

Anthropogenic impacts drive habitat suitability in South Asian bats

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Srinivasulu, A., Senapathi, D. ORCID: <https://orcid.org/0000-0002-8883-1583> and Gonzalez-Suarez, M. ORCID: <https://orcid.org/0000-0001-5069-8900> (2024) Anthropogenic impacts drive habitat suitability in South Asian bats. *Biodiversity and Conservation*, 33. pp. 4099-4120. ISSN 1572-9710 doi: 10.1007/s10531-024-02941-7 Available at <https://centaur.reading.ac.uk/118961/>

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To link to this article DOI: <http://dx.doi.org/10.1007/s10531-024-02941-7>

Publisher: Springer

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Anthropogenic impacts drive habitat suitability in South Asian bats

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Received: 10 January 2024 / Revised: 9 July 2024 / Accepted: 14 September 2024
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Abstract

Despite their diversity and importance as ecological indicators and ecosystem service providers, the macroecology of bats in South Asia is poorly understood, and until recently studies on the ecological niches of these species have been rare. This study analyses the ecogeographic predictors of habitat suitability in South Asian bats by conducting ensemble ecological niche modelling using four algorithms (random forests, artificial neural networks, multivariate adaptive regression splines, and maximum entropy) to define suitability envelopes for 48 selected bat species, based on topographic, hydrographic, land-use, land-cover, and other anthropogenic impact factors. Anthropogenic impact variables showed high importance with Median Night-time Light being the biggest driver of habitat suitability for most of the study species with generally lower suitability of brighter areas. Projected suitable areas for individual species covered between 6.28% and 22.98% of the study area. Regions such as the Thar desert of northwestern India were consistently identified to have low suitability. The Western Ghats in India, the Himalayas in Bhutan, northern India, and Nepal, and Sri Lanka were identified as suitability hotspots for more than half the studied species overlapping with human-impacted habitats. This study offers insight into the impacts of anthropogenic pressure on the macroecology of bats in a megadiverse region and stresses the importance of analysing ecogeographic effects on ecological niches and habitat suitability, which can be vital to inform conservation planning and policymaking in the future.

Keywords Ecological niche modelling · Species distribution modelling · Habitat selection · Ecogeographic factors · Ensemble modelling · Human impacts

Introduction

South Asia is host to 151 species of bats across nine families (Srinivasulu et al. 2023), yet there is very little information known about their distribution and ecology in this region (Bates and Harrison 1997). Despite their high diversity and importance as ecological indicators and ecosystem service providers (Jones et al. 2009; Kunz et al. 2011; Altringham

Communicated by Daniel Hending.

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et al. 2011), bats are relatively underrepresented in macroecological studies, especially in Asia (*but see* Srinivasulu et al. 2024). Subject to persecution and superstitions across many regions of Asia (Frembgen 2006), they are also given very little conservation value, an issue further complicated after the recent COVID-19 pandemic (MacFarlane and Rocha 2020).

A recent trend in ecology has been the study of abiotic and biotic factors on occurrence and distribution patterns across various scales, ranging from small communities to global populations (Leach et al. 2016; Lewis et al. 2017; Lopez et al. 2019). Most studies tend to focus on climate change as a major factor of species distributions (Araújo et al. 2019; Srinivasulu et al. 2021). However, analyses of biotic [including vegetation, land use and land cover (LULC)], topographic (elevation and hydrology), and anthropogenic factors are also vital to understanding distributions and ecological niches (Hughes et al. 2012). Due to effects of both climate-based and ecological cues (Bates and Harrison 1997) on bat behaviour, ecology, and habitat ‘selection’ and suitability, analyses must consider the influence of both to understand bat distributions and niches. Additionally, a deeper understanding of the specific impacts of ecogeographical factors on habitats and species can better inform local management and guide species- and site-specific conservation planning and policy.

In South Asia, bats are distributed across a wide range of habitats from forests to urban and suburban areas and previous work has offered insight into factors that affect habitat suitability for regions or groups. Wordley et al. (2015) analysed the association of bats with agricultural areas and riparian habitats in the Western Ghats, showing that structural diversity within agricultural habitats improves bat abundance and richness. Other studies have also shown that bat distribution in urban and suburban areas is affected by factors like artificial night-time light and distance from the nearest waterbody (Lewanzik et al. 2022), but the level of association with urban and suburban regions varies between species with some bats more likely to be distributed in ‘wilder’ areas (Gili et al. 2020). Forest bats have been found to depend on vegetation structure, and bats in arid and scrubland habitats are influenced by distance to wetlands and riparian vegetation (Razgour et al. 2018). While past studies show that bat distributions can be influenced by ecogeographical factors, there has been no large scale assessment to identify broader drivers and patterns of habitat suitability in South Asian bats.

Ecological niche modelling (ENM) is a method that analyses the known distribution of a species and measured conditions describing climate, geography, and ecology to extrapolate an envelope of spatial suitability approximating the species’ niche and quantify the importance of the different conditions in shaping that niche (Guisan & Thuiller 2005; Araújo and Guisan et al. 2006; Soberón & Arroyo-Peña, 2017). Importantly, ENM can be used to gain knowledge of cryptic, rare, or otherwise difficult to study species because these approaches can identify potential suitable habitat (which may guide monitoring efforts), as well as revealing the set of environmental conditions that influences potential presence (Rebello & Jones 2010; Jeliaskov et al., 2022). Diverse types of environmental conditions can be considered, but often ENM studies focus on climate variables to project species’ current and future distributions and quantify potential climate change impacts (Guisan & Thuiller 2005). Some models do analyse ‘biotic’ ecogeographical factors, including biotic interactions and human activities, and these can offer critical insights and inform conservation planning and policy (Leach et al. 2016; Cosentino et al. 2023). For example, Hughes et al. (2012) conducted an ENM study combining abiotic climate and biotic ecogeographic variables that projected northward shifts in Southeast Asian bats. Combining multiple abiotic and biotic factors can create challenging model complexity, but separate models can be defined with the predicted climatic and ecogeographical suitability areas then compared

and combined to provide a more comprehensive approximation of a species' niche (Johnson et al. 2019). Additionally, there are many ENM algorithms available which can offer distinct results; thus, it is advisable to use various algorithms that are then aggregated into ensemble models for offer better performance and a clearer understanding of model reliability through a combination of goodness-of-fit metrics and inter-algorithm agreement (Thuiller et al. 2009). Ensemble ENMs can be highly reliable and interpretable even with presence-only data if robust approaches for generating pseudoabsences (Barbet-Massin et al. 2012) and standardised protocols for parameterisation (Feng et al. 2019) are applied.

