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ORIGINAL PAPER

Chiropteran diversity and the key determinants of their distribution in Eastern Ghats, India

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Abstract

Understanding the patterns of biodiversity is central to species conservation planning. Here we illustrate chiropteran diversity and distribution pattern of the hill ranges of the Eastern Ghats of Odisha state, India using roost survey and mist net survey techniques. The present study recorded 23 bat species including two newly recorded species for the study site i.e., *Hipposideros galeritus* and *Megaderma spasma*. The bat capture rate was the highest in the moist deciduous forest describing higher bat populations compared with the places of human habitation. Utilities of 21 climate, three physiographic and two disturbance variables and species distribution modelling could reveal that the north-eastern part was more suitable for bat distributions than the southern part of the region. The climate, physiographic and disturbance variables were crucial in their distributions, where elevation and potential evapotranspiration were highly significant. Unlike other species, *Taphozous melanopogon* showed negative correlation with these variables. The mean diurnal temperature and precipitation seasonality have positive influence on bat distributions, indicating their resilience to seasonal precipitation changes and day time temperature fluctuations. The negative effect of temperature seasonality on the distribution of *Pteropus giganteus* could attribute to its vulnerability to climate change effects. The study provides inputs for monitoring the future spatio-temporal changes, suggesting long term conservation measures. It could generate basic information on the impacts of climate change on bat distribution in the future climate change scenario.

Keywords Chiroptera · Climate change · Diversity · Species distribution modelling · Maximum entropy

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Introduction

Understanding the patterns of biodiversity at the ecosystem, species or genetic levels, within a landscape, is essential for a wide range of fundamental and applied purposes in species conservation planning (Moreno and Halffter 2001; Paliwal and Mathur 2012). Although climate has always been a prominent factor in species distributions (Francis and Currie 2003), it is difficult to assess changes in the ecology and behaviour of any individual species to a single cause. Habitat heterogeneity and local scale environments greatly influences community structure and composition (Xu et al. 2014; Kent et al. 2014). Bats are one of the most diverse mammalian order and significant contributor to global mammalian diversity with more than 1300 species worldwide (Fenton and Simmons 2014). For smooth functioning of the ecosystem, they also play important role in pollination, seed dispersion, insect pest control as well as transfer and redistribution of essential nutrients between habitats (Kunz et al. 2011). Bats have long life span and need sufficient energy to manage their sustained power flight (Mello et al. 2009; Voigt and Lewanzik 2011) and are classic examples of biodiversity indicators. Their reproduction depends on climatic suitability and the temporal availability of food resources (Crichton and Krutzsch 2000) and they are efficient in reading climatic signals for foraging, roosting, parturition, migration, breeding and hibernation (Sherwin et al. 2013). However, their slow rate of reproduction has increased their proneness to environmental stress and steady decline in population (Jones et al. 2009). In general, insect populations vary with climatic conditions, where low temperature retards their growth (Anthony et al. 1981; Burles et al. 2009). More rainfall helps dipterans and lepidopterans to multiply rapidly (Frick et al. 2009). On the contrary, insect availability to bats is regulated due to reduced insect flight during heavy rainfall (Anthony et al. 1981). It has been reported that changes in seasonal temperature and precipitation has great control on flowering and fruiting of food plants, which influences foraging behaviour of fruit bat *Eidolon hevlum* by altering reproductive potential of the species (Richter and Cumming 2008). Some studies also highlight the differences in bat species responses to changes in temperatures owing to disparities in foraging, habitat preferences and reproductive needs. *Myotis daubentonii* is reported to be less sensitive to temperature changes owing to its efficient hunting strategy and availability of insects in plenty (Boonman et al. 1998; Ciechanowski et al. 2007), whereas aerial-hawking bats are more likely to depend on climate changes due to their vulnerability to food supply in time and space. Bats are prone to evaporation due to their large naked flight membranes (Webb et al. 1995); and need constant water supply near roosting sites (Adams and Hayes 2008). The lactating females and roosts with high solar gain are more prone to water stress (Adams 2010).

Although bats are one of the most successful and highly adaptive animals, loss and degradation of roosting and foraging habitats, emerging diseases, hunting, persecution as well as effects of climate change have emerged as major factors for declining bat population worldwide (Mickleburgh et al. 2002). The negative influences of climate change on behaviour of European and north-west African bats have been reported (Sherwin et al. 2013). *Lasiurus borealis*, *Rhinolphus ferrumequinum*, *Tadarida brasiliensis* and *Eidolon hevlum* show temporal changes in their foraging behaviour in response to availability of food resources (Park et al. 2000; Dunbar and Tomasi 2006; Newson et al. 2008; Richter and Cumming 2008). The declination of bat population is more intense in the tropical countries (Kingston 2010) and it has been forecasted to exceed by 40% in coming decades solely owing to habitat related threats (Lane et al. 2006). Therefore, adequate information on diversity and status of bats is essential for region-specific conservation measures (Bates 2013).

Species distribution models (SDM) are extrapolation techniques used to map species distributions and the probability of habitat use (Hirzel et al. 2006). Several modelling protocols are employed to enumerate relationships between species and the environment. Maximum Entropy (Maxent) is a popular SDM technique, very useful for mapping species distributions with presence only data (Phillips and Dudík 2008). Its popularity is attributed to its excellent predictive ability compared with other SDMs (e.g. Elith et al. 2006). Maxent is reported to be a preferred technique in distributions of bats especially for small sample sizes (Wisz et al. 2008) and owing to their nocturnal behaviour that impedes their identification in flight (Razgour et al. 2016). Maxent finds the probability distribution, subject to the constraints imposed by the information available from the observed occurrence of the species and environmental conditions across the study area and maps depicting the species' expected range. It has advantages of clamping and regularisation, with abilities to examine whether projections lie within environmental space or geographic space (Murray et al. 2011).

