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11   Strapline: Original Article

12   **Papua New Guinea terrestrial vertebrate richness: elevation matters most for all except reptiles**

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14   Short running head: Papua New Guinea species richness

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20   **ABSTRACT**

21   **Aims** To examine species richness patterns in Papua New Guinea's terrestrial vertebrates and test for

22   geographical congruence between the four classes, and between lizard and snake subgroups. To assess the

23   environmental correlates of Papua New Guinean terrestrial vertebrate richness, and contrast effects of

24   varying analytical resolution and correction for spatial autocorrelation. We predict congruence in the bird,

25 mammal and to a lesser extent amphibian richness, with weak congruence or incongruence between
26 reptiles and the other taxonomic groups. We further predict these patterns will stem from relative or in
27 the case of reptiles dissimilar, correlative trends with environmental predictors such as elevation and
28 temperature.

29 **Location** Papua New Guinea

30 **Methods** Having created and updated distribution maps for reptiles, we compare them with known ranges
31 of amphibians, birds and mammals and generate species richness grids at quarter-, half-, and one- degree
32 spatial resolutions. We examine congruence in species richness between vertebrate groups and between
33 reptile subgroups. We employed spreading-dye models to simulate species richness according to eight
34 environmental predictors and one random model. We accounted for spatial autocorrelation in all analyses.

35 **Results** Papua New Guinean amphibian, bird and mammal species richness are spatially congruent, a trend
36 which strengthens with decreasing spatial resolution. Reptiles and the lizard and snake subgroups reveal
37 remarkably different spatial richness trends. Elevational predictors, particularly elevational range at coarse
38 resolutions, provide the strongest correlates of species richness. Whereas terrestrial vertebrate richness
39 increases with elevation, reptile richness decreases.

40 **Main Conclusions** Congruent species richness gradients in Papua New Guinea are observed in most
41 terrestrial vertebrates, except reptiles. Topographic heterogeneity and associated climatic clines promote
42 diversity in most terrestrial vertebrates but appear to strongly constrain reptile diversity. The
43 topographical complexity and climatic stratification of tropical mountains clearly present a wealth of
44 opportunities for diversification in most terrestrial vertebrate groups. As reptiles are strongly constrained
45 by temperature, tropical mountains present more of a diversification barrier for them.

46 **Key Words:** cross-taxon congruence, elevation, environmental correlates, Papua New Guinea, spatial
47 autocorrelation, spatial resolution, species richness, topographic heterogeneity.

48

49 **INTRODUCTION**

50   Tropical regions hold the greatest species richness on the planet (Fine, 2015). Species richness
51 patterns and drivers within tropical regions, however, remain poorly known (Tuomisto *et al.*, 2014).
52 Analyses at continental and global scales can mask regional correlations between species richness and
53 environmental predictors and thus fail to identify the underlying causes of regional spatial richness

patterns (Qian & Ricklefs, 2008). Previous research demonstrated temperature to be an important determinant of species richness in temperate high-latitude regions, with primacy shifting to water availability in tropical and subtropical low-latitude regions (Hawkins *et al.*, 2003). It was suggested future studies should focus on assessing the interaction between these two richness predictors, as well as other key factors such as environmental heterogeneity (Stein *et al.*, 2014). Furthermore, assessing the determinants of biogeographical patterns across multiple taxonomic groups provides an insight into how these trends vary with differing attributes, such as ecology and dispersal ability (Keith *et al.*, 2012). A comprehensive understanding of the spatial overlap of species richness, or cross-taxon congruence, particularly within tropical regions, is crucial for efficient conservation planning and assessing the impacts of climate change (Grenyer *et al.*, 2006; Qian & Ricklefs, 2008).

