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

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26 **ABSTRACT**

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

47

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

50

51 **Keywords:** Herpetofauna, altitude, mid-domain effect, Rapoport's rule, range size,

52 distribution patterns, Agasthyamalai Biosphere Reserve, tropical mountain

53

54 **1 INTRODUCTION**

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

69 Mountain regions contain disproportionate numbers of species relative to their geographic
70 area (Rahbek et al., 2019a), and many of the global biodiversity hotspots exist within
71 them (Kozak & Wiens, 2010; Guo et al., 2013). In terms of understanding general
72 mechanisms underlying variation in species diversity, elevational gradients have long
73 been recognized as useful “microcosms” of broader latitudinal patterns in species richness
74 (Stevens, 1992). Latitudinal gradients themselves are challenging to study due to their
75 large spatial extent, but in the case of elevation gradients, individual mountain ranges can
76 act as replicated transects. This provides opportunities to test the underlying causes of
77 species diversity patterns (Sanders & Rahbek, 2012). Finally, while elevational gradients

78 have a wide diversity of topographies and climates (Rahbek et al., 2019b), a key feature
79 of them is the existence of a strong thermal gradient. Temperature, a factor known to
80 influence the distribution and functioning of life across organizational scales (Brown,
81 2014), universally declines with increasing elevation. Temperature is particularly
82 important for reptiles; as ectotherms, they rely on ambient temperature to regulate their
83 body heat and allow them to function (Angilletta, 2009).

84 Elevational patterns in species richness tend to take one of three main forms: (1) a
85 monotonic increase, (2) a monotonic decline and (3) a mid-elevation peak (Rahbek,
86 1995). The prevalence of these patterns can vary across different taxonomic groups and
87 biogeographical regions (Peters et al., 2016), although the hump-shaped, mid-elevational
88 peak is reported to be the most common relationship (Rahbek, 2005). There are several
89 hypotheses which may explain these different richness-elevation patterns, and these can
90 be broadly grouped into two main categories: bioclimatic or spatial hypotheses (Grytnes
91 & McCain, 2007).

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

100 The second category of hypotheses seeking to explain elevational gradients in species
101 richness are spatial. A common explanation for richness-elevation patterns is the

102 influence of available area (Lomolino, 2001). This hypothesis is analogous to the well-
103 known species-area relationship which suggests that more individuals will exist in
104 elevational zones that have more available area, which in turn are more likely to come
105 from a larger species pool (Sanders, 2002; Romdal & Grytnes, 2007). The mid-domain
106 effect (MDE) is another popular spatial hypothesis describing species richness patterns.
107 The MDE predicts mid-elevational peaks in richness, purely as a result of the geometry of
108 a bounded domain, such as that between a mountain top and the coast (Colwell & Hurtt,
109 1994; Colwell & Lees, 2000 ; Jetz & Rahbek, 2001). Through the random placement of
110 varying species ranges, there is a high probability of greater range overlap, and therefore
111 higher species richness, at the centre of the bounded domain (Colwell & Lees, 2000).
112 Although MDE predictions are purely based on geometric constraints on range sizes,
113 recent analyses have modelled this effect in conjunction with bioclimatic variables
114 (Colwell et al., 2016). There is mixed empirical support for the influence of MDE on
115 elevation-richness patterns (Hawkins & Diniz-Filho, 2002; Currie & Kerr, 2008; McCain,
116 2009).

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

126 Rapoport's rule as general phenomenon is mixed (Gaston & Chown, 1999; Sanders,
127 2002; McCain & Knight, 2013).

128 In this study, we are interested in describing and understanding the elevational diversity
129 patterns of reptiles in the Western Ghats of India. Overall, richness-elevation patterns of
130 herpetofauna (reptiles and amphibians) tend to show monotonic declines (Heatwole,
131 1982; Cadle & Patton, 1988; Woinarski & Gambold, 1992; Hofer et al., 1999, 2000;
132 Nathan & Werner, 1999; Chettri et al., 2010). This taxonomic group is largely
133 understudied within India especially on elevational diversity patterns (but see
134 Naniwadekar & Vasudevan, 2007; Chettri et al., 2010). This demands an immediate
135 attention because the Indian subcontinent, and the Western Ghats in particular, is a global
136 hotspot of biodiversity. The unique bioclimatic conditions, topographic features and
137 habitat heterogeneity makes the Western Ghats particularly rich in biodiversity and high
138 in species endemism (Nair, 1991; Myers et al., 2000). In fact, 47.13% of the reptiles that
139 occur here are endemic to the Western Ghats (Srinivasulu et al., 2014). Recent studies
140 have also indicated that each mountain range in the Western Ghats possibly has many
141 local endemics and basal lineages – especially in case of reptiles (Cyriac et al., 2018; Pal
142 et al., 2018; Chaitanya et al., 2019; Mallik et al., 2019; Deepak et al., 2020).
143 Consequently, there is a need to better document and explain patterns of species richness
144 in this region.

