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Climate prevails over habitat in shaping northern range limits of European bats

Liliana S. Ferreira

fc55612@alunos.ciencias.ulisboa.pt

University of Lisbon

Sara A. O. Cousins

Stockholm University

Hugo Rebelo

University of Lisbon

Katrine Eldegard

Norwegian University of Life Sciences

Jorge M. Palmeirim

University of Lisbon

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Title

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Authors and affiliations

Liliana S. Ferreira (corresponding author)
cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Department of Biology, Faculty of Sciences, University of Lisbon, 1749-016, Lisbon, Portugal
Department of Physical Geography, Faculty of Science, Stockholm University, SE-106 91 Stockholm, Sweden
Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden
Address: cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Department of Biology, Faculty of Sciences, University of Lisbon, 1749-016, Lisbon, Portugal
Mobile phone: +351 91 02 94 436
Email: fc55612@alunos.ciencias.ulisboa.pt
ORCID: 0000-0002-8695-9516

Sara A. O. Cousins
Department of Physical Geography, Faculty of Science, Stockholm University, SE-106 91 Stockholm, Sweden
Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden
Email: sara.cousins@natgeo.su.se
ORCID: 0000-0003-2656-2645

Hugo Rebelo
cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Department of Biology, Faculty of Sciences, University of Lisbon, 1749-016, Lisbon, Portugal
Email: herebelo@ciencias.ulisboa.pt
ORCID: 0000-0002-7118-4068

Katrine Eldegard
Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Postboks 5003, 1432 Ås, Norway
Email: katrine.eldegard@nmbu.no
ORCID: 0000-0002-3276-8087

Jorge M. Palmeirim
cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Department of Biology, Faculty of Sciences, University of Lisbon, 1749-016, Lisbon, Portugal
Email: jmpalmeirim@ciencias.ulisboa.pt
ORCID: 0000-0003-4734-8162

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Climate prevails over habitat in shaping northern range limits of European bats

Abstract

Context

Species presence is largely determined by climatic and habitat characteristics. For many European bat species, the northern range limit lies in Scandinavia, where species richness and abundance decline northwards. This pattern may primarily reflect direct climatic constraints from progressively colder conditions, or alternatively, habitat suitability.

Objectives

To investigate whether climate or habitat primarily limits bats at their northern margins.

Methods

We surveyed bats at 433 points across the Scandinavian Peninsula using passive acoustic methods, spanning major climatic zones and land cover types. Bat presence was recorded at 340 points, with calls assigned to nine species. Potential distribution modelling was applied to four highly detectable species: *Cnephaeus nilssonii*, *Myotis daubentonii*, *Pipistrellus pygmaeus* and *Nyctalus noctula*. We compared GLMMs using climate-only, habitat-only and combined habitat-climate predictors, generated potential distribution maps, and examined climate and habitat ordination spaces.

Results

Climate was a stronger predictor of bat occurrence than habitat, with temperature variables dominating the GLMMs, suggesting thermal constraints on species persistence at higher latitudes. Maps generated from habitat-only models predicted suitable areas far north of observed ranges, whereas climate-only and combined habitat-climate models better matched field observations. Ordinations showed that species occupied much of the available habitat space but a more restricted portion of available climate space.

Conclusions

Northern range limits of European bats appear primarily climatically constrained rather than habitat-limited. Suitable habitat seems to be available north of current distributions, but low temperatures likely prevent occurrence there. However, unmodelled environmental factors may also influence distributions. Ongoing warming may allow northward expansion, so monitoring bats at their northern range margins may provide a sensitive indicator of climate-driven biogeographical change.

Keywords: Chiroptera, thermal constraints, landscape, species distribution modelling, presence-absence, passive acoustic sampling

Introduction

Identifying the factors that determine species occurrence and range limits is central to ecology and for the development of adequate conservation policies. Climate and structural habitat are widely recognised as key range determinants and underpin most species distribution models (Radomski 2026). At northern high latitudes, low temperatures, short summers and extreme winter events may impose physiological and energetic limits on animal species. These constraints are especially important for insectivorous bats, whose annual cycle depends on balancing energy intake during the active season, reproductive costs, and energy savings during torpor or hibernation (Fjelldal et al. 2023; Ruf and Geiser 2015). Low summer temperatures can reduce insect activity and shorten foraging periods (Speakman et al. 2000; Lilley et al. 2026; de Jong and Ahlén 1991), while cold roosts may increase thermoregulatory costs during pregnancy and lactation (Rydell 1989a). In winter, severe and prolonged cold may increase hibernation energetic costs or restrict the availability of suitable hibernacula (Bartonička et al. 2026; Blomberg et al. 2026; Willis 2017). For instance, some bat species may be unable to maintain energy balance where roost temperatures remain too low to support efficient thermoregulation (Bartonička et al. 2026), or where short summer nights at high latitudes restrict foraging opportunities below the threshold needed to meet metabolic demands (Rydell 1992; Michaelsen 2016b). However, for species whose climatic thresholds are not exceeded and for which ambient conditions remain physiologically tolerable, range limits are expected to result from habitat-mediated processes rather than from climatic exclusion.

Many European bat species reach their northern range limit in Scandinavia, where richness and abundance decline northwards (de Jong and Ahlén 1991; Ulrich et al. 2007). This pattern may reflect climatic constraints imposed by progressively colder and harsher climates (Lilley et al. 2026; Michaelsen 2016c), shorter summer nights (Speakman et al. 2000; Frafjord 2021b), or a scarcity of suitable habitat (Michaelsen 2016a; Vlaschenko et al. 2022). At the European and global scales, bat species richness is strongly associated with latitude and temperature (Pereira and Palmeirim 2013; Ulrich et al. 2007), suggesting that climatic gradients play a major role in shaping broad-scale diversity patterns, although land use, water availability, forest structure and landscape heterogeneity also shape regional assemblages and species-specific distributions (Mehr et al. 2011; Michaelsen 2016a; de Jong and Ahlén 1991).

Understanding the factors that determine current species distributions is increasingly important under ongoing warming (Festa et al. 2023; Rebelo et al. 2010), a trend that is particularly pronounced in northern regions (Kjellström 2004; Rantanen et al. 2022; Vautard et al. 2014). If northern limits are mostly climatically constrained, warming may enable northward expansion (Kravchenko et al. 2025; Rebelo et al. 2010). If they are limited by habitat availability, roost limitation or prey availability, climatic warming alone may not be sufficient to generate range expansion (Fialas et al. 2025; Rebelo et al. 2010). This distinction is particularly important for bats, because climate change is expected to alter not only thermal suitability but also hibernation conditions (Kravchenko et al. 2025), reproductive timing (Lučan et al. 2013) and the seasonal availability of foraging opportunities (Festa et al. 2023; Sherwin et al. 2013).

Nineteen bat species are present in Scandinavia (de Jong et al. 2020), most concentrated in the south, with only a few extending far north and *Cnephaeus nilssonii* (until recently known as *Eptesicus nilssonii*) almost reaching the northern end of the

peninsula (Rydell et al. 1994). This gradual decline in species richness across a wide range of latitudes makes Scandinavia a particularly suitable region to explore factors that determine the northern range limits of bat species.

The main objective of this study was to better understand the factors shaping bat species occurrence and ranges at their northern distribution limits in Europe. We aimed to determine whether, in northern temperate and boreal regions, bats are prevented from expanding further north primarily by climatic constraints or by the availability of suitable habitat. To our best knowledge, this is the first study to address the determinants of bat species distributions at large regional scales across diverse habitats and climates, from temperate to boreal conditions, at the northern limit of many species' distributions.

In line with previous studies indicating that, in general, climatic factors become increasingly important towards the range margins (Tourani et al. 2023; Ulrich et al. 2007), we hypothesized that climate, rather than structural habitat, is the main determinant of the northern range limits of bat species in Scandinavia. This expectation reflects the likelihood that the harsh climatic conditions of central and northern Scandinavia exceed the physiological and energetic tolerances of these species. If this hypothesis holds, potentially suitable habitat should extend well beyond the current northern range limits.