Broad-scale global analyses typically reveal similar species richness patterns across vertebrate taxa (Grenyer *et al.*, 2006; Qian & Ricklefs, 2008). However, considerable variation in vertebrate congruence at continental and regional scales has also been observed, particularly between lizards and other taxa (Powney *et al.*, 2010; Lewin *et al.*, 2016). Cross-taxon congruence is expected when taxa respond similarly to environmental determinants or share large-scale diversification, colonization and extinction rates (Qian & Ricklefs, 2008). The spatial scale at which range map based richness patterns are examined likely influences perceived patterns and drivers of richness (Rahbek, 2005; Hurlbert & Jetz, 2007; Field *et al.,* 2009), especially within the tropics (Jetz *et al.*, 2008). Despite the recognition of scale effects, fine-scale analyses and cross-taxon comparisons of richness determinants are uncommon (Belmaker & Jetz, 2011). While climatic determinants are strongest at coarse scales, processes such as biotic and abiotic filters regulating local community assemblages may provide better explanations for fine-grained richness (Whittaker *et al.*, 2001; Belmaker & Jetz, 2011).

Attempts to explain broad-scale species richness gradients generally focus on predictors such as energy availability, environmental heterogeneity, study area and evolutionary time (Currie, 1991; Rahbek & Graves, 2001; Hawkins *et al.*, 2003; Field *et al.*, 2009). The energy-richness hypothesis (Wright, 1983) proposes that richness is limited by resource availability. Ambient energy is noted as a principle limiting factor for richness at high cold latitudes, with water availability a strong richness determinant at low warm latitudes (Hawkins *et al.*, 2003). Although ambient energy and water availability may directly constrain richness, their interaction is purported to affect distribution patterns indirectly through plant productivity (Field *et al.*, 2009). Plant productivity may influence animal-species richness through increased potential biomass, but it may also be consistent with the resource-speciation hypothesis in providing a greater diversity of resource types supporting more specialist species (Kaspari *et al.*, 2000; Hurlbert, 2004).

86 Tropical regions have the highest rates of net primary productivity (npp; Gillman *et al.*, 2014); a factor
87 thought to cause a trophic cascade of resource abundance, resulting in diversity peaks (Currie, 1991;
88 O'Brien, 1998).

89 Environmental and topographic heterogeneity (i.e., elevational range) are purported to be among
90 the most important factors influencing species richness (Stein *et al.*, 2014), especially at medium to fine
91 spatial scales (Field *et al.,* 2009). Topographic heterogeneity is thought to increase the number of habitat
92 types and resources available, which in turn increases the potential niche space allowing more species to
93 co-exist (Stein *et al.*, 2014). Topographically heterogeneous regions are thought to be particularly
94 important for narrowly ranging endemics by acting as both cradles and museums of biodiversity (Fjeldså *et*
95 *al.*, 2012). The cradle hypothesis posits that increased range in topography and climate will create greater
96 potential for speciation by isolation and divergent adaptation. According to the museum hypothesis,
97 refuge potential in elevationally diverse regions is greater during periods of climatic fluctuation, increasing
98 species persistence (Currie, 1991; Tews *et al.*, 2004). Topography is suggested to influence richness most in
99 regions experiencing the greatest climatic stability over the longest period of time, such as those in the
100 tropics (Fine, 2015). Indeed, broad-scale studies have often highlighted the significance of tropical
101 montane regions for species diversity (Orme *et al.*, 2005; Cadena *et al.,* 2011). At large spatial scales
102 species turnover in montane regions, caused by environmental heterogeneity and niche availability absent
103 in homogenous landscapes, inflates species richness (McCain & Beck, 2016).

104 New Guinea is among the most biologically diverse regions on the planet (Brooks *et al.*, 2006). The
105 exceedingly rich vertebrate assemblage (~5% of the world's terrestrial vertebrate species on less than 0.2%
106 of the Earths land surface) is thought to be the product of the island's large size (785,753 km^2), tropical
107 climate, complex geological history and extensive mountain ranges (Allison, 2009; Shearman and Bryan,
108 2011). New Guinea has a remarkable degree of tectonic complexity (Baldwin *et al.*, 2012), resulting in
109 extensive mountain uplift (over 31% of its mainland area is above 1,000 m, Allison, 2009). These extensive
110 and often isolated mountain ranges produce high levels of range-restricted species. The climate of much of
111 New Guinea is weakly seasonal, with temperature variation largely influenced by elevation, although the
112 savanna areas have a distinct dry season and reduced precipitation overall (~1000-1500 mm annual
113 rainfall; Allison, 2009). Roughly, two-thirds of the island is covered in broadleaf forests, mostly rain forest,
114 which receive from 2000 to more than 10,000 mm of rainfall annually and lack a pronounced dry season.
115 As the fauna on the eastern side of New Guinea, in the country of Papua New Guinea (PNG), has been
116 more thoroughly surveyed (Heads, 2002), we restrict our study on the terrestrial vertebrates to this region.