145 In this context, we ask the following questions: (1) how is reptile species richness
146 distributed across elevation in the southern Western Ghats? (2) What bioclimatic and
147 spatial hypotheses explain these patterns? We use temperature and tree density as
148 measures of bioclimatic niche variables of relevance to reptiles. We predict that both will
149 relate positively to reptile species richness in this region: reptile metabolism is tightly

150 linked to ambient temperature, and we hypothesize that higher tree densities will provide
151 a greater number of niches that different reptile species can exploit. Tree density is often
152 used as a surrogate of habitat heterogeneity and habitat complexity (McCoy & Bell, 1991)
153 and has been repeatedly shown to alter reptile community structure (Heyer and Berven,
154 1973, Scott, 1976, Voris, 1977, Gillespie et al., 2015). In our case, we hypothesize that
155 more reptiles will be present in areas of higher tree densities.

156 We test each hypothesis separately for the two main subgroups of reptile: snakes and
157 lizards. This is typically done in studies of reptile diversity (Fu et al., 2007, Kryštufek et
158 al., 2008, Chettri et al., 2010) because of their different morphology and life-history
159 strategies (Shine & Charnov, 1992). Snakes tend to occupy higher trophic positions
160 compared to lizards, and being limbless they move through the environment very
161 differently (Gove, 1979, Parker & Plummer, 1987, Da Silva et al., 2018). Furthermore,
162 snakes tend to have larger range sizes compared to lizards, which may be an indication of
163 their higher dispersal abilities (Böhm et al., 2013). In general, large-ranged and small-
164 ranged species tend to show different responses to the mid-domain effect (Dunn et al.,
165 2006, Dunn et al., 2007), with small-ranged taxa less likely to conform to the predictions
166 of the MDE.

167 In this context, we predict that the differences in life-history strategies and range sizes
168 between snakes and lizards will result in different elevation-richness patterns, specifically
169 that snakes, with their larger ranges, will be more likely to conform to a mid-elevational
170 peak. We also predict that endemic species will show a mid-elevational peak or a
171 monotonic increase in richness with elevation. Previous studies on herpetofauna have
172 found mid-elevational peaks in endemic richness (Fu et al., 2006), while globally,
173 increases in endemism with elevation may be explained by the greater topographic

174 isolation of these areas which promotes speciation and endemism (Steinbauer et al.,
175 2016). Finally, given previous work on reptiles which found limited global support for a
176 series of spatial hypotheses (McCain, 2010), we expect to find more support for climatic
177 hypotheses at this local scale in the Western Ghats. Simultaneous tests of these
178 hypotheses have not yet been undertaken for reptiles in the biodiversity hotspot of the
179 Western Ghats. Here, we provide a test.

180

181 2 METHODS

182 2.1 Study area

183 Our study was located within the Agasthyamalai Hills (8.4° to 8.8°N and 77.0° to 77.4°E)
184 which is part of the Agasthyamalai Biosphere Reserve (ABR) on the southern tip of the
185 Western Ghats. We covered only the western slope (windward side) of the Agasthyamalai
186 Hills which comprised of two major protected areas: Neyyar and Peppara wildlife
187 sanctuaries in the Kerala State (Figure 1). The mean temperature of the coldest month in
188 the region ranges from 13 °C to 23°C (Pascal, 1982). The windward side of the
189 Agasthyamalai Hills receives high rainfall: varying between 2000-5000 mm annually
190 with only two to three dry months (Ramesh et al., 1997; Varghese & Balasubramanyan,
191 1998).

192 The Agasthyamalai region is well-known for its high plant diversity and endemism
193 (Nayar, 1996; Ramesh et al., 1997; Manju et al., 2009). The vegetation of the area
194 changes significantly along elevation. Champion & Seth (1968) identified four major
195 vegetation types in the area: southern moist mixed deciduous forest (<400 m a.s.l.), west
196 coast semi-evergreen (400-600 m a.s.l.), west coast tropical evergreen (600-1200 m a.s.l.)
197 and southern hilltop tropical evergreen (>1200 m a.s.l.). The deciduous or evergreen
198 forests up to 1200m a.s.l. are comprised of taller trees with canopy height ranging from
199 10-35 m however, the hill top forest is of a dense, stunted evergreen type with canopy
200 height reaching a maximum up to 10 m, mixed with open rocky and grass areas
201 (Varghese & Balasubramanyan, 1998). Apart from human settlements in the lower
202 elevations (<400 m a.s.l.), trekking and pilgrimage activities also exert significant
203 pressure on the natural habitats of the region (Ramesh et al., 1997). Although we

204 observed some level of habitat disturbance along the main trekking route, our sampling
205 was mostly restricted to undisturbed patches along the elevational gradient.

