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ECOGRAPHY

Research article

Large-scale long-term passive-acoustic monitoring reveals spatio-temporal activity patterns of boreal bats

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The distribution ranges and spatio-temporal patterns in the occurrence and activity of boreal bats are yet largely unknown due to their cryptic lifestyle and lack of suitable and efficient study methods. We approached the issue by establishing a permanent passive-acoustic sampling setup spanning the area of Finland to gain an understanding on how latitude affects bat species composition and activity patterns in northern Europe. The recorded bat calls were semi-automatically identified for three target taxa; *Myotis* spp., *Eptesicus nilssonii* or *Pipistrellus nathusii* and the seasonal activity patterns were modeled for each taxa across the seven sampling years (2015–2021). We found an increase in activity since 2015 for *E. nilssonii* and *Myotis* spp. For *E. nilssonii* and *Myotis* spp. we found significant latitude -dependent seasonal activity patterns, where seasonal variation in patterns appeared stronger in the north. Over the years, activity of *P. nathusii* increased during activity peak in June and late season but decreased in mid season. We found the passive-acoustic monitoring network to be an effective and cost-efficient method for gathering bat activity data to analyze spatio-temporal patterns. Long-term data on the composition and dynamics of bat communities facilitates better estimates of abundances and population trend directions for conservation purposes and predicting the effects of climate change.

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Keywords: acoustic monitoring, bats, long-term monitoring, macroecology, spatial ecology, spatio-temporal patterns

Introduction

Biodiversity is declining globally due to anthropogenic actions (Diaz et al. 2019), and distributions and abundances of species are shifting due to ongoing climate change. Our information on changes in biodiversity comes from various monitoring schemes which are often taxonomically biased. Even though vertebrates are more thoroughly monitored in general compared to non-vertebrates, population trends and seasonal patterns of many mammals exhibiting cryptic behavior are poorly known even in Europe. Nocturnal species have traditionally been monitored using e.g. lethal snap-traps (small rodents, Cornulier et al. 2013), droppings (Wistbacka et al. 2018) or snow tracks (Helle et al. 2016). These methods each have their own limitations, and for example, no methods for effective monitoring of bat populations have been available until recent advances in acoustic monitoring technology (Frick 2013).

For many sedentary insectivorous mammals, the boreal zone represents the northern limit of their distribution range due to the restrictions in seasonal food availability. Although many insectivorous mammals remain active over the winter, insectivorous bats hibernate over periods of food shortage (Kortner and Geiser 2000). However, there is a limit to the length of the hibernation period as a function of stored fat reserves and the negative effects of extended torpor (Boyles et al. 2020). Nevertheless, spatially and temporally isolated reports of bats as far north as the arctic circle, and further, have surfaced (Siivonen and Wermundsen 2008), warranting a more systematic approach to understanding the bat community composition and spatio-temporal distribution of bats at the northern edge of their distribution. This would provide information direly needed not only for practical conservation measures, but also to monitor the effects of climate change.

Long-term, spatially extensive monitoring of bat populations has not taken place in the same manner as for birds and rodents (Gregory et al. 2005, Korpela et al. 2013, Rosenberg et al. 2019), although bat ringing (Hutterer et al. 2005) and location-specific efforts (Alcalde et al. 2021) have yielded some significant results. Bat monitoring could benefit from resolution to observe subtle shifts in population dynamics and spatio-temporal patterns to provide more in-depth data for the effective implementation of conservation efforts. For instance, spatio-temporally extensive monitoring of voles, significant silvicultural pests (Huitu et al. 2009), revealed a dramatic attenuation in well-documented population fluctuations, known as the 'vole cycle' (Korpela et al. 2013). This change in phenology was attributed to an increased frequency of mild winters and subsequent lack of snow cover. Similar changes in species composition and distribution shifts attributed to climate change have been observed in numerous bird species through extensive, coordinated monitoring efforts (Rosenberg et al. 2019, Lehikoinen et al. 2021). However, such monitoring efforts have been lacking for bats due to technical challenges in making reliable observations of these cryptic mammals at a geographically significant coverage (but see Ijäs et al. 2017, Vasko et al. 2020).

Recent advances in technology allow the effective and economical collection of large data sets, without direct effort on part of the researcher (Newson et al. 2015, Lundberg et al. 2021). Passive recording equipment can be deployed by citizens and technical staff to collect high-quality raw data for scientific research. Citizen science approaches have long been in use in monitoring birds and certain groups of insects and mammals. However, citizen science has been unavailable in bat research until recently due to the high-cost of equipment and lack of comparable results due to subjective differences in e.g. species identification. The reliable analysis of large, spatio-temporally distributed acoustic datasets has now been made possible by the development of identification algorithms, which rapidly produce identifications of bats to genus or even species level (Rydell et al. 2017, López-Baucells et al. 2019).

