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Cover: Watercolour illustrations—Striped Tiger *Danaus genutia*, Common Silverline *Cigaritis vulcanus*, Tamil Lacewing *Cethosia mahratta*. © Mayur Nandikar.

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ARTICLE

The past and current distribution of the lesser-known Indian endemic Madras Hedgehog *Paraechinus nudiventris* (Mammalia: Eulipotyphla: Erinaceidae)

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Abstract: The Madras Hedgehog *Paraechinus nudiventris* (Horsefield, 1851) is a species endemic to a few isolated patches in southern India threatened by habitat loss and direct take. Little is known about its historical distribution or present climatic needs, both of which could provide important baselines for conservation and habitat restoration. The current distribution of *Paraechinus nudiventris* was modelled using occurrences collected in the field and from community reports. Based on the current climatic niche estimated from Maxent, Madras Hedgehog distribution was projected into southern India during the last interglacial gap (120,000–140,000 YBP), and last glacial maximum (22,000 YBP) and mid-Holocene (~6,000 YBP). During the (Last Interglacial Gap) LIG the suitable habitat was restricted to the Palghat gap in the southern Western Ghats mountains and a small region in south Sri Lanka, although it is unclear whether the suitable climates in Sri Lanka were occupied and then extirpated, or never colonized. The present climatic niche of the species is confined to lower elevations and semi-arid plains of southern and central Tamil Nadu in India. The contemporary models can be used to update the IUCN range map for *P. nudiventris* in India, as well as identify suitable habitats for this species to guide local conservation strategies.

Keywords: Conservation, endemism, IUCN, Maxent modeling, paleo distribution, Southern Indian Hedgehog, Teri red sands.

Tamil: மெட்ராசு முள்ளெலி எனப்படுபவை தென்னிந்தியாவில் ஆங்காங்கே காணப்படும் ஓரிடவாழ்வி ஆகும். இவை வாழிடச் சிதைவாலும் பிற நேரடி தாக்குதலாலும் பெரிதும் அச்சுறுத்தலுக்காளாகியுள்ளன. இவற்றின் விரவலைப் (பரவல்) பற்றியும் அவை வாழ ஏற்றச் சூழல் எவை என்பது பற்றியும் நாம் அறிந்தவை வெகு சொற்பமே. இது குறித்தான அடிப்படைத் தரவுகளைக் கூடுதலாக அறியும்போது அவற்றைப் பாதுகாப்பதற்கும் அவற்றின் வாழிடத்தை மீட்டெடுப்பதற்கும் உதவக்கூடும். தற்போதைய இதன் விரவல் கள நிலவரத்தின் அடிப்படையில் அவை வாழ்ந்துவருவதற்கான அடையாளங்களை வைத்தும் மக்களிடம் மேற்கொண்ட வாய்மொழித்தகவலின் அடிப்படையிலும் உருவாக்கப்பட்டது. அவை வாழ ஏற்றச் சூழல் எவை என்பதை அளவிட மேச்சென்ட் தரவுகள் உதவியுடன் கணக்கிடப்பட்டுள்ளது. தென்னிந்தியாவில் மெட்ராசு முள்ளெலியின் விரவலானது கடந்த பனிப்பாறை ஊழிக்கால இடைவெளியிலும் (120,000–140,000 YBP), பனிப்பாறை ஊழிக்கால இறுதியிலும் (22,000 YBP) மற்றும் மத்திய ஹோலோசீன் கால (~6,000 YBP) த்திலும் நிகழ்ந்திருக்கலாம். இறுதிப் பனிப்பாறை ஊழிக்காலத்தில் பால்க்காட்டுக் கணவாய்க்குத் தென்மேற்கே அமைந்துள்ள மேற்குத்தொடர்ச்சி மலைக்கு இடைப்பட்டப் பகுதியிலும் தென் இலங்கையிலும் இதன் வாழிடம் நிலைகொண்டிருந்திருக்கலாம். பொருத்தமான காலநிலை அமையாததால் முன்பு இலங்கையில் வாழ ஏற்ற சூழல் இருந்து பின்னர் மட்டுப்பட்டு இருக்கலாமோ என்ற விவரம் தெரியவில்லை. தற்போது இவை மையத் தமிழ்நாட்டிலும் தென் பகுதியிலும் உள்ள அடிவாரச் சரிவிலும் வறண்ட பாலை நிலப்பகுதியிலும், வாழத் தகுந்த சூழல் நிலவுகிறது. இந்த ஆய்வின் வழியே கிடைக்கப்பெற்ற தகவல்கள், IUCNல் - மெட்ராசு முள்ளெலியின் பரப்புப் படத்தை மேம்படுத்தவும், இந்த அழிந்துவரும், அரிய இனத்திற்கான ஏற்ற வாழிடங்களை அடையாளங்காட்டி, உள்ளூர் அளவில் பாதுகாப்பு முயற்சிகளை ஊக்குவிக்க உறுதுணையாய் இருக்கும்.

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INTRODUCTION

Studying the baseline distribution of a species is critical for assessing the conservation status of species (Braun 2005; Solberg et al. 2006). The prediction of a species' distribution is crucial to many applications in ecology, evolutionary history, and conservation science (Guisan & Zimmermann 2000; Elith et al. 2006). Despite being intensively studied, detailed large-scale information on various mammal taxa's distribution has been lacking, which can hinder conservation efforts (Gaston 1991; Rondinini et al. 2011). One of the biggest challenges for conservation is to maintain the integrity and functionality of ecosystems while biodiversity is increasingly threatened by many factors. Species distribution models (SDMs) have been widely used to predict and map species' geographic ranges through time (Elith & Leathwick 2009).