To evaluate this hypothesis, we modelled the potential distribution of bat species based on a large-scale systematic survey of their presence across the Scandinavian Peninsula, and followed three complementary approaches:

i) We assessed the relative contribution of climatic and habitat variables in modelling bat occurrence and predicted that climatic variables would outperform habitat variables as determinants of species presence.

ii) We generated potential range maps using species distribution models built separately for climatic and habitat variables. We predicted that climate-only models would more accurately reproduce the observed northern range limits, whereas habitat-only models would overpredict presence, projecting suitable conditions into northern areas where the species are, in fact, absent.

iii) We produced ordinations summarizing the climate-space and habitat-space available across Scandinavia, and plotted presences and absences in these ordination spaces. We predicted that each species would occupy the almost full extent of habitat-space but only a fraction of the available climate-space, consistent with climate, not habitat, acting as the key determinant of bat ranges.

Materials and methods

Study area and sampling design

The Scandinavian Peninsula covers nearly 800 000 km^2. The broad latitudinal range produces a marked south–north gradient from 55 to 71°N, encompassing ecozones that range from temperate to boreal. Topography is highly varied, with the Scandinavian Mountain Range running along the entire peninsula up to about 70°N, and steep fjord landscapes along the western coast (Wielgolaski 1975). This topography creates a gradient of varied vegetation and climates from the bottom of the fjords to the peninsula's central areas, ranging from temperate to boreal

(Supplementary Material Figure S1). Due to the proximity to the North Atlantic Current and the extensive coastline, the western climate is predominantly temperate, despite the high latitude (Beylich 2021). The vegetation is dominated by boreal coniferous forest, primarily composed of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which forms the main land cover across most of the peninsula. These forests can be mixed with broadleaf tree species and sometimes include patches of broadleaf-dominated woodland. On the eastern, less mountainous, side of the peninsula, the forest consists largely of managed coniferous forests often interspersed with open grasslands. Grasslands occur throughout the peninsula but are especially extensive in the mountainous west, while agricultural land is concentrated in the south and along the east coast. Lakes and rivers are present throughout the peninsula (Statistiska Centralbyrån 2023; Statistisk Sentralbyrå 2025).

Bat species occurrence was extensively surveyed with passive acoustic monitoring across the Scandinavian Peninsula (Fig. 1). To stratify the sampling, we divided the peninsula into 21 rectangular sample areas. Each measured 200 km north-south, while its east-west width varied to accommodate the changing breadth of the peninsula. Within each sample area, we selected two to four sampling sites at least 50 km apart. Site selection was based on land-cover maps and satellite imagery to capture the main habitats, topographic variation, and climatic conditions within each area. At each site, we sampled five points separated from each other by at least 200 m: two points on the edge between forest and lake or river, as close as possible to the water; two points on the edge between forest and open area; and one point in the forest. At higher elevations, the vegetation becomes scarcer and more stunted due to harsh weather conditions, making distinct edges between forest and open areas less pronounced. Where distinct forest edges were not present, the border of larger patches of shrubby vegetation was used as the equivalent of the border between forest and open area. All points were situated at least 300 m from buildings to avoid roost-proximity bias (Frafjord 2013; Rydell 1989b), and at least 100 m from roads to avoid commuting corridor effects (Lesiński et al. 2011). Urban areas were excluded from sampling. This design resulted in a total of 87 sampling sites and 435 sampling points, although equipment failure occurred at two of the latter (Fig. 1).

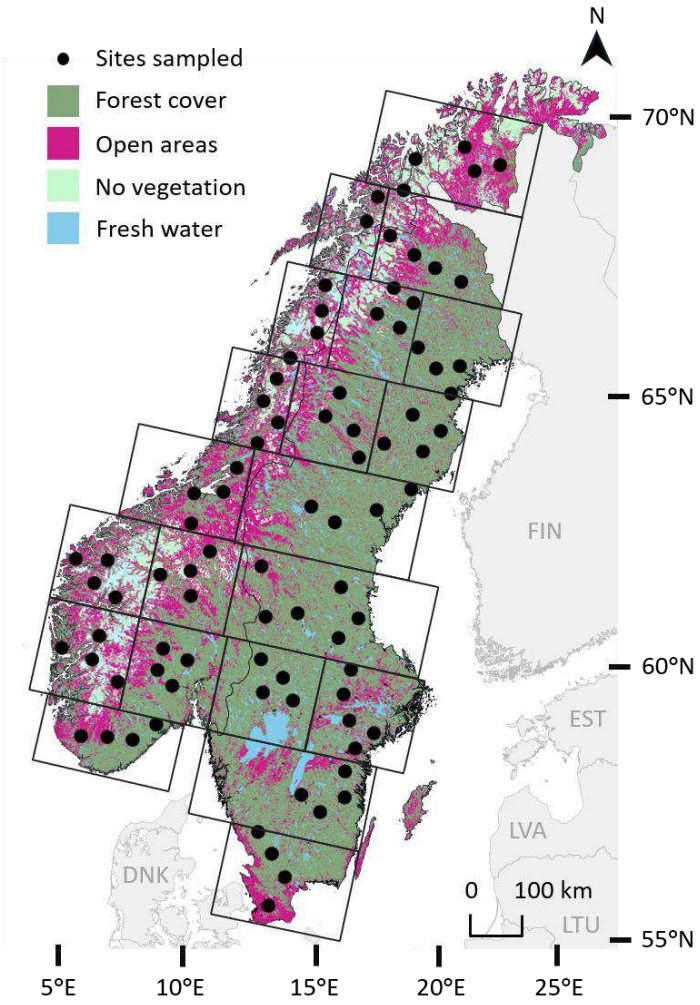


Fig. 1 Map of the study area stratified into sampling areas, showing the sites where bat assemblages were surveyed with acoustic stations in the Scandinavian Peninsula (Norway and Sweden). Each site includes five sampling points. Patches of artificial surfaces and snow and ice are too small to be visible at this scale

Acoustic sampling

Bat species assemblages were sampled using AudioMoth acoustic loggers (Open Acoustic Devices) housed in waterproof electrical junction boxes, with a 500 µm metal mesh covering an opening aligned with the microphone. Fieldwork was conducted from 13 July to 17 August 2022 and from 2 June to 30 July 2023. Recordings were scheduled from 30 min before local sunset to 30 min after sunrise. Sampling began in the southernmost areas in both years to match the seasonal progression of peak bat activity along the peninsula's latitudinal gradient. In Northern Europe bat activity peaks between June and August. At higher latitudes on the Scandinavian Peninsula the active season lasts only 2.5 months, approximately 1.5 months shorter than in the south (Frafjord 2021b). Each point was sampled for three consecutive nights under suitable weather conditions: a minimum air temperature of 7°C (Rydell 1991), no precipitation, and wind speeds below 5 m/s (Froidevaux et al. 2014). Loggers were mounted 2 m above the ground on wooden poles or tree trunks. Microphones were angled slightly downwards to prevent water accumulation on the protective mesh and directed away from nearby vegetation to minimise sound interference. Loggers within forests were

placed in uncluttered, open-canopy clearings to ensure flight accessibility. At forest edges, microphones were positioned parallel to the edge, ensuring that recordings captured comparable portions of both forest and open habitats. Recordings were made at a sampling rate of 192 kHz, using medium gain to minimise signal distortion. Audio was recorded in 59-min cycles separated by 1-min intervals of no recording, using a 10 kHz high-pass filter to reduce ambient and insect noise.

This field sampling methodology is likely to have resulted in some false absences, especially at sites where a species is rare or difficult to detect, although this potential problem was attenuated by including only highly detectable species in the prediction modelling.

Species identification

All recordings were analysed using Kaleidoscope Pro v5.3.9 (Wildlife Acoustics, Inc.). The 59-min files were first segmented into 5-s files. These files were filtered to retain only those containing echolocation pulses with frequencies between 10 and 130 kHz, pulse durations of 1.5–500 ms, and a maximum inter-syllable gap of 500 ms.

