Jins, V. J., Panigrahi, Madhumita, Jayapal, Rajah and Bishop, Tom R. 2021. Elevational gradients of reptile richness in the southern Western Ghats of India: Evaluating spatial and bioclimatic drivers. Biotropica 53 (1) , pp. 317-328. 10.1111/btp.12878

Publishers page: https://doi.org/10.1111/btp.12878

Elevational gradients of reptile richness in the southern Western Ghats of India: evaluating spatial and bioclimatic drivers

VJ. Jins*[1], Madhumita Panigrahi[2], Rajah Jayapal[3] and Tom R. Bishop[4,5]

[1] *Department of Zoology, Sikkim University, Gangtok-737102, Sikkim, India*
[2] *Bombay Natural History Society, Hornbill House, Mumbai-400001, India*
[3] *Sálim Ali Centre for Ornithology & Natural History, Coimbatore-641108, Tamil Nadu, India*
[4] *Department of Earth, Ocean and Ecological Sciences, University of Liverpool, Liverpool L69 3GP, UK*
[5] *Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa*

*Correspondence: VJ. Jins, Department of Zoology, Sikkim University, Gangtok-737102, Sikkim, India. Email: jinsvj@gmail.com

ORCID of all authors:
V.J, Jins- https://orcid.org/0000-0001-8000-720X
Madhumita Panigrahi- http://orcid.org/0000-0002-9502-5424
Rajah Jayapal- https://orcid.org/0000-0003-3656-541X
Tom R. Bishop- https://orcid.org/0000-0001-7061-556X

ABSTRACT

Exploring elevational patterns in species richness and their underlying mechanisms is a major goal in biogeography and community ecology. Reptiles can be powerful model organisms to examine biogeographical patterns. In this study, we examine the elevational patterns of reptile species richness and test a series of hypotheses that may explain them. We sampled reptile communities along a tropical elevation gradient (100-1500 m a.s.l.) in the Western Ghats of India using time constrained visual encounter surveys at each 100m elevation zone for a period of three years. First, we investigated species richness patterns across elevation and the support of mid-domain effect and Rapport’s rule. Second, we tested whether a series of bioclimatic (temperature and tree density) and spatial (mid-domain effect and area) hypotheses explained species richness. We used linear regression and AICc to compare competing models for all reptiles and each of the subgroups: snakes, lizards and Western Ghats’ endemics. Overall reptile richness and lizard richness both displayed linear declines with elevation which was best explained by temperature. Snake richness and endemic species richness did not systematically vary across elevation, and none of the potential hypotheses explained variation in them. This is the first standardized sampling of reptiles along an elevational gradient in the Western Ghats, and our results agree with the global view that temperature is the primary driver of ectotherm species richness. By establishing strong reptile diversity-temperature associations across elevation, our study also has implications for the impact of future climate change on range-restricted species in the Western Ghats.

Data availability statement: Data used in this study will be archived in Dryad, as per the Biotropica policy. Code for analyses will be supplied with datasets.

Keywords: Herpetofauna, altitude, mid-domain effect, Rapoport’s rule, range size, distribution patterns, Agasthyamalai Biosphere Reserve, tropical mountain

1 INTRODUCTION

Why are there different numbers of species in different places? The answer to this question is a major goal in ecology and biogeography (Pianka, 1966; MacArthur, 1972; Brown, 2014). Exploring this question provides us with a greater understanding of how the natural world is organized, but is also a critical activity in a range of conservation planning contexts (Ricketts et al., 1999; Pimm & Brown, 2004). This aim is increasingly important as we enter the Anthropocene and species must either move or evolve if they are to survive (Pecl et al., 2017). Numerous studies across the globe are describing patterns of species diversity and testing them against mechanistic hypotheses (Hudson et al., 2014; Peters et al., 2016). Despite this effort, however, our understanding of species diversity patterns is taxonomically and geographically biased – focussing on patterns of bird and mammal diversity in Europe and the Americas (Hudson et al., 2014). To address this, we explore the variation in species richness of reptiles along an elevational gradient in one of the world's "hottest biodiversity hotspots": The Western Ghats (Nair, 1991; Myers et al., 2000).

Mountain regions contain disproportionate numbers of species relative to their geographic area (Rahbek et al., 2019a), and many of the global biodiversity hotspots exist within them (Kozak & Wiens, 2010; Guo et al., 2013). In terms of understanding general mechanisms underlying variation in species diversity, elevational gradients have long been recognized as useful "microcosms" of broader latitudinal patterns in species richness (Stevens, 1992). Latitudinal gradients themselves are challenging to study due to their large spatial extent, but in the case of elevation gradients, individual mountain ranges can act as replicated transects. This provides opportunities to test the underlying causes of species diversity patterns (Sanders & Rahbek, 2012). Finally, while elevational gradients have a wide diversity of topographies and climates (Rahbek et al., 2019b), a key feature of them is the existence of a strong thermal gradient. Temperature, a factor known to influence the distribution and functioning of life across organizational scales (Brown, 2014), universally declines with increasing elevation. Temperature is particularly important for reptiles; as ectotherms, they rely on ambient temperature to regulate their body heat and allow them to function (Angilletta, 2009).

Elevational patterns in species richness tend to take one of three main forms: (1) a monotonic increase, (2) a monotonic decline and (3) a mid-elevation peak (Rahbek, 1995). The prevalence of these patterns can vary across different taxonomic groups and biogeographical regions (Peters et al., 2016), although the hump-shaped, mid-elevational peak is reported to be the most common relationship (Rahbek, 2005). There are several hypotheses which may explain these different richness-elevation patterns, and these can be broadly grouped into two main categories: bioclimatic or spatial hypotheses (Grytnes & McCain, 2007).

Variation in biologically important variables such as temperature, rainfall or productivity represent climatic hypotheses. In these cases, it is hypothesized that the covariation of these factors along elevational gradients is the cause for various richness-elevation patterns. Compared to endotherms, ectotherm metabolism is highly dependent on ambient temperature (Angilletta, 2009). In consequence, declines in ectotherm richness along elevational gradients have been repeatedly linked to concurrent declines in temperature across space and time (Bishop et al., 2014; Peters et al., 2016), and these patterns can further be explained by the availability of water (Szewczyk & McCain, 2016).

The second category of hypotheses seeking to explain elevational gradients in species richness are spatial. A common explanation for richness-elevation patterns is the influence of available area (Lomolino, 2001). This hypothesis is analogous to the well-known species-area relationship which suggests that more individuals will exist in elevational zones that have more available area, which in turn are more likely to come from a larger species pool (Sanders, 2002; Romdal & Grytnes, 2007). The mid-domain effect (MDE) is another popular spatial hypothesis describing species richness patterns. The MDE predicts mid-elevational peaks in richness, purely as a result of the geometry of a bounded domain, such as that between a mountain top and the coast (Colwell & Hurtt, 1994; Colwell & Lees, 2000 ; Jetz & Rahbek, 2001). Through the random placement of varying species ranges, there is a high probability of greater range overlap, and therefore higher species richness, at the centre of the bounded domain (Colwell & Lees, 2000). Although MDE predictions are purely based on geometric constraints on range sizes, recent analyses have modelled this effect in conjunction with bioclimatic variables (Colwell et al., 2016). There is mixed empirical support for the influence of MDE on elevation-richness patterns (Hawkins & Diniz-Filho, 2002; Currie & Kerr, 2008; McCain, 2009).

Rapoport’s rule on elevational range sizes can also be seen as a “spatial” hypothesis (Stevens, 1992), although it derives from some degree of climatic control (Kendall & Haedrich, 2006). Rapoport’s rule hypothesizes that species at higher elevations have larger range sizes than those at lower elevations. This is due to the broader climatic tolerances required to survive in variable high elevation conditions. There is an underlying assumption that most species have relatively small ranges and cannot tolerate a broad range of climatic conditions. Consequently, ranges accumulate in the climactically stable lowlands to generate a monotonic decline in species richness with increasing elevation (Stevens, 1992; Rahbek, 1997). Like the MDE, support for

Rapoport’s rule as general phenomenon is mixed (Gaston & Chown, 1999; Sanders, 2002; McCain & Knight, 2013).

