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Past influences present: Mammalian species from different biogeographic pools sort environmentally in the Indian subcontinent

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Abstract. Diversity-environment relationships are distinct across species pools, and as a result species from different biogeographic pools have different environmental preferences. Regional communities are drawn from available biogeographic pools, subject to environmental and dispersal constraints. Does shared biogeographic history of taxa lead to similar relationships with the environment? We test this idea in the Indian subcontinent, which is at the confluence of multiple biogeographic regions resulting in species from multiple biogeographic pools being distributed here. Species were classified as belonging to four biogeographic affinities based on their geographic distributions: eastern, northern, western and endemic. We investigated spatial patterns of species richness for all mammals (over 1° x 1° grid cells), for each biogeographic group and for 5 major mammalian orders. Generalized Additive Models (GAM) were used to investigate environment-diversity relationship for all mammals, each biogeographic group, and for major mammalian orders in the Indian subcontinent. Species richness of all mammals was found to be highest in the montane regions of the Eastern Himalayas and the Western Ghats. Species richness of each biogeographic group was highest at the border it shared with Asia, in the direction of immigration from Asia. Environment and spatial variables were both correlated with species richness in the Indian subcontinent and each biogeographic group showed a distinct richness-environment relationship. Additionally, biogeographic groups sorted along environmental space, in keeping with our predictions based on their global distributions. Finally, analyses across mammalian orders had low predictive value, suggesting that shared phylogenetic history is relatively less important than biogeographic ancestry in determining relationships to environment. We conclude that historical factors such as immigration and the distinct evolutionary histories of species impact species richness patterns in the Indian subcontinent. Our results provide insights into drivers of regional community assembly in transition zones where multiple biogeographic species pools co-exist.

Keywords. Indian subcontinent, biogeographic species pools, mammals, endemics, biogeography, Himalayas

Introduction

Species diversity at continental scales is accumulated through speciation and historical immigration (Buschke et al. 2014). Species are also constrained by their environment, requiring adaptation. Speciation, adaptation and historical immigration together result in globally observed species richness gradients, and biogeographic patterns (Gaston 2000). Species belonging to a common biogeographic pool may show similar climatic preferences owing to their shared biogeographic histories, even if they are not phylogenetically related to each other. For instance both squirrel monkeys and three-toed sloths share a

preference for the tropical climates of S. America, despite not being closely related (IUCN 2013).

But how are species accumulated at regional scales? Local communities are sampled from the geographically proximate, larger-scale biogeographic species pool (Buschke et al. 2014, Cornell and Harrison 2014). Data suggests that different species pools interact uniquely with their local environments (Hawkins et al. 2003, Xu et al. 2016). Ecologists suggest that richness and composition of communities at local and regional scales are influenced by environmental filters and interactions within biomes or biogeographic regions (Cornell and Harrison 2014). Additionally,

competition and predation can also influence the presence of species in local communities. Studies focusing on local communities and regional pools tend to be purely ecological or biogeographic, and rarely synthesize these drivers.

Interactions between environmental filters and biogeographic species pools could be particularly relevant in regions where multiple biogeographic species pools overlap. In regions where species from distinct biogeographic pools overlap (such as transition zones; Ferro and Morrone 2014), relationships between species richness and environment can be contingent on biogeographic affinity of the constituent species, as taxa from different species pools may sort out in environmental space. By explicitly considering biogeographic affinity of taxa (i.e., the biogeographic pool they belong to), it is possible to account for history when examining the role of environmental factors in influencing species richness (Lavergne et al. 2006, Harrison and Grace 2007). Recent studies have used multiple analytical approaches to classify biogeographic source pools (Carstensen et al. 2013, Karger et al. 2016), providing a way to investigate the importance of biogeographic affinity and environment to local community assembly.

Apart from the impact that environmental factors (e.g., productivity, evapo-transpiration) have on smaller scale (regional and local) diversity gradients (Hawkins et al. 2003, Ding et al. 2006), other factors like dispersal could also be important. For example, dispersal limitation (the lack of dispersal from the ancestral range) restricts geographical ranges (Cooper et al. 2011). Most species may be unable to colonize suitable habitats very far from their centre of diversification either because they cannot get there, or because the environment is inhospitable. In summary, it is important to disentangle the effects of environment, dispersal limitation and biogeographic affinity on regional species richness gradients.

The Indian subcontinent is at the junction of three biogeographic regions, and although part of the Oriental biogeographic realm, the species pool in the Indian subcontinent is influenced by the surrounding biogeographic pools, such as Saharo-Arabian (Mani 1974). Past climatic transitions,

such as the aridification reported in the late Miocene in western parts of the region, provided opportunities for species to extend their ranges into the Indian subcontinent from the surrounding regions. There is evidence for movement from Africa and the Palaeartic regions into the subcontinent during the Miocene (Neogene) (Wang et al. 2013). Unfortunately the fossil record in the Indian subcontinent is very poor (especially the Neogene mammal fossil record), making it hard to make conclusive inferences. Additionally, many species are also restricted to the Indian subcontinent, and little is known in terms of their evolutionary history. Thus, in addition to endemic species, the Indian subcontinent also shares species with the species pools around it, including the Oriental, Palaeartic and the Saharo-Arabian species pools. This renders the Indian subcontinent a good place to test if shared biogeographic affinities could lead to similar environmental relationships and if different biogeographic groups occupy distinct environments.

To understand if biogeographic history impacts patterns of species richness in the Indian subcontinent, we assigned species to 'biogeographic groups' based on their distributional ranges. We examined spatial patterns of species richness for each group. The richness of each biogeographic group was expected to be highest at the border of the Indian subcontinent with Asia, as most genera show higher richness outside the subcontinent than inside. We investigated whether biogeographic groups differ in the climatic space that they occupy, by determining the relationship between species richness and environment for each group. Each biogeographic group was predicted to occupy distinct climate spaces because shared biogeographic history should result in shared environmental preferences. Finally, we compared the richness-environment relationships for null communities and for all five mammalian orders to investigate impacts of spurious correlations and phylogenetic effects. Null models are increasingly being used in biogeography to explicitly include the effects of geometry on species distributions (Gaston 2000, Diniz-Filho et al. 2002, Rahbek et al. 2007) improv-

ing our understanding of the factors driving richness patterns.