117 The many offshore islands that also comprise a significant portion of PNG are not included in our analyses,

118 consequently our use of "PNG" refers only to the mainland New Guinea portion of that country.

119 We assess species richness, cross-taxon congruence and environmental correlates of PNG's

120 terrestrial vertebrates. To determine the effect of spatial scale on these relationships, we conduct analyses

121 at three spatial resolutions. We predict that the aseasonal tropical climate will result in the highest

122 terrestrial-vertebrate richness predominantly in montane regions. Sharp climatic clines coupled with

123 decreasing connectivity at higher altitudes, are expected to promote species' elevational segregation

124 (Janzen, 1967; Ghalambor *et al.*, 2006) and increase the number of high-elevation range-restricted local

125 endemics. This trend will be most evident in taxa with comparatively poor dispersal ability, such as

126 amphibians. We further predict that PNG amphibian richness will be less constrained by water availability

127 than observed in other, more water-limited, regions (Buckley & Jetz, 2007). While amphibians'

128 physiological and ecological requirements for water (Feder & Burggren, 1992) will remain fundamentally

129 the same, the extremely high degree of precipitation across most of PNG will reduce its level of constraint

130 across the region. We predict that PNG bird and mammal species richness will be strongly positively

131 correlated, exhibiting concordant trends to the environmental predictors due to the equivalent physiology

132 and energetic requirements of endotherms (Grenyer *et al.*, 2006). We predict that PNG reptiles will show

133 the greatest degree of disparity in richness patterns. Reptiles are strongly constrained by temperature due

134 to their physiology and they fundamentally differ from amphibians in their ability to control water loss with

135 dry and scaly skin (Adolph & Porter, 1993). We predict reptile richness will peak in warm lowland regions,

136 thus the ectothermic groups should display incongruent species richness patterns compared with

137 congruent endothermic richness.

138 **MATERIALS AND METHODS**

139 **Species geographical range data**

140 We compiled geographical range data for all 232 PNG native mainland reptile species using ArcGIS

141 10.0, following the taxonomy of Uetz and Hošek (2015), but including three lizards (*Cryptoblepharus*

142 *novaeguineae*, *Gehyra baliola* and *Sphenomorphus anotus*) considered valid by the IUCN Melanesian

143 Reptile Working Group, 2014 (see Appendix S1 and S2 in Supporting Information). We obtained reptile

144 range maps from the Bishop Museum Pacific Biological Survey Project and during the IUCN Melanesian

145 Reptile Redlist Project (July, 2014). We converted all point-locality data to polygons using a 10 km^2 buffer

146 (radius = 1.72 km), in accordance with IUCN mapping standards (http://www.amphibians.org/wp-

147 content/uploads/2013/09/Red-List-Mapping-standards-ARLA-Jan2014-web-version.pdf). To assess trends

in species richness within reptiles, we divided PNG reptiles into lizards (n = 150) and snakes (n = 68), omitting crocodiles (n = 2) and turtles (n = 12) due to their low species numbers. Following the taxonomy of Frost (2015), we obtained ranges for 217 of the 275 PNG amphibian species from the IUCN (2014) and digitized the remaining 58 maps ourselves (see Appendices S1 and S2). We obtained range maps for PNG's 635 breeding-bird species from BirdLife International and NatureServe (2014) and amended 64 of these according to the taxonomy of Pratt and Beehler (2014; see Appendix S1). We obtained range maps for 232 PNG mammal species, 219 were obtained from IUCN (2012) and 13 maps for recently described species were digitized by us (see Appendices S1 and S3).

Species richness for each terrestrial vertebrate group was obtained by collating range maps per group and combining them with three gridded layers of Papua New Guinea (see Appendix S4). Grid cells were either 25x25 km^2 (n = 620), 50x50 km^2 (n = 160), or 100x100 km^2 (n = 41). Equivalence in grid-cell area was ensured using a Behrmann equal-area projection; wherein grid cells areas were 625, 2,500 or 10,000 km^2. For convenience, we refer to these grid layers as 'quarter-degree grid', 'half-degree grid' and 'one-degree grid', as they approximate to these sizes. We omitted grid cells with <50% land area to negate potential species-area relationships.