206 The focal study area encompasses approximately 250 km², spread across an elevational
207 range of 50 to 1868 m a.s.l.. The coast is 30 km from the site - this makes the landscape
208 ideal for testing mid-domain effects as it has geometric constraints on both ends, the
209 mountain summit at the top and the coastline at the bottom.

210 **2.2 Data collection**

211 **2.2.1 Reptile richness**

212 We surveyed reptiles in the Agasthyamalai Hills from April 2012 through to December
213 2014 along an elevation gradient, covering both wet and dry seasons. The total
214 elevational range was categorized into fourteen 100 m wide elevational bands, beginning
215 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
216 of adequate undisturbed habitat, and we did not sample higher than 1500 m a.s.l. due to
217 logistical constraints. Transects of approximately 2000 m in length and 250-300 m in
218 width were laid in each elevational band based on topography and accessibility. We
219 performed time constrained visual encounter surveys (VES) to sample the reptile
220 communities in each elevational band. The VES method surveys an area for a prescribed
221 time, systematically searching for animals in all possible microhabitats covering different
222 vertical strata (Campbell & Christman, 1982, Crump & Scott, 1994). This is an
223 appropriate and well-understood method for both species inventorying and monitoring,
224 and is suitable for examining landscape level patterns especially in mountains. The
225 method is also known for having a higher detection rate of rare species (Crump & Scott,
226 1994) and has successfully been applied before in the Western Ghats (Bhupathy &
227 Nixon, 2011) and Eastern Himalayas (Chettri et al., 2010)

228 We used the transects laid in each elevational band as an approximate spatial guide for
229 our VES sampling. We gradually searched along each transect for reptiles using VES
230 during daylight, from 0800 to 1800 hours, and the search included turning stones and
231 fallen logs, moving leaf litter, scanning the vegetation and, searching on stems and barks
232 of trees. In this sense, VES explores all possible microhabitats from the ground level to
233 the tree branches of approximately 3 m above the ground. Even though active
234 microhabitat search was not possible in higher vertical strata (above 3 m), simple visual
235 scanning of vegetation and tree branches to a maximum height was carried out wherever
236 possible. Repetition of sampling in the same spatial area was avoided as the VES method
237 involves the alteration of microhabitats (turning stones and logs etc.). In our dataset, a
238 single VES “sample” within an elevational band consisted of two person hours (1 hour ×
239 2 people searching = 2 person hours). We were unable to perform equal sampling effort
240 across the elevations, however, due to the differences in spatial and temporal accessibility
241 to some elevational zones (Table S1). We identified all reptiles to species level where
242 possible and assigned a distinct morphospecies identifier where full identification was not
243 possible.

244

245 **2.2.2 Tree density**

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

250

251 **2.2.3 Elevation and available area**

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

258

259 **2.2.4 Environmental variables**

260 We downloaded bioclimatic variables for the study area from the Chelsa` climatic
261 database (<http://www.chelsa-climate.org/>) which is a fine-scale (i.e. 1×1 km), long-term
262 (1979 to 2013) climate dataset with global coverage based on statistical downscaling
263 (Karger et al., 2017). Due to its high resolution, the Chelsa dataset is reported to be more
264 effective for modelling species distributions in geographically complex regions such as
265 mountainous landscapes (Maria & Udo, 2017). Out of the available 19 bioclimatic
266 variables, we retained only mean annual temperature (MAT) and mean annual
267 precipitation (MAP) for analysis as they are most ecologically important for the
268 distribution of reptiles. QGIS Version 3.10 was used for extracting the data from the
269 bioclimatic layer and we used the central point of each elevational transect to represent
270 the climate of each elevation.