The retained files were then processed using the 'Bats of Europe 5.2.1' automatic classifier, restricted to species known to occur in Scandinavia. Files classified as 'noise' were excluded from further analysis, whereas all files assigned to a bat species, as well as those classified as 'no ID' were visually reviewed to verify or determine species identity. This verification consisted of examining call structure on sonograms and measuring five acoustic parameters for at least two pulses per pass: frequency of maximum energy (kHz), maximum frequency (kHz), minimum frequency (kHz), call duration (ms), and inter-pulse interval (Barataud 2020; Russ 2021). A bat pass was defined as a 5-s file containing two or more echolocation pulses. To minimize errors in identification due to the overlap in acoustic parameters across species, non-diagnostic calls were not assigned to species. They were categorized into multispecies groups and excluded from subsequent analyses.

Environmental variables

The land cover classes used in this study were based on the European Space Agency land cover map (Zanaga et al. 2022), with a 10 m cell resolution. The original categories were merged into six classes (Fig. 1): *tree cover* (49.5%, including forest and shrubland - 0.2%), *open areas* (29.6%, encompassing both grassland and 2.3% cropland), *artificial surfaces* (0.5%, including buildings, roads, railways and other artificial structures), *no vegetation* (10%, comprising terrain covered by mosses, lichens, exposed soil, sand, or rocks that never exceed 10% vegetation cover year-round), *snow and ice* (1.6%, representing land persistently covered by snow or glaciers), and *fresh water* (8.8%, including lakes, rivers, and regularly or permanently flooded herbaceous vegetation). Land cover classes were merged based on a combination of knowledge of the biology of the species and past studies on bat spatial ecology (e.g., Razgour et al. 2016).

Landscape variables included the percentage of tree and open area cover within a 100 m radius of each sampled point, the distance to the nearest lake or river, and the Shannon Diversity of habitat types within a 1000 m radius. All these landscape variables have been found to be relevant for European bats (Ferreira et al. 2026; Kirkpatrick et al. 2017; Rainho and Palmeirim 2011). However, we only used variables describing habitat structure, defined here as the physical arrangement, complexity,

and spatial configuration of habitat features, independent of the species that compose them.

Vegetation-structure variables can also influence bat habitat use (Jung et al. 2012; Martins et al. 2024), so we included forest biomass and canopy height, as predictors. These variables were calculated within a 100 m radius around the sampled points using the raster maps generated by Liu et al. (2023), available at https://zenodo.org/records/8154445. Topographic variables—elevation, slope, roughness, and aspect—were derived for each sampling point using a 30 m resolution digital elevation model from Copernicus (European Space Agency 2021). Topographic variables were included in habitat models because they describe physical landscape structure, although elevation also influences climate.

Climatic variables were obtained from CHELSA V2.1 (Karger et al. 2021), representing the 1981–2010 average at a 30 arcsec resolution. From the initial 19 bioclimatic variables (bio1 to bio19), only bio5 (mean maximum temperature of the warmest month), bio6 (mean minimum temperature of the coldest month), and bio12 (annual mean precipitation amount) were retained, as these were the variables that best explained the observed occurrence data. All environmental variables were rescaled to 10 m resolution before analysis. Spatial processing was performed using QGIS (version 3.40 Bratislava).

Statistical analysis

We used three distinct generalized linear mixed models (GLMMs) in R (version 4.5.1) to evaluate and compare the effect of the explanatory variables (habitat variables alone, climate variables alone, and both habitat and climate variables combined) on individual bat species' presence-absence. These models are henceforth referred to as habitat-only model, climate-only model, and habitat-climate model. Topographic variables were considered habitat parameters. Four bat species – *Cnephaeus nilssonii*, *Myotis daubentonii*, *Nyctalus noctula* and *Pipistrellus pygmaeus* – had sufficient number of occurrences for modelling. For modelling purposes, species-specific datasets were restricted by excluding sampling points located more than 200 km north of the northernmost sampling area where each species was recorded. This step reduced the number of trivial absences from latitudes outside the species' observed range, minimizing the risk of zero-inflation in the occurrence data. Furthermore, this approach prevented the disproportionate sampling of cold latitudes from artificially inflating the relative importance of climatic variables over habitat predictors, thereby ensuring a highly conservative test of our hypothesis. This exclusion was unnecessary for *C. nilssonii* because it is distributed almost to the northernmost limits of Scandinavia. All explanatory variables were centred and standardized prior to analysis. Models were fitted using a binomial distribution (R package 'glmmTMB').

As the survey was conducted over two summers, a continuous Julian date (accounting for both day of the year and year of sampling) was included as a random effect to account for potential temporal variation in bat occurrence.

Our sampling design produced clusters of five proximate points per site, which introduced significant spatial autocorrelation, as indicated by Moran's I tests on model residuals. To account for this, all points within 1000 m of each other were grouped into the same cluster, and this categorical variable was then included in the models as a random effect.

All explanatory variables were checked for correlation using Spearman's rank correlation coefficient, and variables with correlations > 0.6 were excluded from modelling (Dormann et al. 2013). For correlated pairs, we retained the variable deemed more ecologically meaningful or more significant in the analysis. In the combined models, temperature and elevation were correlated, and temperature was kept as the more ecologically relevant variable. To prevent multicollinearity, we also calculated variance inflation factors (VIF) for each final model using the 'check_collinearity' function from the R package 'performance', retaining only variables with a VIF < 2.

For each response variable, we then generated all possible models based on different combinations of explanatory variables. These were ranked using the AICc via the 'model.avg' function in the R package 'MuMIn', retaining models with a ΔAICc < 2 (Burnham and Anderson 2002). From the multi-model inference averaging, each predictor relative importance value (RIV) was extracted as the sum of Akaike weights across all candidate models including the predictor. All averaged candidate models had substantially lower AICc values than their corresponding null models.

Model performance was validated by calculating the area under the curve (AUC) of the receiving operating characteristic (ROC) curve and the true skill statistic (TSS). Because models evaluated on their training data can yield overfitted validation metrics, we used 10-fold cross-validation using spatially separated folds with the 'blockCV' package, to account for the spatial clustering of points resultant of our sampling design (Valavi et al. 2019). Out-of-fold predictions were pooled across all spatial folds to calculate global values for both AUC (using the 'pROC' package) and TSS (calculated as sensitivity + specificity - 1; Allouche et al. 2006).

Potential distribution maps for the four bat species were generated across the Scandinavian Peninsula using the variable coefficients from the final averaged models. Although the models were fitted using sampling points restricted to the approximate latitudinal range of each species, they were then projected across the entire peninsula to assess potential distribution beyond the areas used for model calibration. For each model, predictor rasters were multiplied by their respective coefficients and summed with the intercept to obtain the linear predictor. This was then back-transformed using the logistic function to produce a continuous probability surface.

To visualize each species' realised habitat and climate niches across Scandinavia we ran two PCAs using all the sampling points, one on the habitat variables and one on the climate variables retained in the final GLMMs. Species presence-absence records were then projected onto the space defined by PC1 and PC2 of each PCA, showing the portion of the available environmental space occupied by each species. To test whether species presence locations occupied a shifted or restricted subset of the available environmental and habitat space, we performed 9999 random Monte Carlo permutation tests along PC1 and PC2. For each species, we evaluated shifts in both the mean (centroid shift) and variance (niche breadth dispersion) between the presence records and the total available background pool.

Finally, to determine the approximate thermal limits of each species, we generated univariate response curves for minimum and maximum temperatures from univariate GLMMs.

Results

A total of 433 points were acoustically sampled across the peninsula, with bat presence recorded at 340 of these points. Recordings were assigned to nine species: *Barbastella barbastellus*, *Myotis daubentonii*, *Myotis nattereri*, *Nyctalus noctula*, *Cnephaeus nilssonii*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Pipistrellus nathusii*, and *Plecotus auritus*. Most of the presences recorded were of *C. nilssonii* (329 presences), followed by *M. daubentonii* (223), *P. pygmaeus* (127) and *N. noctula* (52). Bat passes that were not possible to identify to species level were identified to groups of species or to genus level and were excluded from further analyses.