In this paper, we provide results from one of the first passive-acoustic monitoring networks for bats worldwide, here, providing large-scale and long term data from Fennoscandia, North Europe spanning over 1000 km. The use of such monitoring scheme has important implications. Bats are protected under the Agreement on the Conservation of Populations of European Bats (UNEP/EUROBATS) set up under the Convention on the Conservation of Migratory Species of Wild Animals. Bats are also covered by the Habitats Directive of the European Union (92/43/EEC) (Hutson et al. 2015). However, the clauses of the agreement are challenging to implement when species distribution ranges are unknown, not to mention annual spatio-temporal changes in activity. Also, with the impending climate change causing range shifts in species (Chen et al. 2011) and the potentially zoonotic pathogens the species carry (Veikkolainen et al. 2014), as well as the extensive wind-farm planning taking place in Europe (Gaultier et al. 2020), it is of crucial importance to assess data provided by a spatially distributed monitoring network. Here, we utilize an acoustic sampling setup covering latitudes from 59°N to 70°N in Finland to describe 1) long-term trend and 2) seasonal changes in activity of boreal bats and 3) how latitude is reflected in bat species composition.

Methods

Acoustic data collection

A passive acoustic monitoring network was set up in 2015 at eleven biological research stations across Finland extending from the southern tip at Tvärminne to the most northern point in Kevo (see Table 1 and Fig 1 for locations and

Table 1. Operating times for each passive detector unit used in this study over the years.

Station/device	WGS84 coordinates		Operating year						
	°N	°E	15	16	17	18	19	20	21
Husö 1	60.279	19.830	x	x	x	x	x	x	x
Husö 2	60.279	19.830	x	x			x		x
Husö 3	60.279	19.830	x	x	x	x			
Seili 1	60.240	21.963	x	x					
Seili 2	60.240	21.963	x	x	x	x	x	x	x
Seili 3	60.240	21.963	x	x	x	x	x	x	x
Tvärminne 1	59.844	23.248	x	x					
Tvärminne 2	59.844	23.248	x	x	x	x	x	x	x
Tvärminne 3	59.844	23.248	x	x	x	x	x	x	x
Lammi 1	61.054	25.041	x	x	x	x	x	x	x
Lammi 2	61.054	25.041	x	x	x	x	x	x	x
Lammi 3	61.054	25.041		x					
Hyytiälä 1	61.845	24.287	x	x					
Hyytiälä 2	61.845	24.287	x	x	x	x	x	x	x
Hyytiälä 3	61.845	24.287	x	x	x	x	x	x	x
Konnevesi 1	62.616	26.347			x	x	x	x	x
Konnevesi 2	62.616	26.347	x	x	x	x	x	x	x
Konnevesi 3	62.616	26.347	x	x					
Oulu 1	65.059	25.466	x	x		x	x		
Oulu 3	65.059	25.466	x			x	x	x	
Oulanka 1	66.370	29.312	x	x	x	x	x	x	x
Oulanka 2	66.370	29.312	x	x	x	x	x	x	x
Oulanka 3	66.370	29.312	x	x					
Kilpisjärvi	69.044	20.803				x	x	x	x
Muddusjärvi 1	69.068	27.113	x		x	x	x		
Muddusjärvi 2	69.068	27.113	x		x	x			
Kevo 1	69.864	27.008	x	x	x	x	x	x	x
Kevo 2	69.757	27.010	x	x	x	x	x	x	x

detailed information). Each station employed two to three Wildlife Acoustics SM2 BAT+ -ultrasound recorders. These were placed in the vicinity of the research stations close (< 10 m) to water bodies and the forest edge. Due to changes in geology and vegetation resulting from the latitudinal extent of our study range, we were unable to apply a more strict standardization in the placement of the units. The recorders were programmed to account for the difference in the dark period which differs between location according to latitude and season. The recording parameters and trigger values on the units were set as follows: starting time 30 min before sunset, ending 30 min after sunrise, sample rate 192 000, high pass filter 16 kHz, trigger 18 dB, gain 36 dB, maximum length 10 s, file format WAV. The data from each recorder, stored on SD-cards, was either sent by mail to the authors, or uploaded onto a cloud service, from which it was downloaded for analysis.

Fennoscandian bat community

The Fennoscandian peninsula defines the northern limits of distribution for many European bat species. Only seven bat species have been confirmed to breed in the country (*Eptesicus nilssonii*, *Myotis daubentonii*, *M. mystacinus*, *M. brandtii*, *M. nattereri*, *Plecotus auritus*, *Pipistrellus nathusii*), and other six species (*Vespertilio murinus*, *Nyctalus noctula*, *Pipistrellus pygmaeus*, *E. serotinus*, *M. dasycneme*) have been recorded, including mostly acoustic observations. Observations and species richness decrease on a south to north gradient (Tidenberg et al. 2019, Lundberg et al. 2021). Especially latitudes between 64°N and 65°N appear to be a cutoff point for both bat species richness and observation effort, with only few reliable scattered observations of *Eptesicus nilssonii* (Tidenberg et al. 2019), *Myotis daubentonii* (Siivonen and Wermundsen 2008) and *M. brandtii/mystacinus* (Siivonen and Wermundsen 2008) recorded further north. To the south of this cutoff point, *P. auritus*, *P. nathusii* and *N. noctula* are frequently observed (Rydell et al. 2014, Ijäs et al. 2017, Tidenberg et al. 2019, Vasko et al. 2020, Lundberg et al. 2021), with all 13 species observed in Finland only encountered in the southern coast. The vast majority of observations in acoustic surveys are from *E. nilssonii*, *P. nathusii*, and the three most common *Myotis* species (*M. daubentonii*, *M. brandtii* and *M. mystacinus*). These are the three reliably acoustically identifiable taxonomic units and the focal taxa in this study.