271

272 **2.3 Data analysis**

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

274

275 2.3.1 Species richness

276 We used rarefaction to generate standardized species richness estimates because sampling
277 effort (hours of VES) varied across the elevational bands. We used the *iNEXT* package in
278 R (Hsieh et al., 2016) to do this. Specifically, we used the function *estimateD* in
279 “incidence_freq” mode (because our raw data are incidences of species in variable
280 numbers of samples from each elevation). We used *estimateD* to estimate species richness
281 for each elevation at the median sampling effort (38 two-person hours). This involved
282 extrapolating richness estimates for elevations that were not sampled for 38 two-person
283 hours, and interpolating samples that were sampled for more than 38 two-person hours.
284 We employed this procedure using four different data subsets: reptiles (all species),
285 snakes, lizards and endemics (of the Western Ghats). We use these estimated species
286 richness values in all the analyses that follow. We assigned status of endemism of each
287 species based on recent assessment of reptiles of the Western Ghats (Srinivasulu et al.,
288 2014). We provide sample completeness estimates from *iNEXT* in Table S1.

289

290 2.3.2 Describing elevational patterns

291 We used linear regressions with Gaussian errors to test whether the species richness of
292 each taxonomic subset had a linear, curvilinear or no relationship with elevation. We used
293 Gaussian errors because the sample size corrected species richness values were not
294 integers. For the linear models, we used only elevation as a predictor variable. For the
295 curvilinear models, we used elevation and elevation² as predictor variables. The null
296 models included only an intercept. We compared models using bias corrected Akaike
297 information criteria (AICc). We calculated the difference in AICc ($\Delta AICc$) between the

298 three models, relative to the one with the lowest AICc, and extracted R^2 adjusted for small
299 sampled sizes. Where competing models are within $2 \Delta AICc$ of each other, we opt to
300 interpret and present the simplest model. We present the model with the lowest AICc
301 along with its adjusted R^2 for each taxonomic subset. None of the models deviated from
302 the model assumptions based on our interpretation of the model diagnostic and residual
303 plots.

304

305 **2.3.3 Testing species richness drivers**

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

317 *Environmental drivers:* We used mean annual temperature ($^{\circ}C$) and tree density (n/ha) to
318 represent environmental drivers. We did not include precipitation because models
319 containing precipitation as well as temperature and tree density, had variance inflation
320 factors (VIF) above 2 (Fox & Monette, 1992). In total there were three environmental
321 models: temperature, tree density and temperature + tree density. We hypothesised that

322 each variable may positively influence reptile species richness independently, or in
323 combination.

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

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

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

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

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

352

353 **RESULTS**

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

358

359 **2.4 Elevational patterns**

360 For reptiles and lizards, species richness declined linearly with increasing elevation
361 (Figure 2a, c; ΔAICc to next best model was 3.99 and 3.86, respectively). In each case,
362 elevation explained a large fraction of the variation in species richness (reptiles adjusted
363 $R^2 = 0.74$, lizards adjusted $R^2 = 0.85$). Neither the linear or curvilinear models fitted well
364 to the patterns of snake and endemic species richness, suggesting that there was no clear
365 systematic variation of species richness with elevation in these groups (Figure 2b, d;
366 ΔAICc to next best model was 2.46 and 1.56, respectively). Full model details can be
367 found in Table S2.

368

369 2.5 Species richness drivers

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

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

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

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

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

396

397 3 DISCUSSION

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

407 Our headline result is the monotonic decline in reptile and lizard species richness which
408 appears to be driven by temperature (Table 2). Fewer reptiles (and lizards) are found in
409 the colder, high elevations (Figure 3, Figure 4). These findings echo results from both the
410 global and the local scale. For example, McCain (2010) found that the most common
411 richness-elevation pattern in reptiles across the globe was a monotonic decline, and that
412 this was largely explained by temperature. Similar findings have been reported for
413 Himalayan reptiles (Chettri et al., 2010), the Costa Rican herpetofauna (Fauth et al.,
414 1989), reptiles in the Dinaric Alps (Kryštufek et al., 2008) and a suite of other ectotherms
415 from around the globe (Bishop et al., 2014; Peters et al., 2016). Although negative
416 richness-temperature relationships are reported for many taxa, including endotherms such
417 as birds and bats (McCain, 2007, 2009), a monotonic decline pattern is most reported for
418 ectothermic taxa (McCain, 2010). Consequently, our results in the Western Ghats feed
419 into the general narrative that temperature is the primary driver of reptile species richness
420 gradients worldwide.

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

435 In terms of endemic species, this potential sampling issue is unlikely to explain our
436 results. Of the species we sampled, 53% were endemic which closely matches the
437 proportion of endemic reptiles in the Western Ghats which is 47% (Srinivasulu *et al.*,
438 2014), and only 20% were found at a single site. Consequently, we are more confident
439 that the patterns we describe for endemic species are reflecting reality – that the number
440 of endemic species does not systematically vary across elevation. An interesting contrast
441 with endemics can be seen in frogs from the Hengduan Mountains, China. In this case,
442 endemics were not influenced by environmental factors, but did fit MDE predictions (Fu
443 et al., 2006). While we do not find strong evidence that endemic species follow the MDE,
444 our data agree with that of Fu et al., (2006) in that the diversity patterns of endemic
445 species do not appear to be driven by bioclimatic variables.