In this study, we are interested in describing and understanding the elevational diversity patterns of reptiles in the Western Ghats of India. Overall, richness-elevation patterns of herpetofauna (reptiles and amphibians) tend to show monotonic declines (Heatwole, 1982; Cadle & Patton, 1988; Woinarski & Gambold, 1992; Hofer et al., 1999, 2000; Nathan & Werner, 1999; Chettri et al., 2010). This taxonomic group is largely understudied within India especially on elevational diversity patterns (but see Naniwadekar & Vasudevan, 2007; Chettri et al., 2010). This demands an immediate attention because the Indian subcontinent, and the Western Ghats in particular, is a global hotspot of biodiversity. The unique bioclimatic conditions, topographic features and habitat heterogeneity makes the Western Ghats particularly rich in biodiversity and high in species endemism (Nair, 1991; Myers et al., 2000). In fact, 47.13% of the reptiles that occur here are endemic to the Western Ghats (Srinivasulu et al., 2014). Recent studies have also indicated that each mountain range in the Western Ghats possibly has many local endemics and basal lineages – especially in case of reptiles (Cyriac et al., 2018; Pal et al., 2018; Chaitanya et al., 2019; Mallik et al., 2019; Deepak et al., 2020). Consequently, there is a need to better document and explain patterns of species richness in this region.

In this context, we ask the following questions: (1) how is reptile species richness distributed across elevation in the southern Western Ghats? (2) What bioclimatic and spatial hypotheses explain these patterns? We use temperature and tree density as measures of bioclimatic niche variables of relevance to reptiles. We predict that both will relate positively to reptile species richness in this region: reptile metabolism is tightly linked to ambient temperature, and we hypothesize that higher tree densities will provide a greater number of niches that different reptile species can exploit. Tree density is often used as a surrogate of habitat heterogeneity and habitat complexity (McCoy & Bell, 1991) and has been repeatedly shown to alter reptile community structure (Heyer and Berven, 1973, Scott, 1976, Voris, 1977, Gillespie et al., 2015). In our case, we hypothesize that more reptiles will be present in areas of higher tree densities.

We test each hypothesis separately for the two main subgroups of reptile: snakes and lizards. This is typically done in studies of reptile diversity (Fu et al.,2007, Kryštufek et al., 2008, Chettri et al., 2010) because of their different morphology and life-history strategies (Shine & Charnov, 1992). Snakes tend to occupy higher trophic positions compared to lizards, and being limbless they move through the environment very differently s (Gove, 1979, Parker & Plummer, 1987, Da Silva et al., 2018). Furthermore, snakes tend to have larger range sizes compared to lizards, which may be an indication of their higher dispersal abilities (Böhm et al., 2013). In general, large-ranged and small-ranged species tend to show different responses to the mid-domain effect (Dunn et al., 2006, Dunn et al., 2007), with small-ranged taxa less likely to conform to the predictions of the MDE.

In this context, we predict that the differences in life-history strategies and range sizes between snakes and lizards will result in different elevation-richness patterns, specifically that snakes, with their larger ranges, will be more likely to conform to a mid-elevational peak. We also predict that endemic species will show a mid-elevational peak or a monotonic increase in richness with elevation. Previous studies on herpetofauna have found mid-elevational peaks in endemic richness (Fu et al., 2006), while globally, increases in endemism with elevation may be explained by the greater topographic isolation of these areas which promotes speciation and endemicity (Steinbauer et al., 2016). Finally, given previous work on reptiles which found limited global support for a series of spatial hypotheses (McCain, 2010), we expect to find more support for climatic hypotheses at this local scale in the Western Ghats. Simultaneous tests of these hypotheses have not yet been undertaken for reptiles in the biodiversity hotspot of the Western Ghats. Here, we provide a test.

2 METHODS

2.1 Study area

Our study was located within the Agasthyamalai Hills (8.4°to 8.8°N and 77.0° to 77.4°E) which is part of the Agasthyamalai Biosphere Reserve (ABR) on the southern tip of the Western Ghats. We covered only the western slope (windward side) of the Agasthyamalai Hills which comprised of two major protected areas: Neyyar and Peppara wildlife sanctuaries in the Kerala State (Figure 1). The mean temperature of the coldest month in the region ranges from 13 °C to 23°C (Pascal, 1982). The windward side of the Agasthyamalai Hills receives high rainfall: varying between 2000-5000 mm annually with only two to three dry months (Ramesh et al., 1997; Varghese & Balasubramanyan, 1998).

The Agasthyamalai region is well-known for its high plant diversity and endemism (Nayar, 1996; Ramesh et al., 1997; Manju et al., 2009). The vegetation of the area changes significantly along elevation. Champion & Seth (1968) identified four major vegetation types in the area: southern moist mixed deciduous forest (<400 m a.s.l.), west coast semi-evergreen (400-600 m a.s.l.), west coast tropical evergreen (600-1200 m a.s.l.) and southern hilltop tropical evergreen (>1200 m a.s.l.). The deciduous or evergreen forests up to 1200m a.s.l. are comprised of taller trees with canopy height ranging from 10-35 m however, the hill top forest is of a dense, stunted evergreen type with canopy height reaching a maximum up to 10 m, mixed with open rocky and grass areas (Varghese & Balasubramanyan, 1998). Apart from human settlements in the lower elevations (<400 m a.s.l.), trekking and pilgrimage activities also exert significant pressure on the natural habitats of the region (Ramesh et al., 1997). Although we observed some level of habitat disturbance along the main trekking route, our sampling was mostly restricted to undisturbed patches along the elevational gradient.

The focal study area encompasses approximately 250 km^2, spread across an elevational range of 50 to 1868 m a.s.l.. The coast is 30 km from the site - this makes the landscape ideal for testing mid-domain effects as it has geometric constraints on both ends, the mountain summit at the top and the coastline at the bottom.

2.2 Data collection

2.2.1 Reptile richness

We surveyed reptiles in the Agasthyamalai Hills from April 2012 through to December 2014 along an elevation gradient, covering both wet and dry seasons. The total elevational range was categorized into fourteen 100 m wide elevational bands, beginning at 100 m a.s.l. and rising to 1500 m a.s.l.. We did not sample at the coast due to the lack of adequate undisturbed habitat, and we did not sample higher than 1500 m a.s.l. due to logistical constraints. Transects of approximately 2000 m in length and 250-300 m in width were laid in each elevational band based on topography and accessibility. We performed time constrained visual encounter surveys (VES) to sample the reptile communities in each elevational band. The VES method surveys an area for a prescribed time, systematically searching for animals in all possible microhabitats covering different vertical strata (Campbell & Christman, 1982, Crump & Scott, 1994). This is an appropriate and well-understood method for both species inventorying and monitoring, and is suitable for examining landscape level patterns especially in mountains. The method is also known for having a higher detection rate of rare species (Crump & Scott, 1994) and has successfully been applied before in the Western Ghats (Bhupathy & Nixon, 2011) and Eastern Himalayas (Chettri et al., 2010)

We used the transects laid in each elevational band as an approximate spatial guide for our VES sampling. We gradually searched along each transect for reptiles using VES during daylight, from 0800 to 1800 hours, and the search included turning stones and fallen logs, moving leaf litter, scanning the vegetation and, searching on stems and barks of trees. In this sense, VES explores all possible microhabitats from the ground level to the tree branches of approximately 3 m above the ground. Even though active microhabitat search was not possible in higher vertical strata (above 3 m), simple visual scanning of vegetation and tree branches to a maximum height was carried out wherever possible. Repetition of sampling in the same spatial area was avoided as the VES method involves the alteration of microhabitats (turning stones and logs etc.). In our dataset, a single VES "sample" within an elevational band consisted of two person hours (1 hour × 2 people searching = 2 person hours). We were unable to perform equal sampling effort across the elevations, however, due to the differences in spatial and temporal accessibility to some elevational zones (Table S1). We identified all reptiles to species level where possible and assigned a distinct morphospecies identifier where full identification was not possible.

2.2.2 Tree density

We laid 10×10 m quadrats along each elevational transect, each quadrat separated by 250 m. This gave 8 quadrats on most transects, although space constraints restricted us from laying 8 quadrats at all elevations. All elevations had at least four quadrats. We counted the number of trees in each quadrat to estimate tree density per hectare.