In this study, we assess habitat suitability in South Asian bats using occurrence records and focusing on ecogeographic factors including land use and land cover, topography, hydrology, and anthropogenic impact variables. We generate ensemble ENMs incorporating multiple replicates of pseudo-absence datasets. Results identify the most important ecogeographic factors and present species habitat suitability maps we use to identify suitability hotspots. We then compare these hotspots with climatically suitable areas defined in a previous study (Srinivasulu et al. 2024) to offer a comprehensive understanding of suitability in the region. The results of this study form a foundation for site- and species-specific bat conservation prioritisation and planning.

Methods

Study area

Our South Asia study area covered approximately 3.75 million sq km, encompassing Afghanistan, Bangladesh, Bhutan, India, the Maldives, Nepal, Pakistan, and Sri Lanka (Fig. 1). Due to the barrier formed by the Himalayas (Gayden et al. 2013; Thapa et al. 2021), trans-Himalayan regions of China that fell under the study extent were excluded. Additionally, due to the isolation and distance between the Nicobar Islands (the most southeastern territory of India) and north Sumatra, Indonesia was also removed from the study extent.

Data collection and preparation

There are 151 bat species found in South Asia, belonging to nine families (Emballonuridae, Hipposideridae, Megadermatidae, Miniopteridae, Molossidae, Pteropodidae, Rhinolophidae, Rhinopomatidae, and Vespertilionidae; Srinivasulu et al. 2023). We limited our analysis to species not endemic to the Andaman and Nicobar Islands, and with more than 30 occurrence records confirmed since 1995. These thresholds were set to ensure temporal consistency with the modelling variables and sufficient occurrence data for robust modelling. Our final dataset included 48 species representing all nine families. Confirmed presence records were collected from various sources (*see* Srinivasulu et al. 2024) including peer-reviewed publications (Bates & Harrison 1997; Srinivasulu & Srinivasulu 2012; Srinivasulu et al. 2021; Raman et al. 2023; Srinivasulu et al. 2024) and museum collections from the Natural History Museum (UK), Harrison Institute (UK), Field Museum of Natural History (USA), Zoological Survey of India (India), and Osmania University Natural History Museum (India). Unpublished records from surveys conducted by the authors from 2002 to 2023, and personal communications from local experts confirmed by photographic or other evidence were also used

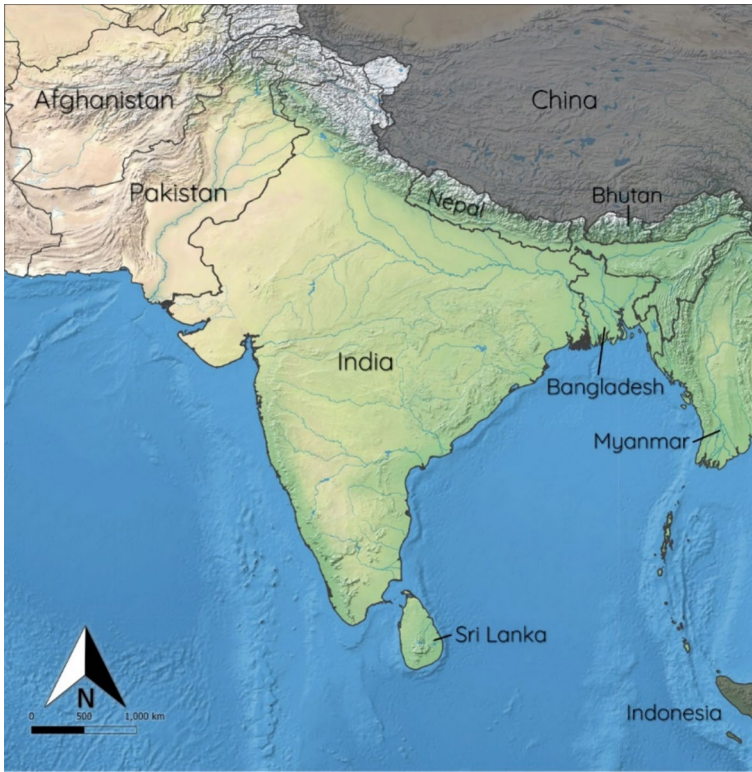


Fig. 1 Map of the study area, with excluded regions indicated in grey

to define occurrence. Records that were published before 1995 and subsequently confirmed through field visit or local experts after 1995 were also included with the original publication as the source.

These occurrence records were spatially rarefied to avoid spatial sampling bias and autocorrelation (Feng et al. 2019) using the *spThin* package (Aiello-Lammens et al. 2015) in R 4.3.1 (R Core Team 2023). Spatial rarefaction was done to 2.5 arc-minutes to match the resolution of the climate data, and duplicate records within the same 2.5 arc-minute grid cell were randomly removed. After data cleaning, a total of 5085 occurrences for a final set of 48 species in nine families were used for the subsequent analysis. The number of occurrences per species ranged from 30 occurrences for *Murina cyclotis* and *Pipistrellus kuhlii* to 439 occurrences for *Pteropus medius* (Supplementary Material 1, 2).