Eptesicus nilssonii and *P. nathusii* are aerial hawking insectivores leaning into utilizing open space and edges of vegetation in their foraging flight (Rydell 1993, Suominen et al. 2020). Especially *E. nilssonii* commonly forage in open environments and do not avoid illuminated areas as actively as the *Myotis* species, which prefer more closed and forested environments (Vasko et al. 2020) and avoid light (Lacoeuilhe et al. 2014, Azam et al. 2018). Foraging habitats

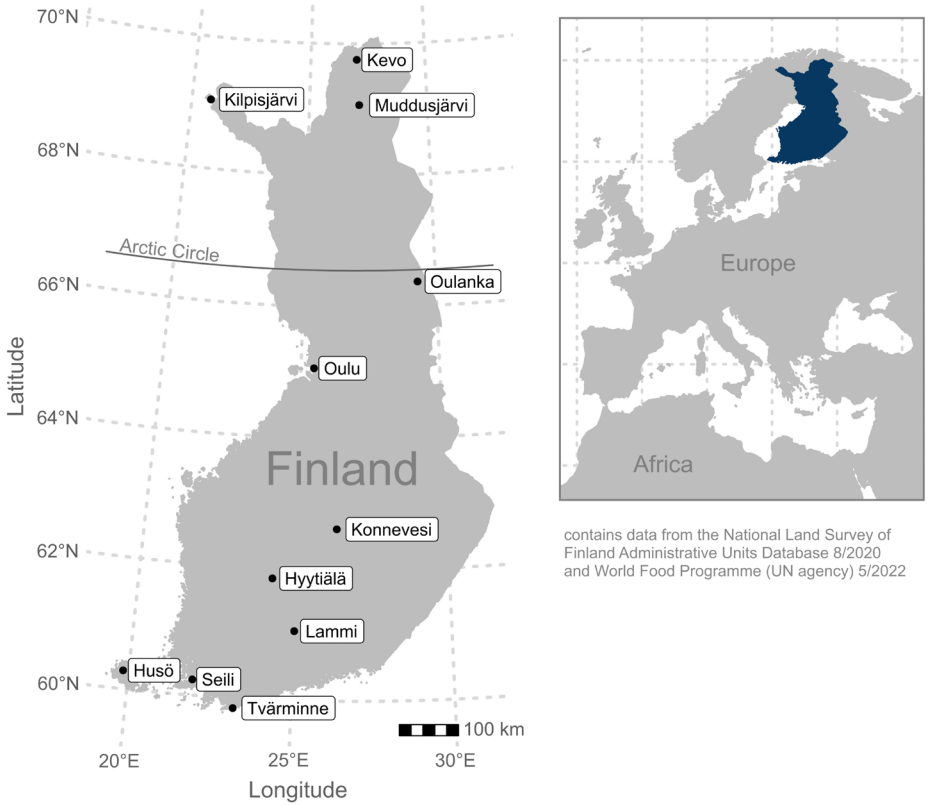

Figure 1. A map of Finland with locations of the research stations participating in long-term monitoring.

differ within *Myotis*, however, with *M. daubentonii* specialized in trawling insects from the water surface, whereas the *M. brandtii* and *M. mystacinus* share similar habits of catching airborne insects in forest edges, openings and passages. Furthermore, with the other taxa adopting more or less sedentary life histories, *P. nathusii* is a long distance migratory species, which has been observed to migrate predominantly to Central Europe for overwintering (Hutterer et al. 2005, Alcalde et al. 2021).

Automated bat identification

Due to the sheer volume of data, comprising seven seasons of acoustic data from a total of 26 devices (2–3 devices per field station, Fig. 1), we chose to utilize automated identification bat species from the collected audio data. We acknowledge the limitations of this method, i.e. the possibility of misidentifications, inability to identify all taxa to species level and omission of some observations due to the algorithm used (Rydell et al. 2017, López-Baucells et al. 2019).

We used SonoChiro 4.0 (Biotope, France) to locate all incidences of our focal bat species: *E. nilssonii*, *P. nathusii* and *Myotis* spp. The following settings were used: classifier NB, call minimum duration 0.5 s, sensitivity 10, minimum number of calls 2. Even though SonoChiro can reasonably well discriminate the three most likely *Myotis* -species in our dataset (*M. brandtii*, *M. mystacinus* and *M. daubentonii*), we opted to pool the genus *Myotis* in our dataset, because 1) we argue that on a large scale, the habitat requirements of all species are similar, and 2) pooling allows the more robust estimates in our model.

Misidentification by software can occur, depending on the hardware, software, recording conditions and taxa (Rydell et al. 2017). To account for this problem, we completed the following quality control protocol: All *P. nathusii* observations north of 61°N and *Myotis* spp. observations north of 64°N were manually checked, because these observations are relatively rare. Additionally, a sample of 33 observations of each three focal taxa, device and year was selected and the software identification of these recordings were then manually checked. There were some quality issues with recordings identified as *Myotis* sp. Consequently, we used the manually identified sample to create custom filters based on quality measurements provided by SonoChiro, and applied these to all of the *Myotis* spp. observations in the data to delete false observations. Based on the manually identified sample, the observations from each station, year and taxa are at least 95% correct after the filtering (>=0.95 precision), and moreover, less than 5% of the real observations are lost in the filtering process (>=0.95 sensitivity). See Supporting information for details.