The Eastern Ghats is one of the oldest, non-contiguous and phyto-geographically important mountain ranges in India that lies parallel to the east coast from Tamil Nadu in southern India to Odisha in the eastern India, spreading over a length of around 1750 km. Recent herpeto-faunal, mammalian and avian inventories along the Eastern Ghats suggests that its forests harbour relict population of once widely distributed wet zone species (Mohapatra et al. 2010, 2014; Agarwal et al. 2013; Nayak et al. 2014; Purohit et al. 2017). Dutta and Mohapatra (2017) reviewed the faunal composition of the Eastern Ghats and reported 32 bat species from eight families to the region. They observed that the northern parts of Eastern Ghats, particularly the Odisha state, have not been adequately explored despite its biological importance. Moreover, the Eastern Ghats landscape has become vulnerable from the rapid land cover changes in recent decades through deforestation, agricultural encroachments and infrastructure development (Reddy et al. 2014) and it might be affecting the bat population occurring in this region.

The present study detailed the inventory of bat fauna of the Eastern Ghats along the hill ranges of Odisha; and explores the underlying causes of their distributions. The habitat suitability maps of some top selected bat species are derived using Maximum Entropy model (Phillips et al. 2006). The influences of elevation, climate and anthropogenic disturbance on bat distributions are highlighted. The findings of this study could provide meaningful insights to monitor the future spatio-temporal changes and suggest long term conservation measures.

Methods

Study area

The study was carried out along the Eastern Ghats hill range in Odisha, eastern India (Fig. 1). The area lies between 17°48′ to 22°33′N and 81°23′ to 86°53′E spreading over an area of 73,700 km^2. The hill ranges of the Eastern Ghats are not contiguous and highly fragmented with hilly and undulating terrain with plain areas. The maximum elevation reaches up to 1672 m, where the southern part has a higher elevation than the northern part. The Eastern Ghats experiences tropical climatic condition with three distinct seasons

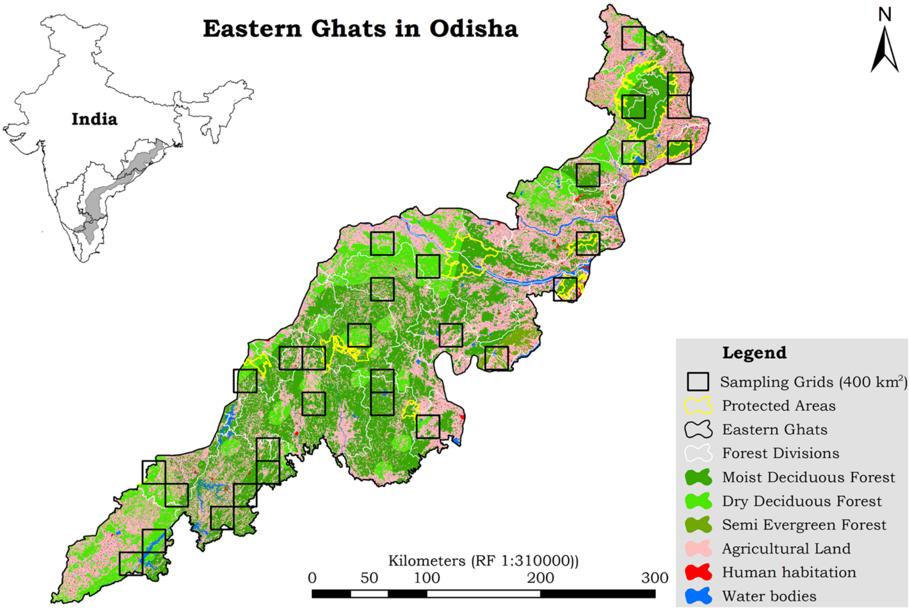

Fig. 1 The study area showing different land cover pattern and bat sampling grids along the Eastern Ghats boundary of Odisha state, India. (Color figure online)

i.e., summer, monsoon and winter. It receives an annual rainfall of 1200–1500 mm from both southwest and northeast monsoon. The temperature varies from a minimum of 12 °C during winter to a maximum of 38 °C during summer (Ray 2005). The forest types of Eastern Ghats hill ranges of Odisha are broadly classified into the tropical moist deciduous, tropical dry deciduous and few patches of semi evergreen forests (Champion and Seth (1968). However, the forest cover of Eastern Ghats has been declined due to agricultural expansion, timber harvesting, shifting cultivation and development of industries (Saranya and Reddy 2016).

Sampling sites

A base map of the study area (Fig. 1) encompassing the known forest cover zone following Champion and Seth (1968) was developed using the Geographic Information System in ArcGIS version 9.3. The detailed land use pattern within each forest zone was then classified as natural forest, agricultural land and human habitation by digitizing over latest Google Earth imagery. 20 km × 20 km grids were overlaid throughout the study area covering all the habitat types (strata); and sampling sites were selected following Guthrie (2012). A total of 30 grids (20 in moist deciduous forest, nine in dry deciduous forest and one in semi evergreen forest) were selected for sampling (Fig. 1). *Tropical moist deciduous forest*, characterised by moderately dense vegetation with heterogeneous canopy layer is widely distributed throughout the study area. Its major plant species are *Shorea robusta*, *Syzygium cumuni*, *Mangifera indica*, *Terminalia tomentosa* and *Anogeissus latifolia*. *Tropical dry deciduous forest* has comparatively open vegetation; and distributed along the central and western parts of the study area. Its dominant plant species are *Tectona grandis*, *Bombax ceiba*, *Madhuca indica* and *Dendrocalamus strictus*. *Tropical semi evergreen forest* is found to occur in the foot hills and valleys > 600 m elevation i.e., in few patches Similipal Biosphere Reserve, Kerandimal hills and Deomali hills along northernmost, central and southern parts of the study area, respectively. The dominant plant species of this forest type are *Terminalia arjuna*, *Mangifera indica* and *Diospyros embryopteris*. *Agricultural lands* include some tree species i.e., *Ficus benghalensis*, *Ficus religiosa*, *Mangifera indica*, *Bombax ceiba*, *Borassus flabellifer*. Non-cultivable areas are dominated by *Lantana camara* and *Chromolaena odorata*. *Human habitation* are with minimal natural vegetation cover, but some seasonal fruiting trees like *Mangifera indica*, *Ziziphus mauritiana*, *Psidium guajava* and *Musa* sp. are witnessed in the backyard.