Methods

Geographical extent

All regions to the south (and inclusive) of the Himalayan mountain range including the political entities of India, Bangladesh, Sri Lanka, Bhutan, Nepal and Pakistan were considered as part of the Indian subcontinent.

Spatial data

Mammal data. The geographical ranges of 358 species of terrestrial non-volant mammals reported from the Indian subcontinent were obtained from an open-access source (IUCN 2013). Out of these species, the subset belonging to the genera *Mus*, *Bandicota* and *Rattus* were excluded as they are commensal with humans, and may affect the patterns we find.

Environmental data. Mean, minimum and maximum annual temperature, mean precipitation, net primary productivity, aridity, habitat diversity, and surface area of each cell were used in this study to quantify the environmental niche of a species. Data for temperature and precipitation were derived from the WorldClim dataset (Hijmans et al. 2005). Net primary productivity was obtained from the Advanced Very High Resolution Radiometer (AVHRR; Prince and Goward 1995). Aridity index—a ratio of the mean annual precipitation to the mean annual evapotranspiration—was derived from the datasets originally provided as part of the WorldClim database, and relates to the rainfall deficit for vegetation growth and the effective evapo-transpiration (Zomer et al. 2008). Habitat diversity was calculated as the number of unique ecoregions per cell based on the terrestrial ecoregions map (Olson et al. 2001). Elevational data was derived from the GTOPO-30 digital elevation maps. Surface area of each cell (discussed in Rahbek et al. (2007)) was calculated based on GTOPO-30 digital elevation model using a freely available extension

for ArcView.

Assigning biogeographic affinities

To assign species to biogeographic groups, for each species we first identified the biogeographic region (eastern, western and northern, Supplementary Figure 1) in which >50% of the species' geographic range overlaps (Bruzgul and Hadly 2007). This was assigned as the biogeographic affinity for the species. Then, each genus was assigned the affinity that was shown by the majority of its constituent species. This affinity was then used to re-assign affinities of the species. In most cases, all species of a genus showed the same affinity, making the assignment straightforward. For a few genera, the species showed different affinities, with no clear majority, making the assignment difficult. These were marked as unclassified (see Supplementary Information).

We used this assignment criterion since individual affinities for species may not be a sufficient indicator of the evolutionary environmental preference of the species, and a higher order classification may be more indicative of that (such as genus or family). Moreover, species within a lineage (or genus) largely show related climatic tolerances and tightly coupled niche and dispersal limitations (Ulrich et al. 2009, Olalla-Tárraga et al. 2011). Hadly et al. (2009) and DeSantis et al. (2012) demonstrate the relative constancy of geographical range sizes in North American mammals suggesting that important ecological and range-related traits are conserved above the species level. Additionally, contemporary species distributions may not be in equilibrium with their environment, and may be influenced by factors other than environmental preference including hunting and habitat loss.

In summary, genera were assigned to one of four groups: 'Eastern' (with distributions predominantly in Southeast Asia and Indo-China), 'Northern' (Palaeartic), 'Western' (arid west Asia and South Asia) and 'Endemic' (restricted to the Indian subcontinent). Note that we use 'eastern', 'western' and 'northern' to denote biogeographic groups created in this study and to differentiate them from the Biogeographic regions Palaeartic,

Oriental and Saharo-African (Holt et al. 2013).

Data analysis

Analyses were conducted at three scales: (1) for all mammals considered together ('all mammals'), (2) separately for the different biogeographic affinities ('biogeographic groups') and (3) separately for five mammalian orders (Rodentia, Soricomorpha, Carnivora, Artiodactyla and Primates). Biogeographic groups consist of species that are not necessarily related to each other, but potentially share a common biogeographic origin. Species from many different orders can be part of a biogeographic group. This is in contrast to members of an order that are more closely related to each other and share a relatively recent ancestor, but may not belong to the same biogeographic group.

What are the species richness patterns in the Indian subcontinent? To obtain counts of species richness, we counted all species with overlapping ranges within each grid cell, even if the range encompassed only 5% the cell. This was done since mammal geographic ranges derived from IUCN are coarse at best and the exact range boundaries are uncertain; the actual range boundary could lie anywhere within a cell. Species richness was the fundamental response variable used in the modeling in this study, and no statistical analyses were conducted at the level of genera. The spatial patterns in species richness were then plotted for each group. We also identified the number of species belonging to each group within a cell, and coloured cells based on which biogeographic group had most species present there.

What are the richness–environment relationships for the different groups? We modeled species richness with environmental predictor variables in a GAM framework. Prior to this, we accounted for multicollinearity and spatial autocorrelation.

Multicollinearity increases variance of estimated coefficients and could result in inflated parameter estimates. We reduced multicollinearity by removing variables contributing to high variance. We did this in two ways. First, we calculated

the variance inflation factor (vif, quantifies inflation in parameter estimates due to multicollinearity (Guisan et al. 2002)), and removed all variables with a vif greater than 3. We did this in a recursive manner, until only variables with $vif < 3$ remained. The vif method reduced the number of variables in our dataset, some of which were initially selected since we thought they might be biologically relevant. Second, we conducted Principal Components Analyses (PCA) for all environmental variables considered in this study, to identify the environmental space that may best discriminate species' responses.

Spatial autocorrelation violates the assumption of independence, central to the regression analysis. We used Moran's I values at ten different distance classes to detect spatial autocorrelation. We then included spatial factors as smoothed terms in subsequent modeling (GAMs, see below), allowing us to explicitly incorporate spatial factors in investigating species responses.