Data curation

We modeled bat activity within the 24 week long season from 1 May to 15 October, annually (Supporting information). The bat observations outside this season were discarded due to

increased inconsistencies in observation effort between research sites. Observation time per device and taxa was grouped into 10 min bins (observation units), which were considered successful if there were at least one observation of the taxa within them. The units were then grouped together with the other units in the same observation period of 14 successive nights (Supporting information). Only the units between sunset and sunrise each night were included at this stage and others were discarded. Therefore the total number of units varied with the length of the night between periods and stations. Moreover, some devices did not record every night during all periods due to technical and practical reasons. Total number of units in each observation period was used as a weight parameter (number of trials) in the model. Hence, the activity was modeled in relation to the observation effort during dark hours.

Statistical analysis

Bat activity, i.e. the response variable, was modeled as a probability of activity occurring during a 10 min observation unit. In the model, we considered the number of units with and without activity in each two-week period. Generalized linear mixed model with binomial error distribution was fitted with the package 'glmmTMB' (Magnusson et al. 2021) in R (www.r-project.org) separately for each taxa. For *E. nilssonii* and *Myotis* spp., the main focus of the study was to model long-term trend and seasonal activity patterns in the latitudinal gradient of Finland between 60° and 66°N. Therefore period, latitude and their interaction were used as predictor variables and year was also included as linear predictor for detecting increasing or decreasing trend. Due to the roughly southwest–northeast oriented geographic pattern of the monitoring stations (Fig. 1), the latitudinal and longitudinal effects cannot be distinguished. We only included latitude, because we expect latitude to be a more important factor within the study region, which is located near the northern limit of *Myotis* spp. especially, but also relatively close to that of *E. nilssonii* (Tidenberg et al. 2019).

Because *P. nathusii* only occurs frequently at the southern coast of Finland, the model was fitted using only the data from the three southernmost stations Husö, Seili and Tvärminne. With only these stations involved, we did not expect a biologically interesting latitudinal pattern to emerge and therefore excluded latitude as a predictor variable. Instead, we used interaction of period and year as a predictor to asses changes in seasonal activity patterns of *P. nathusii* over the years.

Station and device were used as nested random effects (intercept only). The microphones were replaced in 2018 for all devices, and we included that information as an additional random effect (intercept only) to avoid any biases in the results. However, this random effect did not have enough variance for the *Myotis* spp. model to converge, and therefore it was excluded for that taxa.

Detailed information on the model parameters and the code for the model call is available in https://github.com/mhkoti/spatio-temporal. We used Akaike information criterion and model selection approach (Burnham and Anderson 2003) to ensure that our selection of independent variables does not add unnecessary complexity in our model (Supporting information). The model fit was inspected using binned residual plots and visually checking if the binwise average residuals fall within ±2 standard error bounds (Gelman and Hill 2006). The plots were drawn using the package 'arm' ver. 1.13-1 (Gelman et al. 2022) in R (www.r-project.org) (Supporting information). First order autocorrelation of the model errors could arise due to modeling sequential time periods. Therefore, we ran Durbin–Watson test on the model residuals (Fox 2016) using the package 'car' ver. 3.0-13 (Fox and Weisberg 2019) in R (www.r-project.org).

In cases where the statement is based on a coefficient in the fitted glmmTMB model, we consider having a p-value of less than 0.05 significant, and therefore indicating compatibility with the data. However, we also interpret seasonal patterns visually from the plotted period-specific activity estimates. We used the 95% confidence intervals of the modeled estimates calculated with 'effects' package (Fox and Weisberg 2018) in R (www.r-project.org) as rough guidelines in deciding whether difference between any two estimates should be considered indicative or part of the noise.

Results

Long-term changes in activity

The data supports general increase in activity of *Eptesicus nilssonii* and *Myotis* spp. from 2015 to 2021, which is indicated by the signficant model coefficients for year (Supporting information). Depending on the latitude, the mean of periodic activity estimates for *E. nilssonii* and *Myotis* spp. are 1.86–2.01 and 1.34–1.63 times higher in 2021 than in the year 2015, respectively (Supporting information). In contrast, we did not observe clear trend in *P. nathusii* activity.

Latitudinal and seasonal patterns in species activity

In *E. nilssonii*, the interaction between latitude and periods 5–12 had significantly positive coefficients (Supporting information) indicating that the effect of latitude on the periodic estimates is not constant throughout the season (Fig. 2a). There was a strong decline in activity with increasing latitude during the early season, but the latitudinal difference decreased from the period 5 (beginning of July) onwards. In periods 7–12 (August–October) there are no apparent latitudinal differences in activity estimates (Fig. 2a).

Activity of *Myotis* spp. was overall lower in the north than in the south. The interaction coefficient between latitude and period was significantly negative in periods 3–5 (June – early July), resulting in relatively low estimates in the north, and vice versa in periods 6–10 and 12 (Supporting information). At 60°N and 61°N, there is no periodic structure in the activity estimates except for the slight decrease in the end of the season. The more northerly latitudes consistently show a peak in periods 7–10 (August) (Fig. 2b).