During the Last Interglacial period, the rise of sea level caused floods in low areas and isolated populations on temporary islands. Therefore, the current distribution of many species might have occurred due to the Quaternary sea level change and Tertiary geology (Cuffey & Marshall 2000; Rohling et al. 2007; Goelzer et al. 2016). Local geological events and past climatic oscillations are important evolutionary mechanisms that have highly shaped the genetic structure of species (Parmesan & Yohe 2003; Woodruff 2010). In the Asian context, habitat change caused by Quaternary climatic oscillations altered the population structure and evolutionary history of various terrestrial fauna (An 2000; Barry et al. 2002; Blois & Hadly 2009; Ohnishi et al. 2009). However, very little information is available on Indian small mammal species and their paleo-distribution.

The Madras Hedgehog (MH; *Paraechinus nudiventris* Horsefield, 1851), also known as the Bare-bellied Hedgehog, is an endemic species restricted to a few isolated patches of different habitats (Image 1) in the southern Indian states of Tamil Nadu, Kerala, and Andhra Pradesh (Wroughton 1907; Webb–Peploe 1949; Prater 1971; Frost et al. 1991; Xuelong & Hoffman 2013; Marimuthu & Asokan 2014; Kumar & Nijman 2016). It is currently listed as 'Least Concern' by the IUCN Red List (Chakraborty et al. 2017). MH population is declining primarily due to trade, habitat loss, medicinal uses, and hunting (Kumar & Nijman 2016). The MH is declining fast enough to qualify for listing in a more threatened category (Xuelong & Hoffman 2013). MH is only known from the southcentral, southern parts of Tamil Nadu grasslands and dry open landscapes, with a few sightings from high altitude mountains of the Western Ghats (Kumar et al. 2019b). In recognition of such uncertainties, the IUCN has recommended further study, field exploration, and initiation of conservation measures. The first approach to understanding the status of MH is to assess their current distribution, a task previously conducted in certain areas in Tamil Nadu (Kumar & Nijman 2016). The habitat of the Madras Hedgehog includes thorny areas, semi-drylands, bushy deserts, grasslands, edges of cultivated areas, and dried ponds. Thus, knowledge regarding their ecological niche and their present and past distribution is key to better understanding the impacts of climate change and the magnitude of population decline. However, the geographical range and niche of MH remain unclear, and an updated range map for this species is urgently needed to aid conservation planning. Therefore, the identification of climatically suitable areas for the survival and persistence of MH is needed for the conservation of the species. In addition to its restricted distribution and declining population, understanding the Madras Hedgehog's ecological niche and distribution is crucial for effective conservation planning.

Nocturnal behaviour: Madras Hedgehogs are primarily nocturnal, making daytime observations challenging. This behaviour hinders direct visual surveys and necessitates alternative sampling methods that account for their activity patterns. Cryptic nature: The species is known for its cryptic and elusive behaviour, often concealing itself in burrows or dense vegetation. This makes visual detection difficult, requiring specialized techniques for accurate identification and sampling. Limited habitat access: Madras Hedgehogs inhabit diverse landscapes, including areas with restricted access, such as rocky terrains and dense vegetation. Sampling in these habitats poses logistical challenges that need to be addressed for comprehensive data collection. Low population density: The species may have relatively low population densities, making encounters infrequent. This scarcity can impact the efficiency of traditional sampling methods, emphasizing the need for strategic approaches to account for low encounter rates. Seasonal variation: Seasonal changes in behaviour, reproductive patterns, and habitat use may influence the effectiveness of sampling efforts. Considering these variations is crucial for capturing a holistic understanding of the species distribution throughout the year. Madras Hedgehogs might exhibit genetic and morphological variations across their distribution range. Considering all these and integrating these variations into sampling strategies will potentially enhance the accuracy of SDMs, providing a more nuanced depiction of their ecological niche.

There are currently a number of correlative statistical approaches to elucidate the interaction between environmental factors and species' ranges (Guisan & Thuiller 2005). Species distribution models (SDMs) (aka "habitat suitability models", "habitat distribution models" or "climatic niche models" have become a standard approach for estimating the climatic correlates to a species' distribution (Guisan & Zimmermann 2000). SDMs are nowadays a standard for virtually all conservation management projects; it is also used by IUCN (www.iucnredlist.org) to map species' global distribution range. These techniques can be extensively applied to the lesser known and threatened species for conservation concerns. SDMs have been applied in various fields of applied ecology and conservation biology, and are particularly useful for the study of lesser-studied species. A major role of conservation planning is to design reserve networks that protect biodiversity in situ. Research within the field of conservation planning has focused on the development of theories and tools to design reserve networks that protect biodiversity in an efficient and representative manner (Williams & Araujo 2000; Araujo et al. 2002; Cabeza et al. 2004). Among the SDMs, the maximum entropy modelling (Maxent) technique, which requires presence-only occurrence records, is used for the estimation and prediction of a species' geographical range (Phillips et al. 2006). Moreover, the increasing availability of species occurrence data has extended its application in conservation biogeography, especially regarding rare and declining species with incomplete information (Phillips et al. 2006). Consequently, Maxent is an important tool to gain insights into current ranges and potential range -shifts due to climate change effects over time (Franklin 2010). In this study, we aimed to answer the following questions. (I) What are the climatic and topographic conditions related to the Madras Hedgehog species' distribution? (II) Where else do these climatic conditions occur on the landscape presently? (III) Where were these climatic conditions found in the past? We then use the answers to these questions to provide insight into biogeography and conservation of the MH.