Simple predictor variables, temperature and precipitation were also used in addition to vif and PCA reduced variables. Temperature-precipitation is an intuitively easy way of thinking of environmental space (Bonetti and Wiens 2014), because we can make predictions about species' response. We predicted that the eastern group would show positive relationship to both temperature and precipitation, the western group would show positive relationship to temperature but negative relationship to precipitation, and the northern group would show negative relationship to temperature and positive to precipitation. We did not have any specific predictions for the endemic group.

GAMs, assuming a 'Poisson' error distribution, from the package *mgcv* (Wood 2006) were used to model species richness (response variable) as a function of the different groups of predictors. We chose GAMs (Zupan et al. 2014) to account for spatially autocorrelated response distributions. We built models with three sets of predictor variables: (1) final variables selected after vif analyses, (2) PCA analyses, and (3) mean temperature and average precipitation, as these represent *simple predictors* of environmental space. Using different sets of predictors (Pausas et al.

2003) add to better understanding of the richness-environment relationships. We also ran geography-only models (as GAMs) as proxy for the effects of dispersal limitation (Eiserhardt et al. 2013). High explanatory power for geographic distance (or 'geography') indicates the influence of dispersal limitation in driving the observed patterns.

What is the environmental space occupied by each biogeographic group? We quantified environmental space (as defined by temperature and precipitation) occupied by each group. For each species, we obtained the average, minimum and maximum temperature and precipitation across the geographic range within the Indian subcontinent. We then plotted these distributions for the different biogeographic affinities. We repeated with the first principal component by summarizing the average PC score for each species across its range, and then plotting the average scores of each of the biogeographic groups.

Null model analyses. Since the Indian subcontinent is a peninsula, geometric constraints (in addition to climatic preferences) may drive the observed distribution patterns of mammals (See Gaston (2000) for brief discussion, Rahbek et al. (2007)). Null models, simply assume an association between the size and placement of the geographical ranges (within a region) without considering environmental gradients. To quantify the influence of random placement of geographical ranges (with no underlying environmental preferences), we built null models. We retained species range areas (in terms of numbers of cells), but placed them randomly within the bounds of the Indian subcontinent. These are similar to 'range cohesion' or 'spreading dye' models (Rahbek et al. 2007) and assume that ranges are continuous without holes (i.e., all the adjacent cells within range limits were occupied). A species was first assigned to a randomly selected cell, and then the range was extended to the observed value of range size for the species, by randomly selecting any one of the adjacent cells at a time. The environmental space for the randomly distributed spe-

cies was calculated in the same manner as for the observed data. Randomization was repeated 100 times. Observed and null distributions were compared by plotting smoothed frequency histograms. All analyses were carried out in *R* (R Core Team 2014). The function for generating null distributions can be obtained from the package *rangemodelR* v0.1¹.

Results

We were able to assign genera to four biogeographic groups based on distributions: 'Eastern' (47 genera), 'Western' (11 genera), and 'Northern' (47 genera) species and 'Endemic' (22 genera). We were unable to classify 27 genera into any biogeographic group as they had large distributional ranges; many being monotypic (genera with one one species). These were analysed separately to examine if they deviated from the observed patterns (Supplementary Information).

Species richness patterns in the Indian subcontinent

Mammal species richness (SR) is highest in the Himalayas, especially in the Eastern Himalayas with 120–140 species (Figure 1a). The Western Ghats is also very species rich with 80–100 species, although considerably less so than that of the Eastern Himalayas. Peninsular India shows much lower richness, followed by Western India that shows the least richness. Species richness of each group (eastern, western, and northern) is highest close to the border of the Indian subcontinent (with Asia) with which it shares species (Figure 1b–d). For instance, species richness for western species is highest in the west, along the western boundary of the Indian subcontinent (with about 8–11 species), while that of the eastern species is highest along the northeastern parts of the Indian subcontinent (with 50–55 species). In contrast, endemic species richness is highest in peninsular India, away from the borders of the Indian subcontinent. Highest endemic richness is observed in the Western Ghats (Figure 1e).