2.2.3 Elevation and available area

Elevation for each VES was determined during the sampling using an altimeter and GPS. We extracted ASTER global digital elevation model-Version 3 (source: https://earthdata.nasa.gov/, downloaded on 10 January 2020) and calculated the available area of each 100 m elevational band using QGIS Version 3.10. Only the western slope of the Agasthyamalai Hills was considered for this area calculation as it comprises the entire area of the study.

2.2.4 Environmental variables

We downloaded bioclimatic variables for the study area from the Chelsa` climatic database (http://www.chelsa-climate.org/) which is a fine-scale (i.e. 1×1 km), long-term (1979 to 2013) climate dataset with global coverage based on statistical downscaling (Karger et al., 2017). Due to its high resolution, the Chelsa dataset is reported to be more effective for modelling species distributions in geographically complex regions such as mountainous landscapes (Maria & Udo, 2017). Out of the available 19 bioclimatic variables, we retained only mean annual temperature (MAT) and mean annual precipitation (MAP) for analysis as they are most ecologically important for the distribution of reptiles. QGIS Version 3.10 was used for extracting the data from the bioclimatic layer and we used the central point of each elevational transect to represent the climate of each elevation.

2.3 Data analysis

All analyses took place within the R environment (R Core Team, 2018).

2.3.1 Species richness

We used rarefaction to generate standardized species richness estimates because sampling effort (hours of VES) varied across the elevational bands. We used the *iNEXT* package in R (Hsieh et al., 2016) to do this. Specifically, we used the function *estimateD* in "incidence_freq" mode (because our raw data are incidences of species in variable numbers of samples from each elevation). We used *estimateD* to estimate species richness for each elevation at the median sampling effort (38 two-person hours). This involved extrapolating richness estimates for elevations that were not sampled for 38 two-person hours, and interpolating samples that were sampled for more than 38 two-person hours. We employed this procedure using four different data subsets: reptiles (all species), snakes, lizards and endemics (of the Western Ghats). We use these estimated species richness values in all the analyses that follow. We assigned status of endemism of each species based on recent assessment of reptiles of the Western Ghats (Srinivasulu et al., 2014). We provide sample completeness estimates from *iNEXT* in Table S1.

2.3.2 Describing elevational patterns

We used linear regressions with Gaussian errors to test whether the species richness of each taxonomic subset had a linear, curvilinear or no relationship with elevation. We used Gaussian errors because the sample size corrected species richness values were not integers. For the linear models, we used only elevation as a predictor variable. For the curvilinear models, we used elevation and elevation^2 as predictor variables. The null models included only an intercept. We compared models using bias corrected Akaike information criteria (AICc). We calculated the difference in AICc (ΔAICc) between the three models, relative to the one with the lowest AICc, and extracted R^2 adjusted for small sampled sizes. Where competing models are within 2 ΔAICc of each other, we opt to interpret and present the simplest model. We present the model with the lowest AICc along with its adjusted R^2 for each taxonomic subset. None of the models deviated from the model assumptions based on our interpretation of the model diagnostic and residual plots.

2.3.3 Testing species richness drivers

We use an information-theoretic approach to assess the relative evidence for different hypothesized drivers of variation in reptile species richness (Burnham & Anderson, 2002) . We did not build a "global model" and analyse all possible sub-models. Rather, we split our explanatory variables into three classes representing separate, competing hypotheses, and ranked them using AICc. We did this because we do not consider models containing MDE along with other explanatory variables to be biologically meaningful – these hypotheses operate at completely different spatiotemporal scales to those concerning temperature or precipitation, for example. Our goal was to assess the relative weight of evidence in favour of a given hypothesis (represented by one or more actual statistical models). These classes were environmental, area, and mid-domain effects (MDE). Plots of their variation across elevation are presented in Figure S1.

Environmental drivers: We used mean annual temperature (˚C) and tree density (n/ha) to represent environmental drivers. We did not include precipitation because models containing precipitation as well as temperature and tree density, had variance inflation factors (VIF) above 2 (Fox & Monette, 1992). In total there were three environmental models: temperature, tree density and temperature + tree density. We hypothesised that each variable may positively influence reptile species richness independently, or in combination.

Area: We used available elevational area (as described above) to represent the species-area hypothesis.

Mid-domain effect: For MDE, we used the R package *rangemodelR* (Marathe, 2019) to simulate artificial, random range distributions 1000 times. We took the average species richness estimate across the repetitions as the prediction of the MDE hypothesis. This package uses the approach of Wang & Fang (2012), itself an extension of the classic MDE model of Colwell et al. (2004). This model shuffles range midpoints while maintaining range sizes. Midpoints can be shuffled anywhere within the geometric constraints of a bounded domain. We used this procedure separately for each taxonomic subset. Species ranges were interpolated between the highest and lowest elevations we observed them, species recorded at only a single elevation were given a range size of 0.

We modelled each class of drivers separately (1 model for each class, except for the environmental class where there were three candidate models). We constructed linear regressions with Gaussian errors to do this. We compared and ranked all models, including the null intercept only model, using AICc and calculated adjusted R^2 values. We consider the “best” model to be the one with the lowest AICc, but also interpret models within 2 ΔAICc of the top ranked model. We also interpret our models considering the size and direction of the effect sizes (by standardising all explanatory variables prior to running the regressions (Schielzeth, 2010) and the proportion of variance explained (R^2). For example, models for the MDE hypotheses should have a slope of ~1 if they are predicting similar richness-elevation patterns to our observed data.

We performed this modelling procedure four times, once for each of the taxonomic subsets of all reptiles, snakes, lizards and endemic species.

Finally, we tested Rapoport’s rule by correlating species range sizes with their range midpoints (Kwon et al., 2014). We interpolated species ranges, assuming them to be present at all elevations between the highest and lowest observed sighting to generate these data. We performed this test for each subset of reptiles: all, snakes, lizards and endemics.

RESULTS

We sampled 47 species of reptiles across the elevational gradient, including 24 lizards, 22 snakes and one tortoise. Twenty-five of these species are endemic to the Western Ghats. Our full dataset and R code are made available in the public data archiving platform, Dryad.

2.4 Elevational patterns

For reptiles and lizards, species richness declined linearly with increasing elevation (Figure 2a, c; ΔAICc to next best model was 3.99 and 3.86, respectively). In each case, elevation explained a large fraction of the variation in species richness (reptiles adjusted $R^2 = 0.74$, lizards adjusted $R^2 = 0.85$). Neither the linear or curvilinear models fitted well to the patterns of snake and endemic species richness, suggesting that there was no clear systematic variation of species richness with elevation in these groups (Figure 2b, d; ΔAICc to next best model was 2.46 and 1.56, respectively). Full model details can be found in Table S2.

2.5 Species richness drivers

The best supported models explaining overall reptile species richness were those for temperature and temperature + tree density (Table 1). Both were positively related to reptile species richness (Figure 3ab). The inclusion of tree density however, did not explain any additional variance compared to the model containing only temperature: it's ΔAICc was greater than 2, and it's standardised slope was much smaller than that of temperature in the same model (Table 1).

None of the tested hypotheses appear to drive snake species richness (Table 2). The best model was the one containing only an intercept, and none of the candidate models had high R^2 values (expanded version of Table 1 in the supplementary material, Table S3).

For lizard species richness, temperature was the clear best model (Table 1). Lizard species richness was positively related to temperature (Figure 3c). The model containing temperature + tree density was ranked second but, again, the inclusion of this variable did not increase the R^2 and the AICc values clearly indicated that this model was poorer than the one containing only temperature (Table 1). Furthermore, the slope estimate for tree density was smaller than that for temperature and its confidence interval overlapped zero (Table 1).

Endemic species richness was not modelled well by the candidate hypotheses. The best ranked model was the null model containing only an intercept (Table 1). The second ranked model, within a ΔAICc of 2, was for the mid-domain effect. The MDE model had the highest R^2 (0.14) of the candidates and was positively related to endemic species richness (Figure 3d). The unstandardized slope of this model, however, deviated from the expectation of a 1:1 relationship ($b = 0.27 \pm 0.33$, Figure 3d).

Finally, there was no evidence for a positive correlation between species elevational ranges and elevational midpoints, as Rapoport's rule would predict. The Pearson's correlation coefficient was -0.16, -0.12, -0.27 and -0.22 for all reptiles, snakes, lizards and endemics, respectively. All correlations were insignificant ($p > 0.6$ in all cases).