METHODS

Sample Collection

First, MH occurrence records were collected from field surveys carried out between June 2013 to June 2022 in different parts of Tamil Nadu. A thorough review of the literature, and museum occurrence datasets of Kerala, Tamil Nadu, Puducherry, and Andhra Pradesh were screened and analyzed through expert consultation and observer interviews. Surveys were also distributed to gather additional locations. Additionally, reports from newspapers regarding hedgehog sightings in the last 23 years (2000–2022) were searched for. The datasets were cross-verified and confirmed through direct field visits (at select locations) and people surveys (conducted in areas where field verification was not possible). Thirteen districts in Tamil Nadu (Dindugal, Salem, Theni, Erode, Madurai, Karur, Namakkal, Tiruppur, Coimbatore, Tirunelveli, Tuticurin, Kanyakumari, and Virudunagar) were visited, and surveys were conducted to find direct

Image 1. a–b. Madras hedgehog *Paraechinus nudiventris*: a—Juvenile in dry thorny forest, Madurai | b—Adult in rolled up position, Kuthirai Mozhi Theri (Red Sand Dunes), Tuticorin. © Abinesh Muthaiyan.

and indirect evidence of *P. nudiventris*. All the geo-coordinates of the locations were collected from the field (15 locations); a few from the newspaper (34 locations) and literature occurrence points (19 locations) were retrieved from Google Earth. The remaining 32 locations were received from our community interviews with cattle herders and 'Nari Kuravar' tribes. The distribution of the species was then modeled using Maxent, a maximum–entropy approach for species habitat modeling (Phillips et al. 2006), and bioclimatic predictor variables from the BIOCLIM v1.4 databases (Hijmans et al. 2005).

Environmental parameters

Ecological niche modeling methods were applied, where environmental data are extracted from current occurrence records, museum records, local newspapers, field surveys, and urban trade surveys. The relationship between known occurrences of Madras hedgehogs (n = 136) and bioclimatic variables in the present time was examined using Maxent and model selection with AICc using the "dismo" package in R (Hijmans et al. 2011) and custom functions based on (Warren & Seifert 2011). The selected bioclimatic variables included mean annual temperature (BIO1), "isothermality" (BIO3, a measure of the range in daily average temperature versus annual average temperature range), mean temperature of the coldest quarter (BIO11), annual precipitation (BIO12), and precipitation of the wettest quarter (BIO16). These variables were chosen based on prior knowledge of the species' natural history.

Modeling and analysis

The climate niche of *P. nudiventris* was modelled to approximate its current distribution. We then used the relationship between MH occurrence and the climatic variables found there to project their distribution during the mid-Holocene, last glacial maximum (LGM), and last interglacial period distribution (LIG). LGM climate data were down-scaled from the general circulation model (GCM) based on three models. These three models differ in temperature and precipitation. LGM climate as simulated by CCSM3 is cooler and drier than MIROC. The use of the three different climate models enabled us to assess and account for modeling the uncertainty due to LGM and LIG climate data.

The occurrence records of hedgehogs were collected from four South Indian states viz. Kerala, Puducherry, Tamil Nadu and Andhra Pradesh. Due to the concentrated nature of many hedgehog locations in southern India, we also examined model sensitivity in relation to differing levels of "thinned" data using a function from (Smith 2017). Specifically, models were examined with all of the points included; all points more than 10 km apart were included (n = 77), and all points more than 50 km apart were included (n = 19). The study area extent was defined as an area around all of the known occurrences buffered by the maximum pair-wise nearest neighbor distance between occurrences in the full dataset (695.6 km). For each separate set of thinned points, all combinations of predictors were tested, testing a regularization parameter of one, two, and three. Models were ranked based on AICc and candidate models were identified as having greater than 0.05 model weight or less than two ΔAIC from the top model. With the top model identified, we evaluated model fit using a 10-fold cross-validation and examined the area under the curve (AUC), with 0.7 representing 'fair', 0.8 representing 'good', and anything above 0.9 'excellent' Zhang et al. 2018).

RESULTS

The models using the un-thinned data tended to over-represent areas where Madras hedgehogs are known to occur. The predictors included in the top models from thinning up to 10 km and up to 50 km were substantially the same (Table 1), therefore we focus on the results from the 10 km thinned results as a balance between including as much information as possible without over-fitting our results. The top model included: isothermality and either annual precipitation or precipitation during the wettest quarter (Figure 1). MaxEnt provided satisfactory results, with the area under the receiver operating characteristic curve (AUC) values partitioning data into model training and model testing was 0.938. The most suitable climate for Madras Hedgehogs was found within western and southern Tamil Nadu. However, a second, disjunct area of suitable climate appeared in western Andhra Pradesh / eastern Karnataka. There are no known records of Madras Hedgehog in this area. We tested various combinations of predictors across different beta parameters (1, 2, and 3). Results (Table 1) revealed that model selection reduced predictors to just two for isothermal and annual rainfall, a promising indication. Additionally, response curves (Figure 2) showed minimal complexity, contrasting with typical noisy curves associated with overfitting.

