work (Vesterinen et al., 2016). The following PCR program was installed to Mastercycler epgradient S (Eppendorf, Hamburg, Germany): 10 min initial denaturation at 95 °C followed by 38 cycles of 1 min denaturation at 95 °C, 30 s annealing at 56 °C, and 30 extensions at 72 °C. Final extension was conducted at 72 °C for 10 min. The PCR product was run on a 2 % agarose gel stained with GelRed® Nucleic Acid Gel Stain (Biotium, Fremont, USA) gel using electrophoresis with PowerPac™ Basic (Bio-Rad, Hercules, USA) to determine if the amplification was successful. We expected approximately 250 bp long products including primers.

We cleaned successful PCR products with ExoSAP-IT™ PCR Product Cleanup Reagent and sent for Sanger sequencing to FIMM (Institute for Molecular Medicine Finland). Sequences were compared to GenBank nr sequence database using online BLAST tool (Altschul et al., 1990).

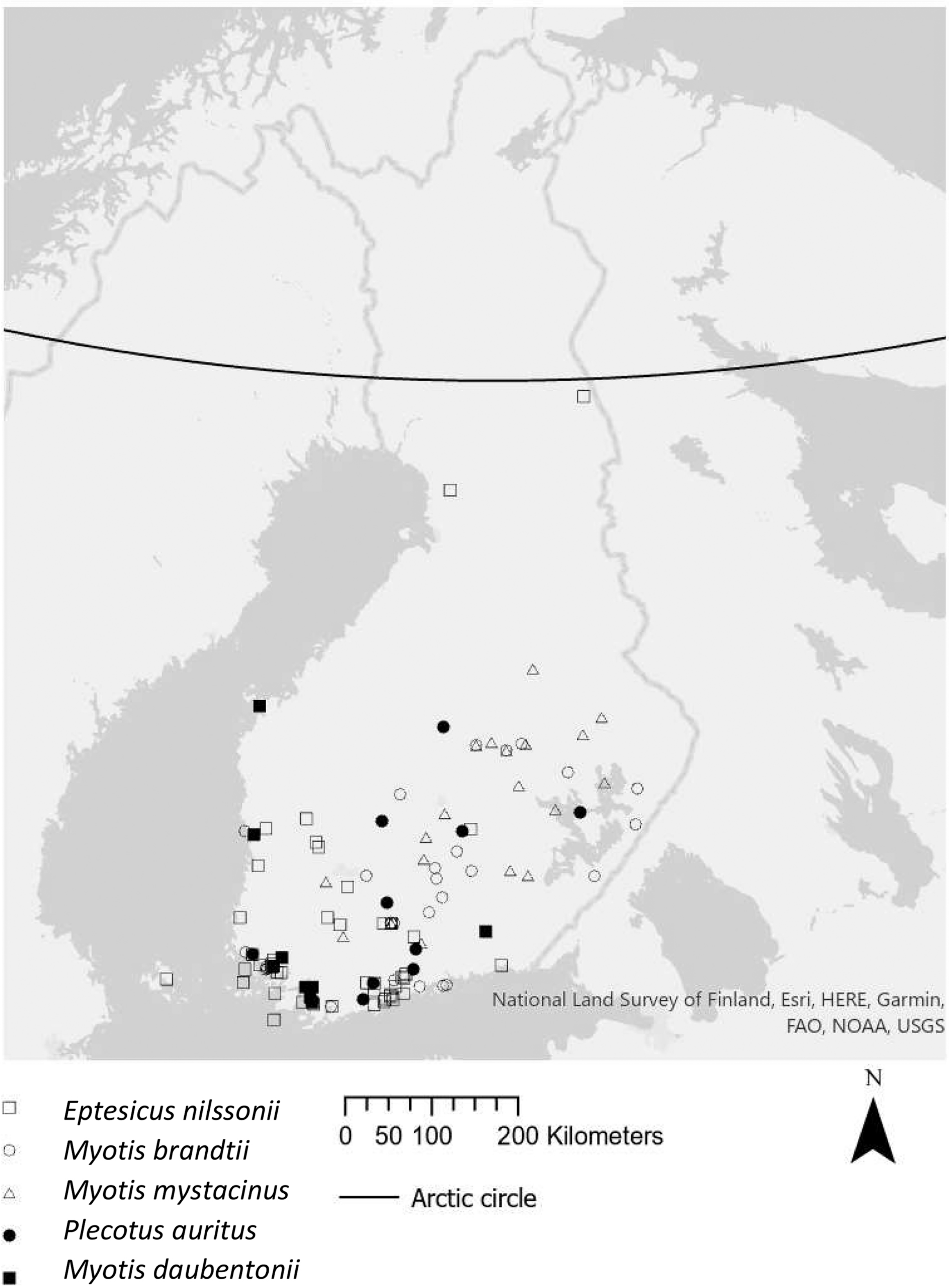

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Fig. 1. A map of the distribution of 173 roost sites where fecal samples obtained in spring 2019 and 2020 from five bat species (*Eptesicus nilssonii*, *Myotis brandtii*, *M. mystacinus*, *Plecotus auritus*, *M. daubentonii*) in Finland. Most samples were collected from the southern and central parts of the country, but two *E. nilssonii* roosts were in the north, close to the Arctic Circle.

2.3. *GIS analysis*

After species were identified for each sampling site, we gathered the information in addition to previously known roost sites and plotted locations based on ETRS-TM35FIN coordinates participants provided using ArcGIS Pro program version 3.0. We drew a 10 km radius buffer around each roost point and generated 4 random points on that buffer for all roost sites to investigate whether the roost sites differed from random points (Oakeley and Jones, 1998; Arthur et al., 2014; Tink et al., 2014).

We used Corine Land Cover 20 × 20 m raster layer as our land use data (Finnish Environment Institute 2018). We drew 100 m, 200 m, 500 m, 1 km, 2 km and 5 km radius buffer zones around each roost site and random point, and calculated the number of raster cells belonging to each of the 48 land-use classes (Supplementary material Table 1) for every buffer zone and