Figure 1f shows which species dominate

¹ <https://cran.r-project.org/web/packages/rangemodelR/index.html>

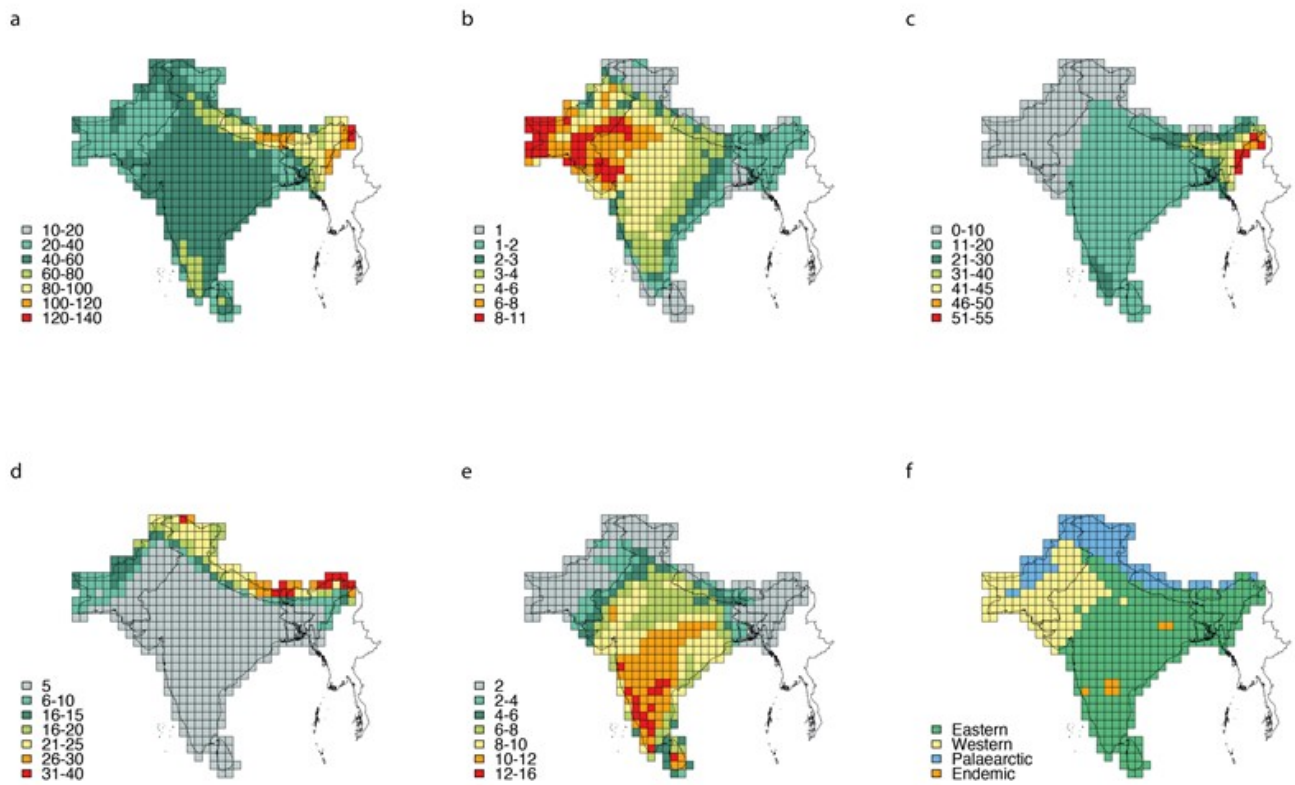


Figure 1. Species richness of mammals in the Indian subcontinent. Species Richness of (a) all mammals (b) Eastern, (c) Western, (d) Northern (e) Endemic and (f) Group with the highest proportion of species in each cell (see below). The total species richness for each group are different - this is reflected in the legend for each group. 1a: displays the direction (with respect to the Indian subcontinent) of the three biogeographic groups - Eastern, Western and Northern. 1f: The proportion of each group in each cell was calculated, and the cells are coloured based on the group with the highest proportion. This group dominates the community in each cell.

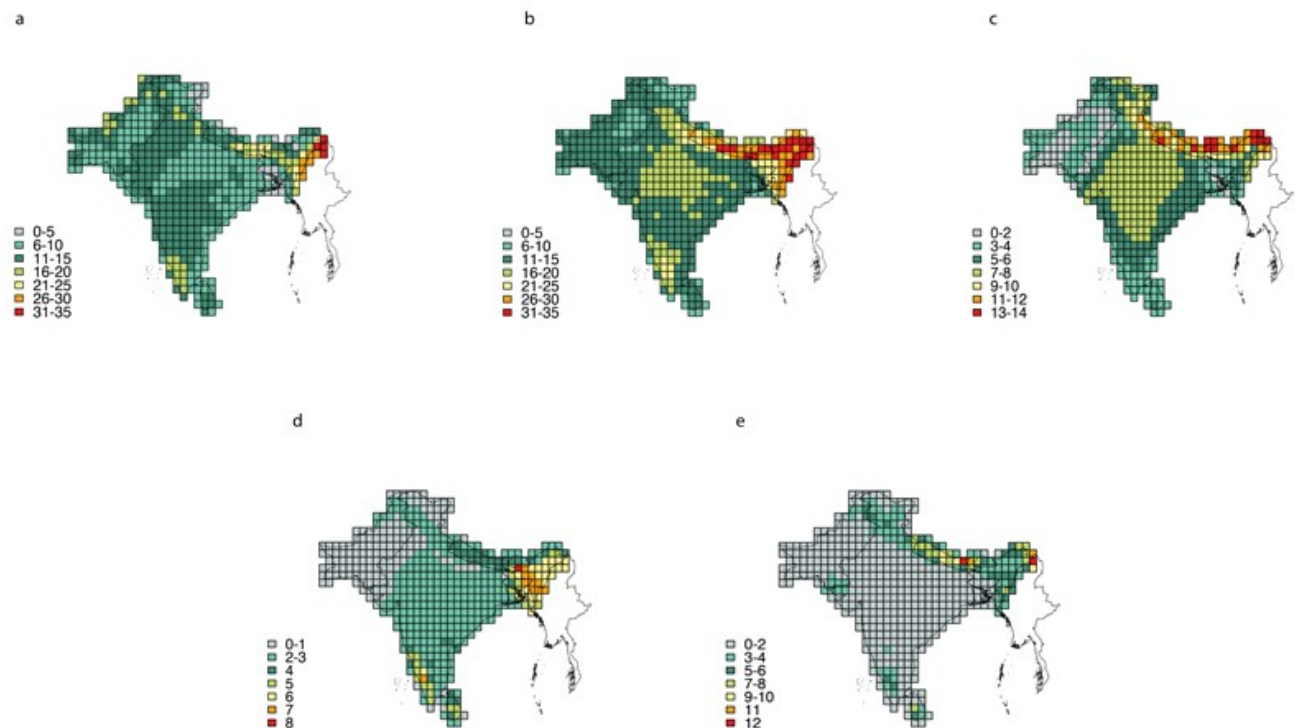


Figure 2. Species richness of mammalian orders in the Indian subcontinent. Species richness of the mammalian orders (a) Rodentia (b) Carnivora (c) Artiodactyla (d) Primates (e) Soricomorpha. The total species richness for each group is different - this is reflected in the legend for each group

communities locally across the subcontinent. Western parts of the subcontinent (where the western species richness is highest) are dominated by these species, while the Himalayas are dominated by the northern species. Most of subcontinent is dominated by species belonging to the eastern group. Very few cells showed high numbers of endemic species. Species richness for each order shows patterns similar to the 'all mammal' patterns within the Indian subcontinent (Figure 2).