Distribution of suitable habitats in the current climate environment

The model results indicated three main regions of *P.*

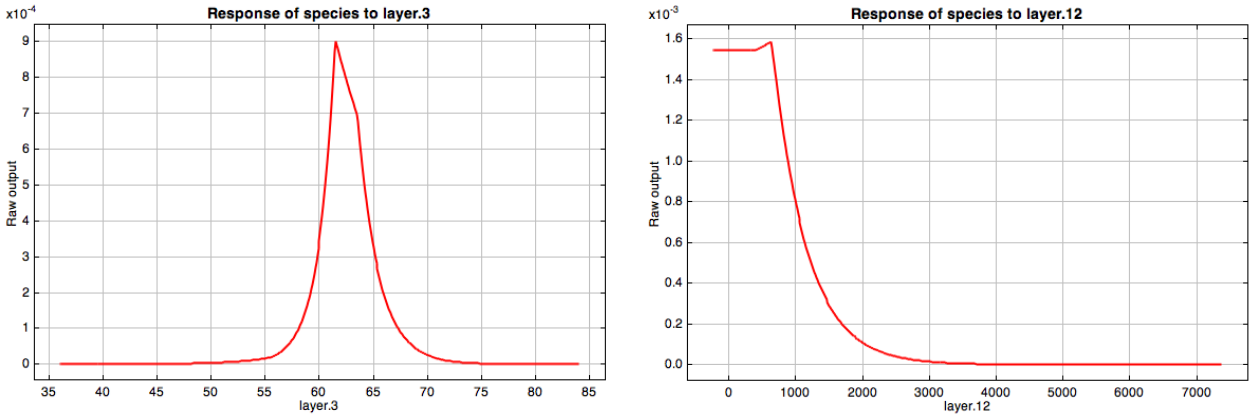

Figure 1. Climatic suitability for Madras Hedgehog *P. nudiventris* relative to Isothermality (C*10, left) and mean annual precipitation (mm, right).

nudiventris distribution (Figure 2). Western and Southern districts of Tamil Nadu in India. Such as Tirunelveli, Kanyakumari, Tuticorin, Viruthunagar, Theni, Madurai, Dindugal, Tiruppur, Coimbatore, Nilgiris, Erode, Salem, Tiruppur, Karur and Namakkal Districts. And a patchy isolated suitable habitat in Andhra Pradesh (Adoni Yemmiganur). Potentially suitable habitat was predicted in areas in Sri Lankan Island districts such as Kurunegala, Puttalam, Anuradhapura, Vavuniya, Thalamannar, and Mullitheevu. The present study predicts the suitable habitat in the coastal Teri dunes, near coastal dunes and inland dunes at the foothills of Western Ghats of Southern and Western Tamil Nadu. Additionally, the Korangaadu grasslands, semi-arid pasture lands, and drylands are predicted as suitable habitat for hedgehogs in Tamil Nadu. The coastal dunes are continuous coast-parallel deposits from Kanyakumari to south Rameshwaram also a suitable habitat. The model predicted the minimal presence of MH within high altitude forests, with the majority located in plains, dry semi-arid bushes on the fringes of urban areas, and grasslands adjacent to sandy red soils.

Table 1. Model selection results for Madras Hedgehog (*P. nudiventris*) Maxent BIOCLIM models, including models constructed for all points; models constructed with points thinned to a minimum of 10km distance; and models constructed with points thinned to a minimum of 50km distance

Model	β	K	AICc	ΔAICc
All points				
Isothermality + Precip Wettest Quarter	1	16	3127.92	0
Thinned 10km				
Isothermality + Annual Precipitation	1	9	1878.05	0
Annual Temperature + Isothermality + Annual Precipitation	1	12	1881.58	3.53
Annual Temperature + Isothermality + Mean Temp Coldest Quarter + Annual Precipitation	1	14	1883.39	5.3
Annual Temperature + Isothermality + Mean Temp Coldest Quarter + Precip Wettest Quarter	2	8	1884.39	6.33
Thinned 50km				
Isothermality + Annual Precipitation	1	7	1872.34	0
Annual Temperature + Isothermality + Mean Temp Coldest Quarter + Annual Precipitation	1	13	1876.32	3.98
Annual Temperature + Isothermality + Annual Precipitation	1	10	1877.9	5.56

Predicted paleo-distribution

The size of suitable habitat in previous climates varied substantially (Figure 3). In the mid-Holocene, the Madras Hedgehog may have been more widespread, including into, areas of south and western Tamil Nadu districts along the plains and foothills of the Western Ghats mountains (Figure 3a). However, during the LIG period, their potential habitat appeared to be restricted to a very small range in the Palghat Gap of the southern Western Ghats in low plains between Kerala and Tamil Nadu. Another small suitable area in southern Sri Lankan Island was also surprisingly revealed. The area of suitable habitat of *P. nudiventris* decreased gradually in LIG (Figure 3b). During the LGM period, the most suitable habitat was only in four distinct areas in southern India and Sri Lanka (Figure 3c). During the LGM, sea levels would have been low enough to allow MH to cross to Sri Lanka, where a large area with suitable climate was found.