3 DISCUSSION

Our study is the first analysis of reptile diversity along an elevational gradient within the Western Ghats. We find a linear decline of reptile richness with increasing elevation (Figure 3a). This pattern is repeated in lizards (Figure 3c), who make up the largest fraction of overall reptile diversity in this area, but not for snakes (Figure 3b) or for endemic species (Figure 3d). We find no clear relationships between snake and endemic species richness with elevation. Furthermore, our data do not support a range of spatial hypotheses concerning the underlying drivers of reptile species richness (i.e. low R^2s and high ΔAICcs of these models, Table 1, Table S3). Instead, our data suggest that temperature is the primary factor driving the diversity of reptiles in this area.

Our headline result is the monotonic decline in reptile and lizard species richness which appears to be driven by temperature (Table 2). Fewer reptiles (and lizards) are found in the colder, high elevations (Figure 3, Figure 4). These findings echo results from both the global and the local scale. For example, McCain (2010) found that the most common richness-elevation pattern in reptiles across the globe was a monotonic decline, and that this was largely explained by temperature. Similar findings have been reported for Himalayan reptiles (Chettri et al., 2010), the Costa Rican herpetofauna (Fauth et al., 1989), reptiles in the Dinaric Alps (Kryštufek et al., 2008) and a suite of other ectotherms from around the globe (Bishop et al., 2014; Peters et al., 2016). Although negative richness-temperature relationships are reported for many taxa, including endotherms such as birds and bats (McCain, 2007, 2009), a monotonic decline pattern is most reported for ectothermic taxa (McCain, 2010). Consequently, our results in the Western Ghats feed into the general narrative that temperature is the primary driver of reptile species richness gradients worldwide.

Despite this overall finding, however, we do not detect any systematic patterns in snake or endemic richness patterns (Figure 3b, d). For snakes, at least, this may be a consequence of our sampling. Compared to lizards, snakes are rare and can be difficult to observe during VES. This results from their cryptic behaviours, frequent use of inaccessible microhabitats (e.g., burrows, boulders and tree holes) and low rates of activity (Parker & Plummer, 1987, Durso et al., 2011). In our dataset, 40% of snake species were recorded at only a single site, whereas this was the case for only 12% of lizards. This high proportion of singleton observations suggests that this sampling difficulty may well be obscuring any systematic patterns in snake richness. Consequently, we suggest that further standardised and repeated sampling across the Western Ghats is needed to fully disentangle the issue of snake elevational-diversity patterns in the region. Note, even at a global-scale, data scarcity is a major issue in deriving broad scale diversity patterns in snakes and in assessing their conservation status or extinction risks (Böhm et al., 2013, Böhm et al., 2017).

In terms of endemic species, this potential sampling issue is unlikely to explain our results. Of the species we sampled, 53% were endemic which closely matches the proportion of endemic reptiles in the Western Ghats which is 47% (Srinivasulu *et al.*, 2014), and only 20% were found at a single site. Consequently, we are more confident that the patterns we describe for endemic species are reflecting reality – that the number of endemic species does not systematically vary across elevation. An interesting contrast with endemics can be seen in frogs from the Hengduan Mountains, China. In this case, endemics were not influenced by environmental factors, but did fit MDE predictions (Fu et al., 2006). While we do not find strong evidence that endemic species follow the MDE, our data agree with that of Fu et al., (2006) in that the diversity patterns of endemic species do not appear to be driven by bioclimatic variables.

How representative are our results in the Agasthyamalai Hills of the Western Ghats as a whole? The Western Ghats largely consist of conical shaped mountains, as do the hills sampled here (Elsen & Tingley, 2015). Compared to the windward side we focused in the present study, the ranges towards the leeward side of the Ghats slightly differ in their habitat types and rainfall intensities (Nair & Daniel, 1986; Nair, 1991), but are unlikely to differ in their temperature-elevation patterns. Critically, the unique high elevation tropical montane cloud forest known as Shola, a natural matrix of forests and grasslands (found only above 1500m a.s.l) is scarce in the Agasthyamalai landscape compared to most of the northern hill ranges (e.g. Anaimalai Hills- 2695m a.s.l.). Sholas are known for the presence of some endemic reptiles (Deepak & Vasudevan, 2008), and this has been further proved by recent discoveries (Deepak et al., 2020). Consequently, studies exploring such high elevation habitats could alter the endemic-elevation pattern that we see here. Finally, a recent phylogeographic analysis of frogs highlighted that the Palghat Gap (a natural biogeographical barrier within the Western Ghats) could potentially be a barrier to dispersal and influence larger macroevolutionary patterns (Vijayakumar et al., 2016). Whether this biogeographical barrier also causes differences in the patterns and drivers of reptile richness, however, remains to be tested – we suspect that it is unlikely.

In this study, we have not analyzed beta diversity across elevation because our sampling effort differed across the gradient. For alpha diversity (species richness) we could correct for this using known interpolation and extrapolation techniques (Hsieh et al., 2016). While similar corrections exist for beta diversity (Chao et al., 2005), this is beyond the scope of the current manuscript. Regardless, there is a clear opportunity and need for more comparative analyses of elevational patterns (including beta diversity) between different ranges within the Western Ghats. Regardless, considering the largely similar habitat types across the region and the repeated temperature-elevation gradients, we suggest that our alpha diversity analyses are likely to be representative of the entire Western Ghats.

In summary, we provide the first evidence of reptile species richness-elevation patterns in the Western Ghats, a global biodiversity hotspot. Despite the strong geometric constraints (mountain summit and coastline) present in the study range, the observed richness patterns were not shaped by the mid-domain effect or the available-area effect in the Agasthyamalai Hills. Temperature is the clear driver of these patterns for reptiles, and for lizards but not for snakes and endemic species. These temperature relationships result in a monotonic decline in reptile and lizard richness with increasing elevation. These findings agree with those at the global scale which report a tight link between temperature and reptile diversity patterns (McCain, 2010). Since external temperatures directly determine metabolic rates in ectotherms (such as reptiles and amphibians), they show higher affinities with temperature and are more vulnerable to changing climates than endotherms (i.e. birds and mammals) (Rolland et al., 2018). This becomes a critical issue for the large number of range-restricted reptiles in the Western Ghats where many species are endemic and confined to certain hill ranges. As global temperatures rise, these species may find themselves pushed to new elevational ranges, or they may run out of appropriate thermal environments entirely (Colwell et al., 2008). The next steps are to extend this kind of standardized sampling, throughout the Western Ghats, to confirm if the patterns are repeatable and to further generalize our understanding of how biodiversity is maintained in these ancient landscapes.

ACKNOWLEDGEMENTS

This publication is an outcome of a larger project on reptiles and birds of Agasthyamalai Hills funded by Department of Biotechnology (DBT), Govt. of India. We dedicate this work to late Dr. S. Bhupathy of SACON who was the principal investigator of the project and Ph.D. supervisor to J.V.J initially. We are grateful to Kerala Forest Department for all the research permissions and logistic support in the field. We thank Director, SACON for the support at different stages of the study. Special thanks to Dr. P.V. Karunakaran, SACON for his help in vegetation sampling. Dr. Nathan J. Sanders, University of Vermont, USA gave comments on earlier drafts of MS and facilitated collaborations. We thank Dr. Arun P. R, SACON and Dr. Bhoj K. Acharya, Sikkim University for the guidance and constant support to J.V.J. We appreciate the help provided by the field assistants and local communities during the field study.

Author contribution statement: J.V.J conceived the questions and designed the study. J.V.J and M.P conducted field data collection. J.V.J along with T.R.B designed MS, carried out data analysis and led the writing. R.J and M.P provided comments for improving the MS at different stages.

REFERENCES

Angilletta, M. (2009). *Thermal adaptation: a theoretical and empirical synthesis*. Oxford, UK: Oxford University Press.

Aliabadian, M., Roselaar, C. S., Sluys, R., & Nijman, V. (2007). Low predictive power of mid-domain effect to explain geographic species richness patterns in Palearctic songbirds. *Contributions to Zoology*, 76, 197-204.

Bhupathy, S. & Nixon, A.M.A. (2011). Status of reptiles in upper Nilgiris, Nilgiri Biosphere Reserve, Western Ghats, India. *Journal of the Bombay Natural History Society*, 108, 103–108.

Bishop, T.R., Robertson, M.P., Rensburg, B.J. & Parr, C.L. (2014). Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. *Journal of Biogeography*, 41, 2256–2268.