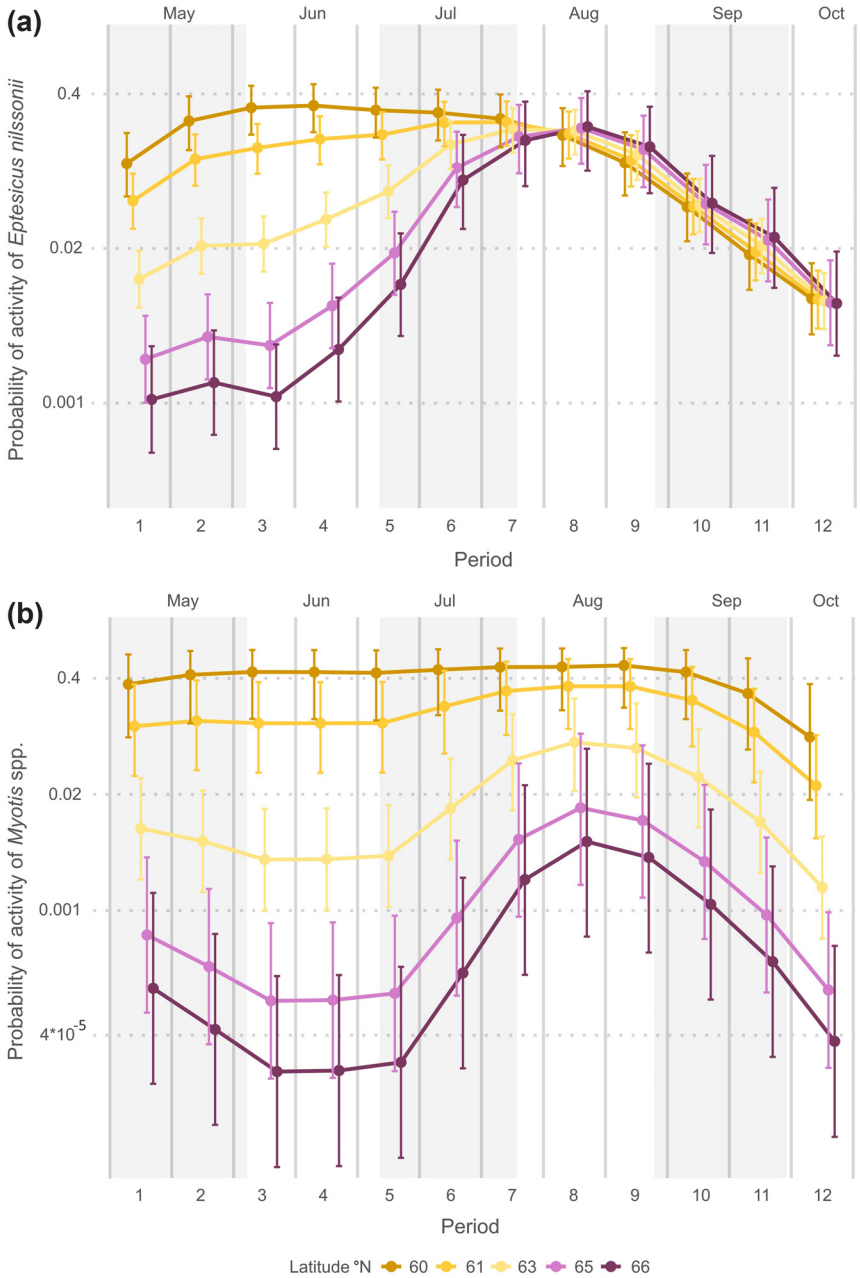

Figure 2. Estimated probablility of activity of *E. nilssonii* (a) and *Myotis* spp. (b) across the modeled periods and latitudes. The values correspond to the probablity of at least one bat call being recorded in 10 min. Only the time between sunset and sunrise are considered each night. The error bars marking 95% confidence intervals of the estimated activity values are calculated with Effect-function in the package 'effects' (Fox and Weisberg 2018). The raw values are available in the Supporting information.

There was an activity peak of *Pipistrellus nathusii* centered around periods 3 and 4 (June), but the peak only emerges over the years (Fig. 3) as dictated by the positive and significant interaction coefficients. Similarly, interaction of periods 11 and 12 (September–October) and year was positive and significant (Supporting information) resulting in increased late-season activity estimates for *P. nathusii* (Fig. 3). In periods 6–9, however, activity decreased significantly over the years (Fig. 3, Supporting information).

The full models had smaller AIC values than any reduced versions, indicating that all fixed predictor values are necessary (Supporting information). The model fit was visually inspected using binned residual plots. In *E. nilssonii*, *Myotis* spp. and *P. nathusii* models, less than 95% of binwise average residuals are within the ±2 standard error bounds (88, 88 and 76%, respectively), which indicates a model fit issue. The bad fit is related to certain years, that deviate considerably from the fitted linear relationship. Otherwise, the model fit appears decent as there are no clear patterns (see Supporting information for details). There was no first order autocorrelation between the observation periods in the models for *E. nilssonii*, *Myotis* spp.