DISCUSSION

Over-fitting with MaxEnt often is a concern. We have used the model selection approach and varied the "beta" parameter. The beta parameter in MaxEnt controls the

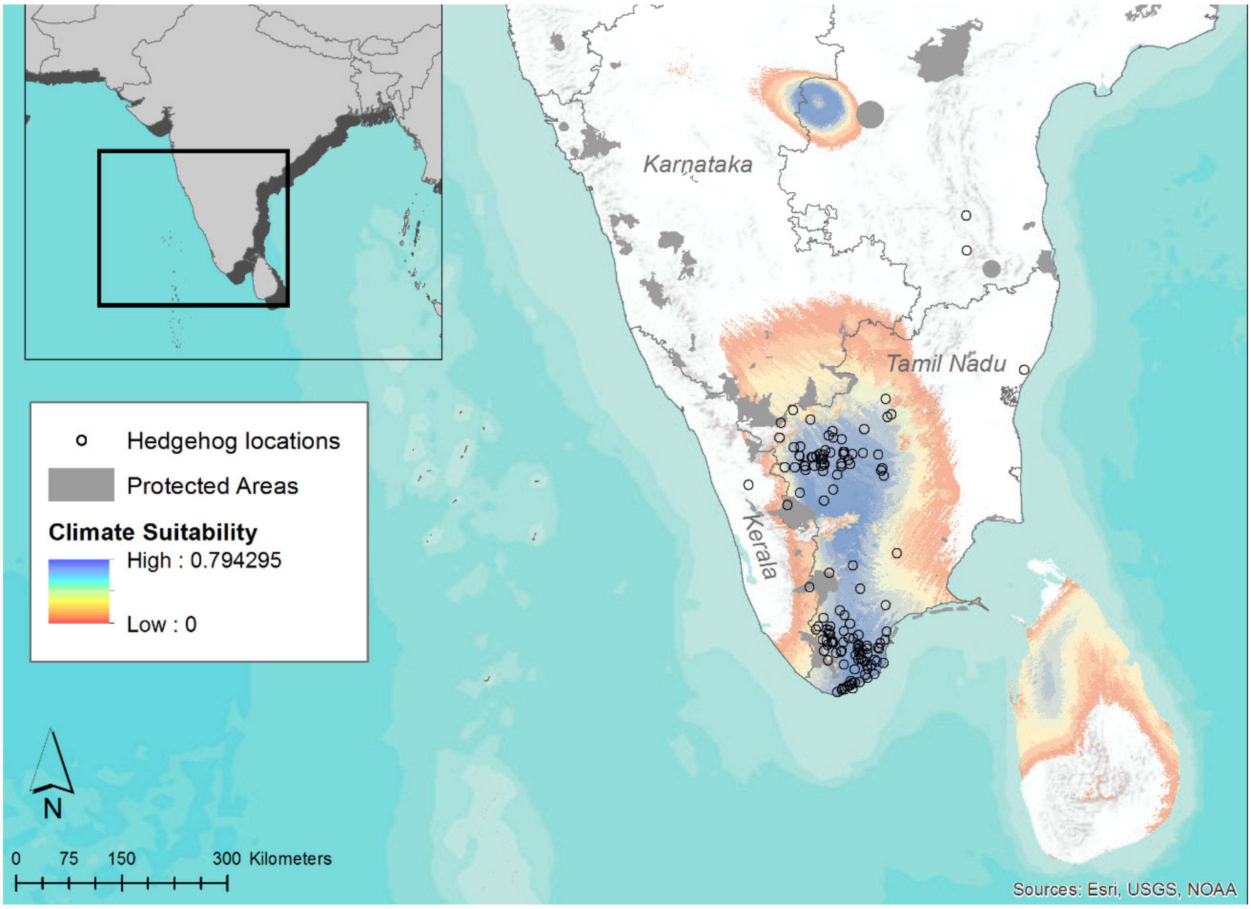

Figure 2. Climatic suitability model for Madras hedgehog (P. nudiventris) using BIOCLIM (Isothermality and Mean Annual Precipitation) and Maxent. All known occurrences are shown, but points were thinned to a minimum distance of 10 km for this model. The potential highly suitable distribution areas are shown in blue. The map was processed in ArcGIS version 10.2 (ESRI, Redlands, California, USA) (http://www.esri.com/).

complexity of the model – a higher number means fewer parameters and less over-fitting. We ran all of our models with each combination of predictors across a number of beta parameters (one, two, and three). As Table 1 shows, the model selection approach reduced the total number of predictors to just two, isothermality and either annual precipitation or precipitation of the wettest quarter. This shows a good sign that it is not over-fitting. In addition, the Figure 2, the response curves show very little complexity. The typical problem with MaxEnt is shown in response curves that are very "noisy" – these look more like a typical parametric response. In short, we used the best available tools to reduce over-fitting using MaxEnt, and our results suggest that we have minimized that problem.

Environmental variables

Current distribution records and previous literature provide evidence that medium-altitude mountains, shrublands, grasslands and dry semi-arid regions are very suitable for MH in southern India (Wroughton 1907; Webb-Peploe 1949; Manakadan 2013; Marimuthu & Asokan 2014; Kumar & Nijman 2016; Kumar et al. 2019a, b; Kumar et al. 2020). Both the variables are more related to the habitat of the species. However, for our study, we modelled the macro climate. Although most predicted habitat from southern Tamil Nadu shrub lands, sandy red dunes along grasslands and near water sources, these habitat features are present throughout most of southern India. The percent arid vegetation was a positive limiting factor for this species inferred in Table 1. These results are consistent with our fieldwork observations. Questionnaire surveys found only a few individuals inside high altitude forests; the majority were found in plains, dry semi–arid bushes on the edges of urban environments, grasslands near sandy red soils.