for all sites. We then combined the 48 land-use classes into six classes for data analyses. The classes were: Built environment (consists of all human-built structures), mixed forest (which also included deciduous forests), coniferous forest, open landscape and shrubbery (which also included pastures, fields, golf courses and other open, vegetated areas as well as areas with shrubbery), wetland, and water.

2.4. *Statistical analyses*

We transformed the sum of each land-use variable for each radius and each species first to percentages, and further to ln+ 1 to decrease correlation using equation $\ln(Xi/Xtot*100 + 1)$, where Xi is a land-use class and Xtot is the sum of all land-use classes on given radius. We tested autocorrelations of land-use classes by variance inflation factor (VIF). Acceptable VIF values are below 5 (Fox and Monette, 1992) and all the values met this criterion; hence we conducted a binomial generalized linear model (GLM) where we tested the influence of different compositions of land use types on the occurrence of roosts. In our model the presence of the roost is a dependent variable and each land-use type an explanatory variable (Ancillotto et al., 2022). We first ran the model separately for all radiuses and all species to detect the landscape variables that were associated with roosts. We considered land-use types significant for roost site selection if the P-value was below 0.05. After running the model separately on each species and each radius, we compared the models for different radiuses to identify the models best explaining the presence of roosts of given species by using the Akaike information criterion method with correction for small sample sizes (AICc) (de Leeuw, 1992). The model with the lowest AICc value and delta-AICc value below 2 best explained the presence of the roosts in given habitat.

3. Results

We received fecal pellets from 79 locations and complemented our analysis by including 94 previously known bat roosts, for a total of 173 roost sites. Of these, 72 were used by *E. nilssonii*, 44 by *M. brandtii*, 26 by *M. mystacinus*, 20 by *P. auritus* and 11 by *M. daubentonii*. We also found co-occurrence of *M. brandtii* and *M. mystacinus* as well as *M. brandtii* and *P. auritus*.