Relative importance of explanatory variables in GLMMs

In general, in the GLMMs the climatic variables, namely the mean minimum temperature of the coldest month and mean maximum temperature of the warmest month, were the strongest predictors of bat species distributions (Table 1). Higher temperatures consistently increased predicted species presence in climate-only models (for all four species) and in habitat-climate models (for *C. nilssonii*, *N. noctula* and *P. pygmaeus*). In contrast, habitat variables had comparatively weaker effect in both habitat-only models and in habitat-climate models.

The performance across all models was good, as indicated by the relatively high cross-validation AUC scores (range 0.71–0.91) and TSS scores (range 0.40–0.72) (Table 1).

Table 1 Results of GLMMs predicting the probability of species occurrence using habitat variables only, climatic variables only, and combined habitat and climatic variables, based on bat species presence-absence data. Estimates were obtained using multimodel inference and model averaging, retaining models with ΔAICc < 2. Significant variables are shown in bold. RIV indicates the relative importance value of predictor variables; AUC is the area under the receiver operating characteristic curve, measuring discrimination between presences and absences; TSS is the true skill statistic, assessing model performance from sensitivity and specificity

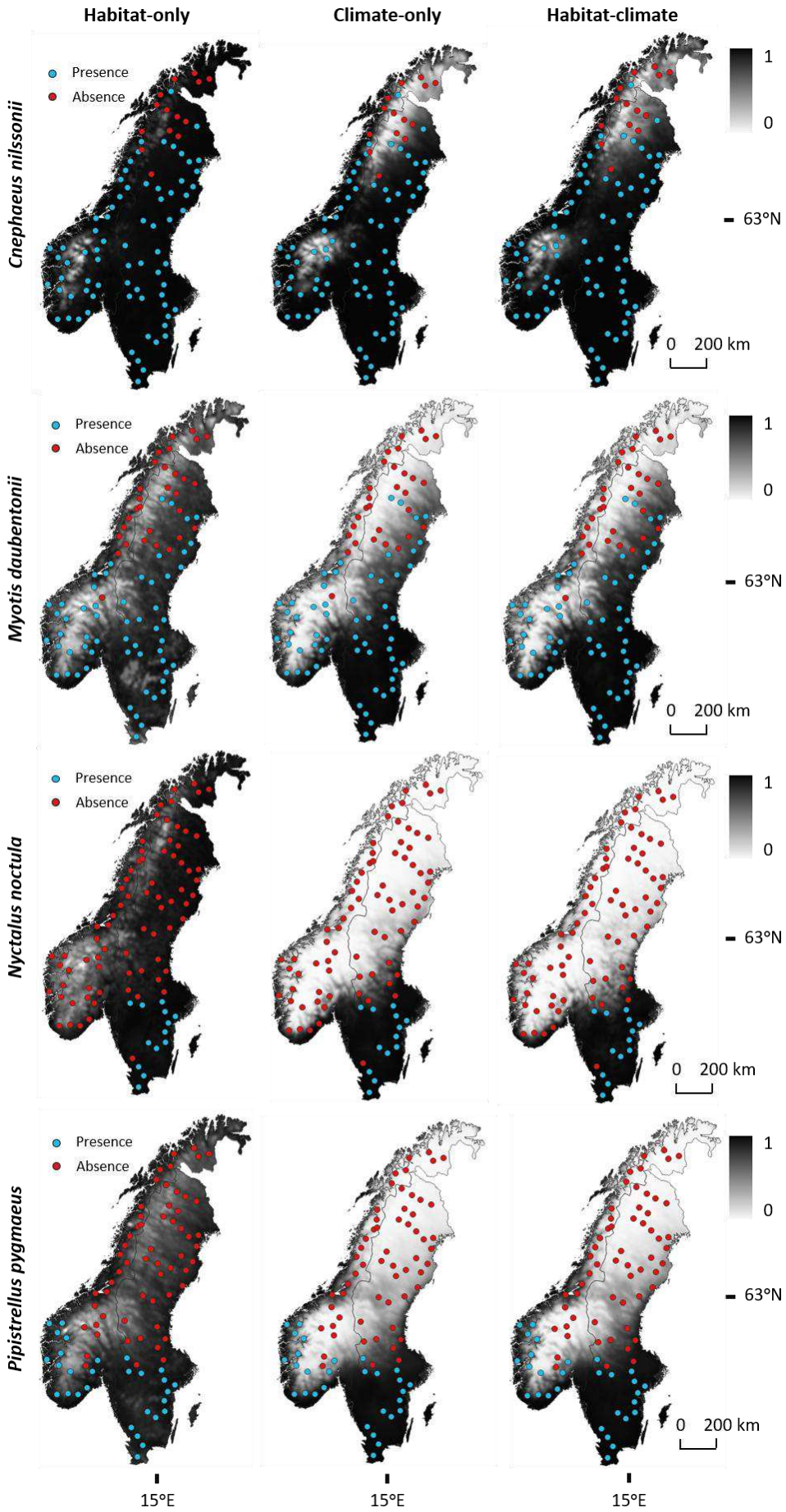
Species	Variable type	Predictor variable	Direction of effect	Estimate	Standard error	p-value	RIV	AUC	TSS
Cnephaeus nilssonii	Habitat variables	**Intercept**		**4.21**	**1.34**	**0.00 ****			
		Elevation		-1.02	0.62	0.10	0.72		
		Open area		0.46	0.31	0.14	0.57	0.87	0.68
		Distance to water		0.23	0.33	0.50	0.20		
		Canopy height mean		0.20	0.38	0.60	0.10		
	Climatic variables	**Intercept**		**3.62**	**0.72**	**0.00 *****			
		Maximum temperature	↑	**1.74**	**0.80**	**0.03 ***	**1.00**	0.89	0.67
		Minimum temperature	↑	**2.62**	**0.90**	**0.00 ****	**1.00**		
		Annual precipitation		0.76	0.84	0.37	0.36		
	Habitat and climatic variables	**Intercept**		**3.63**	**0.71**	**0.00 *****			
		Maximum temperature	↑	**1.87**	**0.78**	**0.02 ***	**1.00**		
		Minimum temperature	↑	**2.58**	**0.86**	**0.00 ****	**1.00**	0.89	0.68
		Open area		0.52	0.30	0.08 .	0.68		
		Distance to water		0.47	0.35	0.18	0.47		
		Annual precipitation		0.81	0.83	0.33	0.23		

		Canopy height mean		-0.51	0.38	0.18	0.10		
		Shannon diversity index		-0.15	0.40	0.71	0.08		
Myotis daubentonii	Habitat variables	Intercept	↑	0.12	0.76	0.87		0.90	0.68
		Canopy height mean		**0.53**	**0.26**	**0.04 ***	**0.96**		
		Elevation		-0.61	0.38	0.11	0.60		
		Shannon diversity index		0.42	0.27	0.13	0.59		
		Slope		0.34	0.26	0.20	0.45		
		Distance to water		-0.31	0.23	0.18	0.48		
	Climatic variables	Intercept	↑	0.15	0.45	0.74		0.91	0.69
		Maximum temperature	↑	**2.01**	**0.45**	**0.00 *** **	**1.00**		
		Minimum temperature		**1.02**	**0.46**	**0.03 ***	**1.00**		
	Habitat and climatic variables	Intercept	↑	0.17	0.45	0.71		0.91	0.68
		Maximum temperature		**2.10**	**0.47**	**0.00 *** **	**1.00**		
		Minimum temperature		0.87	0.47	0.06 .	0.86		
		Slope		0.46	0.25	0.06 .	0.85		
		Shannon diversity index		0.33	0.25	0.18	0.30		
		Canopy height mean		0.26	0.24	0.28	0.26		
		Distance to water		-0.17	0.20	0.42	0.08		
		Annual precipitation		-0.15	0.46	0.74	0.06		
		Tree cover		0.05	0.20	0.79	0.06		
Nyctalus noctula	Habitat variables	**Intercept**		**6.21**	**1.57**	**0.00 *** **		0.78	0.50
		log(Elevation)	↓	**-7.13**	**1.67**	**0.00 *** **	**1.00**		
		Shannon diversity index	↑	**0.48**	**0.24**	**0.05 ***	**1.00**		
		Slope	↓	**-0.70**	**0.29**	**0.02 ***	**1.00**		
		Open area		-0.19	0.23	0.42	0.25		
		Canopy height mean		-0.16	0.24	0.49	0.23		
	Climatic variables	**Intercept**		**-2.15**	**0.49**	**0.00 *** **		0.87	0.62
		Maximum temperature	↑	**2.44**	**0.52**	**0.00 *** **	**1.00**		
		Minimum temperature		**2.34**	**0.57**	**0.00 *** **	**1.00**		
	Habitat and climatic variables	**Intercept**		**-2.43**	**0.55**	**0.00 *** **		0.84	0.58
		Maximum temperature	↑	**2.23**	**0.57**	**0.00 *** **	**1.00**		
		Minimum temperature	↑	**2.87**	**0.69**	**0.00 *** **	**1.00**		
		Shannon diversity index	↑	**0.81**	**0.32**	**0.01 ***	**1.00**		
		Canopy height mean		-0.43	0.31	0.17	0.42		
		Open area		-0.31	0.28	0.27	0.34		
		Slope		-0.27	0.42	0.52	0.13		
Pipistrellus pygmaeus	Habitat variables	**Intercept**		**3.98**	**0.63**	**0.00 *** **		0.71	0.40
		Canopy height mean		0.26	0.18	0.15	0.60		
		Distance to water		-0.23	0.16	0.15	0.51		
		log(Elevation)	↓	**-4.00**	**0.62**	**0.00 *** **	**1.00**		
		slope	↑	**0.63**	**0.18**	**0.00 *** **	**1.00**		