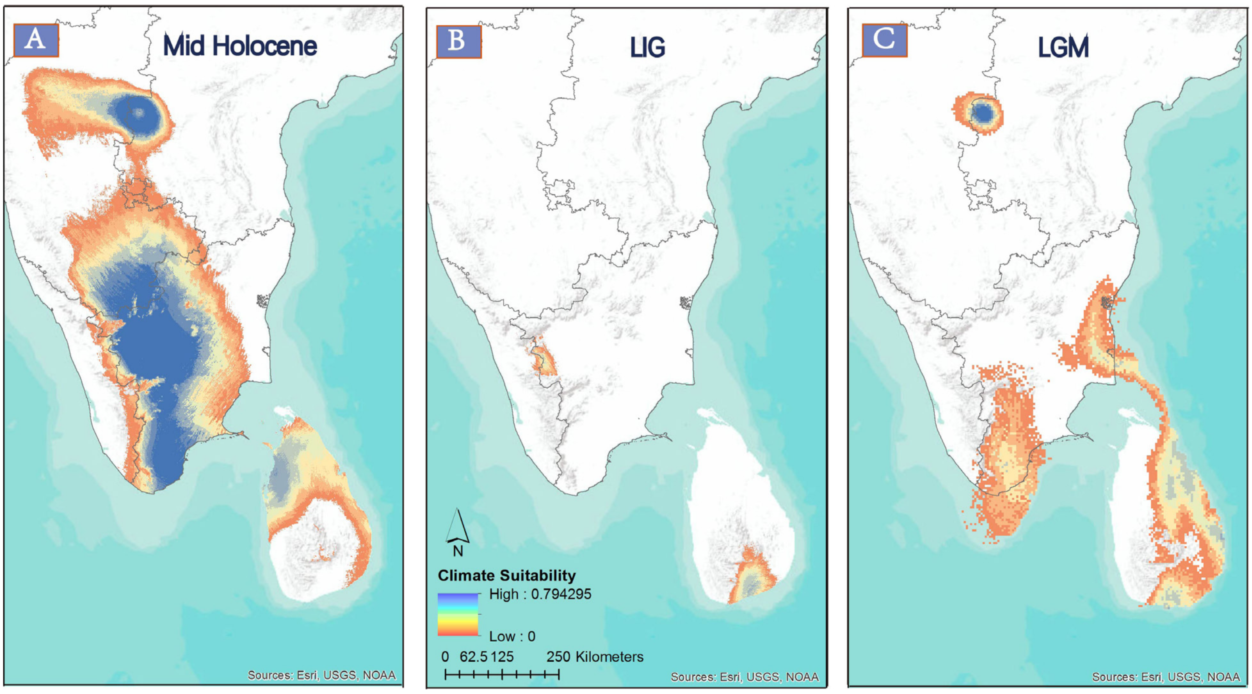

Figure 3. Madras Hedgehog (MH) distribution models created with Maxent at three spatial projections. The predicted distributions of Madras Hedgehog *P. nudiventris* projected to southern India and Sri Lanka under (A) Mid Holocene (B) Last Inter Glacial (LIG) and (C) Last Glacial Maximum (LGM). The colour shows habitat suitability value, with orange corresponding to low suitability, and blue with high suitability. These models were created using low-resolution climate data (BIOCLIM), while the models were created with higher-resolution data for Isothermality and mean annual precipitation. Suitability values are represented from low (orange) to high (blue). The representation of sea level during the LGM is from WorldClim ((Hijmans et al. 2005), http://www.worldclim.org). All models were developed using the ''maximum entropy model'' as implemented in the software MAXENT 3.3.3e.

Distribution ranges and ecological drivers

The occurrence of *P. nudiventris* from Keelakarai near Gulf of Mannar coast (Wroughton 1907), edges of Tuticorin coastal areas (Kumar & Nijman 2016), clearly show a unique pattern of occupying the sandy areas of the coastal plain districts in Tamil Nadu. Tirunelveli District holds the alluvial zone, red soil zone (Sand dunes and Teris) in the Tamirabarani river basin (Mani 1974) which holds a few isolated populations of *P. nudiventris*. "Teri" habitat heavily populated with insects, grasshoppers, and fan throated lizards, would be an excellent foraging ground for hedgehogs. The thorny bushes provide them with shelter and protection from the hot sun and predatory animals. As per the predicted results, the suitable habitat within low to medium rainfall plains, warm temperature drylands, water bodies occupied vegetated areas, and edges of coastal lands could act as a survival ground for the hedgehogs apart from the mountains.

In the year of 1917, there were about nine million of palmyras in lower elevations of Tirunelveli district (Pate 1917). This clearly indicates a higher number of suitable hedgehog habitat in a wider range in Tamil Nadu. The present rarity of this species in Tamil Nadu is therefore due to the rapid loss of the palmyra tree forests that is currently patchy and fragmented. Increasing human population and windmills is also a major threat of the rapid declining in hedgehog's population (Kumar & Nijman 2016; Kumar et al. 2019a,b).