We found that 98.8 % of the roosts were in the southern and central parts of the country (Fig. 1), but fecal pellets were also obtained from two *E. nilssonii* roosts in the proximity of the Arctic Circle. We observed a more easterly distribution of *M. brandtii* and *M. mystacinus* roosts as compared to *E. nilssonii* and *P. auritus* roosts.

Results of the general linear model showed that the essential habitat patches for *E. nilssonii* roost occurrence were built environment, open and shrubbery and water within a 200 m radius of the roost site. Wetlands had a negative impact on the occurrence of a roosts (Tables 1 and 3). For *M. brandtii* built environment and mixed forest had a negative impact on the roost occurrence at a 5 km radius (Tables 2 and 4). We did not find enough roost sites to include *M. mystacinus, M. daubentonii* and *P. auritus*, for further analyses.

Within the 200 m surrounding habitat for *E. nilssonii*, land-use cover was 24.46 % built environment, 19.35 % mixed forest, 20.78 % coniferous forest, 21.87 % open and shrubbery, 4.22 % wetlands and 9.31 % water (Fig. 2). The radius that gave the best model for *M. brandtii* was 5 km, and the land-use type covers within that buffer were 11.14 % of built environment, 22.61 % of mixed forest,

Table 1
Results of generalized linear models assessing the impact of various land use types within a 200 m-buffer on 72 roost occurrences for *Eptesicus nilssonii*. The analysis examines the relationship between land use types and roost selection, highlighting the influence of different environmental features. The presence of built environment, open and shrubbery areas, and water bodies positively affect roost occurrence, while wetlands exhibit a negative effect on the presence of a roost.

	Estimate	Std. Error	z value	Pr (>|z|)
(Intercept)	-5.039	1.182	-4.262	< 0.001
Built	0.976	0.177	5.507	< 0.001
Mixed	0.204	0.204	0.998	0.32
Coniferous	0.254	0.167	1.524	0.13
Open	0.412	0.187	2.2	< 0.05
Wetland	-1.828	0.258	-7.1	< 0.001
Water	0.681	0.196	3.475	< 0.001

Table 2
Results of generalized linear models assessing the impacts of various land use types within a 5 km-buffer on 44 roost occurrences for *Myotis brandtii*. The analyses examine the relationship between land use types and roost selecting, highlighting the influence of different environmental features. The presence of built environment and mixed forest negatively affect the roost occurrence.

	Estimate	Std. Error	z value	Pr (>|z|)
(Intercept)	3.011	6.525	0.461	0.65
Built	-1.036	0.411	-2.519	< 0.05
Mixed	-1.676	0.682	-2.456	< 0.05
Coniferous	0.985	0.903	1.091	0.28
Open	-0.275	0.691	-0.397	0.69
Wetland	-0.471	0.287	-1.64	0.10
Water	0.290	0.394	0.735	0.46

Table 3
Comparison of generalized linear models to identify the radius best explaining the presence of *Eptesicus nilssonii* roosts. The lowest AICc value was for the 200 m radius and Delta AICc for all other radiuses was above 2; hence the model for 200 m best predicted the presence of a roost.

	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
200 m	7	243.09	0	0.99	0.99	-114.38
100 m	7	253.39	10.3	0.01	1	-119.53
5 km	7	278.77	35.69	0	1	-132.23
500 m	7	282.86	39.78	0	1	-134.27
2 km	7	304.06	60.97	0	1	-144.87
1 km	7	306.52	63.43	0	1	-146.1

Table 4
Comparison of generalized linear models to identify the radius best explaining the presence of *Myotis brandtii* roosts. The model with the lowest AICc value was the for the 5 km radius and the Delta AICc for all other radiuses was above 2; hence the model for 5 km best predicted the presence of a roost for the species.