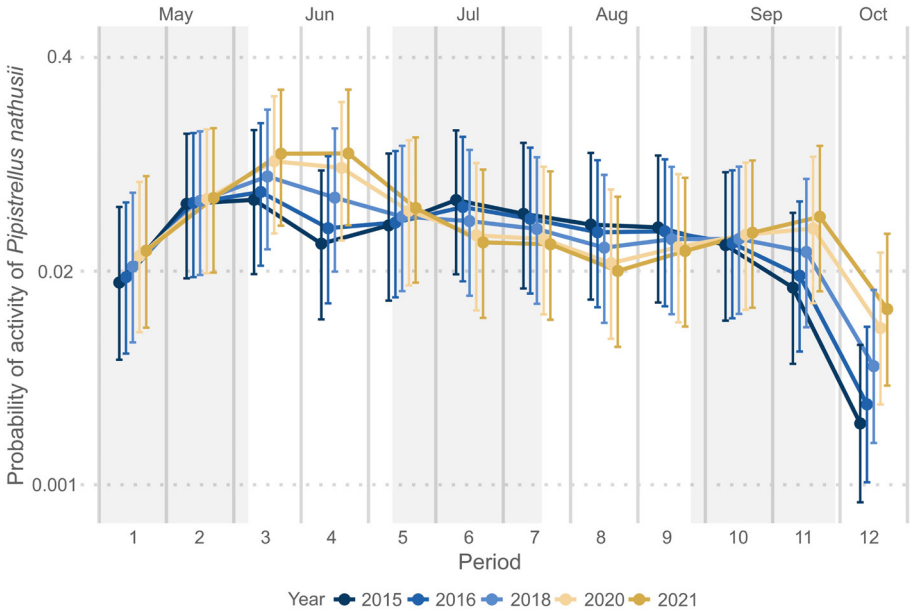

Figure 3. Periodic pattern of the *P. nathusii* observations visualized on a logarithmic scale: The values correspond to the probablity of at least one bat call being recorded in 10 min. Only the time between sunset and sunrise are considered each night. The error bars marking 95% confidence intervals of the estimated activity values are calculated with Effect-function in the package 'effects' (Fox and Weisberg 2018). The raw values are available in the Supporting information.

or *P. nathusii* (Durbin–Watson Test: 2.08, 1.97 and 2.12, respectively).

There were very few bat observations in the three northernmost stations, Muddusjärvi, Kevo and Kilpisjärvi, and we excluded them from the modeling. All observations from these stations are presented in Table 2. Only *V. murinus* and *P. nathusii* were observed at these stations apart from a single *E. nilssonii* in 2021. However, the recordings lack acoustic features of *E. nilssonii* and *V. murinus* that would allow 100% certain distinction. Therefore, we consider these identifications probable but not certain.

Discussion

Our study assessed the potential for long-term, extensive monitoring of bat activity using a passive acoustic monitoring network. The activity was further used to model spatio-temporal changes and annual trends in bat activity and phenology across a latitudinal gradient. Until now, coordinated passive acoustic monitoring has not been performed at this scale. Our results suggest it could provide a feasible method to generate information on activity trends of particularly insectivorous bat species globally (Mancini et al. 2022; Meramo et al. 2022). In the seven years our network has operated, we have identified patterns in bat activity, both between and within years for boreal bat species. Surprisingly, *E. nilssonii* and *Myotis* spp. showed an increasing trend in annual activity, and a distinguished activity peak in late summer and autumn. In addition, we found decreasing bat activity with increasing latitude for *Myotis* spp. For instance, latitude had a remarkable negative effect on the activity of *Myotis* spp. with almost no activity at 66°N, which is in line with the known northern limit of the genus (Siivonen and Wermundsen 2008).

Table 2. All bats observed at the northernmost research stations Kilpisjärvi, Muddusjärvi and Kevo.

Station	Species	Date
Kevo	*V. murinus* cf.	16 September 2015
Kevo	*V. murinus* cf.	19 September 2015
Kilpisjärvi	*P. nathusii*	30 August 2018
Kevo	*P. nathusii*	31 August 2018
Kevo	*P. nathusii*	3 September 2018
Kevo	*P. nathusii*	4 September 2018
Kevo	*P. nathusii*	5 September 2018
Kevo	*V. murinus* cf.	13 October 2018
Kevo	*P. nathusii*	6 September 2019
Kilpisjärvi	*E. nilssonii* cf.	27 August 2021

Across-seasons trends

Both *E. nilssonii* and *Myotis* spp. showed an increasing yearly trend in activity. For *E. nilssonii*, this contrasts recent observations in southern Sweden, where encounters of *E. nilssonii* have decreased drastically, categorizing the most common bat species in Sweden in the 1980s to presently endangered in their national Red List of Threatened Species (Rydell et al. 2020). While our time series is too short to make inferences on the effect of climate change, particularly when taking into consideration that we did not include climate variable in our analyses, we can still allow ourselves some room for speculation to allow formulation of research questions for further research. For instance, the positive trend in bat activity

could be due to suitable milder climatic conditions during our monitoring period on the northern edge of the species range (Jiguet et al. 2010). Bats benefit from high ambient temperature due to the increased availability of arthropod prey (Speakman and Rowland 1999) and enhanced development of the fetus (Racey and Speakman 1987). Furthermore, favourable climatic condition could also lead to increased overwintering success through extended foraging time, allowing bats to gain energy resources to survive the winter, and in addition, possibly affect the positive activity pattern.