Bat survey

The bat fauna survey was carried out for three years during May 2015 to June 2018. The roost survey and mist net survey techniques were adopted following the guidelines and field protocols of Bat Conservation Trust (2007). In each sampling grid, information on occurrence of bat roosting sites were collected by interviewing the local people and Forest Department staffs owing to their adequate knowledge on local biodiversity. Subsequently, the identified bat roosting sites were surveyed involving them. Additionally, caves, crevices, tree holes, deserted buildings and old temples situated nearby the surveyed roosts were searched. The roost survey was carried out during the day. At each active roost, some bats were captured using an entomological net directly or mounted over an extendable pole to identify species with a minimum disturbance. Species were identified following Bates and Harrison (1997) and Srinivasulu et al. (2010) adopted for the Indian bats. For the present study, species with confirmed identification were considered. For identification of those preferring to roost in crevices, tree holes and other inaccessible locations, we used mist nets. In each 30 grids selected for sample survey, three different locations were considered on the basis of their natural vegetation, agricultural land and human habitation. Total 90 locations covering 20 in moist deciduous vegetation, nine in dry deciduous vegetation, one in semi evergreen vegetation, 30 in agricultural lands and 30 in human habitation were sampled (Table 1). Sampling sites were revisited for at least

Table 1 Sampling effort and capture rate of bats in the five sampled habitats of study area (2015–2018)

Habitat type	Number of sampling sites	Total number of sampling nights	Total duration of sampling (h)	m^2nh	S	S/m^2nh	N	N/m^2nh
Moist deciduous forest	20	90	270	4050	19	0.0047	140	0.0345
Dry deciduous forest	9	89	267	4005	16	0.0040	84	0.0209
Semi evergreen forest	1	87	261	3915	12	0.0030	50	0.0128
Agricultural land	30	90	270	4050	12	0.0029	98	0.0242
Human habitation	30	90	270	4050	12	0.0029	99	0.0244
Overall	90	446	1338	15,974	21	0.0013	470	0.0294

m^2nh total sampling effort, S species richness, S/m^2nh capture rate of individual species, N number of individual species, N/m^2nh capture rate of individual bats three times during the study period. Netting activities at each location was carried out for three hours per sampling night just after sunset.

For mist netting, one 15 m^2 net with 13 mm mesh size and four sleeves (Avinet USA) was used and deployed across forest trails, streams and near water bodies along flyways of bats (Barlow 1999). Before mist netting, a preliminary investigation on availability of space, surrounding vegetation, availability of water holes, suspected flight path and kind of obstructions was carried out during daytime. Nets were set below canopy level either by stalking them with bamboo poles or with tree canopies following the techniques described by Humphrey et al. (1968). One additional mist net was kept for reserve to replace the damaged ones as bats damage nets after entanglement. Whenever nets were placed over water bodies or streams, intensive care was taken not to keep the lowest edge of the net near water surface as far as possible ensuring that it is high enough to prevent any bats that are captured in the bottom of the mist net from hanging in the water (Kunz 1988). After deployment, nets were checked at every 15 min interval to ensure that all the captured bats are removed quickly and prevent any of them from escaping. Bats captured in the net were immediately released with utmost care without any physical injury. If any pregnant or lactating bat was caught in the mist net, it was immediately released without further examination. All captured bats were kept in hung up position in cloth bags, and none were kept for more than one hour of capture. The number of individuals captured or located in roosts, habitat type, elevation and geographic location of sampling site were recorded.

Data analysis

The mist netting sampling effort (m^2 nh) was calculated by multiplying the net area (m^2) with total duration of sampling (nh) following Kingston (2009). The capture rate of individual species and individual bats were calculated by dividing the total number of species (S) and individual bats (N) by each sampling effort, respectively. Overall species richness of bats considered both roost survey and mist net data, whereas mist net data was used to enumerate diversity and abundance. To quantify the species diversity of bats between different habitats, the Shannon Diversity Index (H′), Dominance (D) and Simpson’s index of diversity were calculated.

The Shannon Diversity Index (H′) is calculated by the following equation (Shannon 1948):

$$H' = -\sum_i \frac{n_i}{n} \ln \frac{n_i}{n}$$

where, n_i is the number of individuals in a particular habitat and n is the total number of species.

The dominance index is computed using the formula (Hammer et al. 2001):

$$\mathrm{D} = \sum_i \left(\frac{n_i}{n}\right)^2$$

where, n_i is the number of individuals of taxon i.

Simpson’s index of diversity is computed using the formula (Simpson 1949):

$$1 - \sum \left(\frac{n}{N}\right)^2$$

where, n is the total number of individuals of a species and N is the total number of individuals of the species.

The relative abundance was calculated by dividing the number of individuals of a species by the total number of all species. To investigate the species abundance distributions between habitats, a rank abundance plot of bats in the sampled habitats were developed in *BioDiversity Professional* version 2 (McAleece et al. 1997). To test the significant differences in observed species richness between habitats, Chi square (χ^2) test was performed. The t test (t) was carried out to evaluate the Shannon and Simpson diversity indices; and Kolmogorov–Smirnov test was used to assess the significant difference in abundance distributions between habitats. Calculations of diversity indices, χ^2 test and *t* test and preparation of graphs were done using *PAST* version 3.20 software (Hammer et al. 2001).

To understand the influence of variables on species responses, a total of 26 variables were considered from three correlate types: 21 climate, three physiographic and two disturbance variables. Nineteen climate variables were procured from WorldClim database (http://www.worldclim.org; Hijmans et al. 2005); and two other climate variables (potential evapotranspiration and aridity index) were obtained from CGIAR_CSI database (Trabucco and Zomer 2009). We acquired elevation and aspect from the GMTED 2010 database (https://lta.cr.usgs.gov), and derived the terrain ruggedness index from the differences of the elevation values of adjacent cells relative to the central cell (Riley et al. 2000). Two socio-ecological indicators: the human appropriation of net primary productivity and global human footprint were obtained from WCS_CIESIN database (WCS_CIESIN 2005). Each variable was assigned a common coordinate system of WGS84 datum and conformed to 1 km^2 spatial resolution. The selection of environmental variables for this study was done as per Schoeman et al. (2013). Organisation and pre-processing of environmental data layers were done using ArcGIS 10 and R version 3.5. For species with ≥ 20 sample point locations were considered for analysis. We examined the correlation between variables by using the package ‘GGally’ (Schloerke et al. 2014); and a threshold of 0.75 correlation was assigned to select variables to avoid overestimation in model performances owing to high correlation. To evaluate the importance of variables, the principal component analysis, which involved simultaneous centring and scaling was performed by the package ‘factoextra’ (Kassambara and Mundt 2017). We prepared the habitat suitability maps using Maximum Entropy (Maxent) model (Phillips et al. 2006). Maxent was performed using the package ‘dismo’ by setting default parameters (Hijmans et al. 2017). Validation was done by k-fold partitioning with 80% training and 20% test data. We used area under (receiver-operator) curve (AUC) to assess the performances of Maxent. A model above random (AUC > 0.50) was nominated for mapping species distributions.