	Tree cover		-0.13	0.20	0.52	0.18		
Climatic variables	**Intercept**		**-0.48**	**0.20**	**0.02 ***		0.91	0.71
	Maximum temperature	↑	**0.49**	**0.20**	**0.01 ***	**1.00**		
	Minimum temperature	↑	**2.49**	**0.30**	**0.00 *****	**1.00**		
Habitat and climatic variables	**Intercept**		**-0.54**	**0.21**	**0.01 ** **		0.91	0.72
	Maximum temperature	↑	**0.83**	**0.23**	**0.00 ** **	**1.00**		
	Minimum temperature	↑	**2.42**	**0.31**	**0.00 *****	**1.00**		
	Slope	↑	**0.74**	**0.26**	**0.00 ** **	**1.00**		
	Canopy height mean		0.20	0.21	0.35	0.36		

Predicted distribution maps

Distribution maps from habitat-only models show broader potential ranges than climate-only models for all species (Fig. 2). For *M. daubentonii*, *N. noctula*, and *P. pygmaeus*, they identify extensive northern areas as suitable despite these regions not being occupied. In contrast, the maps generated by climate-only models closely match the ranges confirmed by field data, excluding those northern areas.



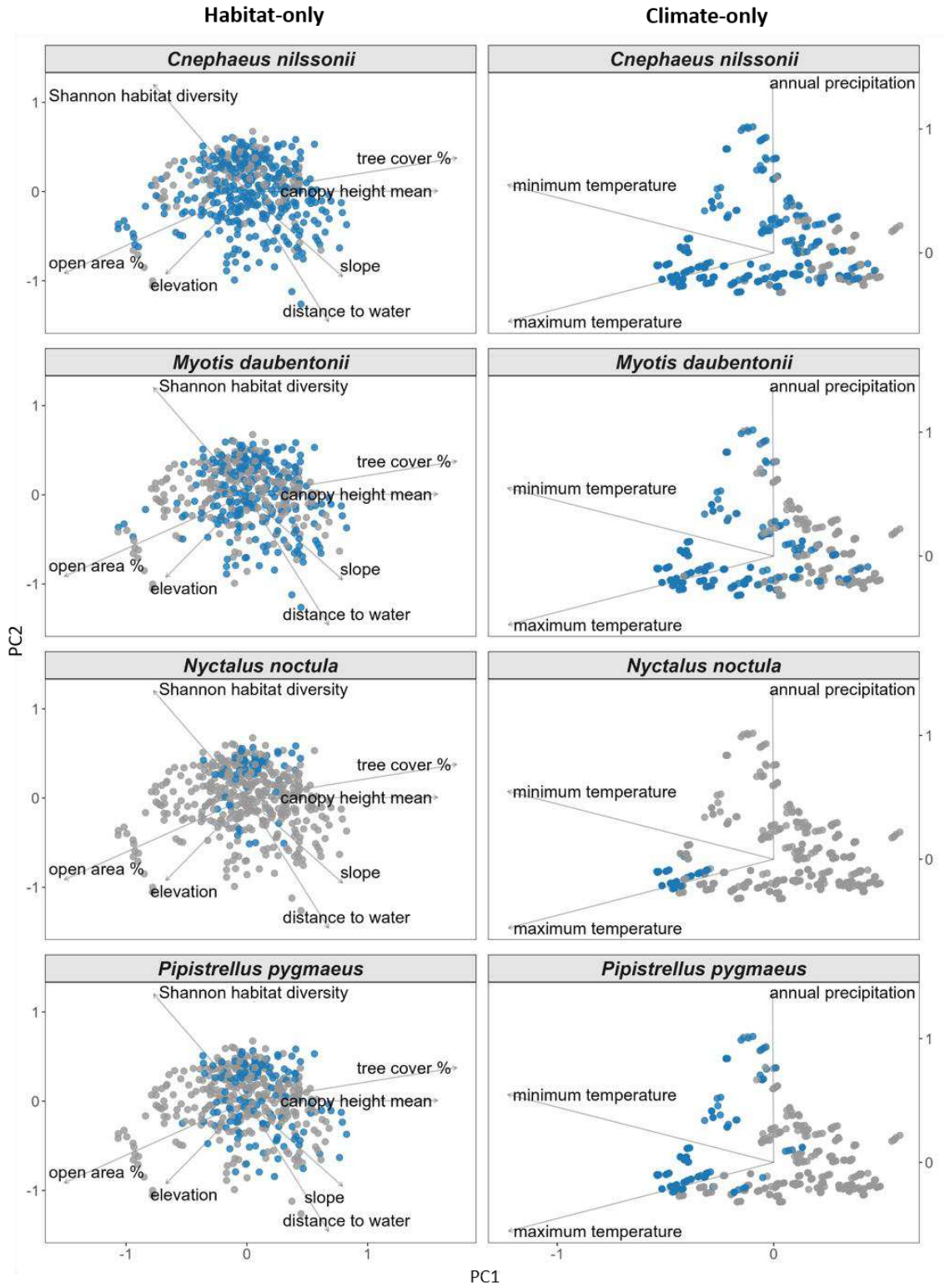
417 **Fig. 2** Potential distribution maps for each species based on averaged best-performing

GLMMs including habitat-only variables, climate-only variables, and both habitat and climate variables. Habitat suitability is depicted in grayscale, ranging from white (lowest) to black (highest). Dots represent sampling sites where each species was recorded as present (blue) or absent (red). Most habitat-only maps indicate suitability across vast northern areas where the species was not recorded, whereas maps including climatic variables are more accurate. Presences in areas predicted as unsuitable are usually in mountain regions, at sites located in low valleys that are suitable but not visible at the scale of the maps

Distribution of species presences in climate and habitat ordination spaces

The first two axes of the climate PCA explained 95% of the variance, and those of the habitat PCA explained 60.2%. When presence and absence points were projected onto the habitat ordination, presences of all species extended across almost the entire range of habitat PC1 and PC2 scores, broadly overlapping the cloud of available sites (Fig. 3). This indicates that bat occurrences were associated with a wide range of habitat conditions across the peninsula. In contrast, in the climate ordination, presences were concentrated mainly on the left side of the space, corresponding to warmer regions, and were sparse or absent from the colder portion of the climate space, depending on the species (Fig. 3). Thus, bat occurrences covered most of the available habitat space but only a more restricted subset of the available climate space.