Various ecogeographic factors may influence habitat suitability in bats, including land use and land cover (LULC), hydrography, and topography (Rebelo et al. 2010; Hughes et al. 2012; Raman et al. 2023; Tuan et al. 2023), but current and accurate data for South Asia are only available for a limited subset. We selected an initial set of 21 ecogeographical variables (EGVs) based on various ecological hypotheses (See Table 1 in Appendix). All variables were analysed at 2.5 arc-minute resolution to assess spatial patterns on a moderately-fine resolution (approximately 5×5 km). Variables with

different resolutions were resampled to 2.5 arc-minutes using the *terra* package (Hijmans 2023) in R; all variables were cropped and masked to our study area.

While modern ENM algorithms can account for (or are not greatly impacted by) issues caused by multicollinearity in variables, the initial set of variables was reduced to allow for accurate model transfer and clarity of interpretation. The EGVs were filtered based on a combined test of variance inflation (VIF) and correlation in the *usdm* package (Naimi et al. 2014) in R, such that variables with absolute pairwise Pearson's $r \leq 0.7$ were selected. When the correlation was higher than 0.7, the variable with the highest VIF was removed to decrease the overall variance inflation in the analysis. A final set of 19 EGVs was selected for the analysis (See Table 1 in Appendix).

Pseudoabsence data, a prerequisite for presence-only ecological niche modelling (Feng et al. 2019), were generated for the analysis broadly following Barbet-Massin et al. (2012). For each species, a minimum of 1000 pseudoabsences were generated; to balance the number of occurrences and pseudoabsences for the species with fewer occurrences, multiple pseudoabsence replicate sets were created, each with the same number of pseudoabsences as selected occurrences for the species. The number of replicate sets was calculated by dividing 1000 by the number of occurrences and rounding up to the nearest whole number. Replicate sets ranged from 3 for *Pteropus medius* (439 occurrences) to 34 for *Pipistrellus kuhlii* (30 occurrences). This allowed a minimum of 1000 pseudoabsences for each species and incorporated a measure of intra-species uncertainty through resampling for the species with fewer localities (Supplementary Material 2).

Ensemble ecological niche modelling

Ensemble ecological niche models were created for each species using *biomod2* (Thuiller et al. 2023), an R package that implements the BIOMOD (Thuiller et al. 2009) niche modelling framework. The ensemble models included four algorithms known to be robust at large distribution scales (Meller et al. 2014): multivariate adaptive regression splines (MARS), artificial neural networks (ANN), random forests (RF), and maximum entropy (MAXENT). Five-fold cross-validation was used to validate the models, and model performance was assessed using area under receiver operating character (ROC) curve (AUC), and true skill statistic (TSS). To estimate the importance of each EGV to ecogeographic suitability, we averaged variable contribution, estimated as the difference in model performance (AUC) after removal of the variable, over five permutations. Variable importance was also described based on a ranking of mean permutation importance for each variable in each species.

For each species a consensus model was created by averaging all individual models with $TSS > 0.5$. Predictions from ensemble models for each species were reclassified into binary output to define ecogeographically suitable and unsuitable areas using a maximum TSS threshold. Binary hotspot maps of ecogeographic suitability were created by adding binary predictions of all species to reflect the number of species for which each cell was ecogeographically suitable (cell values could range from 0 to 48). Hotspots were then defined exploring three thresholds that reflected suitability for at least 25% (suitable for ≥ 12 species), 50% (suitable for ≥ 24 species), and 75% (suitable for ≥ 36 species) of the 48 study species. Model uncertainty was reported considering model agreement across individual replicates within a species, and then averaging across species so that low values represent

highly certain unsuitability, high values represent highly certain suitability, and values in between represented uncertainty.

Post-hoc analyses

To understand potential impacts and conservation challenges in detected areas of suitability, we described the land use and land cover (LULC) variables using six main types: Forests (including needleleaf, evergreen broadleaf, deciduous broadleaf, and mixed trees), Scrubland (including shrub and herbaceous vegetation), Anthropogenic regions (including cultivated vegetation, and urban and suburban and suburban and suburban areas), Wetlands (including open water and flooded vegetation), and Barren regions (including barren rock, and snow and ice). Anthropogenic impacts were described using the respective means of the Human Footprint Index and Median Night-time Light variables. The values of each variable type for all the cells of species binary models and the suitability hotspot models were then averaged. In the case of the LULC variables, this showed the average representation of each LULC type in suitable areas (represented as % of the suitable areas covered by a particular LULC type). For the anthropogenic impact variables, this showed averages of human footprint and night-time light in suitable areas. Finally, we mapped the overlap and discrepancies between ecogeographically suitable area models and previously identified climatically suitable areas (Srinivasulu et al. 2024).

Results

Ecogeographic variables

Variables that best described suitability varied across species, but overall, variables associated with Anthropogenic Impact had high importance. Amongst these, *Median Night-time Light* had the highest average variable contribution values (mean \pm SD across all species: $29.03\% \pm 15.48\%$, min–max: 4.45%–52.8%; Fig. 2; Supplementary Material 2) and was the top variable for 30 of the 48 study species, across all nine families. All species had potential suitable areas in ‘dark’ regions, with *Median Night-time Light* values ranging from 0.87 to 10.77 DN (digital number units; see Table 1 in Appendix), with high inter-cell variability across their potential suitable area. The Common Pipistrelle *Pipistrellus pipistrellus* and Naked-rumped Tomb bat *Taphozous nudiventris* were the only species for which *Median Night-time Light* averaged > 10 DN. Within these dark regions, for 40 species relatively brighter areas (average cell values for *Night-time Light* > 5 DN) were projected to be suitable. For 8 species, suitability was associated with relatively darker areas (average cell values for *Median Night-time Light* < 5 DN). The average *Median Night-time Light* across South Asia is 2.75 ± 5.95 DN, and human-inhabited areas across the region had *Median Night-time Light* values above 20 DN, with the brightest cells in the study area (63 DN) seen in large cities in India including Bengaluru, Hyderabad, Kolkata, Mumbai, and New Delhi, and in Karachi, Pakistan.