Böhm, M., Collen, B., Baillie, J. E., Bowles, P., Chanson, J., Cox, N., ... & Rhodin, A. G. (2013). The conservation status of the world’s reptiles. *Biological Conservation*, 157, 372-385.

Böhm, M., Kemp, R., Williams, R., Davidson, A. D., Garcia, A., McMillan, K. M., ... & Collen, B. (2017). Rapoport's rule and determinants of species range size in snakes. *Diversity and Distributions*, 23, 1472-1481.

Brown, J.H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, 41, 8–22.

Burnham, K.P. & Anderson, D.R. (2002), *Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition,* Springer-Verlag, New York.

Cadle, J.E. & Patton, J.L. (1988). Distribution patterns of some amphibians, reptiles, and mammals of the eastern Andean slope of southern Peru. In *Proceedings of a Workshop on Neotropical Distribution Patterns*, pp. 225–244. Academia Brasileira de Ciencias Río de Janeiro.

Campbell, H.W. & Christman, S.P. (1982). Field techniques for herpetofaunal community analysis. *Herpetological Communities*, 13, 193–200.

Cardelús, C. L., Colwell, R. K., & Watkins Jr, J. E. (2006). Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology*, 94, 144-156.

Chaitanya, R., Giri, V.B., Deepak, V., Datta-Roy, A., Murthy, B. & Karanth, P. (2019). Diversification in the mountains: a generic reappraisal of the Western Ghats endemic gecko genus Dravidogecko Smith, 1933 (Squamata: Gekkonidae) with descriptions of six new species. *Zootaxa*, 4688, 1–56.

Champion, H.G. & Seth, S.K. (1968). *Revised forest types of India.* Govt, of India Publications, New Delhi.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology letters*, 8, 148-159.

Chettri, B., Bhupathy, S. & Acharya, B.K. (2010). Distribution pattern of reptiles along an eastern Himalayan elevation gradient, India. *Acta Oecologica*, 36, 16–22.

Colwell, R.K. & Hurtt, G.C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *The American Naturalist*, 144, 570–595.

Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, 15, 70–76.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004). The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, 163, E1–E23.

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322, 258-261.

Colwell, R. K., Gotelli, N. J., Ashton, L. A., Beck, J., Brehm, G., Fayle, T. M., ... & Klimes, P. (2016). Midpoint attractors and species richness: modelling the interaction between environmental drivers and geometric constraints. *Ecology Letters*, 19, 1009-1022.

Crump, M. L. & N. J. Scott. 1994. Visual encounter surveys. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. A. C. Hayek, and M. S. Foster (Eds.): Biological diversity handbook series; measuring and monitoring biological diversity: Standard methods for amphibians. pp. 84–92. Smithsonian Institution Press, Washington, DC

Cyriac, V.P., Johny, A., Umesh, P.K. & Palot, M.J. (2018). Description of two new species of Cnemaspis Strauch, 1887 (Squamata: Gekkonidae) from the Western Ghats of Kerala, India. *Zootaxa*, 4459, 85–100.

Da Silva, F. O., Fabre, A. C., Savriama, Y., Ollonen, J., Mahlow, K., Herrel, A., ... & Di-Poï, N. (2018). The ecological origins of snakes as revealed by skull evolution. *Nature communications*, 9, 1-11.

Deepak, V. & Vasudevan, K. (2008). Density and microhabitat association of Salea anamallayana in Eravikulam National Park, Western Ghats, India. *The Herpetological Journal*, 18, 165-170.

Deepak, V., Narayanan, S., Rajkumar, K.P., Easa, P.S., Sreejith, K.A. & Gower, D.J. (2020). Description of a new species of Xylophis Beddome, 1878 (Serpentes: Pareidae: Xylophiinae) from the Western Ghats, India. *Zootaxa*, 4755, 231–250.

Dunn, R. R., Colwell, R. K., & Nilsson, C. (2006). The river domain: why are there more species halfway up the river?. *Ecography*, 29, 251-259.

Dunn, R. R., McCain, C. M., & Sanders, N. J. (2007). When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. *Global Ecology and Biogeography*, 16, 305-312.

Durso, A. M., Willson, J. D., & Winne, C. T. (2011). Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation*, 144, 1508-1515.

Elsen, P.R. & Tingley, M.W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, 5, 772–776.

Fauth, J.E., Crother, B.I. & Slowinski, J.B. (1989). Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica*, 21, 178–185.

Fox, J. & Monette, G. (1992). Generalized collinearity diagnostics. *Journal of the American Statistical Association*, 87, 178–183.

Fu, C., Hua, X., Li, J., Chang, Z., Pu, Z. & Chen, J. (2006). Elevational patterns of frog species richness and endemic richness in the Hengduan Mountains, China: geometric constraints, area and climate effects. *Ecography*, 29, 919–927.

Fu, C., Wang, J., Pu, Z., Zhang, S., Chen, H., Zhao, B., ... & Wu, J. (2007). Elevational gradients of diversity for lizards and snakes in the Hengduan Mountains, China. *Biodiversity and Conservation*, 16, 707-726.

Gaston, K.J. & Chown, S.L. (1999). Why Rapoport's rule does not generalise. *Oikos*, 84, 309–312.

Gillespie, G. R., Howard, S., Stroud, J. T., Ul-Hassanah, A., Campling, M., Lardner, B., ... & Kusrini, M. (2015). Responses of tropical forest herpetofauna to moderate anthropogenic disturbance and effects of natural habitat variation in Sulawesi, Indonesia. *Biological conservation*, 192, 161-173.

Gove, D. (1979). A comparative study of snake and lizard tongue-flicking, with an evolutionary hypothesis. *Zeitschrift für Tierpsychologie*, 51, 58-76.

Grytnes, J.-A. & McCain, C.M. (2007). Elevational trends in biodiversity. *Encyclopedia of Biodiversity*, 5, 1–8.

Guo, Q., Kelt, D.A., Sun, Z., Liu, H., Hu, L., Ren, H. & Wen, J. (2013). Global variation in elevational diversity patterns. *Scientific reports*, 3, 3007. doi: https://doi.org/10.1038/srep03007.

Heatwole, H. (1982). A review of structuring in herpetofaunal assemblages. *US Fish and Wildlife Service Wildlife Research Report*, 13, 1–19.

Heyer, R.W., Berven, K.A., 1973. Species diversities of herpetofaunal samples from similar microhabitats at two tropical sites. *Ecology*, 54, 642–645.

Hofer, U., Bersier, L.-F. & Borcard, D. (1999). Spatial organization of a herpetofauna on an elevational gradient revealed by null model tests. *Ecology*, 80, 976–988.

Hofer, U., Bersier, L.-F. & Borcard, D. (2000). Ecotones and gradient as determinants of herpetofaunal community structure in the primary forest of Mount Kupe, Cameroon. *Journal of tropical ecology*, 16, 517–533.

Hsieh, T.C., Ma, K.H. & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456.

Hu, J., Xie, F., Li, C. & Jiang, J. (2011). Elevational patterns of species richness, range and body size for spiny frogs. *PLoS One*, 6, e19817.

Hudson, L. N., Newbold, T., Contu, S., Hill, S. L., Lysenko, I., De Palma, A., ... & Choimes, A. (2014). The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. *Ecology and Evolution*, *4*, 4701-4735.

Jetz, W. & Rahbek, C. (2001). Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences*, 98,

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... & Kessler, M. (2017). Climatologies at high resolution for the earth’s land surface areas. *Scientific Data*, *4*, 170122.

Kendall, V.J. & Haedrich, R.L. (2006). Species richness in Atlantic deep-sea fishes assessed in terms of the mid-domain effect and Rapoport’s rule. *Deep Sea Research Part I: Oceanographic Research Papers*, 53, 506–515.

Kozak, K.H. & Wiens, J.J. (2010). Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *The American Naturalist*, 176, 40–54.

Kryštufek, B., Janžekovič, F. & Donev, N.R. (2008). Elevational diversity of reptiles on two Dinaric mountains. *Journal of Natural History*, 42, 399–408.

Kwon, T.-S., Kim, S.-S. & Chun, J.H. (2014). Pattern of ant diversity in Korea: An empirical test of Rapoport's altitudinal rule. *Journal of Asia-Pacific Entomology*, 17, 161–167.