Two measurements based on scores along the main axis of each ordination supported this pattern. First, the shift between the centre of the used space and the centre of the available space was much smaller in habitat space than in climate space, with mean values of 0.07 and 0.26, respectively. This indicates that occurrences were nearly centred within the available habitat gradient, but displaced towards one end of the climate gradient, corresponding to warmer conditions. Second, mean niche breadth was twice as high in habitat space as in climate space, 0.08 versus 0.04, indicating broader use of existing habitat conditions than climatic conditions. Overall, both metrics support the visual interpretation that bat distributions appear to be more constrained by climate than by habitat.



450 **Fig. 3** Principal component analysis (PCA) biplots representing habitat-space (left) and
451 climate-space (right) in Scandinavia, and their occupation by bat species. Dots
452 represent sampled sites where each species was absent (grey) or present (blue).
453 Arrows indicate environmental variables. All species occupy most of the available
454 habitat-space, but some occupy only the left part of the climate-space, which is
455 associated with higher temperatures
456

457
458 Climatic limits of species
459 Univariate plots of the mean minimum temperature of the coldest month indicate
460 that, for all species, the predicted probability of occurrence declines substantially at
461 lower temperatures, even within each species' latitudinal range (Fig. 4). In the coldest
462 locations within those ranges, the predicted probability of occurrence is zero or nearly
463 zero. This pattern is also observed for the mean maximum temperature of the
464 warmest month. The effect is evident across all species, although it is more
465 pronounced in those with less northward penetration, such as *N. noctula*, for which no
466 presences were recorded at mean minimum temperatures below -6.4°C or mean
467 maximum temperatures below 19.8°C, and *P. pygmaeus*, for which no presences were
468 recorded at mean minimum temperatures below -10.6°C.
469

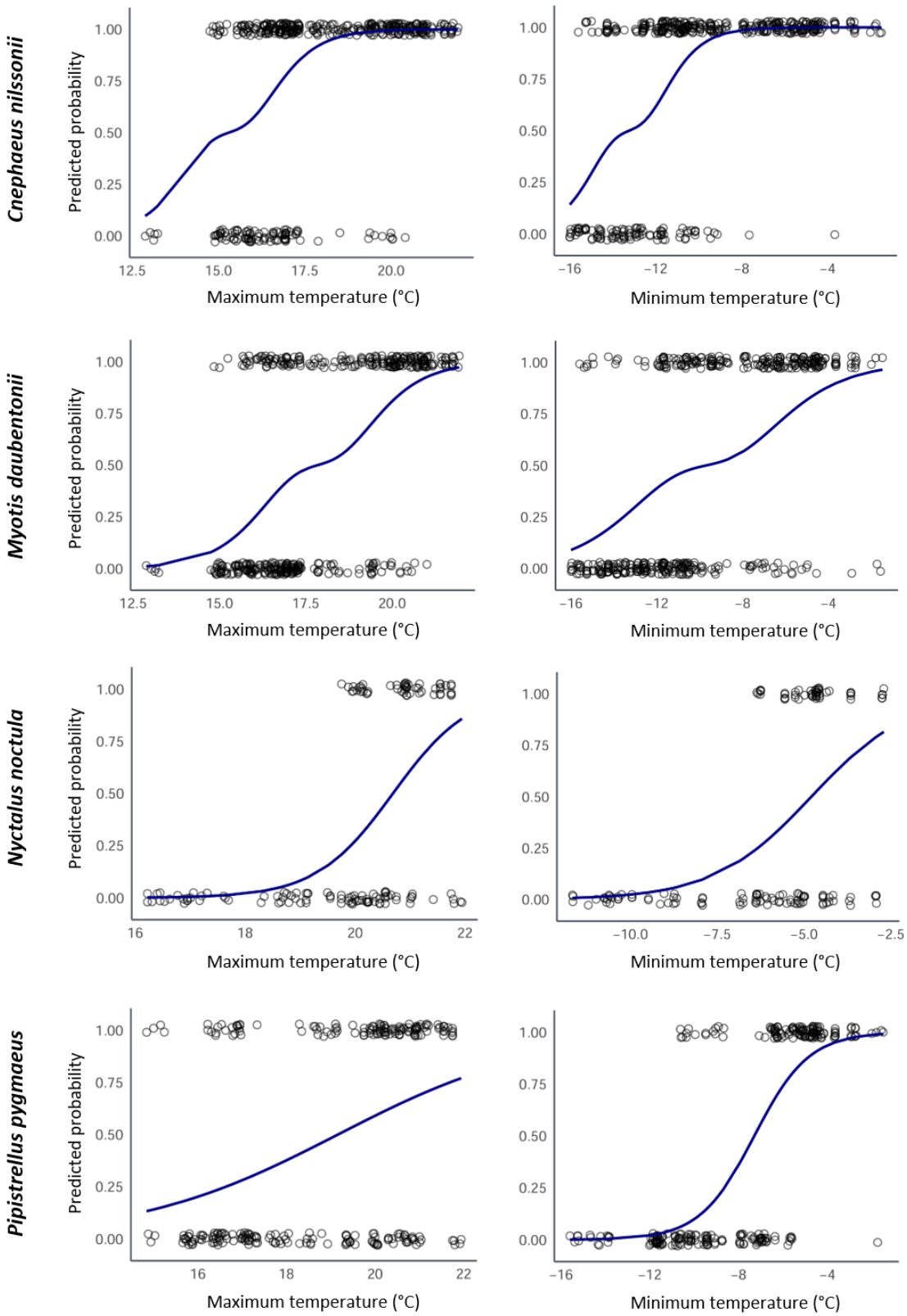


Fig. 4 Predicted probability of presence of each species as a function of mean maximum temperature of the warmest month (left) and mean minimum temperature of the coldest month (right), within the latitudinal range where each species is present. Lines represent logistic regression curves and open circles represent sampled points. The probability of occurrence declines markedly at lower temperatures and is zero or nearly zero at the coldest points within the occupied latitudinal range

Discussion

In the following sections, we first discuss the relative importance of climatic and habitat variables in explaining species occurrence, then evaluate whether modelled distributions match observed ranges, examine how species occupy available climate and habitat space, and finally consider potential confounding factors and limitations, including night duration, prey availability, roost availability, and latitudinal changes in habitat structure.

Climatic variables are stronger predictors of species distributions than habitat variables In all climate-only models, the strongest predictors were the mean minimum temperature of the coldest month and the mean maximum temperature of the warmest month.

The importance of the mean minimum temperature suggests that hibernation is a critical bottleneck at high latitudes. During hibernation, bats require suitable hibernacula with stable microclimatic conditions that prevent freezing, minimizing energetic costs from arousals (Blomberg et al. 2026; Siivonen and Wermundsen 2008), and allowing survival through long periods without feeding (Culina et al. 2017; Willis 2017). Very cold and long winters may increase hibernation costs, as bats arouse near freezing temperatures, depleting stored energy reserves and potentially reducing overwinter survival (Willis 2017). Low external temperatures may also reduce the availability of thermally suitable roosts (Bartonička et al. 2026).

The importance of the mean maximum temperature of the warmest month indicates that summer temperatures may also constrain bat occurrence. Warmer summers may increase prey availability, expanding nightly and seasonal foraging opportunities (de Jong and Ahlén 1991; Michaelsen 2016c). This is especially important at high latitudes, where the active season is short, nights are brief (Michaelsen 2016b), foraging windows are reduced, and insect availability declines rapidly after sunset as temperatures fall (Fjelldal et al. 2023; Frafjord 2021b; Lilley et al. 2026). Warmer nights increase bat activity and probably help maintain prey availability (de Jong and Ahlén 1991; Michaelsen 2016c). Moreover, warmer summers accelerate gestation by reducing the time pregnant females spent in torpor (Rydell 1989a), allowing juveniles more time to develop and accumulate reserves before hibernation, potentially increasing overwinter survival. Winter migration to milder areas can reduce hibernation constraints, but not all bat species have evolved this behaviour, and long southward migrations are limited by hibernaculum availability and the energetic trade-off between migrating and staying resident (Lagerveld et al. 2024).