Environmental data

Three climatic predictors (temperature, precipitation and net primary productivity) and one topographic predictor (elevation) were used to derive eight environmental predictors (see Appendix S5). Temperature and precipitation data were obtained from the PNG Resource Information System (3rd Edition; Bryan & Shearman, 2008) and used to produce mean-annual and annual-range measures for both temperature (a proxy for ambient energy availability) and precipitation (a proxy for water availability). Net primary productivity (npp) data were obtained from Imhoff *et al.* (2004) and used as a proxy for rate of biomass production in primary producers (Hurlbert, 2004). Insufficient variance in npp heterogeneity precluded its use as a richness predictor. Elevational data were obtained from the PNG Resource Information System (3rd Edition; Bryan & Shearman, 2008) and used to create three topography predictors: mean elevation, elevational range (maximum - minimum elevation per grid cell) and a 'mid-elevation' predictor (see below). The 'mid-elevation' model predicts that species richness has a unimodal relationship with elevation, thus within a given grid cell richness will increase with the proportion of area at Papua New Guineas elevational mid-point. The function to simulate this follows the formula:

$$E_{mid} = 1 - ((|E_i - E_{jmid}|) / E_{jmid})$$

178 where $_j$ represents the total gridded domain of PNG, and $_i$ a given cell within the grid. E_i represents the

179 mean elevation in cell $_i$, and E_{jmid} is half the difference between the maximum and minimum mean

180 elevation recorded in grid $_j$.

181 **Simulation models**

182   Richness patterns are typically investigated through curve-fitting analysis (Rahbek *et al.,*

183 2007) and as such cannot model species ranges directly or generate quantitative predictions of species

184 richness (Gotelli *et al.*, 2009). Spreading-dye models (termed "Geometric constraint models" in Jetz and

185 Rahbek, 2001) were developed as an alternative method for assessing richness gradients in heterogeneous

186 landscapes. These spatially explicit models can simulate speciation, dispersal and extinction of species in

187 heterogeneous landscapes (Gotelli *et al.*, 2009). Spreading-dye models reconstruct distributions by

188 assigning cells to a species' range within the gridded domain. After the initial cell has been selected the

189 range is allowed to expand to adjacent cells, with the cell number in each species' predicted range

190 equivalent to its observed range. The initial grid cell and subsequent adjacent cell selection can either

191 occur stochastically, with all grid cells equal in selection probability, or be weighted according to underlying

192 environmental predictor values across the gridded domain (Storch *et al.*, 2006; Rahbek *et al.*, 2007; Szabo

193 *et al.*, 2009).

194   To simulate species richness according to our predictors, we used spreading-dye models at a

195 quarter-, half- and one-degree grid scale (Jetz & Rahbek, 2001; Storch *et al.,* 2006). For each terrestrial

196 vertebrate group we developed nine species richness simulation models, eight simulation models derived

197 from environmental predictors and one null model. The null model specifies a single geographic origin for

198 each species, and allows each range to spread cohesively and randomly within the gridded domain (Gotelli

199 *et al.*, 2009). Simulations were modified to assess the role of environmental gradients on species richness

200 by weighting cells according to the predictor values (Storch *et al.*, 2006; Rahbek *et al.*, 2007; Szabo *et al.*,

201 2009). The gridded predictors: mean elevation, elevational range, mean annual npp, mean annual

202 temperature, annual temperature range, mean annual precipitation and annual precipitation range were

203 rescaled to between 0 and 1, using minimum and maximum values for each predictor. This ensured that a

204 given proportional change resulted in an equivalent change in cell selection probability across all

205 environmental predictors (Rangel *et al.*, 2007). The relative probability of initial cell and subsequent

206 adjacent cell selection was determined by variation in the environmental predictor values. Thus

207 environmental determinism per cell ranged from completely random ($_i$ = 0) to strongly deterministic ($_i$ = 1).