Elevated annual ambient temperatures have been beneficial for *P. nathusii* in the United Kingdom (Lundy et al. 2010) and Sweden, where *P. nathusii* has expanded its distribution to the north (Gerell and Lundberg 1985, de Jong et al. 2020). *Pipistrellus nathusii* activity increased during the June activity peak, and late September and October but decreased in July and August, which suggests migratory activity could be higher through Finland, but the population may still be too small to show an increase in activity at a local level (i.e. in the vicinity of the research stations). Importantly, our network will continue to produce data for future analyses and these knowledge of current patterns will pave the way for more sophisticated models including climatic variables.

Within-season trends

Seasonal activity patterns in *E. nilssonii* and *Myotis* spp. changed significantly with latitude. Activity at the southernmost latitudes was roughly uniform throughout the summer months, after which it decreased in late summer and as the autumn proceeded. In contrast, we observed a distinct activity peak above 63°N for *E. nilssonii* and above 61°N for *Myotis* spp. during late summer and early autumn. At least for *E. nilssonii*, the activity peak at northern latitudes occurs after the pups are weaned in the south (Kosonen 2013), and coincides with declining activity in the south. Although we have no data on timing of breeding across latitudes, this pattern could stem from delayed breeding season and subsequent wave of pups entering their independent life and scouting for potential hibernation and foraging sites (Fenton 1969). Alternatively, bats could migrate to feed in the north, where the conditions for breeding may not be optimal, but insect prey is abundant nevertheless (de Jong and Ahlén 1991). This type of mid-distance, within-season vagrant behaviour could be more expected of *E. nilssonii* due to its tendency for mid-distance migratory behaviour (Hutterer et al. 2005, Suominen et al. 2020), but would be a novel and unexpected finding for *Myotis* spp. Similar post-breeding, northwards vagrant behaviour prior to the southwards autumn migration has been observed in several bird species and is potentially linked with prospecting of the future breeding sites (Newton 2007).

Discrepancies in timing of activity across latitudes within a season may also be due to prevailing climatic conditions. For instance, due to long winters at high latitudes, pups are born later in the season, hence weaning and independent flight is observed later. However, excluding coastal Norway in the case of *E. nilssonii* (Rydell et al. 1994), there are no confirmed maternity colonies at the latitudes where our most northern devices are located (Tidenberg et al. 2019). The lack of observed breeding sites does not necessarily mean that they do not exist, as the observation effort at northerly latitudes has been significantly lower so far (Tidenberg et al. 2019).

The relatively steady period, or even a slight dip in activity as latitude increases, in June in *E. nilssonii* and *Myotis* spp. coincides with the shortest night and the reproductive period; hence, bats could be avoiding open areas or retreating to maternity colonies. In contrast to the light-sensitive *Myotis* spp., *E. nilssonii* is considered a light-tolerant species that does not avoid artificially lit (Rydell 1992, Lacoeuilhe et al. 2014) or open areas for foraging (Rydell 1986). Nevertheless, Vasko et al. (2020) observed similar a dip in the activity of *E. nilssonii* during mid-summer, followed by increasing activity as nights began to lengthen and grow darker towards the autumn. In addition, they reported higher activity for both *Myotis* spp. and *E. nilssonii* in mature, closed forests in June and July, and increased activity in open areas in August. This suggests *E. nilssonii* may also be sensitive to light during the breeding time, although feeding around street lights is not uncommon later in the summer (Rydell 1992). Activity in both taxa begin decreasing by the end of August and continued to decrease until a drop at the end of the season, most likely due to a drop in ambient temperature limiting bat activity (Gorman et al. 2021).

Pipistrellus nathusii: an example of the importance of long-term monitoring

Our third focal taxa, *P. nathusii*, is considered rare in Finland (Tidenberg et al. 2019) and is listed as vulnerable (VU) in the Red List of Finnish Species (Hyvärinen et al. 2019). In accordance with this, activity was minimal at all but three of the most southern stations (Supporting information). At these stations, our results suggest a yearly increase in *P. nathusii* activity in the periods corresponding to June and September/early October, but a decrease was observed in July and August (Fig. 3). Considering that *P. nathusii* is predominantly a migratory species (Hutterer et al. 2005), the increased activity in June and September/early October could represent migrating individuals from north or inland. An autumn peak in activity related to migration has been previously documented in Finland (Ijäs et al. 2017). In contrast, the decreased activity in July and August probably indicates changes in the locally breeding bat community. With the temporal extent of this study, we cannot conclude whether this stems from a couple of bad years for *P. nathusii* or an ongoing trend. Nevertheless, this observation calls future monitoring. Based on the recent observation of hibernating *P. nathusii* in SW Finland (Blomberg et al. 2021) and increasing late activity in our data, local overwintering should also be considered and carefully monitored in the future.