	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
5 km	7	190.13	0	0.71	0.71	-87.8
2 km	7	192.3	2.17	0.24	0.96	-88.88
100 m	7	196.65	6.52	0.03	0.98	-91.06
500 m	7	197.75	7.62	0.02	1	-91.61
200 m	7	203.4	13.27	0	1	-94.44
1 km	7	207.54	17.41	0	1	-96.51

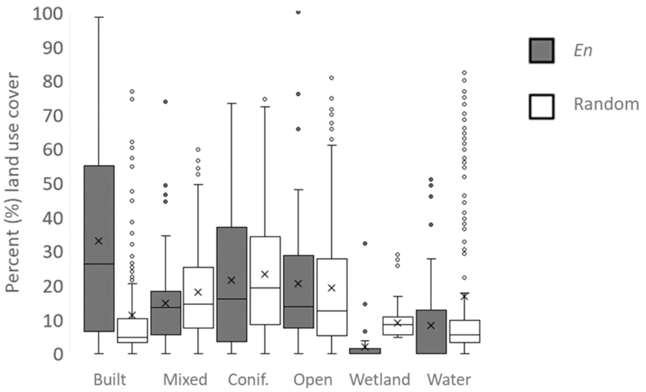

Fig. 2. Percent land use cover (built environment, mixed forest, coniferous forest, open & shrubbery, wetland, and water) for sites occupied by *E. nilssonii* (En) and for randomly selected sites (Random) within a 200 m radius. Error bars represent the 95 % confidence interval, the bottom and top of the box are the 25th and 75th percentiles, the line inside the box is the 50th percentile (median), and any outliers are shown as closed circles.

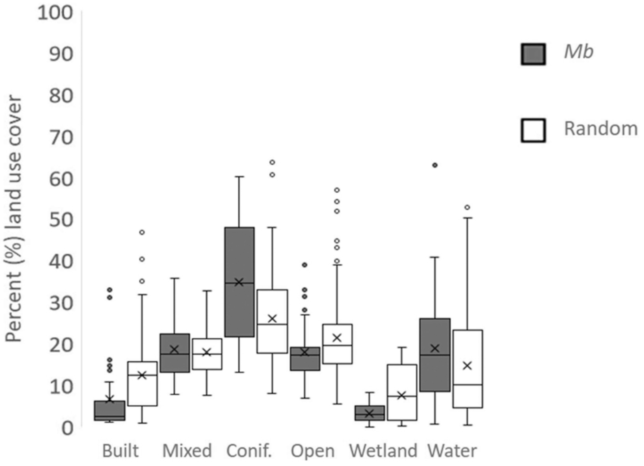

Fig. 3. Percent land use cover (built environment, mixed forest, coniferous forest, open & shrubbery, wetland, and water) for sites occupied by *M. brandtii* (Mb) and for randomly selected sites (Random) within a 5 km radius. Error bars represent the 95 % confidence interval, the bottom and top of the box are the 25th and 75th percentiles, the line inside the box is the 50th percentile (median), and any outliers are shown as closed circles.

23.89 % of coniferous forest, 20.82 % of open and shrubbery, 8.81 % of wetland and 12.71 % water (Fig. 3).