MacArthur, R.H. (1972). *Geographical ecology: patterns in the distribution of species*, Princeton University Press.

Mallik, A.K., Achyuthan, N.S., Ganesh, S.R., Pal, S.P., Vijayakumar, S.P. & Shanker, K. (2019). Discovery of a deeply divergent new lineage of vine snake (Colubridae: Ahaetuliinae: Proahaetulla gen. nov.) from the southern Western Ghats of Peninsular India with a revised key for Ahaetuliinae. *Plos One, 14, e0218851*

Manju, C.N., Rajesh, K.P. & Madhusoodanan, P.V. (2009). Bryophyte Diversity in Kerala Part of Agasthyamalai Biosphere Reserve in Western Ghats. *Taiwania*, 54, 57–68.

Marathe, A. (2019). rangemodelR: mid-domain effect and species richness. *R package Version*, 1. https://cran.r-project.org/web/packages/iNEXT/

Maria, B. & Udo, S. (2017). Why input matters: Selection of climate data sets for modelling the potential distribution of a treeline species in the Himalayan region. *Ecological Modelling*, 359, 92–102.

McCain, C.M. (2005). Elevational gradients in diversity of small mammals. *Ecology*, 86, 366–372.

McCain, C. M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and biogeography*, 16, 1-13.

McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346-360.

McCain, C.M. (2010). Global analysis of reptile elevational diversity. *Global Ecology and Biogeography*, 19, 541–553.

McCain, C.M. & Knight, K.B. (2013). Elevational Rapoport's rule is not pervasive on mountains. *Global Ecology and Biogeography*, 22, 750–759.

McCoy, E.D. & Bell, S.S. (1991). Habitat structure: the evolution and diversification of a complex topic. *Habitat structure: the physical arrangement of objects in space* (ed. by S.S. Bell, E.D. McCoy and H.R. Mushinsky), pp. 3– 27. Chapman & Hall, London.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

Nair, N.C. & Daniel, P. (1986). Floristic diversity of the Western Ghats and its conservation: a review. *Proceedings. Animal sciences-Indian Academy of Sciences*. (Animal Science/Plant Science), Supplement: 127-163.

Nair, S.C. (1991). *The southern Western Ghats: a biodiversity conservation plan*. Indian National Trust for Art and Cultural Heritage, New Delhi.

Naniwadekar, R. & Vasudevan, K. (2007). Patterns in diversity of anurans along an elevational gradient in the Western Ghats, South India. *Journal of Biogeography*, 34, 842–853.

Nathan, R. & Werner, Y.L. (1999). Reptiles and breeding birds on Mt. Hermon: patterns of altitudinal distribution and species richness. *Israel Journal of Zoology*, 45, 1–33.

Nayar, M.P. (1996). *Hot spots of endemic plants of India*, *Nepal and Bhutan*, Tropical Botanic Garden and Research Institute, Thiruvananthapuram.

Ogwu, M.C., Takahashi, K., Dong, K., Song, H.-K., Moroenyane, I., Waldman, B. & Adams, J.M. (2019). Fungal elevational Rapoport pattern from a High Mountain in Japan. *Scientific Reports*, 9, 1–10.

Oommen, M.A. & Shanker, K. (2005). Elevational species richness patterns emerge from multiple local mechanisms in Himalayan woody plants. *Ecology*, 86, 3039–3047.

Pal, S., Vijayakumar, S.P., Shanker, K., Jayarajan, A. & Deepak, V. (2018). A systematic revision of Calotes Cuvier, 1817 (Squamata: Agamidae) from the Western Ghats adds two genera and reveals two new species. *Zootaxa*, 4482, 401–450.

Parker, W. S. & Plummer, M. V. (1987). Population ecology. In *Snakes: ecology and evolutionary biology* (ed. R. A. Seigel, J. T. Collins & S. S. Novak), pp. 253–301. New York: Macmillan

Pascal, J.P. (1982). *Bioclimates of the Western Ghats at 1/250, 000*. French Institute of Pondicherry, Pondicherry.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... & Falconi, L. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*, eaai9214.

Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., ... & Haas, M. (2016). Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications*, *7*, 13736.

Pianka, E.R. (1966). Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, 100, 33–46.

R core Team. (2018). *R: A language and environment for statistical computing. R Foundation for Statistical Computing. Austria: Vienna*. https://www.R-project.org.

Pimm, S.L. & Brown, J.H. (2004). Domains of diversity. *Science*, 304, 831–833.

Rahbek, C. (1995). The elevational gradient of species richness: a uniform pattern? *Ecography*, 18, 200–205.

Rahbek, C. (1997). The relationship among area, elevation, and regional species richness in neotropical birds. *The American Naturalist*, 149, 875–902.

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology letters*, 8, 224–239.

Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G., Nogues-Bravo, D., Rasmussen, C.M., Richardson, K., Rosing, M.T. & Whittaker, R.J. (2019a). Building mountain biodiversity: Geological and evolutionary processes. *Science,* 365, 1114–1119.

Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J. & Fjelds\aa, J. (2019b). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, 365, 1108–1113.

Ramesh, B.R., Menon, S. & Bawa, K.S. (1997). A vegetation based approach to biodiversity gap analysis in the Agastyamalai region, Western Ghats, India. *Ambio*, 26, 529–536.

Ricketts, T.H., Dinerstein, E., Olson, D.M. & Loucks, C. (1999). Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. *BioScience*, 49, 369–381.

Rolland, J., Silvestro, D., Schluter, D., Guisan, A., Broennimann, O., & Salamin, N. (2018). The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nature Ecology & Evolution*, 2, 459-464.

Romdal, T.S. & Grytnes, J.A. (2007). An indirect area effect on elevational species richness patterns. *Ecography*, 30, 440–448.

Sanders, N.J. (2002). Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography*, 25, 25–32.

Sanders, N.J. & Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography*, 35, 1-3.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103-113.

Scott, N. J. (1976). The abundance and diversity of herpetofaunas of tropical forest litter. *Biotropica*, 8, 41–58.

Srinivasulu, C., Srinivasulu, B. & Molur, S. (2014). *The Status and distribution of reptiles in the Western Ghats, India.* Conservation Assessment and Management Plan (CAMP). Wildlife Information Liaison Development Society, Coimbatore, Tamil Nadu, 148pp.

Steinbauer, M. J., Field, R., Grytnes, J. A., Trigas, P., Ah-Peng, C., Attorre, F., ... & De Sanctis, M. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, *25*, 1097-1107.

Stevens, G.C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, 133, 240–256.

Stevens, G.C. (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, 140, 893–911.

Szewczyk, T. & McCain, C.M. (2016). A systematic review of global drivers of ant elevational diversity. *Plos One*, 11, e0155404

Varghese, A. O., & Balasubramanyan, K. (1999). Structure, composition and diversity of the tropical wet evergreen forest of the Agasthyamalai region of Kerala, Western Ghats. *Journal of South Asian Natural History, 4,* 87-98.

Vijayakumar, S.P., Menezes, R.C., Jayarajan, A. & Shanker, K. (2016). Glaciations, gradients, and geography: multiple drivers of diversification of bush frogs in the Western Ghats Escarpment. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20161011.doi: https://doi.org/10.1098/rspb.2016.1011.

Voris, H.K. (1977). Comparison of herpetofaunal diversity in tree buttresses of evergreen tropical forests. *Herpetologica*, 33, 375–380.

Wang, X. & Fang, J. (2012). Constraining null models with environmental gradients: a new method for evaluating the effects of environmental factors and geometric constraints on geographic diversity patterns. *Ecography*, 35, 1147–1159.

Wiens, J. J., Brandley, M. C., & Reeder, T. W. (2006). Why does a trait evolve multiple times within a clade? Repeated evolution of snakeline body form in squamate reptiles. *Evolution*, 60, 123-141.

Woinarski, J.C.Z. & Gambold, N. (1992). Gradient analysis of a tropical herpetofauna: distribution patterns of terrestrial reptiles and amphibians in Stage III of Kakadu National Park, Australia. *Wildlife Research*, 19, 105–127.