Similarly, *Human Footprint Index* was among the top variables for several species (ranking second and third in contribution for 12 and 7 species respectively). For 33 species areas with relatively higher human footprint (> 15 units) were more likely to be occupied, whereas for 15 species suitability was associated with lower human footprint values (< 15 units). *Relative elevation*, which describes topography relative to the mean elevation of

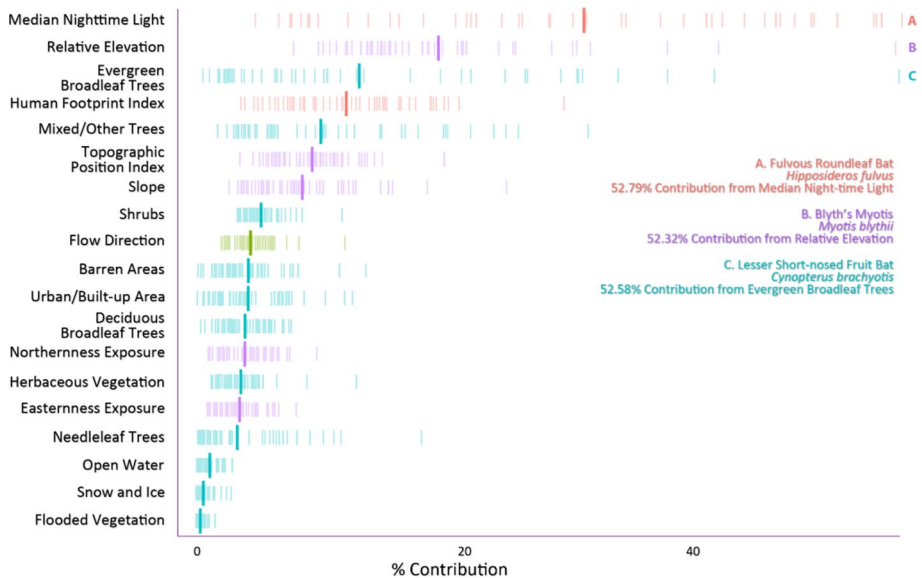


Fig. 2 Percentage importance of each variable included in the analysis. Each line represents the percentage contribution of each variable for one species. Thicker lines represent the mean percentage contribution of that variable across all species. Variable colours correspond to the group (red—Anthropogenic Impact, purple—topography, blue—LULC, green—hydrography)

South Asia, was one of the most important non-anthropogenic variables, being the top variable for eight species, and the second and third top variable for 17 and 19 species respectively. For 35 species, areas lower than 900 m asl were projected to be suitable, whereas for 13 species areas higher than 900 m asl had projected suitability.

Across all species, an average of 13.40% (SD=4.82%) of the study area was ecogeographically suitable, ranging from 6.28% in the Least Horseshoe bat *Rhinolophus pusillus* to 22.98% in Dormer's Pipistrelle *Scotozous dormeri*. Ecogeographically suitable areas were identified in diverse sites across the study area, in various combinations of four patterns: generally distributed suitable areas, suitable areas clustering mainly in the Western Ghats and/or the northeast of the study region, suitable areas clustering mainly in the Himalayas, generally distributed suitable areas with clusters also in northwest South Asia (Fig. 3). The pattern of suitable areas in some species matched the distribution of occurrence records (Supplementary Material 1, 3), but this varied greatly among species. There were consistently large areas of low suitability seen in the Thar desert of Rajasthan (in northwest India), although for some species there were small suitable areas in this region (Supplementary Material 3). Some species, along with a general distribution of small suitability across the region, showed large contiguous projected suitable areas in certain regions. For example, Kelaart's Pipistrelle *Pipistrellus ceylonicus*, a widely distributed species commonly found near human-inhabited areas, had a generally distributed pattern of suitability with more suitable areas in the Western Ghats and Nilgiri Hills of south India, the tropical regions of Sri Lanka (Central, Southern, Western, and Sabaragamuwa provinces), and the river valleys of northern India and Pakistan (ranging from Delhi to the northern Indus River valley). Similarly, the Lesser False Vampire bat *Megaderma spasma* showed a general distribution of predicted suitability combined with high-density areas of