Biogeographic groups differ in their relationships to environment factors

Environment and space together were very good predictors of species richness for all mammals. Within each of the biogeographic groups, they explained more than 90% of the variation in species richness (with the exception of the western group) (see deviance explained in Table 1). Biogeographic groups differed in their relationships to environmental variables, irrespective of the predictor variables used (vif-reduced, PCA or only temperature-precipitation).

Temperature-Precipitation models: The eastern group shows a significant positive relationship to precipitation, while the western group shows a negative relationship with precipitation (Table 1). The northern group shows a negative relationship with temperature, as predicted. The endemic

group does not show strong significant relationship with either of the environmental variables.

Vif reduced variables: The final set of variables included based on vif < 3 were (measured for each cell in the dataset) net primary productivity, Maximum Elevation, Surface area (to control for undulating landscape), Habitat diversity and Aridity index. Biogeographic groups show distinct relationships to environmental variables (Table 1). Primary productivity is a significant predictor for all mammals, and for the eastern group. Surface area of the cell is a significant predictor of the western group, but not for northern/paleartic, where diversity is highest at high elevations. Habitat diversity is a significant predictor for the northern and the eastern groups, while aridity was significant for all except the western groups. Maximum elevation was a significant predictor for all groups.

PCA variables: The first principal component axes had high explanatory power (93.6%). The model results when the first component of the PCA was used are similar to the other results, with high explanatory power to the models (see model summaries in the Supplementary Information).

Table 1. Model summaries for the different generalized additive models built to determine the diversity-environment relationship for the various predictor combinations and the groups. All values are the actual parameters from the models, and have not been inverse transformed. The numbers in bold refer to significant results. The first six columns reports the model summaries for models that used the individual environmental variables (Npp - Net Primary Productivity, Ema - Max. Elevation, S - Surface area, H - Habitat diversity and A - Aridity Index). The last three columns represent the model summaries when temperature and precipitation were used as the predictors.

Group	Deviance explained (in %)	Individual environment variables (vif reduced)					Temp-Prec space		Deviance explained (in %)
		Npp	Ema	S	H	A	Temp	Prec	
All mammals	91.4	3.56x10 ⁻³	>0.01	>0.01	1.41x10 ⁻²	>0.01			
Eastern	95.5	5.95x10 ⁻³	>0.01	>0.01	1.67x10 ⁻²	>0.01	0.0014	0.0015	92.6
Western	86.2	1.12x10 ⁻³	>0.01	>0.01	1.60x10 ⁻²	>0.01	0.0409	-0.0018	86.3
Palaeartic	95.3	-6.20x10 ⁻⁴	1.38x10 ⁻⁴	>0.01	2.03x10 ⁻²	>0.01	-0.0334	0.0034	93.7
Endemic	93.5	4.66x10 ⁻³	>0.01	>0.01	1.38x10 ⁻²	>0.01	0.0022	0.0006	91.3

Geographic distance (proxy for dispersal limitation) also shows high R^2

Geographic space had a higher explanatory power (Table 2) than environmental variables for all groups, when the two were considered independently. The details of the model summaries are provided in Supplementary Table 2.

Table 2. The explanatory power for geography (space) versus environment for mammal species diversity patterns in the Indian subcontinent using the first component of the principal axes. Goodness of fit measures, R^2 , are used as an indication of the explanatory power, and are expressed in %

Group	PC axis	
	Geography	Environment
All mammals	43.1	3.76
Eastern	66.08	7.54
Western	46	20.25
Palaeartic	68.8	21.5
Endemic	33	12.5

Mammalian orders

The mammal orders also differed in their relationships to environmental variables, when the vif-reduced variables were chosen (Table 3). These models also had lower explanatory power (R^2) than the corresponding models for the biogeographic groups (Table 1). Across orders, maximum elevation and aridity index (except for Artiodactyl-

la) were consistently important predictors of species richness. For Rodentia habitat diversity, for Carnivora net primary productivity and habitat diversity, for Primates primary productivity and for Soricomorpha surface area and habitat diversity are important predictors.

Biogeographic groups sort in environmental space

The environmental space occupied by each of the biogeographic groups is distinct (Figure 3a,b) for both mean temperature–precipitation space and first PCA across the range of each species in every biogeographic group. The environmental niche space occupied by the biogeographic groups mirrors the results of the environmental regression models, and is consistent with our predictions. For instance, the northern groups occupy a low temperature niche space, thus sorting from the other groups that seem to occupy a mid- to high-temperature space.

Observed distributions differ from null expectations of occupied climate space

Observed climate space distributions of the biogeographic groups differed from climate space distributions based on random species ranges in at least one environmental parameter (Figure 4). Specifically, for the eastern group, the observed distribution was different from random for both temperature and precipitation. The western group tended to occupy drier areas than random, while

Table 3. The model summaries for all the Orders. R^2 is used as an indication of the explanatory power, and expressed in %. All numbers in bold refer to significant results.