446 How representative are our results in the Agasthyamalai Hills of the Western Ghats as a
447 whole? The Western Ghats largely consist of conical shaped mountains, as do the hills
448 sampled here (Elsen & Tingley, 2015). Compared to the windward side we focused in the
449 present study, the ranges towards the leeward side of the Ghats slightly differ in their
450 habitat types and rainfall intensities (Nair & Daniel, 1986; Nair, 1991), but are unlikely to
451 differ in their temperature-elevation patterns. Critically, the unique high elevation tropical
452 montane cloud forest known as Shola, a natural matrix of forests and grasslands (found
453 only above 1500m a.s.l) is scarce in the Agasthyamalai landscape compared to most of
454 the northern hill ranges (e.g. Anaimalai Hills- 2695m a.s.l.). Sholas are known for the
455 presence of some endemic reptiles (Deepak & Vasudevan, 2008), and this has been
456 further proved by recent discoveries (Deepak et al., 2020). Consequently, studies
457 exploring such high elevation habitats could alter the endemic-elevation pattern that we
458 see here. Finally, a recent phylogeographic analysis of frogs highlighted that the Palghat
459 Gap (a natural biogeographical barrier within the Western Ghats) could potentially be a
460 barrier to dispersal and influence larger macroevolutionary patterns (Vijayakumar et al.,
461 2016). Whether this biogeographical barrier also causes differences in the patterns and
462 drivers of reptile richness, however, remains to be tested – we suspect that it is unlikely.

463 In this study, we have not analyzed beta diversity across elevation because our sampling
464 effort differed across the gradient. For alpha diversity (species richness) we could correct
465 for this using known interpolation and extrapolation techniques (Hsieh et al., 2016).

466 While similar corrections exist for beta diversity (Chao et al., 2005), this is beyond the
467 scope of the current manuscript. Regardless, there is a clear opportunity and need for
468 more comparative analyses of elevational patterns (including beta diversity) between
469 different ranges within the Western Ghats. Regardless, considering the largely similar
470 habitat types across the region and the repeated temperature-elevation gradients, we

471 suggest that our alpha diversity analyses are likely to be representative of the entire
472 Western Ghats.

473 In summary, we provide the first evidence of reptile species richness-elevation patterns in
474 the Western Ghats, a global biodiversity hotspot. Despite the strong geometric constraints
475 (mountain summit and coastline) present in the study range, the observed richness
476 patterns were not shaped by the mid-domain effect or the available-area effect in the
477 Agasthyamalai Hills. Temperature is the clear driver of these patterns for reptiles, and for
478 lizards but not for snakes and endemic species. These temperature relationships result in a
479 monotonic decline in reptile and lizard richness with increasing elevation. These findings
480 agree with those at the global scale which report a tight link between temperature and
481 reptile diversity patterns (McCain, 2010). Since external temperatures directly determine
482 metabolic rates in ectotherms (such as reptiles and amphibians), they show higher
483 affinities with temperature and are more vulnerable to changing climates than endotherms
484 (i.e. birds and mammals) (Rolland et al., 2018). This becomes a critical issue for the large
485 number of range-restricted reptiles in the Western Ghats where many species are endemic
486 and confined to certain hill ranges. As global temperatures rise, these species may find
487 themselves pushed to new elevational ranges, or they may run out of appropriate thermal
488 environments entirely (Colwell et al., 2008). The next steps are to extend this kind of
489 standardized sampling, throughout the Western Ghats, to confirm if the patterns are
490 repeatable and to further generalize our understanding of how biodiversity is maintained
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506 J.V.J and M.P conducted field data collection. J.V.J along with T.R.B designed MS,
507 carried out data analysis and led the writing. R.J and M.P provided comments for
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509

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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. Δ AICc is calculated relative to the top ranked model for each taxonomic subset. R^2 is adjusted R^2 . Standardised slopes are also given \pm 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.