TABLES

Table 1. Results of modelling to test hypotheses of species richness drivers. For each taxonomic subset, summaries of the top three linear regression models are shown. AICc is the bias corrected Akaike information criterion. ΔAICc is calculated relative to the top ranked model for each taxonomic subset. R^2 is adjusted R^2. Standardised slopes are also given ± the 95% CIs. Slope 1 refers to the first, or only explanatory variable. Slope 2 refers to the second, where applicable, which is always tree density.

Taxon subset	Explanatory variable	Slope 1	Slope 2	AICc	ΔAICc	R^2
Reptiles	Temperature	4.27±1.54		72.08	0	0.73
	Temperature + tree density	4.87±2.07	0.91±2.07	74.97	2.9	0.73
	Area	2.52±2.65		87.39	15.31	0.2
Snakes	Null			55.89	0	0
	Temperature	0.48±1.13		58.39	2.49	-0.01
	Tree density	0.09±1.17		59.33	3.44	-0.09
Lizards	Temperature	3.63±0.99		59.78	0	0.83
	Temperature + tree density	3.45±1.38	-0.26±1.38	63.61	3.83	0.82
	Tree density	-2.54±1.9		78.11	18.33	0.36
Endemics	Null			57.93	0	0
	MDE	0.9±1.12		58.14	0.21	0.15
	Tree density	-0.7±1.18		59.51	1.58	0.06

FIGURES

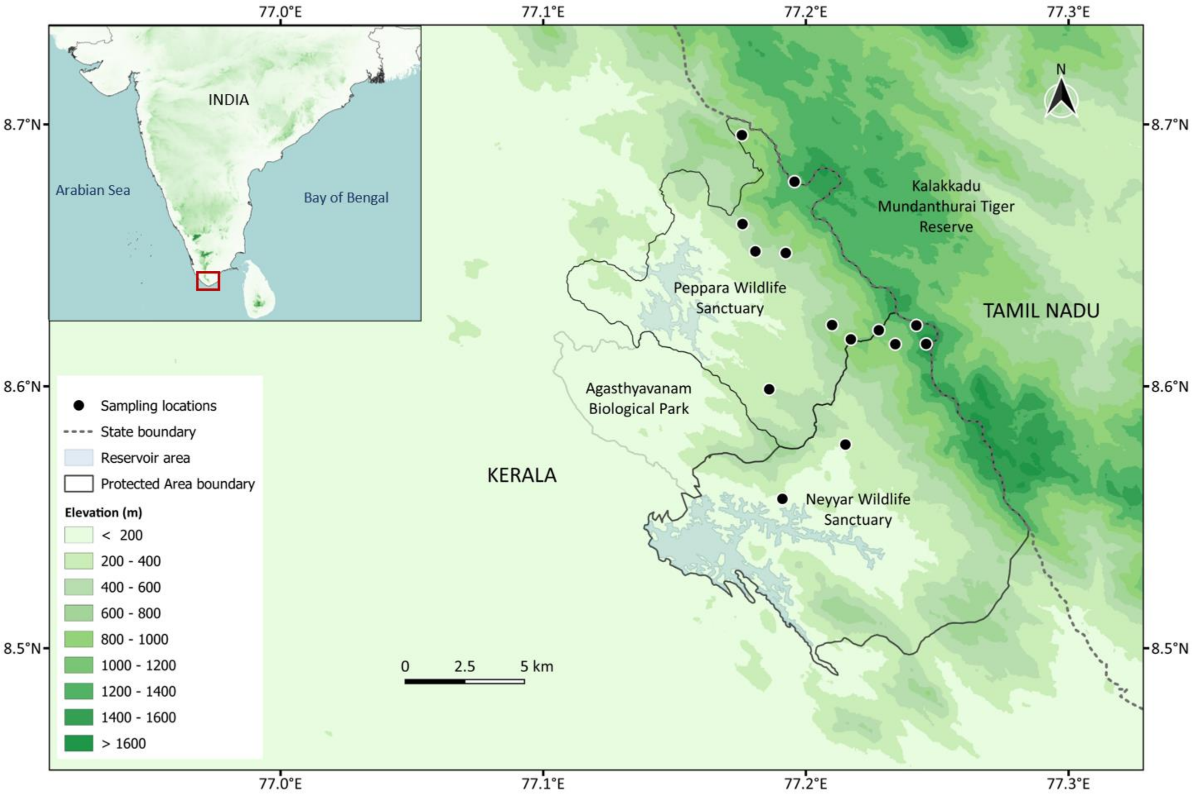

Figure 1. Sampling locations along the elevation gradient. Inset: location of Agasthyamalai Hills in the Indian subcontinent.

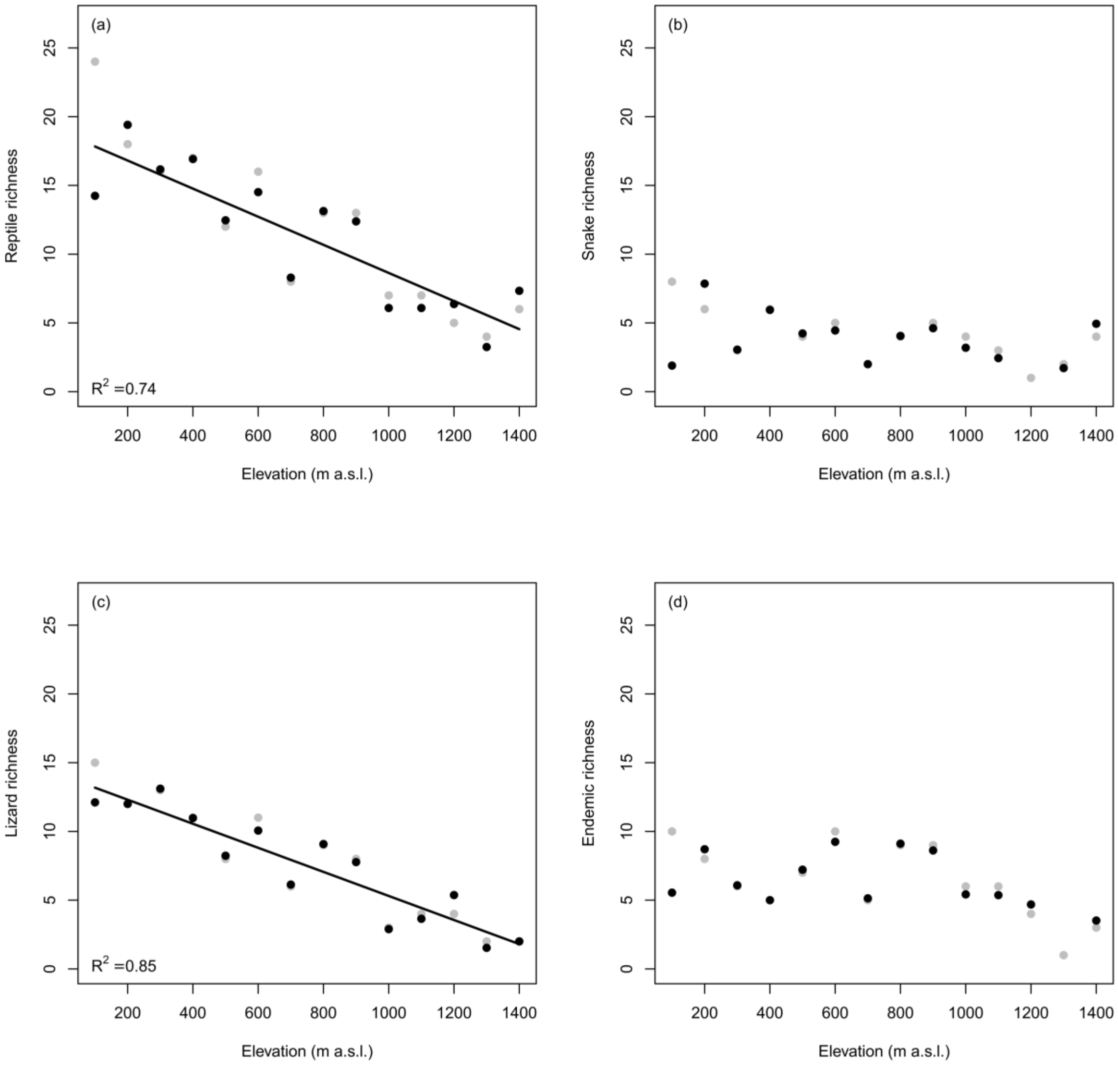

Figure 2. Patterns of species richness across elevation for (a) all reptiles, (b) snakes, (c) lizards and (d) endemic species. Data points represent elevational sampling sites. Black points are the analysed data, interpolated or extrapolated to correct for sampling biases. Grey points represent the raw, observed species richness values. Lines represent linear regression lines.