Group	% Deviance explained	Individual environmental variables				
		Net primary Productivity	Maximum elevation	Surface area	Habitat diversity	Aridity Index
Rodents	74.7	3.26×10^{-3}	>0.01	>0.01	1.65×10^{-2}	>0.01
Carnivora	89.1	3.51×10^{-3}	>0.01	>0.01	1.39×10^{-2}	>0.01
Artiodactyla	85.4	3.62×10^{-4}	>0.01	>0.01	1.36×10^{-2}	>0.01
Primate	80.8	9.78×10^{-3}	>0.01	>0.01	1.68×10^{-2}	>0.01
Soricomorpha	73.8	2.14×10^{-3}	1.43×10^{-4}	>0.01	3.32×10^{-2}	>0.01

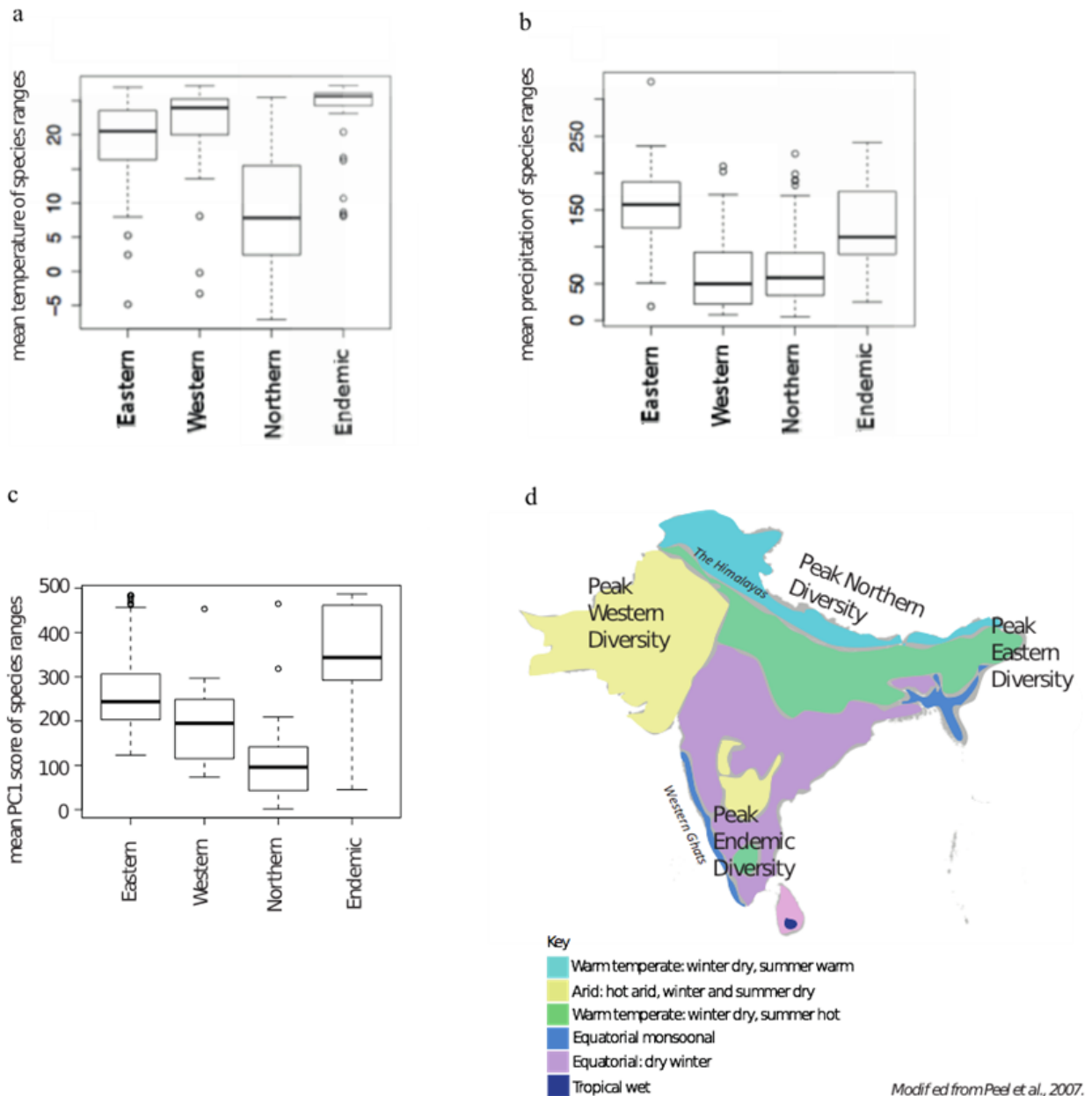


Figure 3. Environmental sorting of mammal groups in the Indian subcontinent. Biogeographic groups sort along (a) temperature and (b) precipitation space. Each boxplot represents the mean temperature/precipitation space occupied by each species in each of the groups. (c) Biogeographic groups sort along a composite environmental space (PC axis). (d) An illustration of the Koppen climate space in the Indian subcontinent, with the center of diversity for each group in the subcontinent overlaid on the climate map.

northern groups tended to occupy colder areas than random. The endemic group overlapped well with the random environmental space.

Discussion

Species richness is highest in the montane regions

Montane regions are known to harbor high diversity due to their topographic heterogeneity, and this is true in the Indian subcontinent as well (reviewed in Ghalambor et al. (2006)). Species

richness in the Indian subcontinent, when all mammals are considered together, peaks in the montane regions of Himalayas (especially Eastern Himalayas) and in the Western Ghats (Figure 1a). Western India and parts of peninsular India are characterized by arid and semi-arid ecosystems which are associated with lower diversity, as observed with our data as well. The geographic location of the Indian subcontinent and subsequent movement of mammals from Asia has left a strong signature in the distribution of mammal diversity