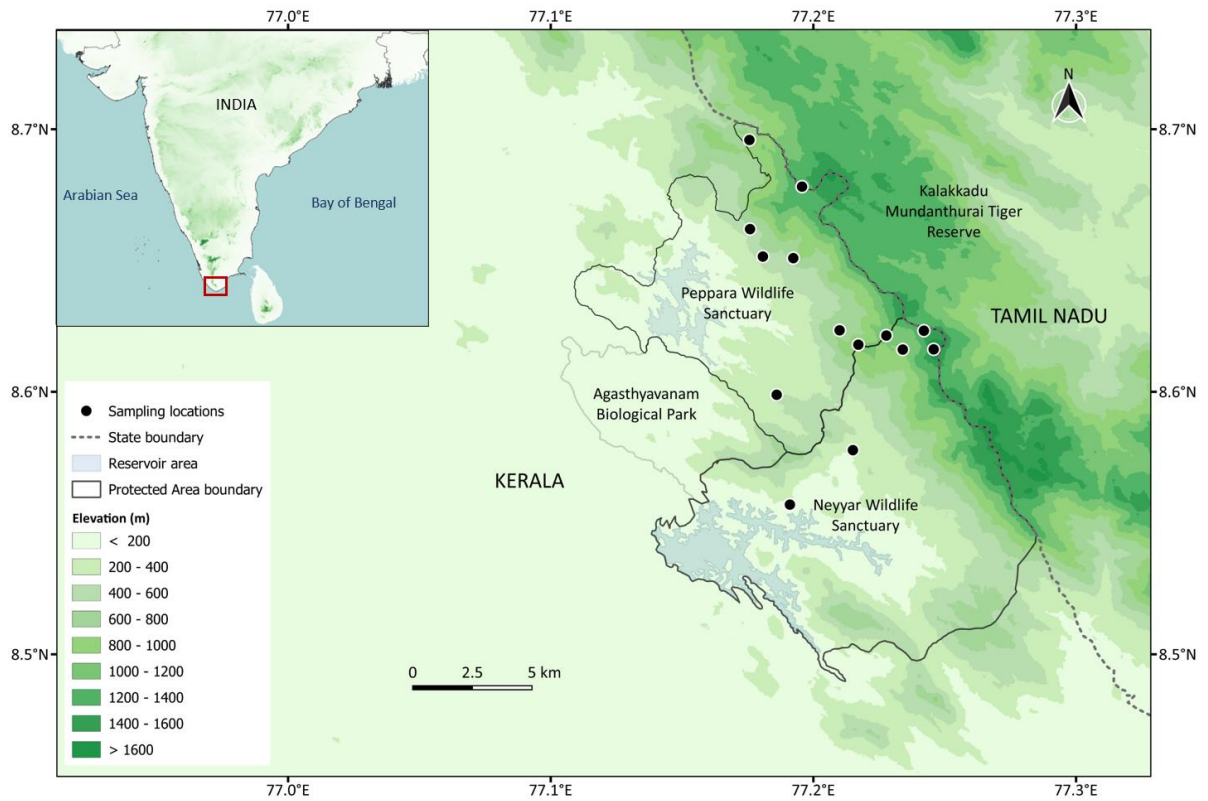
Taxon subset	Explanatory variable	Slope 1	Slope 2	AICc	Δ AICc	R^2
Reptiles	Temperature	4.27 \pm 1.54		72.08	0	0.73
	Temperature + tree density	4.87 \pm 2.07	0.91 \pm 2.07	74.97	2.9	0.73
	Area	2.52 \pm 2.65		87.39	15.31	0.2
Snakes	Null			55.89	0	0
	Temperature	0.48 \pm 1.13		58.39	2.49	-0.01
	Tree density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

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FIGURES



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791 **Figure 1.** Sampling locations along the elevation gradient. Inset: location of