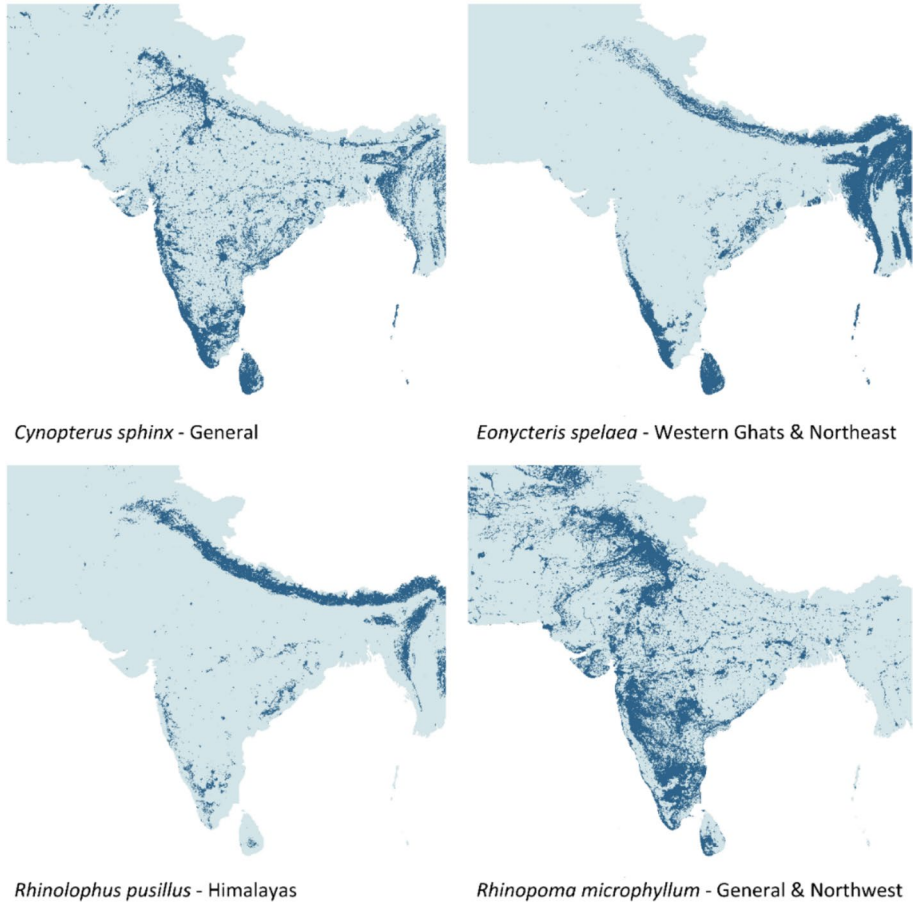


Fig. 3 Example from four species that represent the four main patterns of suitability found across species

suitability in the Western Ghats and Sri Lanka, the Andaman and Nicobar Islands, north-east India, and northern Myanmar. The Greater Mouse-tailed bat *Rhinopoma microphyllum*, a species found from northern and western Africa to northeastern India and Bangladesh, was the only species which had predicted suitability in the northwest of the study area, with regions of Afghanistan shown to be suitable in addition to northern India and Pakistan, and the Deccan Plateau (Supplementary Material 3).

Suitability hotspots

Based on the explored thresholds of ≥ 12 , ≥ 24 , and ≥ 36 species, hotspots of ecogeographic suitability occupied 21.28%, 7.07%, and 1.04% of the study area respectively. Hotspots were identified in various locations across the study area, but generally in urban and suburban areas and along linear features like roads, rivers, and hill ranges (Fig. 4). There was no area suitable for all 48 studied species.

Hotspots of suitability (for ≥ 12 species) were located across the study area, but distribution was not uniform (Fig. 4). The Western Ghats and the Nilgiris, the central and

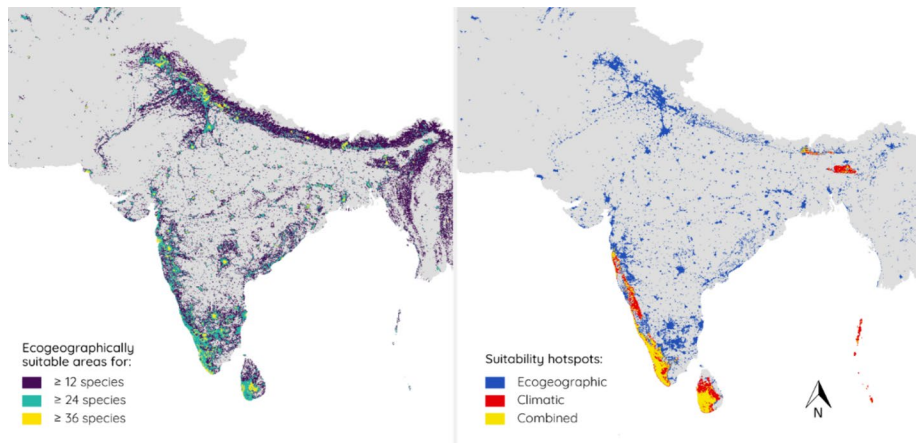


Fig. 4 Map of ecogeographically suitable hotspot areas based on three thresholds (areas identified as suitable for ≥ 12 , ≥ 24 , and ≥ 36 species); and comparative map of ecogeographic and climate suitability hotspots (for ≥ 24 species) highlighting the relatively few areas of combined ecogeographic and climatic suitability

southwestern provinces of Sri Lanka, the Himalayas extending from northern Pakistan to northeastern India, and the Andaman and Nicobar Islands showed large amounts of suitability hotspots, while there were fewer suitable areas in the Thar desert and northwest South Asia. Central India and the plains of northern India comprised fragmented areas of suitability centred most often around cities and towns, but with a contiguous area of suitability from Jaipur, through Delhi, to Jammu, through northern Pakistan, continuing southward following the Indus River valley (Fig. 4). Similar areas were identified when defining hotspots based on the threshold for ≥ 24 species, although contiguous patches of hotspot areas became less frequent in the Himalayas. For ≥ 36 species, only small patches of suitable area were seen across the study area, often corresponding to large cities and towns. The only relatively large contiguous patches were seen in the mountainous regions of northern India and Pakistan, the central highlands of Sri Lanka, and the southern Western Ghats and Malabar coast (Fig. 4; Supplementary Material 3).

The Urban and Built-up areas LULC class covered on average approximately half of each cell in suitability hotspots (mean and SD percentage of each cell covered: $50.04\% \pm 44.76\%$ for hotspots with ≥ 12 species, $50.18\% \pm 45.08\%$ for ≥ 24 species, $50.68\% \pm 46.74\%$ for ≥ 36 species). This exceeds the per-cell average percentage cover of anthropogenic areas across the study area ($25.34\% \pm 35.06\%$) indicating that regions of potential suitability for multiple species are more often found associated with anthropogenic features than expected. However, the per-cell cover of anthropogenic habitats were relatively low within each family, ranging from $1.39\% \pm 1\%$ for Rhinolophidae to $9.61\% \pm 2.15\%$ for Rhinopomatidae. Barren areas were the second most common LULC type in suitability areas ($19.09\% \pm 33.19\%$ for ≥ 12 species, $17.24\% \pm 32.03\%$ for ≥ 24 species, $16.73\% \pm 31.68\%$ for ≥ 36 species), also exceeding the average barren land cover across the study area ($9.51\% \pm 7.14\%$). The association to barren areas may capture roosting areas, as many of the study species roost in rocky caves, crevices, and subterranean features (Bates and Harrison 1997). Suitability hotspots representing more species (> 36 species) were often seen around human habitation (Fig. 4) but also within ‘wilder’ areas like the southern Western Ghats, capturing a wide relationship with human-impacted areas in most species, with preferences for different

types of more natural areas varying more widely (and thus, less likely to show consistently as suitable in hotspots for many species).