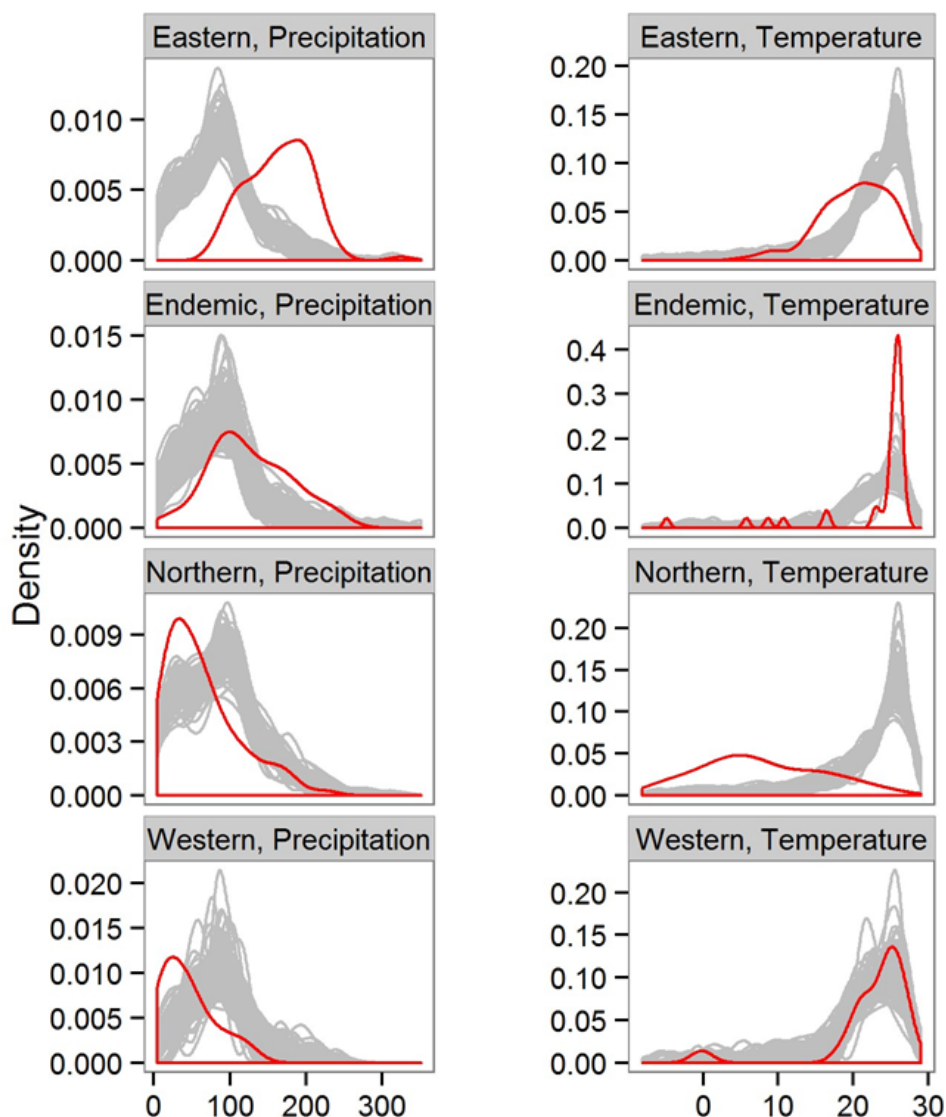


Figure 4. Observed and null distributions of climate spaces for the biogeographic groups. The null distributions describe the spurious correlations with climate due to geometric constraints. The deviation of the empirical climatic spaces from the null represents the non-random associations of biogeographic groups with climate. For each group we have plotted the kernel densities of the distribution in climate space based on random placement of the ranges of the constituent species, in gray. The empirical distribution in climate space is denoted by the red curve.

in the subcontinent and the species richness of each biogeographic group reflects this. The richness of each group peaks along the border of the Indian subcontinent with the region with which species are shared (Figure 1b, 1c, 1d). For instance, western species richness peaked along the western boundary of the Indian subcontinent; many western species had ranges that extended into west Asia (e.g., *Tatera indica*, the Indian gerbil). Similarly, the species richness of the eastern group peaks along the eastern boundary of the Indian subcontinent with Asia; many eastern spe-

cies have ranges that extend into south China, Myanmar and Southeast Asia (e.g., *Catopuma temminckii*, Golden cat).

Most of the modern families of mammals evolved during the Paleocene (Meng and McKenna 1998), during which time the Indian plate was not yet part of the Asian landmass. It is widely thought that many mammals moved to the Indian subcontinent from Central Asia (and not from the Indian subcontinent into Asia) (Bown and Rose 1990). Some authors challenge this paradigm with respect to Artiodactyls (Rose 1996), although

there are very few Paleocene mammal fossils recorded from the Indian subcontinent (Rose et al. 2014). Subsequent to the collision, especially during the Miocene, there were many instances of movement of mammals from northern Asia and the Afro-Arabian regions (African and Eurasian faunal elements). Fossil deposits from Kutch, West India, suggest faunal exchange between Afro-Arabian regions and the Indian subcontinent during early Miocene (Bhandari et al. 2010). Others have suggested a mixture of Southern-Russian and African forms in the Indian subcontinent. We suggest that historical processes, such as immigration from a source pool and niche constraints may have influenced the spatial patterns of diversity and distribution in the Indian subcontinent. While evidence and understanding of historical immigration on macroecological patterns has been shown from North America (Morales-Castilla et al. 2012), our knowledge for the Indian subcontinent remains poor from a paleontological perspective. From a phylogenetic perspective, genetic data suggests that macaques expanded their ranges into the Indian subcontinent (Chakraborty et al. 2007). Knowledge about the timescale of these migrations into the subcontinent remains poor.

Spatial and environmental niche based sorting in the Indian subcontinent

The spatial gradients of species richness in the Indian subcontinent (for all mammals, and biogeographic groups) could be a result of two processes: environmental niche based sorting (Gravel et al. 2006) and spatial limits on distributions of species. Our results demonstrate that both geography (space) and environment influence the distribution of diversity in the subcontinent, consistent with results from other studies (Özkan et al. 2013), indicating that both niche-based and neutral processes may be involved in assembling diversity here (Rominger et al. 2009).

Except for the eastern group, environment is a good predictor of species richness patterns for all biogeographic groups (including endemic). Further, the environment-richness relationship is more pronounced (higher R^2 values) in the case of the biogeographic groups than mammalian or-

ders, suggesting a tighter coupling of biogeographic groups to their environments. The different biogeographic groups occupy distinct environmental spaces (Figure 3), consistent with our predictions for the temperature-precipitation space based on the environments that most species are exposed to outside the Indian subcontinent. For instance, western species show a positive relationship to temperature that is consistent with their distributions and known history. These species inhabit arid and semi arid regions both inside and outside the subcontinent, and thus as expected, show positive relationship to temperature. The results remain consistent even when other environmental variables were included. Null models that remove associations of species to climatic variables further validate this inference.