4. Discussion

Our data show that at least five species of bats use human-constructed diurnal roosts during the reproductive season in Finland, which is in accordance with our predictions and previous findings from Europe (Marnell and Presetnik, 2010). The roosts occupied by *E. nilssonii* were the most common in our research, followed by roosts occupied by *M. brandtii*, *M. mystacinus* and *P. auritus*. *Myotis daubentonii* was likely underrepresented in our research due to different roost site requirements; while other species often choose to roost inside spaces in human occupied buildings, such as in attics and roof spaces, *M. daubentonii* is found to favor bridges, churches, and other buildings with no human residency (Marnell and Presetnik, 2010) and they also roost frequently in woodpecker cavities (Lučan and Radil, 2010). *Plecotus auritus* has been considered to favor trees as roost sites at more southerly latitudes, although the species is commonly found in buildings (Marnell and Presetnik, 2010). The number of observed roosts with *M. mystacinus* was contrary to our expectations, because this species is not often caught in ringing surveys, and it is difficult to distinguish from other *Myotis* in acoustic surveys (Finnish museum of Natural History, Ringing and recovery database of birds (TIPU) http://tun.fi/HR.48; Barataud, 2015). Furthermore, we found some bat species sharing diurnal summer roost sites. Two *M. brandtii* colonies shared a roost location with *P. auritus* and one roost site location was shared by *M. brandtii* and *M. mystacinus*. *Eptesicus nilssonii* and *M. daubentonii* did not share roosts with other species in our study.

In accordance with our predictions, *E. nilssonii* had the most comprehensive distribution and the most northerly roost sites in our study. The species is known to have the most northerly range of all bat species in the world (López-Baucells et al., 2019; Suominen et al., 2022), and breeding colonies are known well above the Arctic Circle in Norway (Rydell et al., 1994). However, most of the roosts in our research were concentrated in the southern and central parts of the country (Fig. 1), with only two roosts above 63 N, still well below the breeding sites in Norway. No breeding colonies of the species are known above the Arctic Circle in Finland, even though observations of individual bats exist across the Finnish Lapland (Tidenberg et al., 2019; Kotila et al., 2023). The absence of breeding colonies from Finnish Lapland might be due to colder, more continental climate in Finland compared to Atlantic, milder climate in north coast of Norway, or they might not yet have been discovered due to low human population density and lack of search effort in the area (Tidenberg et al., 2019).

Myotis brandtii was the second most frequent species in our data set and roosts of the species were found in the southern and central parts of the country (Fig. 1). *Myotis mystacinus* was the third most frequent species, which is surprising as the species is seldom caught during ringing censuses (Finnish museum of Natural History, Ringing and recovery database of birds (TIPU) http://tun.fi/HR.48). A roost site for *M. mystacinus* was also the third most northern roost site (Fig. 1) in our study. Roost sites of *P. auritus* were located mostly in the southern and central parts of Finland, and all *M. daubentonii* roosts were on the southwestern coast of the country. However, both species are common in Finland and regularly found in the southern and central parts of the country (Tidenberg et al., 2019).

Our research confirms that important landscape variables around the roosts and the distance that these variables impact differs between the two boreal bat species. While landscape features within 200 m impacted on the roost site selection of *E. nilssonii*, the distance was 5 km for *M. brandtii*. *Eptesicus nilssonii* favored built environment and open and shrubbery and water 200 m around its roosts. The species is not considered to be sensitive to light (Frafjord, 2013; Lacoeuilhe et al., 2014), which is an advantage in human modified landscape. The species has been documented to forage around streetlamps (Rydell, 1992), and hence can adjust to environmental changes and even benefit from urbanization. *Eptesicus nilssonii* is a strong flyer (Rydell, 1993a; Norberg, 1987) that can escape from predators and has been considered to favor semi-open areas as its foraging grounds, which is in accordance with open and shrubbery as important land use type around the roosts we found (Haupt. et al., 2006; Frafjord, 2013; de Jong, 1994; Smirnov et al., 2021). However, the known range size of the species extends way beyond the 200 m radius from the roost (e.g., de Jong, 1994; Haupt at al, 2006; Frafjord, 2013). It is possible, that the 200 m radius only highlights the important land use types around the roost to provide suitable conditions for roosting. Individuals from breeding colonies often forage close to the roost (e.g., Racey and Swift, 1985; Henry et al., 2002, Rydell, 1993b; Mackie and Racey, 2007). Water provides not only a possibility to drink, but also abundant food resources when hatched insects emerge from the water surface (Lilley et al., 2012a, 2012b; Korine et al., 2016; Parker et al., 2019; Mas et al., 2021). Our results highlight the generalist behavior of the species that can adjust to and benefit of landscape fragmentation if food resources are secured.