The Sankarankovil, western Kovilpatti, uplands of Ambai, Tirunelveli, the greater part of Naanguneri, and north of Srivaikundam hold wide areas of red sandy lands, spotted with a number of small tanks, paddy lands and broken steep watercourses which the rains scour from year to year. This indicates that palymra forests along the red sand were a suitable habitat from that time itself. All of them provided good hiding places and enormous densities of invertebrates for MH. The most interesting division is red sand in the Teri landscape. They are in the southern part of Naanguneri Taluk and Tiruchendur Taluk occupying 388 km^2 of Palmyra forest (Pate 1917). Back to 1917, the Kuthirai Mozhi Theri formed as a reserved forest and the barren masses of sand were fertile patches of land found at intervals along their bases. Another interesting unique place occupied by the hedgehogs is Tharuvais, which comprises great inland lakes in Naanguneri Talk. The soil structure has changed a lot in the last 100 years due to flooding in many of the areas of the district.

Paleo – distribution ranges and potential refugium

The phylogenetic relationship and divergence of the genus *Paraechinus* are very poorly known. Based on molecular analyses of the hedgehog species, the spiny hedgehogs had formed four distinct lineages by the end of Miocene to early Pliocene, (Erinaceus, Atelerix, Hemiechinus and Paraechinus) over a two Myr time period (Bannikova et al. 2014).

Red dunes in the east coast were classified as inland, coastal and near-coastal (Teris) dunes (Joseph et al. 1997). The east and west coastal dunes of Tamil Nadu belong to the middle to late Holocene (Kunz et al. 2010; Alappat et al. 2011). But the extreme southeastern coast of Tamil Nadu holds the vast majority of the red sand soils called as Teri's, which are imprints of Late Pleistocene coastal sediments and originally developed because of the lower sea levels (Gardner & Martingell 1990; Jayangondaperumal et al. 2017). These shallow marine conditions have also been confirmed by previous studies in southern Tamil Nadu coastal districts. The large vertebrate fossils, gastropod and bivalve shells from the Tirunelveli-Tuticorin road, proboscidians fossil from Sayarmalai areas in southern Tamil Nadu (Tirunelveli) indicated that during the Pleistocene, the area was occupied by water and lagoons (Easterson 1966). During the last glacial maximum (LGM) continental shelves were exposed with a vast reservoir of sediments with strong landward winds (NE/E) to form Aeolian Teri and the north-east monsoon helped to form fluvial Teri sediments. The south-west monsoon direction also plays a vital role in carrying sediments from one place to another but this depends also upon the loose sediments, at the time of transport (Anburaj et al. 2015). During the mid-Holocene, these areas were covered by sand dunes. The North East wind and arid conditions reduced the red sands during the last glacial period. Later the higher humidity and denser vegetation cover intensified in the red dune areas. The modern sediments occur on the coastal edge of the earlier Holocene deposits. A stable, well-vegetated land surface, raised above but close to the sea (Gardner & Martingell 1990). As per the analysis, the widest, habitat is suitable in mid-Holocene, we believe the sand dunes were a good habitat for the fossorial hedgehog during that time. There was a single observation of a hedgehog in the eastern province of Sri Lanka (Green 1913). The lowered sea levels, at an easy land route across the Palk Strait, linking India and Sri Lanka (Voris 2000) could have acted as a dispersal mode for the hedgehogs. In the Western Ghats mountains of India, the three natural, geographical breaks such as the Goa gap (65–80 MYA, Palghat and Shenkottah gaps were formed 500 MYA (Soman et al. 1990; Unnikrishnan-Warrier et al. 2009; Nandini & Robin 2012). As per the SDM maps, the Palghat gap in the southern Western Ghats mountains and southern part of Sri Lankan Island likely acted as a refugium during LIG for the hedgehog, because of the floristic similarity of the wet forests of the Eastern Ghats and southern Sri Lanka (separated from India only by the Palk Strait) to the Western Ghats (Gunatilleke & Gunatilleke 1990). There were regular regional species exchanges between southern India and Sri Lanka, that might have influenced the range shifts and speciation events of the endemic plants in these regions (Bose et al. 2016).

The late Pleistocene deposition of sand in the upper terrace was associated with abundant sand supply owing to the lower sea level. The second stage of dune accretion at 4.5 ka was observed at the lower level relative to the present-day coast. It was presumably associated with late Holocene higher sea level in the coasts of southern India and deposition of sand in the backshore region on top of the previous indurated aeolian deposits. The elevated topography of the area acted as an obstruction to trap the sand-laden onshore winds and facilitated accumulation (Alappat et al. 2017).

The vegetation in the Shola habitat during the last glacial maxima (18,000 years ago) was affected by drier climate, and the landscape was dominated by C4 grasslands with forests restricted to more humid valleys or bogs (Farooqui et al. 2010). Since then, forests have been expanding as the climate has become more humid, and these fluctuations have possibly affected the population structure of the species found in these specific habitats (Gadagkar et al. 2010). The weakening of pre-monsoonal and post-monsoonal rainfall was most likely due to the LGM towards late Pleistocene and increased aridity during the late Holocene (Kumaran et al. 2013). While considering the Mid Holocene was more suitable for the hedgehog, the aridification could have driven their dispersal towards the different areas.