When considering suitability hotspots for at least half the study species (≥ 24 species) we found that only 1.17% of the study area was projected to be both ecogeographically and climatically suitable (2.19% for only climatically suitable area, *see* Srinivasulu et al. (2024); and 7.07% for only ecogeographically suitable area, Fig. 4). Based on future climatic suitability projections averaged across two global climate models (Canadian Earth System Model v5 and Hadley Centre Global Environment Model v3), 0.98% and 0.82% of the study area is expected to be ecogeographically and climatically suitable in 2050 according to the SSP2-RCP4.5 and SSP5-RCP8.5 socioeconomic pathways respectively. This represents a reduction in the suitable area under future climate conditions.

Model evaluation

Model performance varied across species, and all four algorithms were used in the final ensemble for each species. RF had the highest validation scores on average (mean \pm SD) across all species (TSS: 0.984 ± 0.017 ; AUC: 0.999 ± 0.002), followed by MAXENT (TSS: 0.811 ± 0.108 ; AUC: 0.908 ± 0.050), MARS (TSS: 0.804 ± 0.120 ; AUC: 0.943 ± 0.045), and ANN (TSS: 0.738 ± 0.190 ; AUC: 0.896 ± 0.094). Regions of high certainty of suitability were seen around urban areas including towns and cities, and small highly certain areas were seen along major road features, indicating the importance of linear features in habitat suitability across bats. Additionally, a large proportion of the cells in the Indian state of Kerala, the Central, Western, Sabaragamuwa, and Southern provinces of Sri Lanka, and the northern Himalayas extending from Afghanistan to India were found highly certain to be suitable. Regions of highly certain unsuitability were restricted to the Thar and arid regions of Pakistan and Afghanistan, and smaller areas in various Indian states in the Gangetic plain. Uncertainty of suitability was recovered across the study region, but mostly in the Himalayas, the Western Ghats, the northern Eastern Ghats, northeast India, and the surrounding regions of major metropolitan cities (Supplementary Material 4).

Discussion

Our study identifies Median Night-time Light as the ecogeographical factor with the highest importance to map habitat suitability in South Asian bats. Artificial night-time light is prevalent across many regions in South Asia due to the high human population in the region, increasing in brightness steadily with higher rates of urban and suburban expansion and growth (Kaushik et al. 2022). Night-time light impacts bat flight, behaviour, foraging, and roosting in varied but largely adverse ways (Stone et al. 2015; Spoelstra et al. 2017), yet to our knowledge, no study has been conducted in South Asia to specifically quantify the effects of night-time light on bat movement, feeding, and roosting. While generally important, it is noteworthy that the importance of night-time light varied among species. Species with differing ecologies and behaviours are likely to be impacted by light levels differently. Some bats are quite sensitive to light disturbance. For example, Median Night-time Light was a the most important variable for the fulvous roundleaf bat *Hipposideros fulvus* (variable contribution 52.80%), a species generally found in relatively darker areas

(Median Night-time Light across its projected suitable area is 0.87 ± 3.89 DV). Cooler lighting with white and green components have been shown to cause significant decreases in the abundance of species like *Rhinolophus* (horseshoe bats), and *Myotis* (mouse-eared bats; Spoelstra et al. 2017), which are not usually found in or near human habitation. However, other bats like Pteropodids are more synanthropic and from our analyses appear to commonly occur in areas with high night-time light values. For example, Median Night-time Light was a very important variable for Kelaart's pipistrelle *Pipistrellus ceylonicus* (51.32%) and the naked-rumped tomb bat *Taphozous nudiventris* (47.97%), and in contrast with *Hipposideros fulvus* both species were projected to occur in relatively lighter environments (Median Night-time Light in projected suitable areas 7.07 ± 10.03 DV, and 10.49 ± 9.98 DV respectively. For comparison human-inhabited areas in the region had values > 20 DN). These species may be more resilient to anthropogenic changes (able to cope with some artificial night-time light) and some may even benefit—some urban insectivore species are known to use streetlights in urban and suburban areas as feeding grounds (Hermans et al. 2024). Variation can also occur within groups of related species. Bats from families generally considered to be light-sensitive, like Pteropodidae which primarily use sight and smell rather than echolocation for navigation (Bates and Harrison 1997), can be associated with urban areas—e.g., greater short-nosed fruit bat *Cynopterus sphinx* is commonly found in city suburbs due to its association with fruiting trees (Bates and Harrison 1997), and Indian flying fox *Pteropus medius* has been observed in large colonies in various cities and towns (Pandian and Suresh 2021; Roy et al. 2024). Even for species that can tolerate higher levels of artificial night light, it is important to carefully consider lighting practices to ensure natural communities and ecosystem services are not disrupted (Rowse et al. 2016; Voigt et al. 2021).