208 Simulated terrestrial-vertebrate species richness, derived from the nine predictors at three spatial

209   resolutions, was carried out 999 times for each group, and the gridded mean species richness calculated

210   from all models.

Statistical analysis

212   All statistical analyses were carried out in R 3.3.0 (R Development Core Team, 2016). Cross-taxon

213   congruence among PNG terrestrial-vertebrate group richness was initially assessed using Pearson's

214   correlation coefficient; however, non-independence in the spatial data was detected using Moran's *I* (see

215   Appendix S6). Spatial autocorrelation arises when neighbouring locality values in spatial data are more

216   similar than expected by chance (Legendre, 1993), leading to increased type-1 error rates and incorrect

217   parameter estimates (Lennon, 2000). To account for spatial autocorrelation we used Dutilleul's modified *t*-

218   test (Dutilleul *et al.*, 1993), provided in the package 'SpatialPack' (Osorio & Vallejos, 2014).

219   To identify the strongest environmental correlates of each PNG terrestrial vertebrate group, we

220   regressed observed species richness against richness simulated by the eight environmental predictors and

221   the single stochastic predictor. We initially conducted ordinary least squares (OLS) regression, then

222   accounted for spatial autocorrelation in model residuals by using simultaneous autoregressive (SAR)

223   models (Kissling & Carl, 2008), provided in the package 'spdep' (Bivand & Piras, 2015). The spatial

224   structure was specified as the eight nearest neighbours to each cell, and neighbour cells were weighted

225   according to the row-standardized coding scheme. We assessed the relative explanatory power in the OLS

226   and SAR models using Akaike's information criterion (AIC_c).

RESULTS

Species richness

229   PNG bird and mammal richness have generally concordant patterns at the quarter-degree grid

230   scale, whereas amphibian and reptile richness patterns are distinct from these and from each other (Fig.

231   1). Amphibian richness (13 - 55 species per grid cell, mean 27 ± 8 SD; Fig. 1) peaks within the Central

232   Highlands and north-western Bewani and Torricelli mountain ranges, with less pronounced peaks on the

233   south-eastern Owen Stanley mountain range. Lowest amphibian richness occurs in the south-western

234   Trans-Fly, north-western Sepik, and coastal lowland areas. Bird richness reveals a strong affinity to the

235   Papuan peninsula, with greatest richness bordering the Owen Stanley mountain ranges and lowest within

236   the interior of the Central Highlands, south-western Trans-Fly and north-western Sepik lowlands (133 - 411

237   species per grid cell, mean: 289 ± 47; Fig. 1). Mammal richness peaks trace the Central and southern Owen

238   Stanley Mountains periphery, with lowest richness in the Trans-Fly and Sepik lowlands (35 - 118 species per

239   grid cell, mean: 76 ± 21). Reptile richness peaks occur within the lowlands of the Trans-Fly, Huon Gulf and

240   south-central Papuan Peninsula, with richness decreasing towards the major mountain range interiors (11 -

241   89 species per grid cell, mean 56 ± 15; Fig. 1). Dividing PNG reptiles into lizards (n = 150) and snakes (n =

242   68) reveals strikingly different richness peaks (Fig. 1). Lizard richness peaks in northern lowland areas along

243   the Huon Gulf and north-west West Sepik Province, whereas snake richness peaks in the lowlands of the

244   Trans-Fly and south-central Papuan Peninsula.

245   **Cross-taxon congruence**

246   Cross-taxon congruence between PNG amphibian, bird and mammal species richness is positive

247   irrespective of spatial autocorrelation or resolution (Table 1). Mammal richness exhibits the strongest

248   degree of congruence with amphibian and bird richness, across the three spatial resolutions (Pearson's r =

249   0.61 - 0.87, P <0.01). In contrast, once corrected for spatial autocorrelation, reptile richness is not

250   significantly correlated with amphibian, bird or mammal richness at any of the spatial resolutions. Lizard

251   and snake richness largely exhibit no correlation with the other three terrestrial vertebrate groups. Lizard

252   and bird richness are positively correlated at the quarter-degree resolution (Pearson's r = 0.39, P <0.01),

253   however, this relationship becomes insignificant at the coarser resolutions. A positive correlation between

254   lizard and snake richness, also diminishes with decreasing spatial resolution (Pearson's r = 0.69 [P <0.01],

255   0.54 [P <0.01] and 0.36 [P 0.02] at the quarter-degree, half-degree and one-degree resolutions).