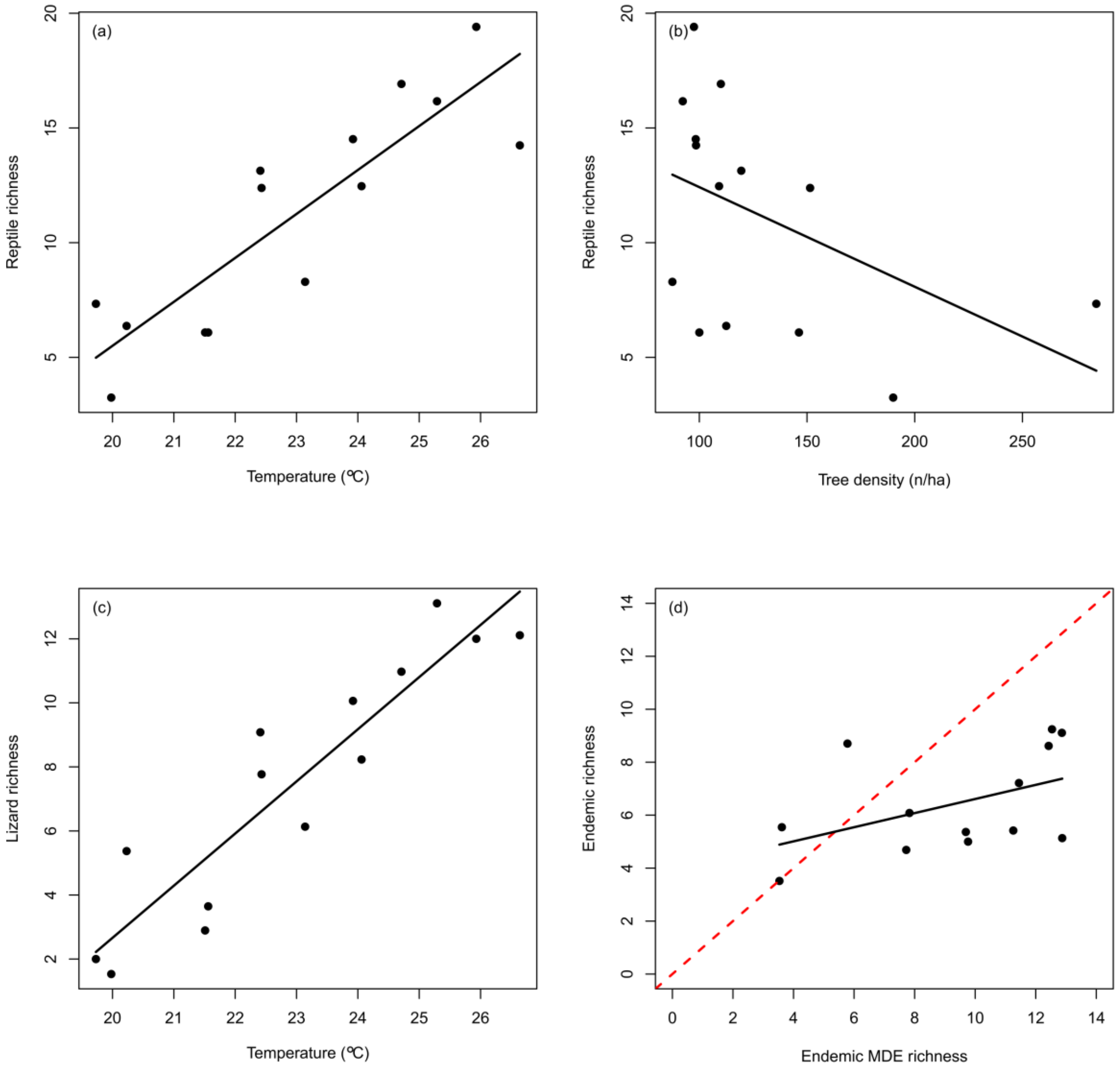

Figure 3. Select relationships between species richness of different reptile subsets and different potential drivers. Data points are elevational sampling sites. Black solid lines represent linear regression lines. Red dashed line in (d) represents a 1:1 relationship, which would be expected if the mid-domain effect (MDE) predictions of species richness match observed richness patterns. Relationships displayed here were top-ranked by AICc, or within ΔAICc of the top-ranked models and are displayed here for illustration.

SUPPLEMENTARY MATERIAL

Table S1. Table showing sample completeness calculated using the *iNEXT* function in the *iNEXT* package of R. Sampling effort is recorded in two-person hours (1 = 2 people searching for 1 hour).

Elevation (m)	**Sampling effort**	**Species observed**	**Sample completeness**
100	152	24	0.9639
200	27	18	0.9056
300	35	16	0.9054
400	37	17	0.9628
500	32	12	0.9413
600	44	16	0.9106
700	31	8	0.9539
800	35	13	0.8651
900	39	13	0.8109
1000	54	7	0.9378
1100	50	7	0.9129
1200	22	5	0.6818
1300	47	4	0.4086
1400	26	6	0.6753

828

Table S2. Table showing modelling details for elevational diversity patterns.

Taxon subset	Elevational model	AICc	ΔAICc	R^2
Reptiles	Linear	71.88	0	0.74
Reptiles	Curvilinear	75.88	3.99	0.76
Reptiles	Null	88.36	16.48	0
Snakes	Null	55.89	0	0
Snakes	Linear	58.36	2.47	0.07
Snakes	Curvilinear	62.69	6.80	0
Lizards	Linear	58.25	0	0.85
Lizards	Curvilinear	62.12	3.87	0.86
Lizards	Null	82.26	24.00	0
Endemics	Null	57.93	0	0
Endemic	Curvilinear	59.49	1.56	0.38
Endemics	Linear	59.50	1.57	0.13

829

830

Table S3. Expanded version of table 2 in the main text. Results of modelling to test hypotheses of species richness drivers. For each taxonomic subset, summaries of the top three linear regression models are shown. AICc is the bias corrected Akaike information criterion. ΔAICc is calculated relative to the top ranked model for each taxonomic subset. R^2 is adjusted R^2. Standardised slopes are also given ± the 95% CIs. Slope 1 refers to the first, or only explanatory variable. Slope 2 refers to the second, where applicable, which is always tree density.

Taxon subset	Explanatory driver	Slope 1	Slope 2	AICc	ΔAICc	R^2
Reptile	Temperature	1.92±0.69		72.08	0	0.73
Reptile	Temperature + tree density	2.19±0.93	0.02±0.04	74.97	2.9	0.73
Reptile	Area	0.13±0.14		87.39	15.31	0.2
Reptile	Tree density	-0.04±0.05		88.21	16.13	0.15
Reptile	Null			88.36	16.29	0
Reptile	MDE	0.03±0.52		91.65	19.58	-0.08
Snake	Null			55.89	0	0
Snake	Temperature	0.22±0.52		58.39	2.49	-0.01
Snake	Tree density	0±0.02		59.33	3.44	-0.09
Snake	MDE	-0.03±0.5		59.35	3.45	-0.09
Snake	Area	0±0.06		59.35	3.46	-0.09
Snake	Temperature + tree density	0.55±0.76	0.02±0.03	60.66	4.76	0.05
Lizard	Temperature	1.63±0.44		59.78	0	0.83
Lizard	Temperature + tree density	1.55±0.62	0±0.03	63.61	3.83	0.82
Lizard	Tree density	-0.05±0.04		78.11	18.33	0.36
Lizard	Area	0.13±0.1		78.96	19.18	0.32
Lizard	Null			82.26	22.48	0
Lizard	MDE	0.03±0.68		85.56	25.78	-0.08

Endemic	Null			57.93	0	0
Endemic	MDE	0.27±0.33		58.14	0.21	0.15
Endemic	Tree density	-0.01±0.02		59.51	1.58	0.06
Endemic	Temperature	0.33±0.55		59.52	1.59	0.06
Endemic	Area	0±0.06		61.4	3.47	-0.09
Endemic	Temperature + tree density	0.2±0.73	-0.01±0.03	63.35	5.42	0