792 Agasthyamalai Hills in the Indian subcontinent.

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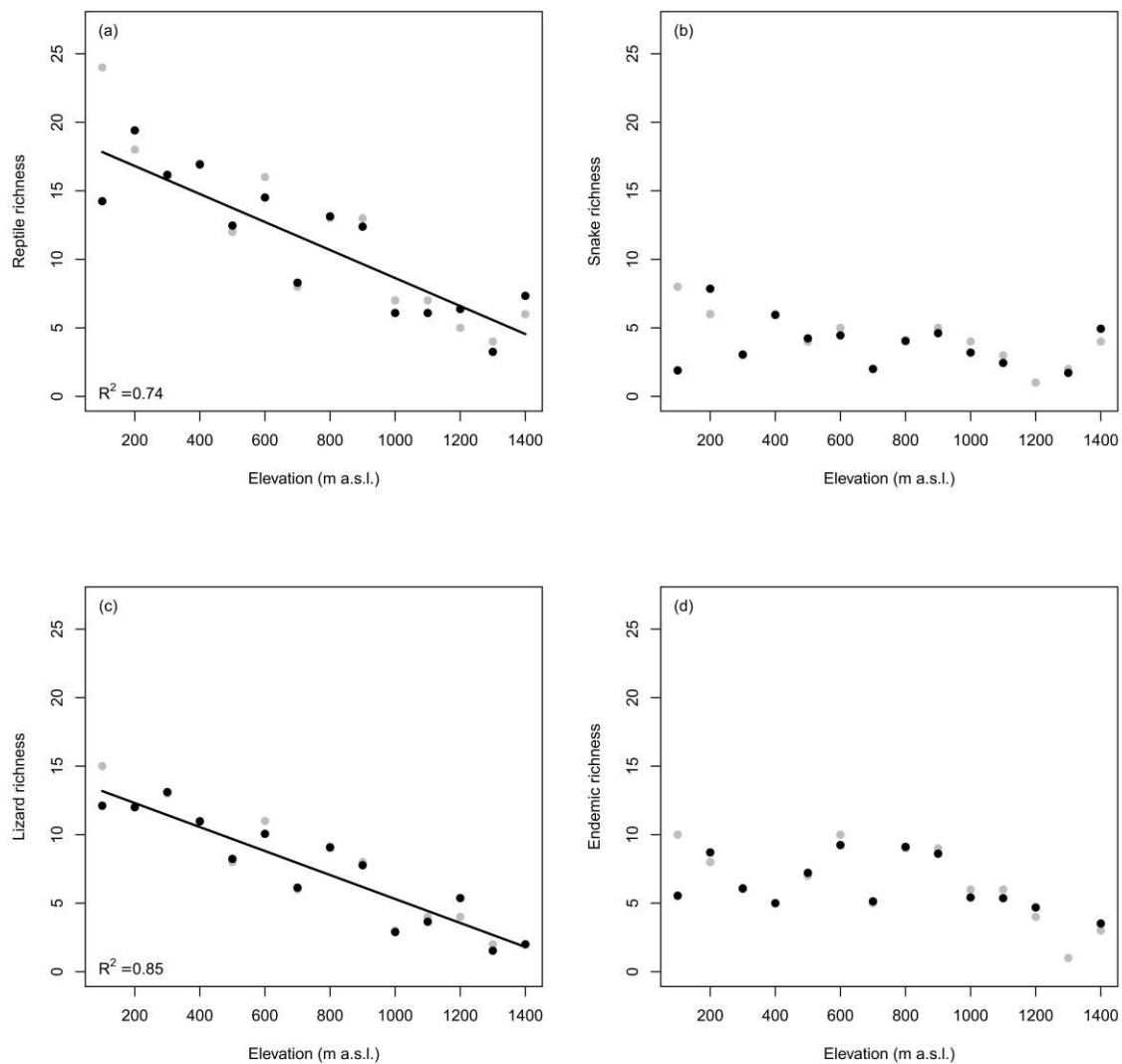
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810 **Figure 2.** Patterns of species richness across elevation for (a) all reptiles, (b) snakes, (c)