Monsoon rainfall plays a vital role in the spatial distribution of old and modern forests (Shukla et al. 2014; Srivastava et al. 2016). The west coast of India receives annually a maximum rainfall of 2,000–2,900 mm; the northeast receives 1,530–2,200 mm whereas central India receives a moderate rainfall of 700–1,200 mm and the northwestern and southwestern parts receive the least (Beltrando & Camberlin 1993; Srivastava et al. 2016). However, at present two monsoons are responsible for these precipitation patterns: The south-west monsoon (June–September) responsible for about 70–90% of the annual rainfall (Boucher 1998) and the north-east monsoon (October–December) contributes to 50% of annual rainfall (Kumar et al. 2006). During the last phase of the late Pleistocene and Holocene, the wet evergreen plant species in southern India were replaced by the moist deciduous species (Kumaran et al. 2013). Whereas, in southern Asia, the arrival of the south-west monsoon dates back to the early Miocene (Shukla et al. 2014). Srivastava and coworkers suggested that pre–monsoonal, monsoonal, and post-monsoonal rainfalls were responsible for the extended rainfall period in the late Pleistocene, which supported the growth of the wet evergreen element in India (Srivastava et al. 2016).

Conservation implications

The success of any conservation programme for a threatened species depends on a sound understanding of its habitat requirements. If the habitat that is critical for a species' persistence is understood, important areas can be identified and protected, and searches for further populations may be efficiently targeted (Somaweera et al. 2015). In the year 1917, the human population size was 513,234 in Tirunelveli district (Pate 1917), increasing to 2,723,988 in 2001 and 3,077,233 in 2011 (Census India 2011). Habitat and vegetation are key factors for small mammals, including insectivores such as the MH. The ongoing changing land use and effects of climate change in Tamil Nadu (Jha et al. 2000; Jayakumar & Arockiasamy 2003; Prakasam 2010; Kumar et al. 2011; Magesh & Chandrasekar 2017) could reduce the future distribution of this fossorial hedgehog species. Rapid human expansion and low land use policy could affect the land-use areas of cultivated land, barren land, shrubs, and water bodies, which are important for the survival of the hedgehog. The new data on the species will be key to deciding factors if a change in its conservation status is needed. We are especially concerned about our finding that a relatively lesser studied species may suffer severe reductions in its potential distribution, as per previous studies, those individuals reported from the open canopy, semi-arid, thorny, shrub and grasslands (Kumar & Nijman 2016). Compared with the high elevation, there are vast majority of individuals recorded from the lowlands and plains of Tamil Nadu, which is also predicted by our present analysis. Thus, the lowlands and semi-arid regions need protection and further surveys. The species is fragmented and within a restricted range in a few districts in Tamil Nadu, Kerala, and Andhra Pradesh. The population size, density, and rate of extinction are directly linked with the isolation and patch size of the animal. Small populations are generally susceptible to demographic stochasticity (Gibbs 1998; Hicks & Pearson 2003). Demographic stochasticity may also play a role in the hedgehog species population decline. The few fragmented/isolated populations in the range within Tamil Nadu might be in danger and dramatically in a declining phase. The uncontrolled collection of this species for food and medicine for the past 100 years, in the dry areas of Tamil Nadu, triggered the MH towards the verge of local extinction (Kumar & Nijman 2016). As a solitary nature, the ongoing threats limited the individual's intercourse possibilities in the highly fragmented landscapes of southern Tamil Nadu along with predatory pressure (Brawin Kumar pers. Obs.). This species is listed in Schedule II of the Wild Life (Protection) Act, 1972 (amendment, 2022).

From the prediction map, only ten of the locations fall inside the protected areas of southern India, and most of the high-altitude mountains are less suitable. The predicted cells are suitable in eastern and southern districts of Pothais (Tamil: low altitude hillocks), Tharuvais (Tamil: larger inland lake edges), Palmyra forests, Teri red sand dunes, grasslands, savannah, and shrub-dominated urban areas. The drylands of the plains act as a suitable habitat and these habitats are in danger. However, the conservation of drylands and their associated habitats such as grasslands (Paruthipaadu, Korangaadu) and unique soil types (Teri red soil) and lower elevation forests in Tamil Nadu hold a most suitable habitat for this hedgehog species. If conservation happens all associated flora and fauna will be conserved with great importance for them in this region. Moreover, the implementation of conservation education at local levels would be important to preserve the last remaining individuals of hedgehogs.

Overall, our model predictions for *P. nudiventris* is the well–established hypothesis that Indo-Sri Lankan faunal exchange is important for this lesser-known fossorial species. They were confined to small refugia during Pleistocene glacial periods in the low lands of southern Western Ghats, Palghat gap and in the south of the Sri Lankan Island. The refugium during the glacial periods shows a very large unsuitable environment for this species in most of the other areas in Tamil Nadu. The LIG could have played a major role in isolating populations and that played a profound phenomenon in phylogeographical patterns. We hypothesize that this may be the result of important geological and environmental changes that have happened in that time. Our results show a lowland migration pattern during the LIG and towards the Sri Lankan Islands, as refugia for *P. nudiventris*. In that context, larger high-altitude mountains could also have provided a suitable habitat during LGM for this arid-adapted species in southern India. The changes in alluvium soil, red sand dunes and vegetation are a positive mode for this species. Thus, they might have a wider distribution range than previously. The recent aridification could lead a demographic change in this species. More attention on the molecular-based phylogeographical works in this arid regional fauna could help to understand more about the biogeography of this region.

Future surveys could be strategically targeted in regions characterized by plains, dry semi-arid bushes, and savannahs, on the outskirts of urban areas, south Deccan plateau areas, Deccan thorn scrub forests and grasslands of Tamil Nadu and other adjacent states. Additionally, focusing on areas with a historical hedgehog presence, as indicated by our previous work, could enhance the effectiveness of future surveys.

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