Despite having significantly less data than the other two focal taxa of this study, *P. nathusii* well exemplifies the importance of long-term monitoring. Although our data set is still limited, we can draw a careful conclusion that the species

maybe increasing its activity in the north and possibly delaying its autumn migration. Also, by comparing the temporal positioning of the activity peaks in our dataset to those produced for *P. nathusii* at both Pape, Latvia (Pētersons et al. 2021) and southern Sweden (Rydell et al. 2014, Seebens-Hoyer et al. 2021), we could begin to deduce potential migratory pathways in the Baltic to assist in conservation action planning, e.g. windpark development projects (Gaultier et al. 2020). Knowledge on temporal activity, migratory pathways, and furthermore, the population structure of the species, can also assist in monitoring for novel zoonotic pathogens for which bats can act as effective vectors, especially as a consequence of climate change (Laine et al. 2013, Veikkolainen et al. 2014, Kivistö et al. 2019). These not only warrant the continuation of long-term acoustic data collection at research station, but also prompts collaboration with researchers from other countries surrounding the Baltic to gain a more holistic view on open questions surrounding migratory behaviour in *P. nathusii* (Rydell et al. 2014).

Northern vagrants

We also found individual observations of *P. nathusii* and possible *Vespertilio murinus* from the most northern locations; Kevo and Kilpisjärvi. *Pipistrellus nathusii* is known to breed in southern Finland below 61°N (Hagner-Wahlsten and Kyheröinen 2008), but there are no known *V. murinus* roosts in Finland. Both species are migratory (Hutterer et al. 2005) and all observations occurred late in the season, which might indicate that the calls are made by vagrant, possibly young individuals. The majority of the *P. nathusii* observations at sampling locations north of 61°N were from 2018, when the species was ten times more active than any other year (Supporting information). The activity was not radically high in Tvärminne, Husö and Seili that year, suggesting that the northern vagrants could be coming from further away. During the same year, a record number of migrating *P. nathusii* was observed in Pape, east side of the Baltic Sea, while numbers in Måkläppen, in the west side, were not above average. This suggests an influx of vagrant individuals from the east. Such events may have implications for gene flow and pathogen transmission, and should be monitored in the future.

Methodological issues

The passive detector network provides a method to study long-term spatio-temporal changes in the activity of bats across the country. An increase in activity might suggest a peak in abundance. However, the passive acoustic method itself does not provide a reliable method for assessing the number of individuals, i.e. population size. Also, the spatial patterns in activity might change during the season because bats could concentrate around certain resources like the roost sites and foraging spots. The location of these concentrations in relation to the monitoring sites might consequently affect the observed activity and lead into interpreting changes in bat behaviour as change in overall abundance.

The placement of the units has a pronounced effect on detected species composition; thus, study sites must be selected carefully, preferable using systematic or random stratified sampling design. For instance, the activity of *Myotis* spp. will most likely be underestimated if the devices are located at a distance from forest edges, especially during short and light midsummer nights. The devices in this study were placed in proximity of both trees and open areas in order to target the focal taxa as evenly as possible. Furthermore, some species, e.g. *Plecotus* spp., have very quiet echolocation calls that are most likely grossly underrepresented in the records leading to a potentially biased interpretation of the results. Hence, we excluded *Plecotus* calls for this study and focused on more audible species that can be quantified based on recordings.

Because longitude was not included in the model and the monitoring stations were located roughly in a southwest–northeast axis, it should be noted that latitudinal effects might be increased or weakened by non-modeled longitudinal effects. Additionally, the three southernmost stations also represent three out of four coastal stations. Therefore, the observed latitudinal effects could be radically different should the monitoring arrangement follow the coastline.

Finally, the residual plotting revealed a model fit issue regarding year-variable (Supporting information). This indicates that a lot of variation between years is not well described by the continuous linear predictor. This does not necessarily invalidate the estimated coefficients but, instead of projecting into the future, the observed trend should be considered as a depiction of the 7 modeled years. An obvious solution for the fit problem would be longer time series that would increase signal-to-noise-ratio and potentially clarify the trend. Alternatively, allowing model intercept to vary between years (random intercept model) or using year as a categorical predictor could improve model fit in technical sense. However, this would be in expense of interpretable temporal trend, which was one of the main objectives of this study.

Conclusions

Estimating relative abundances and trends in bat populations is challenging due to the lack of reliable, long-term data. A permanent acoustic monitoring network enables the study of these processes and provides feasible tools for conservation and management planning. The monitoring method presented here can be applied at different locations around the globe due to affordable new passive acoustic devices on the market. As our network continues to operate, the models become more reliable and especially long term trends, such as the effects of the climate change, become more accurate. Furthermore, models can be expanded by adding variables, e.g. landscape or weather parameters, to improve detail. Climate change can drive northerly distribution shifts (Chen et al. 2011), as has been suggested to occur with *E. nilssonii* (Rydell et al. 2020) and *P. nathusii* (Gerell and Lundberg 1985) in Sweden. Simultaneously, Fennoscandia may witness more southerly species to disperse towards the

north. The results presented here highlight the importance of research station networks in monitoring and understanding long-term changes of bat species distribution. We also emphasize the use of more descriptive studies to describe trends and dynamics in less-studied phenomena to be able to build more intricate, hypothesis-driven research.

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Supporting information

The Supporting information associated with this article is available with the online version.

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