Results

Species richness and composition

During the study 470 individual bats from 21 species were captured in mist nets. The individual species capture rate was highest ($S/m^2nh = 0.0047$) in moist deciduous forest and lowest ($S/m^2nh = 0.0029$) in semi evergreen forest. Similarly, the capture rate of individual bats was highest ($N/m^2nh = 0.0345$) in moist deciduous forest and lowest ($N/m^2nh = 0.0128$) in both agricultural land and human habitation (Table 1). A total of 23 species of bats (21 from mist net capture) under seven different families were recorded. They comprised of three frugivore species and 20 insectivore species (Table 2). The family Vespertilionidae was well represented by six species, followed by Hipposideridae (5 species), Pteropodidae and Emballonuridae (3 species each), Rhinolophidae, Megadermatidae and Rhinopomatidae (2 species each) (Table 2). Moreover, during the study two species of insectivorous bats: *Hipposideros galeritus* and *Megaderma spasma* were reported to occur in Odisha for the first time. Among these, 17 species were recorded from their roosts and foraging sites, four species exclusively from their foraging sites and two species exclusively from their roosting sites (Table 2).

Species diversity and abundance

The Shannon diversity index (H′) was highest in moist deciduous forest (2.540) followed by dry deciduous forest (2.250), agricultural land (2.062), human habitation (2.053) and semi evergreen forest (2.003). The dominance (D) was highest in semi evergreen forest (0.214) followed by dry deciduous forest (0.178), agricultural land (0.161), human habitation (0.160) and moist deciduous forest (0.124). The Simpson index of diversity was recorded highest in moist deciduous forest (0.875) followed by agricultural land and human habitation (0.839 each), dry deciduous forest (0.821) and semi evergreen forest (0.785). However, the diversity between natural and anthropogenic habitats showed statistically significant differences with Shannon index (t test = 4.55, $p < 0.05$), but statistically insignificant diversity with Simpson index (t test = - 0.49, $p > 0.05$).

Rhinolophus lepidus was the most abundant species with a relative abundance of 24.68, followed by *Cynopterus sphinx* (15.11%), *Scotophilus heathii* (13.19%), *Pipistrellus ceylonicus* (6.81%), *Scotophilus kuhlii* (5.96%), *Hipposideros lankadiva* (4.68%), *Pipistrellus tenuis* (3.83%), *Hipposideros ater* (3.62%), *Rousettus leschenaultii* (3.40%), *Megaderma lyra* and *Taphozous melanopogon* (2.98% each), *Saccolaimus saccolaimus* (1.91%), *Hipposideros speoris*, *M. spasma* and *Rhinopoma microphyllum* (1.70% each), *Pipistrellus coromandra* (1.06%), *Rhinopoma hardwickii* (0.85%), *Taphozous longimanus* (0.64%), *Hipposideros fulvus* and *H. galeritus* (1.49% each) and *Rhinolophus rouxii* (0.21%) (Table 2).

The rank abundance plot exhibited *R. lepidus* as the most abundant species in moist deciduous forest, dry deciduous forest and semi evergreen forest with the relative abundances of 30.22, 38.10 and 42%, respectively. *S. heathii* was the most abundant species in agricultural land with relative abundance of 25.51%. *C. sphinx* and *S. heathii* were the most abundant species in human habitation (Fig. 2). The Kolmogorov–Smirnov test indicated no significant difference in abundance distribution of bats between habitats ($p > 0.05$) except when moist deciduous forest was compared with that of semi evergreen forest (Kolmogorov–Smirnov test = 0.5714, $p < 0.05$) and human habitation (Kolmogorov–Smirnov test = 0.4285, $p < 0.05$).

Co-linearity among variables

After multi co-linearity test, we considered ten least correlated variables for the analysis. This included elevation, global human footprint, human appropriation of net primary productivity, mean diurnal temperature range, mean annual temperature, mean annual precipitation, precipitation of driest quarter, potential evapotranspiration, precipitation seasonality and temperature seasonality (Fig. 3). The mean diurnal temperature range is found to have weak correlation with disturbance variables and mean annual precipitation and temperature. Its correlation with potential evapotranspiration and two seasonal climate variables

Table 2 Number of bats captured from the five major sampling habitats of the study area (2015–2018)

Species[a]	Abbreviation	Record location[b]	Roost type[c]	Feeding habit[d]	Moist deciduous forest	Dry deciduous forest	Semi evergreen forest	Agriculture land	Human habitation
Pteropodidae (fruit bats)									
Pteropus giganteus[#]	Pte	R	Tr	Fr					
Cynopterus sphinx	Csp	R, F	Fl, Cv	Fr	11	8	5	23	24
Rousettus leschenaultii	Rles	R, F	Bl, Cv	Fr	5	3	5	1	2
Rhinolophidae (horseshoe bats)									
Rhinolophus lepidus	Rlep	R, F	Cv, Bl, Th	In	42	32	21	10	10
Rhinolophus rouxii	Rro	R, F	Cv	In	2				
Hipposideridae (leaf-nosed bats)									
Hipposideros ater	Hat	R, F	Cv	In	7	7	2		
Hipposideros fulvus	Hfu	R, F	Cv	In	4	3			
Hipposideros galeritus[*]	Hga	R, F	Cv, Bl	In	7				
Hipposideros speoris	Hsp	R, F	Cv	In	8				
Hipposideros lankadiva	Hla	R, F	Cv, Bl	In	7	4	2	4	5
Megadermatidae (false vampire bats)									
Megaderma lyra	Mly	R, F	Cv, Bl	Ca	6	2	3	2	1
Megaderma spasma[*]	Msa	R, F	Cv	In	4	3	1		
Rhinopomatidae (mouse-tailed bats)									
Rhinopoma microphyllum	Rmi	R, F	Cv, Bl	In	3	5			
Rhinopoma hardwickii	Rha	R, F	Cv, Bl	In	2	2			
Emballonuridae (sheath-tailed bats)									
Taphozous longimanus	Tlo	R, F	Bl	In		3			
Taphozous melanopogon	Tme	R, F	Cv, Bl	In	7	1	1	3	2
Saccolaimus saccolaimus	Ssa	F		In	4	1	3		1