The suitability hotspots in the study area showed large contiguous clusters in northern India, the Indus River valley in Pakistan, the Himalayas of Bhutan, India, and Nepal, the Western Ghats in south India, and the highlands of Sri Lanka. This spatial distribution of hotspots broadly aligned with the Myers et al. (2000), with the highest amount of suitable area seen in the Indian Western Ghats and across the Sri Lanka hotspot, further emphasising the importance of this region as a South Asian biodiversity hotspot (Fig. 4). However, it is important to note that this hotspot also comprises large cities, towns, and complex infrastructure, and may be threatened by habitat destruction due to lateral expansion. While there is active conservation in place across the Western Ghats and Sri Lanka (Das et al. 2006; Bambaradeniya 2006), this tends to focus more on charismatic species and there is a need for bat-specific conservation efforts. Spatial suitability patterns were broadly consistent at all species suitability thresholds; regions suitable for ≥ 24 and ≥ 36 species were less contiguous than those suitable for ≥ 12 species, but the largest contiguous regions consistently remained in the Western Ghats and southwestern Sri Lanka (Fig. 4). Hotspots for half of the studied species revealed a large area of fragmented suitability in the Western Ghats of northern Karnataka, roughly situated between Sharavati Valley Wildlife Sanctuary in the south and Anashi National Park in the north, while the western coast was still projected to be suitable. The contiguity of suitability hotspots in the Nilgiri and Vindhya hill ranges, and the lower Himalayas—all regions with very specific and unique ecosystems, habitat structures, and vegetation (Olson et al. 2001)—was also lower when mapping suitability for more species (Fig. 4). River valleys, cities and towns, and large wilderness areas were consistently projected to be suitable for multiple species, and linear structures including forest corridors and urban and suburban structures such as roads also showed suitability,

indicating the importance of such features as movement pathways. In some cases, these linear features may be used by forest- or scrubland-dominant species as corridors between suitable habitats, therefore making them vital for connectivity. While the higher suitability of conurbations and roads could be interpreted as an artefact of bias in the collection of occurrence data, this is not immediately apparent when viewing the occurrence data for our study species (Supplementary Material 3) and must be explored more deeply. It is important to note that these results are applicable only for a relatively small subset of the large diversity of bats in South Asia (~16% of the 151 species present in South Asia).

Suitability hotspots included relatively high proportions of Anthropogenic habitats, which likely captured common patterns from generalist species that can adapt to human impacts, but we found variation among groups and species. The lowest cover of anthropogenic habitats was found in the suitable areas of Rhinolophidae (horseshoe bats), a family distributed mostly in forests, caves in South Asia, had, while the highest were found in the Rhinopomatidae (mouse-tailed bats), a family associated with human habitation and features such as tombs, ruins, etc., and known anecdotally to be resilient to disturbance. Common species (e.g., greater short-nosed fruit bat *Cynopterus sphinx*, and Indian flying fox *Pteropus medius*) showed higher association with urban and suburban and human-inhabited areas than more specialist and more uncommon species (e.g., great roundleaf bat *Hipposideros armiger*, and intermediate horseshoe bat *Rhinolophus affinis*), likely due to the formers' generalist ecological niches allowing more resiliency to anthropogenic disturbance.

Assessing habitat suitability can inform conservation planning and ENM is an especially effective approach (Jeliaskov et al. 2022). Suitability analyses tend to be climate-focused, occasionally incorporating topographic variables (Festa et al., 2023), but in regions of high habitat, species, and structural diversity such as South Asia (Myers et al. 2000; Srinivasulu and Srinivasulu 2012; Ramankutty et al. 2018; Raman et al. 2023), it is imperative that ecogeographic factors are also assessed. Regions shown to be climatically suitable may not be ecogeographically suitable or vice versa. Srinivasulu et al. (2024) defined climatic suitability for 110 species of South Asian bats revealing large contiguous suitability hotspots in the Himalayas, the Western Ghats, and Sri Lanka, similar to the hotspots described in this study. While broad area coincided, the overlap of climate and ecogeography suitability area for the 48 species reveal a much smaller suitable area. Moreover, these combined suitability areas face anthropogenic threats of habitat disturbance and destruction, and in some cases like the northern Western Ghats, appeared quite fragmented (Anand et al. 2010). Our results show that failing to consider both climate and ecogeography suitability can overestimate suitability, and we highlight the value of combined appraisal. Bats are likely to show large responses to climate change (Festa et al., 2023), these may outweigh the influence of ecogeographic factors in future distributions (Wani et al. 2021). However, ecogeographic factors will likely respond to climate change and socioeconomic development, while we did not consider projected changes to these factors in our study future studies could further evaluated these changes under projected shared socioeconomic pathways (O'Neill et al. 2017; Bukovsky et al. 2021).

The results of any ENM study are impacted greatly by various factors including the quality and filtering of the variables and occurrence data, how pseudoabsence are generated and results validated (Feng et al. 2019). In our analysis, we selected species with

a minimum number of occurrences considering representation and model requirements. We acknowledge that by doing so, rarer species and those occurring in more remote area were more likely to be excluded. To identify ecogeographical variables we focused on proposed hypothesised relationships and then filtered to avoid high correlations that could affect inference. While we aimed to include a wide range of relevant variables, lack of available information at this scale prevented us from considering some likely important variables including those related to availability of food resources. We implemented a robust approach to define pseudo-absences that combines geographic constraints and replicated random sampling (Srinivasulu et al. 2024). This approach could be further improved using ecological filtering in niche space (Barbet-Massin et al. 2012; Iturbide et al. 2015), and a deeper analysis of survey and observation biases in the data. Finally, we used five-fold crossvalidation which is a widely used method but could be further improved by spatial block crossvalidation (Valavi et al. 2019). Ensemble ENMs are relatively new and quite powerful but can be computationally intensive and complex to interpret, thus often requiring a compromise between performance and feasibility.

Our study offers insight into the role of various ecogeographic factors on bat habitat suitability in South Asia, highlighting a role of anthropogenic factors, identifying suitable habitat hotspots, and revealing a worrying projected loss of ecogeographic and climatically suitable areas in the near future. We focused on describing broad patterns and effects, but to support conservation and policy we provide species-level results (Supplementary Material 2, 3) that can be used to consider effects within particular regions and for particular species. Bats in South Asia are a diverse group that faces some challenges. Some resilient generalist species, like pipistrelles, may be able to cope with human expansion, but others may be left with few suitable areas. Future work to further our understanding of bat ecological niches and distributions, including projected changes, would be needed and benefit from additional occurrence data and improved information on ecological variables and their projected changes.