Myotis brandtii is considered a light-sensitive species (e.g., Lacoeuilhe et al., 2014) that avoids illuminated areas as far as 50 m from light sources (Azam et al., 2018), which might explain why built environment had a negative effect on the roost occurrence of the species in our research. Forests are seldom lit in Finland and the canopy dims the nighttime light. Interestingly however, the distances from the roosts where land use types had an impact on roost site selection were relatively long at 5 km and is more reflective of the actual home range size (Kurek et al., 2020), rather than the land-use characteristics in the immediate vicinity of the roost that influence roost site selection in *E. nilssonii*. Although forest cover was not significant land use type in our model in determining roost site selection for *M. brandtii* at the large scale, it was important at smaller distances (Supplementary tables 6–9) and has been recognized as an important habitat in other studies, and the species is forest specialist (de Jong and Ahlén, 1991; Wermundsen and Siivonen, 2008; Vasko et al., 2020). Vasko et al. (2020) found that the activity of *Myotis* sp. is highest in mature forests in Finland, although they could not distinguish their acoustic results to species level. However, at more southerly latitudes *M. brandtii/mystacinus* were observed to favor more fragmented, discontinuous woodland habitat (Kaňuch et al., 2008; Buckley et al., 2013; Gili et al., 2020; Kurek et al., 2020). This interesting latitudinal difference of habitat use might be due to differences in the forest type when continuous forests are mainly pinewood plantations, discontinuous forests offer more habitat patches for the species (Gili et al., 2020). However, another explanation could be the darker summer nights at southerly latitudes, during which light-sensitive species do not require as much cover from the vegetation compared to the north, where the temporal extent of twilight is longer. Either way, our results highlight the importance of latitudinal aspect in implementing conservation measures; species may have differing environmental requirements at different latitudes.

The landscape changes in the surrounding habitat might have a species-specific effect; generalist and light-tolerant species, such as *E. nilssonii*, may not be as sensitive to environmental changes around the roost and can even benefit from the urbanization (Haupt et al., 2006) while forest-dwelling species that rely on canopy cover, such as *Myotis* species in Finland (Vasko et al., 2020) may abandon their roost site if logging alters their surrounding habitat to a greater degree. Moreover, the distance from the roost where land use types predict the occurrence of the roost varies between species. Hence, species-specific environmental requirements should be carefully considered in land use planning. For some species, such as *E. nilssonii*, conservation efforts can be targeted directly at protecting nursery roosts (Ciechanowski, 2015). However, for other species, species-specific preferences should be considered more efficiently in conservation efforts (Uhrin et al., 2017), and the habitat surrounding the roost itself should also be protected.

Besides the immediate habitat surrounding the roosts, habitat connectivity is also important for bats and the relationship between habitats, fragmentation and configuration is species-specific and scale dependent (Hale et al., 2012). However, most studies of connectivity concerning boreal species are conducted in the southern parts of their distribution range, and thus are not applicable directly to Fennoscandia. Nevertheless, a habitat model considering connectivity was accurate at predicting the activity of forest species but failed to predict the number of species (von Hirschheydt et al., 2020) in Sweden. In central Europe bat species with short range echolocation calls, such as forest *Myotis* and *P. auritus*, have been found to suffer from fragmentation to a greater extent compared to species that use long range echolocation calls and favor more open environments, such as *E. nilssonii* and *P. nathusii* (Frey-Ehrenbold et al., 2013; Gili et al., 2020; Ancillotto et al., 2022). As human disturbance was an important feature in roost site selection for *M. brandtii* in Finland, the species might suffer from forest fragmentation also higher latitudes. Although our research did not measure connectivity, we now know which key habitats that are essential for roost site selection in boreal bats and can include them in further research concerning connectivity and furthermore, in conservation actions. For example, green passageways might offer a safe route through unfavorable habitat patches, such as highways (Martínez-Medina et al., 2022), when species-specific preferences on habitat use have been included in planning. Species flying in an open habitat, such as Pipistrellus spp., have been found to use green bridges crossing highways, while clutter-adapted species from genus *Myotis* use underpasses more frequently (Martínez-Medina et al., 2022). Building underpasses in areas with high *Myotis* spp. activity would increase their mobility and connectivity. Also, reducing artificial light radiation can improve connectivity for light-intolerant species (Laforge et al., 2019). By gaining more detailed information at species level and improving the model by adding more detailed information on important connectivity features, it would be possible to get more precise predictions on spatial activity and species richness for conservation purposes. For example, in Sweden, the number of bat species was positively correlated with the amount of deciduous woodland, but not coniferous forests (de Jong, 1995). In Finland however, forest cover is dominated by coniferous forests and deciduous forests are a minority (e.g., Mönkkönen et al., 2022). Still these species exist in Finland, suggesting habitat requirements are different at higher latitudes.