The low predictive value of the habitat variables in the combined habitat-climate GLMMs, relative to that of the climate variables, is a consequence of the numerous absences in areas where basic habitat conditions appear to be met but climate conditions are unsuitable. This pattern is consistent with the expectation that, at the scale of the Scandinavian Peninsula, climate exerts a stronger influence than habitat on species distributions.

However, the models still indicate that some habitat variables were ecologically relevant. Higher mean canopy height reflects older and more developed forest stands,

which benefit forest specialists such as *M. daubentonii* (Jung et al. 2012; Vlaschenko et al. 2022; Węgiel et al. 2019). Similarly, greater habitat diversity, previously shown to benefit several bat species in Scandinavia at smaller geographic scales (Ferreira et al. 2026), also appears relevant at larger scales, as suggested by the models for *N. noctula*. Elevation constrained species mostly restricted to the southern part of the peninsula, such as *N. noctula* and *Pipistrellus pygmaeus*, presumably because higher elevations are associated with lower temperatures. Increased slope may benefit some bats by creating shade from steep mountains during periods without dark nights. Such shaded areas may extend foraging time relative to flat landscapes (Michaelsen et al. 2011). This has not been reported for *N. noctula*, that seems to not benefit from increased slope.

Overall, these findings fit Scandinavia's biogeographic context: tree cover, water bodies, habitat diversity and vegetation-related structural elements used by bats extend well north of observed species ranges. Habitat therefore does not appear to limit northern-edge distributions, explaining its low model relevance or exclusion. Consistent with our first prediction, climate-only, habitat-only and habitat-climate models show that, at high latitudes, climate variables better predict species presence, supporting climate as the main driver shaping northern bat ranges. This pattern is also consistent with large-scale species distribution modelling more generally, in which climatic variables often provide the strongest descriptors of species' ranges (Pearson and Dawson 2003).

Species range maps from habitat-based models suggest that suitable habitat at higher latitudes remains unoccupied

Overall, the range maps predicted by the models that included climate predictors matched the occurrence data quite well and show that the four modelled species represent a gradient from ranges covering virtually all of the peninsula to those restricted to its southern part. In contrast, the maps based on habitat variables alone yielded predicted ranges that covered almost the entire study region and, in general, did not match the occurrences.

Most potential distribution maps classify high-elevation areas along the Scandinavian Mountains as unsuitable, despite our recording bats there. This is because our observations were made in valleys too narrow to appear at the map's scale, which are climatically and ecologically very different from the surrounding highlands. *C. nilssonii* was the only species both predicted and observed near the northernmost part of the Scandinavian Peninsula, consistent with records of breeding up to 69°N in Norway (Rydell et al. 1994; Speakman et al. 2000), as well as our own northernmost record at 69.2°N. Of the four studied species, it seems to be the least limited by the harsh climate of high latitudes, although occurrences declined with both mean minimum temperature of the coldest month and mean maximum temperature of the warmest month. This tolerance is due to multiple behavioural and physiological adaptations (Rydell 1989a; Michaelsen 2016b; Frafjord 2021b), including mechanisms that allow it to withstand very low ambient temperatures (Fjelldal et al. 2023; Sørås et al. 2023). Not surprisingly, *C. nilssonii* is the bat species that occurs furthest north in the world (Sørås et al. 2023).

The modelled maps also show *M. daubentonii* reaching very high latitudes, although not quite as far as *C. nilssonii*. This agrees with the literature (Siivonen and

Wermundsen 2008) and with our field records, which extend to 66.9°N. Prolonged and deep torpor bouts, described at high elevations, may facilitate the persistence of *M. daubentonii* at high latitudes (Nardone et al. 2015), However, its occurrence decreased with lower mean minimum and maximum temperatures, and the species has never been found breeding north of the Arctic Circle. This apparent limitation is possibly linked to energetic constraints in very harsh climate and may help explain why it does not extend as far north as *C. nilssonii*. *M. daubentonii* is known to make short regional migrations, typically 10–100 km, but occasionally up to 304 km (Encarnação and Becker 2023), which may account for individuals occurring north of the species' breeding range.

For *N. noctula*, the map generated by the habitat-only model indicates a range covering virtually all of Scandinavia, even though the species occurs only in the south, as correctly shown in the maps produced by our models that include climate variables. This strongly suggests that climate, rather than habitat availability, limits its northward expansion. *N. noctula* uses both open areas and forests, and its fast flight allows it to exploit fragmented or open forest landscapes (Mackie and Racey 2007). Structurally, the habitats dominating central and northern Scandinavia therefore appear suitable for the species, which explains its inflated predicted distribution visible on the habitat-only maps. The sensitivity of *N. noctula* to cold climates is supported by its long north-south migrations, with migratory pressure reportedly higher in northern populations (Lehnert et al. 2018). Scandinavian individuals are known to cross the Baltic Sea to hibernate in milder climates farther south (Rydell et al. 2014).

The situation revealed by the predicted maps for *P. pygmaeus* is similar to that of *N. noctula*; habitat-only maps show suitability much farther north than observed, whereas climate-based models generally match known occurrences. This is consistent with the presence of apparently suitable habitats throughout the peninsula that are not occupied due to climate constraints. The strong influence of temperature on the occurrence of *P. pygmaeus* near the northern edge of its range in Norway had already been demonstrated by Michaelsen et al. (2011), who suggested that day length may also be a limiting factor. At higher latitudes, increased energetic demands to remain active and support juvenile growth (Fjelldal et al. 2023), likely explain why climate, especially summer temperature, limits its range despite apparent habitat availability. As in the case of *N. noctula*, the apparent occurrence of north-south migrations to spend the winter in milder climates across the Baltic (Rydell et al. 2014) also underlines the sensitivity of the species to low temperatures, although hibernation also occurs in southern Scandinavia (Frafjord 2021a).

The better match of the range maps generated by climate-only and habitat-climate models with the field observations and published ranges (de Jong et al. 2020; Mitchell-Jones et al. 2026; Russo 2023) points to climate as a key factor shaping the species' northern limits. As expected, this aligns with the results of the GLMMs. The broader suitability predicted by habitat-only models at higher latitudes suggests that appropriate habitat may extend beyond the observed range, but that its availability alone is insufficient to explain the species' occurrences. This contrast supports the interpretation that climatic constraints, rather than a lack of suitable habitat, are likely limiting northward species expansion, as hypothesized in the introduction.

Ordination spaces indicate climate, rather than habitat, as the dominant range constraint at high latitudes

We predicted that each species would occupy the full extent of the available habitat-space but only a fraction of the available climate-space. The ordinations support this prediction: the realised Scandinavian distributions of the four focal species are constrained mainly by climate rather than by habitat availability. Suitable structural habitat occurs within and beyond current ranges, but species are absent from many areas where habitat appears suitable but climate is unfavourable. This is clearest for *N. noctula* and *P. pygmaeus*, which occupy only a restricted portion of the available climatic space, while habitat-space shows suitable conditions extending well beyond their realised ranges. This is consistent with climate-based maps yielding more restricted predictions than habitat-only models. *M. daubentonii* has one of the broadest Scandinavian distributions, but declines in the coldest areas, mirroring the climate ordination, in which presences become sparser at lower temperatures, corroborating that climatically extreme areas still constrain its range. *C. nilssonii* has the broadest climatic and habitat niche, reaches furthest north, and occupies the widest portion of both ordination spaces, persisting under colder conditions. This aligns with the extensive range predicted by the climate-only and habitat-climate models. The scarcity of presences at the rightmost extreme of the climate ordination matches the low occurrence probability shown in those maps.

Overall, the ordinations support the map-based patterns: these species occupy most of the available habitat space, but only part of the climate-space across Scandinavia, although *C. nilssonii* occupies nearly the full climate-space.

Potential roles of night duration, prey, roosts, and habitat integrity

The predictive models used in this study to identify factors influencing bat occurrence include only climate variables and relatively broad structural habitat variables. However, several parameters that may influence occurrence could not be incorporated in the modelling, either because they were strongly correlated with other predictors – as in the case of summer night duration, which depends on latitude and is therefore highly correlated with temperature – or because spatially explicit data were not available (prey availability, roost availability, and habitat integrity). Their potential roles are discussed in this section.