Appendix

See Table 1

Table 1 Initial set of ecogeographical variables used in this study, with hypothesis for selection and notes on inclusion for the final analysis

Group	Name	Description	Source	Hypothesis	Included?
Land-use and Land cover (LULC)	Evergreen and Deciduous Needleleaf trees	% Cover of each land-use and land cover class	EarthEnv Consensus Land cover (Tuanmu and Jetz 2014)	Species, particularly those more specialized, have preferences (or are restricted) to specific habitats and can vary on their adaptation to modified environments	Yes
	Evergreen Broadleaf trees				Yes
	Deciduous Broadleaf trees				Yes
	Mixed and Other trees				Yes
	Shrubs				Yes
	Herbaceous vegetation				Yes
	Cultivated and Managed vegetation				No
	Flooded vegetation				Yes
	Urban and suburban and Built-up				Yes
	Snow and Ice				Yes
	Barren				Yes
	Open water				Yes
	Relative elevation	Difference between the elevation of a cell and the mean elevation of the study area (900 m asl), in metres	CGIAR-CSI SRTM (Jarvis et al. 2008)	Species habitat and thermal preferences influence their presence across the altitudinal gradient	Yes
	Slope	% degree of inclination, calculated through dividing the amount of change in elevation by the horizontal distance covered		Suitable caves and preferred types of vegetation in and around preferred roosting, feeding, or transit sites are associated with specific slopes	Yes

Table 1 (continued)

Group	Name	Description	Source	Hypothesis	Included?
	Aspect	Compass direction that the terrain surface faces, ranging from 0 to 360 (where 0 and 360 denote north)		Important for calculations of northerness and easternness exposure variables	No
	Northerness exposure	Calculated as $\sin(\text{Slope}) * \cos(\text{Aspect})$; describes the northerness and exposure of the cell, ranging from -1 (vertical and south-facing) through 0 (flat) to 1 (vertical and north-facing)		Cool and north-facing may be preferable for species in alpine conditions; additionally, south-facing roosts may be more sensitive to annual daytime light patterns, impacting roost selection	Yes
	Easternness exposure	Calculated as $\sin(\text{Slope}) * \sin(\text{Aspect})$; describes the eastness and exposure of the cell, ranging from -1 (vertical and west-facing) through 0 (flat) to 1 (vertical and east-facing)		Degree of eastness exposure may impact post-dusk emergence and pre-dawn return times to roosts, influencing roost selection	Yes
	Topographic position index (TPI)	Calculated as the absolute difference in elevation between a point and the average elevation of all points at a radius of 2.5 km around it, interpolated over each cell. Reflects the topographic heterogeneity in each cell (Guisan et al., 1999); lower values represent valleys, ditches, and canyons; higher values represent hilltops, mountains, and ridges		Heterogeneous topographies provide more complex habitat structure, and may influence habitat suitability in bats which depend on structural complexity; rougher topographies also offer microhabitats that can help with thermoregulation in hot conditions (Burakowski et al. 2018)	Yes

Table 1 (continued)

Group	Name	Description	Source	Hypothesis	Included?
Hydrography	Flow direction	Calculated using the D8 method (O'Callaghan and Mark 1984); represents the direction of the steepest downward slope from each cell	CGIAR-CSI SRTM (Jarvis et al. 2008)	Direction of the steepest slope may impact the ambient temperature and post-rainfall water retention of the roost and its surroundings, affecting roost suitability (e.g., northeastward flow direction in a region may make it sensitive to waterlogging and landslides resulting from southwestward rainfall)	Yes
Anthropogenic impact	Human footprint index	Cumulative index of the human pressure on the environment, rescaled to 0–128, where 0 represents least human pressure, and 128 represents highest human pressure on the biome	2018 release of the Global Human Footprint Index, 2009 (Venter et al. 2018)	Some species show affinity to, and others avoid human-modified and -impacted landscapes (Wolf et al. 2022)	Yes
	Median night-time light	Median from 1992 to 2018 of the annual mean global night-time light intensity, ranging from 0 to 63 Digital Number (DN) values, where values < 10 DN are considered 'dark'	Harmonised global night-time light dataset (Li et al. 2020)	Night-time light intensity may affect the suitability of a habitat for roosting and foraging; different species may respond to night-time light patterns differently (Mathews et al. 2015)	Yes

Table 1 (continued)

Group	Name	Description	Source	Hypothesis	Included?
	Total Road Density	Density of all roads (including highways and primary, secondary, tertiary, and local roads) in each cell, as metres per square kilometre	Global Roads Inventory Project (Meijer et al. 2018)	Roads provide linear structures for flight generally clear of vegetation or comprising parallel vegetation features (e.g. plantations on road medians and margins), but are also sources of noise and light pollution, and bats may avoid them due to risk of collision (Altringham and Kerth 2016; Ramalho and Aguiar 2020)	No

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02941-7>.

Acknowledgements AS was funded by a University of Reading (UK) International Research PhD Studentship [GS21-026]. We thank the University of Reading (UK) for their research facilities and support. AS also acknowledges Chelmala Srinivasulu and Bhargavi Srinivasulu for their instrumental assistance in data collection and analysis. We thank our various collaborators, colleagues, and friends for sharing their information, resources, and data, and are grateful for their support in this work.

Author contributions AS, DS, MGS: Conceptualization; AS, DS, MGS: Methodology; AS: Software; AS, MGS: Writing—Original Draft; DS, MGS: Writing—Review & Editing; AS, DS, MGS: Visualisation; DS, MGS: Supervision.

Funding University of Reading (UK) International Research PhD Studentship [GS21-026].

Data availability Data used in this study is available on Mendeley Data at: <https://data.mendeley.com/datasets/7hydcb3pff>.

Declarations

Competing interests The authors declare no competing interests.

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