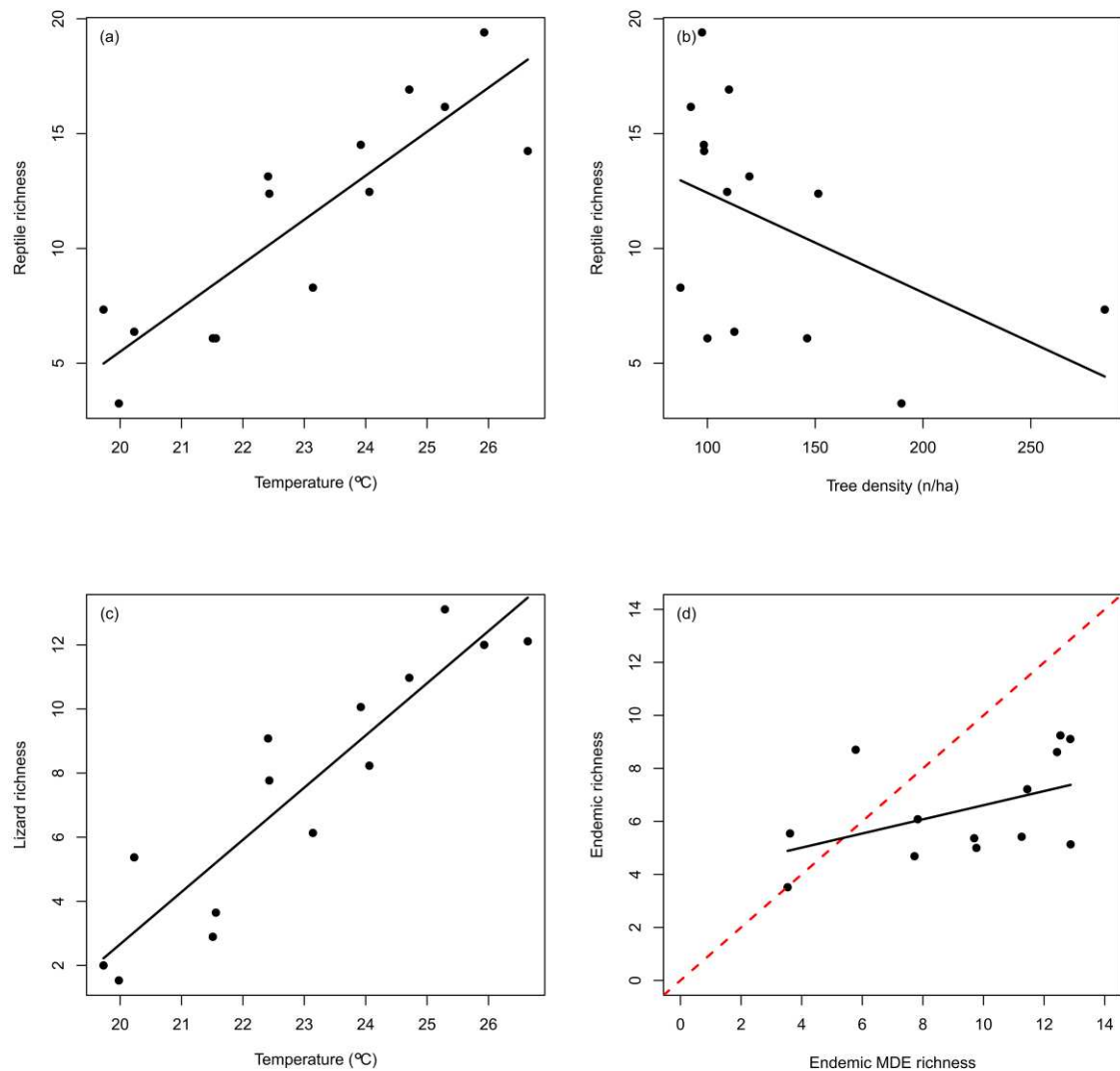
811 lizards and (d) endemic species. Data points represent elevational sampling sites. Black

812 points are the analysed data, interpolated or extrapolated to correct for sampling biases.

813 Grey points represent the raw, observed species richness values. Lines represent linear

814 regression lines.

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818 **Figure 3.** Select relationships between species richness of different reptile subsets and

819 different potential drivers. Data points are elevational sampling sites. Black solid lines

820 represent linear regression lines. Red dashed line in (d) represents a 1:1 relationship,

821 which would be expected if the mid-domain effect (MDE) predictions of species richness

822 match observed richness patterns. Relationships displayed here were top-ranked by AICc,

823 or within Δ AICc of the top-ranked models and are displayed here for illustration.

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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

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

Taxon subset	Elevational model	AICc	ΔAICc	R²
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

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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. Δ AICc is calculated relative to the top ranked model for each taxonomic subset. R^2 is adjusted R^2 . Standardised slopes are also given \pm 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	Δ AICc	R^2
Reptile	Temperature	1.92 \pm 0.69		72.08	0	0.73
Reptile	Temperature + tree density	2.19 \pm 0.93	0.02 \pm 0.04	74.97	2.9	0.73
Reptile	Area	0.13 \pm 0.14		87.39	15.31	0.2
Reptile	Tree density	-0.04 \pm 0.05		88.21	16.13	0.15
Reptile	Null			88.36	16.29	0
Reptile	MDE	0.03 \pm 0.52		91.65	19.58	-0.08
Snake	Null			55.89	0	0
Snake	Temperature	0.22 \pm 0.52		58.39	2.49	-0.01
Snake	Tree density	0 \pm 0.02		59.33	3.44	-0.09
Snake	MDE	-0.03 \pm 0.5		59.35	3.45	-0.09
Snake	Area	0 \pm 0.06		59.35	3.46	-0.09
Snake	Temperature + tree density	0.55 \pm 0.76	0.02 \pm 0.03	60.66	4.76	0.05
Lizard	Temperature	1.63 \pm 0.44		59.78	0	0.83
Lizard	Temperature + tree density	1.55 \pm 0.62	0 \pm 0.03	63.61	3.83	0.82
Lizard	Tree density	-0.05 \pm 0.04		78.11	18.33	0.36
Lizard	Area	0.13 \pm 0.1		78.96	19.18	0.32
Lizard	Null			82.26	22.48	0
Lizard	MDE	0.03 \pm 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

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