Summer night length decreases markedly from southern to northern Scandinavia. At higher latitudes, shorter and brighter summer nights may influence bats independently of habitat and climate, by increasing predation risk, decreasing or increasing insect availability, and reducing foraging time, especially in light-sensitive species (Rydell 1992; Michaelsen 2016b). In the most extreme situations, species occurring furthest north must forage under the midnight sun, when they must tolerate light levels two to four times brighter than further south (Frafjord 2021b). Because both night length and temperature vary strongly with latitude, their effects on bat occurrence are difficult to separate. Nevertheless, the univariate plots relating temperature to probability of occurrence provide useful evidence. For all species, occurrence probability declined substantially with decreasing temperature and became virtually zero at the coldest sites, even within the latitudinal range occupied by the species. This was especially clear for *N. noctula* and *P. pygmaeus*, whose ranges are restricted to southern Scandinavia. This suggests that, at least in the case of these

species, and of the many other species that do not occur at the highest latitudes, their lower thermal limits are encountered well before reaching the latitudes where summer nights are short. In other words, they are absent not only from northern regions with short summer nights, but also from colder southern uplands and interior areas, despite relatively longer nights. This pattern indicates that low temperatures are likely a stronger constraint on their Scandinavian distributions than summer night length. This is further supported by the presence of several species at higher latitudes—and thus under shorter summer nights—along the warmer peninsula coastal regions than in the colder interior, though robust distributional data for Scandinavian bats remain scarce. Some species appear able to cope, at least partly, with the limitations imposed by short nights through behavioural adjustments, such as shifting the timing of foraging or by hunting in areas shaded by topography or trees (Frafjord 2021b; Lilley et al. 2026; Michaelsen 2016b). However, very short summer nights may still play a relevant role in limiting ranges, especially because they are likely to compound the challenges imposed by lower temperatures. The shortest nights do not coincide with the warmest part of the summer, as the highest temperatures often occur in August, when nights have already started to lengthen. Therefore, bats face substantial challenges during the breeding season in June and July — when nights are shortest and weather conditions might be unfavourable — while simultaneously raising their young.

Insect prey availability could also be a relevant factor constraining the occurrence of bat species beyond their current northern distribution limits. Studies conducted at different latitudes in Scandinavia and Finland show that, in regions dominated by boreal forest, some insect groups are abundant during the bat active season, although different groups peak at different times and in different habitats, forcing bats to track energetically profitable feeding opportunities (de Jong and Ahlén 1991; Vasko et al. 2020). Prey availability is clearly a key determinant of spatial and temporal variation in the foraging activity of several bat species in this region (de Jong and Ahlén 1991). However, this local-scale importance does not imply that prey availability prevents species from occurring north of their current ranges. Most bat species occurring in Scandinavia seem to have the plasticity to adjust foraging behaviour to the variable spatial and temporal nature of prey availability (Kotila et al. 2023; Vasko et al. 2020). Moreover, the main insect groups in their diets broadly overlap, despite interspecific dietary variation (Vesterinen et al. 2018). Therefore, it is plausible that some species could sustain themselves north of their present distributions, but do not occur there due to climatic constraints. However, a species-by-species comparison between diet composition and prey availability at different latitudes would be needed to further validate this hypothesis.

Suitable roosts are an essential component of bat habitat, and their availability could in principle help explain the absence of *P. pygmaeus* and *N. noctula* from northern regions. However, *P. pygmaeus* is an adaptable species that roosts mainly in buildings, which occur throughout the Scandinavian Peninsula. Indeed, *C. nilssonii*, one of the species most dependent on buildings for roosting (Frafjord 2013; Rydell 1989b), is the commonest bat in the boreal regions of Scandinavia (de Jong et al. 2020; Rydell 1992). This suggests that the availability of building roosts is unlikely to be a critical factor limiting the northern distribution of bats. *N. noctula* is known to roost mainly in tree cavities, preferring those excavated by nesting woodpeckers (Boonman 2000). In

northern Sweden, Andersson et al. (2018) found that woodpecker excavation was by far the most important source of cavities in both natural and managed forests. Moreover, the two most important cavity excavators in boreal Scandinavia, the great spotted woodpecker *Dendrocopos major* and the black woodpecker *Dryocopus martius* (Angelstam and Mikusiński 1994), breed up to the northernmost forests, and the cavities they excavate are widely used by *N. noctula* (Boonman 2000). Therefore, suitable cavities are necessarily available, and cavity availability is unlikely to explain the complete absence of *N. noctula* from central and northern Scandinavia. These considerations likely apply to all bat species in Scandinavia, as they rely mainly on roosts in buildings, tree cavities, or both, with some species also occupying rock crevices (Michaelsen et al. 2013). Although the availability of these roost types varies across the peninsula and such variation may affect local bat species abundances, the evidence discussed above indicates that roost availability is unlikely to explain their complete absence from central and northern Scandinavia.

Most bat species in Scandinavia are, to some extent, dependent on forests, so their scarcity or low quality is another candidate explanation for the absence of most species from central and northern regions. Indeed, much of the peninsula is now dominated by industrial forests, which generally provide lower-quality habitat for bats than natural forests (Russo et al. 2016). However, unlike southern Scandinavia, the north still contains vast expanses of natural and biodiversity-rich forest, especially along the foothills on the eastern side of the Scandinavian Mountain Range (Svensson et al. 2020). Still *N. noctula* and *P. pygmaeus*, as well as most other Scandinavian bats, do not occupy these forests. This suggests that climatic factors, rather than a lack of suitable habitat, are preventing bats from colonizing the northern regions, although a potential role of subtle habitat-related factors, not included in our analysis, cannot be excluded.

Although none of the factors discussed in this section contradict the hypothesis that low temperatures are the main barrier preventing Scandinavian bats from colonizing northern regions, they may still play a role. The situation of each factor is distinct, but because all of them can be linked to temperature, and some may interact with it, it is not possible to clearly untangle their relative effects.

Conclusions

By combining species distribution modelling with extensive field data from Scandinavia our results show that climate, rather than habitat availability, primarily determines the northern distribution limits of the studied European bats. Climatic variables predicted occurrence better than habitat variables, and climate-based models matched observed northern limits more closely than habitat-only models, which identified suitable areas far north of current ranges. Ordinations further showed that bats occupied most of the available habitat space but only a restricted portion of the climate space. Together, these results demonstrate that suitable broad-scale habitat exists beyond the realised distributions of several species, and that thermal constraints are the main limitation to northward expansion of bat species in Scandinavia. However, unmodelled factors, particularly prey availability and night length, may also contribute and interact with climate.

The importance of temperature-related variables is consistent with the idea that high-latitude occurrence depends on the capacity of species to maintain a positive energy balance for survival and reproduction under cold conditions that act through multiple mechanisms. Although winter and summer temperatures covary geographically and cannot be fully disentangled here, the thermal environment emerged as the dominant correlate of northern range limits.

Short and bright summer nights also challenge northern bats, but they do not alone explain range limits, as species were absent not only from northern areas with short nights, but also from colder high-elevation areas farther south where nights are longer. This supports the interpretation that low temperature is the stronger broad-scale constraint, although night length may interact with thermal conditions and influence how far some species can persist northwards.

Our main conclusion is likely to apply to most Scandinavian bats, all of which are vespertilionids, although species-specific exceptions may occur. The four studied species belong to distinct genera that span major evolutionary lineages within Vespertilionidae, yet showed similar responses, suggesting a general pattern. This also matches macrogeographical range-limit theory, which predicts that climate should dominate over habitat constraints at cold northern range edges.

Overall, our study supports the view that the northern distribution limits of European bats are primarily thermally constrained rather than habitat-limited. Continued warming is therefore likely to relax these constraints and allow some species to expand northwards, consistent with observed range shifts (Kravchenko et al. 2025; Lundy et al. 2010). However, for *C. nilssonii*, the only species occurring almost to the northernmost limit of Scandinavia, warming may increase competition from southern species. Because warming is particularly pronounced at high latitudes, monitoring bat distributions at their northern margins provides a sensitive indicator of climate-driven biogeographical change.

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Statements and declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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