Table 2 (continued)

Species[a]	Abbreviation	Record location[b]	Roost type[c]	Feeding habit[d]	Moist deciduous forest	Dry deciduous forest	Semi evergreen forest	Agriculture land	Human habitation
Vespertilionidae (evening bats)									
Kerivoula picta[#]	Kpi	R	Fl	In					
Pipistrellus coromandra	Pco	R, F	Bl	In	1			2	2
Pipistrellus ceylonicus	Pce	F		In	8			11	13
Pipistrellus tenuis	Pte	F		In		2	3	7	6
Scotophilus kuhlii	Sku	F		In	5	4	2	8	9
Scotophilus heathii	She	R, F	Fl, Bl	In	7	4	2	25	24
Grand total					139	84	50	98	99

*New additions to the bat species of Eastern Ghats in Odisha are indicated by asterisks

[#] Species were recorded from their roosting sites only

[a] Nomenclature follows Srinivasulu and Srinivasulu (2012)

[b] Recorded location: *R* roosting sites; *F* foraging sites

[c] Information on roost type was collected from observation: *T* exposed branches of trees, *Fl* foliage, *Cv* cave, *Bl* abondoned buildings

[d] Feeding habits follows Bates and Harrison (1997): *Fr* Frugivore, *In* Insectivore, *Ca* Carnivore

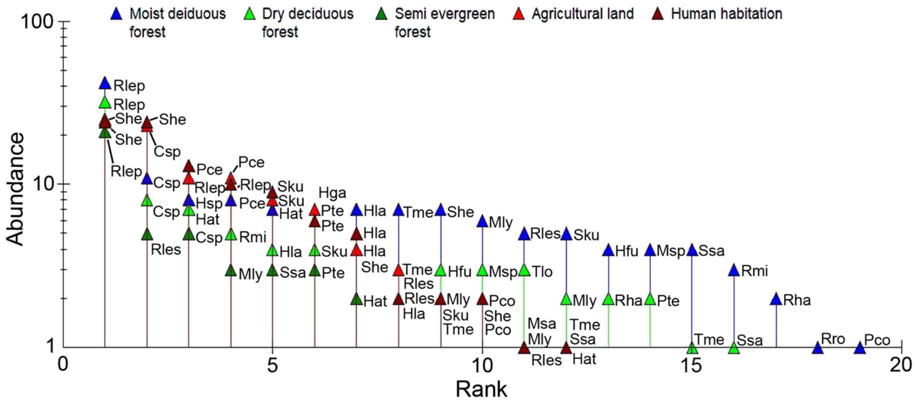

Fig. 2 Rank abundance plots for bats recorded in five sampled habitats in the Eastern Ghats. Species abbreviations are given in Table 2. (Color figure online)

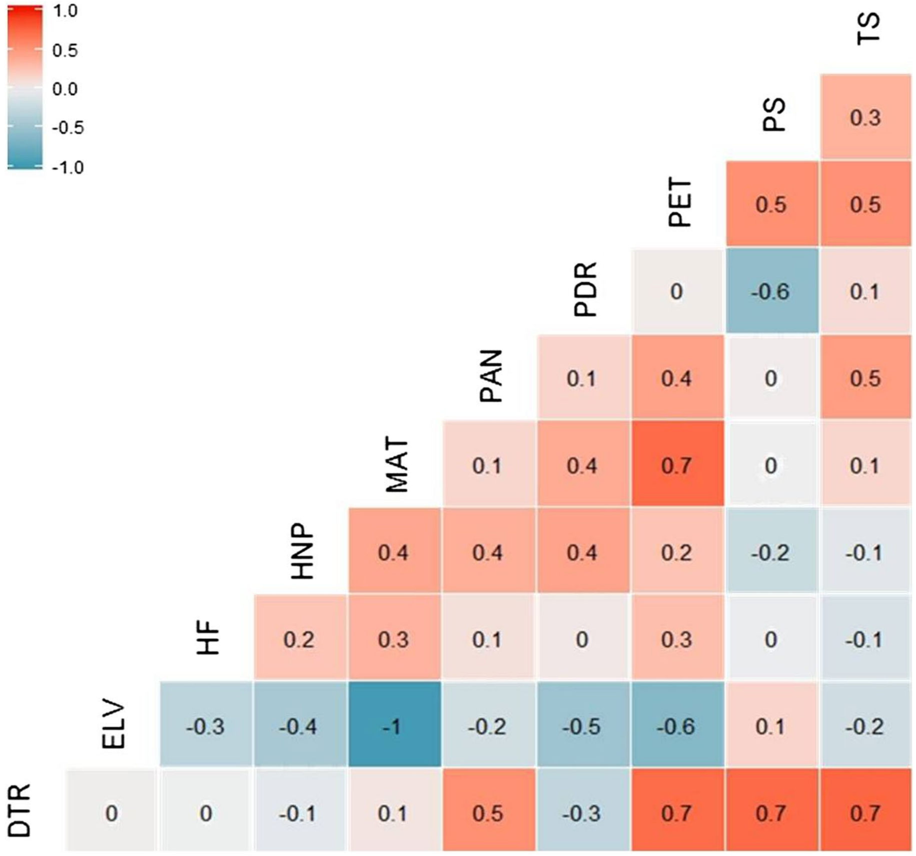

Fig. 3 Correlation plot of selected variables. *DTR* mean diurnal temperature range, *ELV* elevation, *HF* global human footprint, *HNP* human appropriation of net primary productivity, *MAT* mean annual temperature, *PDR* precipitation of driest quarter, *PAN* annual precipitation, *PET* potential evapotranspiration, *PS* precipitation seasonality, *TS* temperature seasonality. (Color figure online)

(precipitation- and temperature- seasonality) was good (r = 0.70). Elevation showed weak and negative correlation with other variables, except in case of precipitation seasonality, where a weak and positive correlation existed. Both disturbance variables are weakly correlated. Similarly, climate variables (except mean diurnal temperature range) are weak, but positively correlated. The mean annual temperature and potential evaporation showed a good correlation (r = 0.70).