Our null model analyses allowed us to simulate communities where relationships with climate could arise spuriously, or by geometric constraints on range size. These null models represent climate spaces occupied by species based on the random placement of ranges within the Indian subcontinent, and any deviation from the null distributions suggests a non-random association with environment. In the Indian subcontinent, we find a non-random association of mammal ranges with environment, since the observed distributions in climate space deviated from the null distributions. In Figure 4, the modal positions of the distributions are different. The modal positions are also different between the different groups supporting our results from the GAMs, showing that the different groups occupy distinct environmental spaces. Together, our results from the GAMs and the null analyses suggest that different biogeographic groups occupy distinct environmental spaces (although there is overlap, since many species are also found in central India).

We propose that shared biogeographic history could result in similar climatic niche spaces for species within the Indian subcontinent. Taken along with a pattern of immigration for mammal species into the Indian subcontinent, this could indicate some conservatism in trait space across space and time for mammals within the Indian subcontinent. Addi-

tionally, this implies that species with shared biogeographic histories show similarity in climatic spaces, even if they are not closely related genetically (which is necessary condition for phylogenetic niche conservatism). Importantly, the conservatism that we seem to observe is historical than phylogenetic. It is possible that that within genera, there could be additional evidence for phylogenetic niche conservatism. Thus the results of our study do not follow the commonly accepted definition for phylogenetic niche conservatism.

Geography is also a good predictor of the spatial patterns of species richness in the Indian subcontinent. For all mammals, and for eastern group, geography had more explanatory power than environmental variables. The eastern group as a whole has a much larger distribution and richness than the other groups, and is found across different climate spaces, which may result in weak relationship to environment. This wide distribution results in geography being a better predictor of spatial patterns in species richness than is environment. For the other groups, the explanatory power of geography could potentially reflect dispersal limits to species distributions. This is consistent with many other studies that show dispersal limitation also being an important correlate of diversity distributions (Myers et al. 2013). An additional reason for the high explanatory power for geographic space could be the strong spatial pattern for climate and habitat in the Indian subcontinent (Figure 3C). If species are indeed tracking their environments then they will also show strong spatial signatures. Cooper et al. (2011) partitioned niche conservatism into spatial and phylogenetic components, and observed that spatial effects drove the patterns of niche conservatism in mammal environmental niches. Without underplaying the role of phylogeny, their results suggest that species ranges tend to aggregate in similar environmental spaces due to lack of dispersal from ancestral ranges. Thus, all three scenarios are consistent with high explanatory power of spatial components.

Endemics distributed mainly in peninsular India

Endemic mammals, distributed mostly in peninsular India (reaching a peak richness in the Western Ghats) (Figure 1e), occupy an environmental space that is distinct from the other three biogeographic groups (Figure 3). Many of these endemic genera are monotypic (e.g., *Madromys*, *Golunda*) although some are speciose (e.g., *Funambulus*; Wilson and Reeder 2005). In many cases, their relationships to other lineages are not clearly resolved in phylogenies published so far (e.g., Schenk et al. 2013), and resolving their evolutionary history will shed light on the origin of their niche preference. One possible scenario is that endemic genera represent lineages that diverged from ancestors derived from the other biogeographic groups. This divergence, driven by isolation, could have resulted in the observed geographic (and environmental) distribution of the endemic lineages. Alternatively, they could represent older lineages, which may have an independent evolutionary history compared to the species that are shared with other regions in Asia. Based on what is known of the history of mammal evolution and the fossil record from the Indian subcontinent (Wang et al. 2013) so far this scenario seems unlikely. It is possible that the endemic lineages represent older immigrants into the Indian subcontinent, followed by range expansions of the other groups.

We could not assign affinities to 27 genera (with a total of 72 species); these species also show diversity patterns that are consistent with what we observe for all the groups so far with high species richness in the Himalayas followed by the Western Ghats (Supplementary Figure S2). Additionally, environment (specifically surface area of the cell) is an important correlate of this richness gradient (Supplementary Information).

In this study we limit ourselves to quantifying and studying the environmental niche of a species as reflected by its geographic range (realised environmental niche) within the Indian subcontinent. Greater insights can be gained by looking at the environmental space occupied by species across their range, and by incorporating phylogenetic measures of trait evolution (Terribile et al. 2012). Unfortunately, the geographical ranges of

species across taxonomic groups are coarsely defined within the Indian subcontinent. Developing better range maps will aid in better definition of the environmental niches of species. We used species distribution maps to classify species into biogeographic groups. It would be ideal to use other means of reconstructing their biogeographic affinity, including fossil data and phylogenetic reconstructions of ancestral ranges. We are confident that our classification will reflect those that will be obtained through these other classifications. We were not able to classify some taxa because of no distinct patterns of distributions of the species. For such groups, which are currently not included in any of the groups, it will be important to get phylogenetic data to classify them correctly.

In summary, we demonstrate strong spatial patterns in the distribution of mammal species and biogeographic groups in the Indian subcontinent. High predictive power of spatial and environmental variables suggests that both are equally important in determining species distributions. Different biogeographic groups show distinct environment-diversity relationships. Our study demonstrates that in addition to contemporary environment, historical factors influence the observed spatial richness patterns in the Indian subcontinent. Species from distinct species pools may interact with their environments in unique ways. We provide predictions for regions which can be colonized by species from multiple species pools, and expect that historical factors could predispose bias species' response to available environmental space, impacting the assembly at diversity at smaller spatial scales.

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Author Contributions

KT and UR conceived the study, KT and AM did the analysis, KT, AM and UR wrote the paper. The authors declare no competing interests.

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