Our results highlight the need for a greater perspective on conservation planning and land use. Protecting roosts is not enough; species-specific variation in the habitat surrounding roosts must also be considered in conservation management plans. For example, if the aim is to protect an area for *M. brandtii* in Finland, we now know that avoiding further urban expansion around the roost is a key factor for preserving the colony, while for *E. nilssonii*, reforestation might change the roosting location to a more open location. Future research should continue to focus on studying land-types around roosts, and include connectivity of the important habitat features, forest volume and tree data, to gain exact information on the roosting habitat requirements of species. However, locating roost sites or identification of bat species can be challenging if only traditional methods such as radiotracking and acoustic surveys are used

(Mitchell-Jones and McLeish, 2003). Citizen science proved to be a useful method for locating roosts and collecting fecal pellets for species identification. Citizen science bolstered the dataset from collected private buildings, assisting with the identification of several roosts that would not have been found using traditional methods or would have required a vast research effort that was not possible with given resources. We acknowledge that despite the combination of sampling methods, our sample size was rather small considering the number of species and we would have more conclusive results with a larger data set. Hence, further research should focus on the topic.

5. Conclusions

Our results show that bat species have differing preferences on landscape parameters around roosts. Roosting is one of the most fundamental periods in the lives of bats with the entire colony being vulnerable to unfavorable conditions, predators, and other disturbances. Hence, the surrounding habitat plays an essential part in protecting bats against weather conditions and predators when exiting the roost and providing a safe passageway to foraging sites. More attention should be paid, and more research is needed around the topic of roost site selection. These results show that in conservation matters, just preserving a roost is not enough; the surrounding habitat plays an important role as well and should be considered when land use actions are planned. We also demonstrated that including citizen science may allow reducing the costs of field operations and increase roost search efficiency. When instructed carefully, citizens can provide high-quality data for research purposes (Lundberg et al., 2021). Moreover, engaging the greater public in data collection can also raise interest in nature in general as well as nature conservation.

CRediT authorship contribution statement

Kati M. Suominen: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Visualization, Writing – original draft, Writing – review & editing. Funding acquisition. **Eero J. Vesterinen**: Conceptualization, Methodology, Resources, Supervision, Writing – review & editing. **Ilkka Kivistö**: Methodology, Investigation, Writing – review & editing. **Maria Reiman**: Methodology, Investigation, Writing – review & editing. **Tarmo Virtanen**: Methodology, Software, Supervision, Writing – review & editing. **Melissa B. Meierhofer**: Methodology, Software, Formal analysis, Data curation, Writing – review & editing. **Ville Vasko**: Software, Resources, Writing – review & editing. **Tarja Sironen**: Resources, Writing – review & editing. **Thomas M. Lilley:** Conceptualization, Resources, Supervision, Writing – review & editing, Project administration.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests Kati Suominen reports financial support was provided by Kone Foundation.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02589.

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