Description of variables

The elevation range for the study area was 23–1672 m. Elevation is found to have maximum variation (277.4 SD). Aspect is low with a mean value of 178.3°. The terrain ruggedness showed variations (163.4 SD); and its value ranged between 6 and 777.2. The aridity index ranged between 0.07 and 0.11, with a mean of 0.09. The standard deviation and standard error was negligible. The mean annual precipitation ranged between 1194 and 1608 mm, with a mean of 1415.7 mm. The precipitations during the coldest and driest quarters were low (34.8 ± 8.7 mm). The precipitation of the driest month was almost dry with 4.7 mm rainfall. The mean precipitation of wettest and warmest quarters match (mean 311 mm) and their value ranged between 230 and 381 mm. The mean precipitation seasonality value was 98.75 CV. It ranged between 87 and 124 CV. The mean diurnal temperature range was 10 °C (8.1–11.3 °C). The mean isothermality value was 42.85. The mean annual temperature ranged between 20.9 °C and 27.5 °C, with the mean at 25.56 °C. Its standard deviation was low at 1.41 SD. The mean annual temperature range was 23.16 °C and ranged between 20.9 °C and 27.5 °C. The minimum and maximum temperatures of the coldest and warmest months were 13.2 °C and 40.8 °C, respectively. Temperature seasonality showed a greater mean (354.9 CV). The mean global human footprint was 30.28, whereas the mean human appropriation of net primary productivity was nearly double this value i.e. 59.7. The standard deviation and standard error were higher in human appropriation of net primary productivity than the global human footprint (Table 3).

Potential distribution

Out of 23 species identified, 11 species were represented with ≥ 20 sample location points. Therefore, predictions were made for 11 species using Maxent. The habitat suitability maps of nine species showing AUC > 0.5 prediction accuracy have been represented (Fig. 4). In general, the north-eastern part is found to be suitable places for chiropterans compared with southern part. *C. sphinx* is observed to be a well distributed species (Fig. 4a). *H. ater* is predicted to be distributed in the upper most eastern parts of the region (Fig. 5b). *M. lyra* is found to occur in upper most western parts of study area, in contrast to occurrences of *C. sphinx* (Fig. 4c). *P. ceylonicus* was confined to mid-upper eastern parts of the region (Fig. 4d). *P. giganteus* is observed to be more prominent in eastern regions, and additionally in southern parts of the study area (Fig. 4e). *P. tenuis* is predicted to exist in mid to upper eastern parts of the region (Fig. 4f). *R. leschenaultii* showed a similar habitat preference with that of *P. tenuis* (Fig. 4g). *S. heathii* was well distributed over the entire study area. Unlike *C. sphinx*, its distribution was not suitable in mid-south region of the study site (Fig. 4h). *T. melanopogon* exhibited a similar distribution structure like that of *M. lyra* (Fig. 4i).

Table 3 Descriptive statistics of variables

Variables	Min	Max	Mean	SD	Skew	SE
AI	0.07	0.11	0.09	0.01	0.29	0.00
ASP (°)	0.00	359.73	178.31	100.33	0.10	4.77
Mean diurnal temperature range (°)	8.10	11.30	10.01	0.65	− 0.75	0.03
Elevation (m)	23	1211	349.44	277.4	0.82	13.19
Global human footprint	15	84	30.28	10.65	1.61	0.51
Human appropriation of net primary productivity	15.16	629.49	59.67	56.12	4.27	2.67
Isothermality	40	46	42.85	1.35	0.45	0.06
Mean annual temperature (°C)	20.90	27.50	25.56	1.41	− 0.81	0.07
Annual precipitation (mm)	1194	1608	1415.74	100.82	− 0.25	4.80
Precipitation of coldest quarter (mm)	17	72	43.50	10.10	0.35	0.48
Precipitation of driest quarter (mm)	13	50	34.80	8.61	− 0.61	0.41
Precipitation of driest month (mm)	1	8	4.73	1.55	0.23	0.07
Potential evapotranspiration (ha/year)	1365	1711	1559.29	74.10	− 0.54	3.52
Precipitation seasonality (CV)	87	124	98.75	6.32	0.98	0.30
Precipitation of wettest quarter (mm)	230	381	311.31	34.58	− 0.02	1.64
Precipitation of warmest month (mm)	232	424	325.64	33.61	− 0.37	1.60
Precipitation of warmest quarter (mm)	230	381	311.31	34.58	− 0.02	1.64
Annual temperature range (°C)	17.80	27.40	23.16	1.93	− 0.66	0.09
Temperature of the coldest month (°C)	9	16	13.22	1.48	− 0.20	0.07
Temperature of coldest quarter (°C)	16.30	22.80	20.59	1.39	− 0.51	0.07
Temperature of driest quarter (°C)	16.30	22.90	20.71	1.37	− 0.53	0.07
Terrain ruggedness index	6	777.21	190.22	163.43	1.03	7.77
Temperature seasonality (CV)	277.50	421.70	354.89	35.53	− 0.19	1.69
Temperature of wettest quarter (°C)	21.10	28.70	26.75	1.65	− 0.92	0.08
Temperature of the warmest month (°C)	30.80	40.80	36.38	1.81	− 0.61	0.09
Temperature of warmest quarter (°C)	24.80	32.70	29.90	1.46	− 0.86	0.07

Significance of variables

The principal component analysis of respective species was evaluated to assess the significance of variables (Fig. 5). In general, elevation was predicted to be a significant determinant for their distributions. Its influence was positive except in case of *T. melanopogon*, where elevation showed negative effect. The mean annual temperature is found to have negative influence on their distributions, but in case of *T. melanopogon,* its relationship was positive. Potential evapotranspiration showed a significant effect in their distributions. The impact of this variable is less in *T. melanopogon*. The precipitation in driest quarter exhibited a negative influence on bat distributions except in case of *P. giganteus*, where the variable showed a positive influence. The mean annual precipitation is found to have positive influence on distributions of *C. sphinx*, *P. ceylonicus*, *P. tenuis*, *R. leschenaultii* and *T. melanopogon*. However, the mean annual precipitation exhibited negative correlation with distributions of *H. ater*, *M. lyra*, *P. giganteus* and *S. heathii*. The temperature seasonality showed a general positive correlation with bat distributions except in the distribution of *P. giganteus*, where it showed a negative correlation. The mean diurnal temperature and precipitation seasonality were predicted

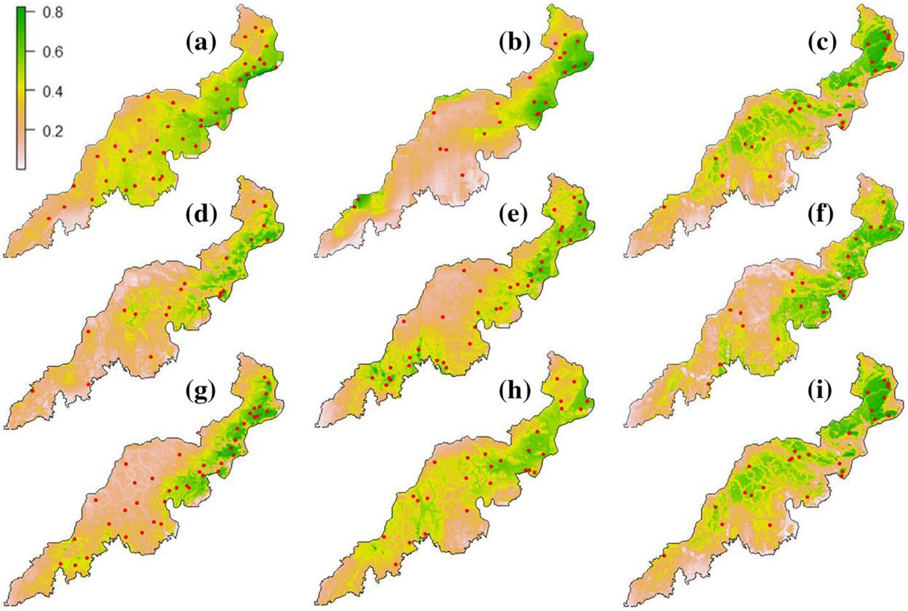

Fig. 4 Potential distribution maps of **a** *Cynopterus sphinx*, **b** *Hipposideros ater*, **c** *Megaderma lyra*, **d** *Pipistrellus ceylonicus*, **e** *Pteropus giganteus*, **f** *Pipistrellus tenuis*, **g** *Rousettus leschenaultii*, **h** *Scotophilus heathii* and **i** *Taphozous melanopogon* in eastern parts of the Eastern Ghats. Maps were derived by maximum entropy distribution modelling (Phillips et al. 2006). (Color figure online)

along the 2nd principal component axis and both exhibited positive correlation with bat distributions.

Discussion

The present study identified 23 bat species existing in the study area. This includes 12 species newly recorded along the Eastern Ghats in Odisha, and two species i.e., *H. galeritus* and *M. spasma* newly recorded for the Odisha state. The bat fauna of the hill ranges of Eastern Ghats of Odisha is more than 90% of the total bats of Odisha (Debata et al. 2016); and around 69% of the total bats of the Eastern Ghats (Dutta and Mohapatra 2017). Earlier studies reported 11 bat species in the Eastern Ghats of Odisha i.e., *C. sphinx*, *P. giganteus*, *R. leschenaultii*, *R. lepidus*, *R. rouxii*, *M. lyra*, *T. longimanus*, *T. melanopogon*, *P. coromandra*, *P. tenuis* and *S. heathii* (Das et al. 1993; Ramkrishna et al. 2006). The dominant presence of two bat families: Vespertilionidae and Hipposideridae corroborates with the earlier reports from the Western Ghats (Korad et al. 2007), Andaman and Nicobar Islands (Aul et al. 2014; Srinivasulu et al. 2017), and the Himalayas (Saikia et al. 2011). The dominance of both families has also been reported in tropical countries like Borneo (Struebig et al. 2012), China (Luo et al. 2013), Malaysia (Kingston et al. 2003), Thailand (Phommexay et al. 2011) and Vietnam (Furey et al. 2010). The dominant presence of insectivore species is in congruence with the tropical bat communities (Mickleburgh et al. 1992; Hutson et al. 2001).

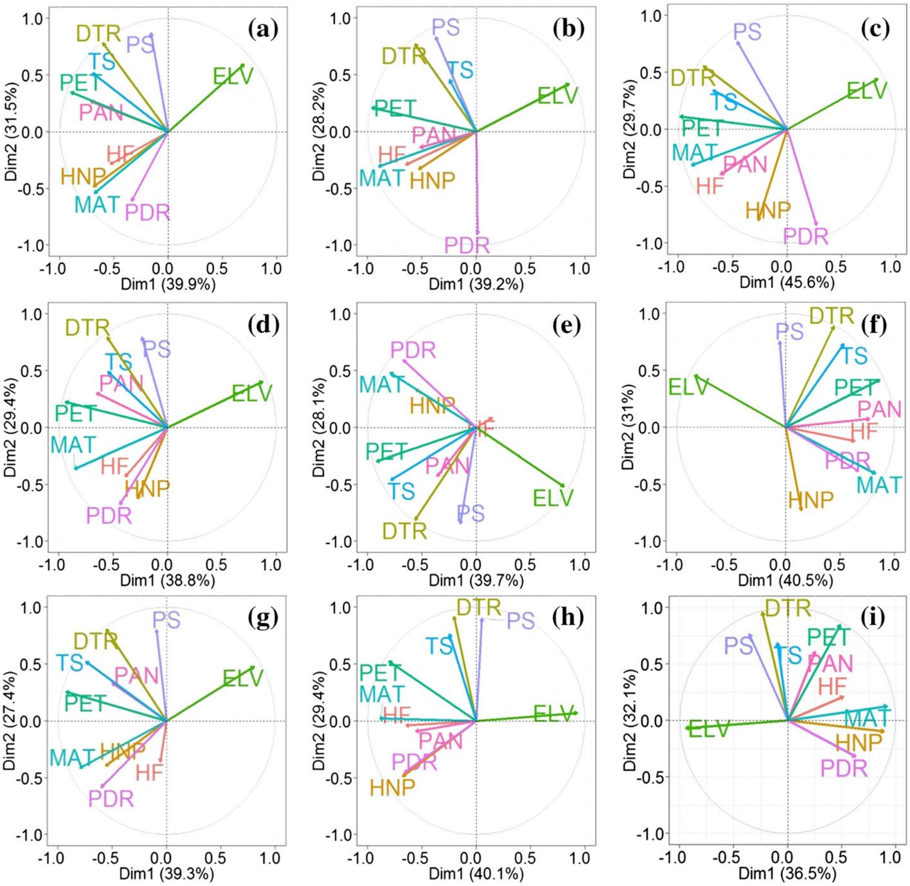

Fig. 5 Biplots showing coefficients of variables on principal components **a** *Cynopterus sphinx*, **b** *Hipposideros ater*, **c** *Megaderma lyra*, **d** *Pipistrellus ceylonicus*, **e** *Pteropus giganteus*, **f** *Pipistrellus tenuis*, **g** *Rousettus leschenaultii*, **h** *Scotophilus heathii* and **i** *Taphozous melanopogon*. Abbreviations are same as in Fig. 3. (Color figure online)

The frequency of bat capture rate was higher in the natural forest than that in anthropogenic habitats. It could be attributed to greater heterogeneity in natural habitats (moist deciduous forest, dry deciduous forest and semi evergreen forest) owing to multiple layers of stratification providing wide ranges of foraging niches for different species (Struebig et al. 2008; Deshpande 2012). The availability of food resources and availability of preferable roosting sites greatly influence bats and increase their presence in similar landscapes (Kingston 2010; Furey et al. 2010; Phommexay et al. 2011; Struebig et al. 2012). Loss of natural habitats due to human induced activities is a major threat to bats (Mickleburgh et al. 2002). It is in congruence with earlier studies that many bat species from Hipposideridae, Megadermatidae, Emballonuridae and Vespertilionidae families are true forest dwellers, and seldom occur in places of human habitation (Bates and Harrison 1997). However, the relative abundance of *C. sphinx*, *R. leschenaultii* and *S. heathii* was maximum in anthropogenic habitats. The availability of shrubs and bushes in the home gardens and across roadsides are preferred foraging sites for *R. lepidus*, a forest dwelling species.

R. lepidus, *C. sphinx*, *S. heathii*, *P. coromandara* and *P. tenuis* are highly abundant in the study area. Maxent predictions also reveal the same, i.e., *C. sphinx* and *S. heathii* are well distributed for the region (Fig. 5). These species are common to south Asia (Srinivasulu and Srinivasulu 2012) and in disturbed habitats (Bates and Harrison 1997). The availability of flowering and fruiting trees and agricultural crops attract insect pests, and it may attribute to assemblage of these bats in places of available food resources (Faria et al. 2006). In contrast, *S. saccolaimus*, *H. galeritus*, *H. lankadiva* and *T. melanopogon* showed less relative abundance indicating that they are habitat specialists preferring forests. *T. melanopogon* has comparatively less habitat suitability to the region. On the other hand, *P. tenuis*, *R. lepidus*, *T. melanopogon* and *M. lyra* exhibited similar distribution pattern. It may ascribe to their common feeding habits and climatic dependence. Probably due to the same reason, *H. ater* and *M. lyra* have different niche. However, further investigations are necessary to substantiate feeding habits and climatic dependence on their habitat preferences (Fig. 5).

In general, elevation is a significant determinant for chiropteran distributions. It indicates physiography has greater significance in their distributions. The availability of rocks and crevices could provide them to roost safely at elevated surfaces. The availability of forests might support their preferences at elevated regions. The low human interference at higher elevation also helps them grow safe. These findings corroborate with the earlier studies that elevation and habitat characteristics are reported to be significant determinants for chiropteran diversity (Arita 1993; McCain 2007). However, elevation has negative influence on the distribution of *T. melanopogon*, indicating its dependency on temperature. Unlike other species, the prediction showed its positive correlation with the mean annual temperature. Due to the same reason, potential evapotranspiration, which showed significant effects in distributions of other species, was less effective in the distribution of *T. melanopogon*. Overall, precipitation in the driest quarter showed a negative association with their species distributions, indicating significance of water availability during driest period. The positive influence of this variable in the distribution of *P. giganteus* might attribute to its efficiency to manage water stress better compared with other species. The positive influence of mean annual precipitation on distributions of *C. sphinx*, *P. ceylonicus*, *P. tenuis*, *R. leschenaultii* and *T. melanopogon* describe their water dependencies. However, the negative effects of the mean annual precipitation exhibited on distributions of *H. atar*, *M. lyra*, *P. giganteus* and *S. heathii* suggests their greater ability to manage water stress or less dependent on water. A general positive correlation between temperature seasonality and species distributions indicates their less vulnerability to fluctuations in temperature. The negative correlation between temperature seasonality and the distribution of *P. giganteus* could attribute to its inefficiency to regulate thermal stress due to fluctuations in temperature regime and climate change effects. The mean diurnal temperature and precipitation seasonality are positive determinants of species distributions, attributing to their resilience to seasonal precipitation changes and day time temperature fluctuations.

Conclusions

The study recorded 23 bat species. It includes the first distribution record of two species i.e., *H. galeritus* and *M. spasma* for the region. The bat capture rate was the highest in the moist deciduous forest describing higher bat diversity than in the places of human habitation. Use of Maxent could reveal the north eastern part of the hill ranges of Eastern Ghats of Odisha is more suitable for chiropterans. Elevation and potential evapotranspiration are significant determinants for their distributions except in the distributions of *T. melanopogon*, which showed negative correlation with both. The mean diurnal temperature and precipitation seasonality are positive determinants of bat species distributions, which may be attributed to their resilience to seasonal precipitation changes and day time temperature fluctuations. The negative effect of temperature seasonality on the distribution of *P. giganteus* could indicate its vulnerability to climate change effects. However, global studies on the impacts of climate change on bats are still at a preliminary stage and need further investigations. Inclusion of *H. galeritus* and *R. rouxii* as Nationally Threatened species by the Conservation Assessment and Management Plan of south Asian bats (Molur et al. 2002) is a major concern for conservation. The effects of climate change on the distribution of *P. giganteus* are also significant from conservation point of view. The present study generated baseline information on bat species distributions along the Eastern Ghats of Odisha; and could provide useful inputs for monitoring the future spatio-temporal changes and long term conservation measures.

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