256   **Simulated environmental predictors**

257   Our analyses reveal that elevation provides the best predictor of PNG terrestrial vertebrate richness

258   (Table 2 and see Appendix S7). Correcting for spatial autocorrelation affected the variance explained by

259   each predictor model. This altered the best-fit predictor models for amphibian and mammal richness at the

260   finest resolutions and for birds at the two coarser resolutions. Spatial resolution similarly affects the best-

261   fit predictor models, primarily between the quarter- and half degree for all terrestrial vertebrates except

262   reptiles. PNG reptile richness exhibits a distinct, negative correlation with mean elevation at quarter-

263   degree (OLS r^2 = 0.48, P <0.01; SAR Naglekerke r^2 = 0.71, P <0.01) and half-degree resolutions (OLS r^2 =

264   0.25, P <0.01; SAR Naglekerke r^2 = 0.49, P <0.01). At the quarter-degree resolution, PNG bird richness is

265   strongly correlated with the mid-elevation richness model (OLS r^2 = 0.20, P <0.01; SAR Naglekerke r^2 = 0.63,

266   P <0.01). Variance in amphibian richness is best explained by temperature range (OLS r^2 = 0.42, P <0.01;

267   SAR Naglekerke r^2 = 0.80, P <0.01), and mammal richness by elevational range (OLS r^2 = 0.76, P <0.01; SAR

268   Naglekerke r^2 = 0.88, P <0.01). Further, elevational range best explains the variance in amphibian, bird and

269   mammal richness at both the half- and one-degree resolution, following correction for spatial

270   autocorrelation. The stochastic spreading-dye and net-primary-productivity richness models consistently

271   provide the worst predictors of PNG terrestrial vertebrate species richness.

272   **DISCUSSION**

273   This study provides a comprehensive assessment of the biogeographical patterns of species

274   richness for terrestrial vertebrates in Papua New Guinea, a remarkably diverse but understudied region.

275   Our analyses reveal congruent richness patterns in all Papua New Guinea terrestrial vertebrates except for

276   reptiles and the constituent lizard and snake groups. Our findings are generally consistent with the cross-

277   taxon congruence observed in most groups at the global scale (Grenyer *et al*., 2006; Qian & Ricklefs, 2008),

278   and reptiles being outliers within regions such as Australia (Powney *et al*., 2010), and Africa (Lewin *et al*.,

279   2016). As in previous studies (Grenyer *et al*., 2006; Belmaker & Jetz, 2011) spatial resolution influenced the

280   degree of congruence among richness patterns for PNG amphibians, birds and mammals, but had no effect

281   on reptile incongruence. These congruent versus contrasting patterns are evidently linked to the

282   underlying abiotic and biotic factors governing each species' distribution, a trend increasingly apparent at

283   finer spatial scales.

284   Climatic variables are frequently considered to provide the strongest predictors of broad-scale

285   species richness (Hawkins *et al*., 2003; Field *et al*., 2009), while other studies have suggested topographic

286   heterogeneity measures may strongly regulate species richness gradients, especially at small spatial scales

287   (Kerr & Packer, 1997; Whittaker *et al*., 2001; Ricklefs, 2006; Rahbek *et al*., 2007; Stein *et al*., 2014).

288   Belmaker & Jetz (2011) noted that measures of global amphibian, bird and mammal richness patterns

289   display contrasting relationships with climate, but similar relationships with topographical heterogeneity.

290   The primacy of topographical heterogeneity in predicting species richness is particularly evident in high-

291   energy regions such as the tropics (Orme *et al*., 2005; Grenyer *et al*., 2006; Davies *et al*., 2007; Kreft & Jetz,

292   2007; Thomas *et al*., 2008; Qian, 2010). Our analyses reveal that elevational range strongly correlates with

293   PNG amphibian, bird and mammal richness at coarser spatial resolutions. Furthermore, in accordance with

294   Belmaker & Jetz (2011), we show that all terrestrial vertebrates, except reptiles, display similar

295   topographical-heterogeneity-richness slopes (Table 2). We thus provide evidence for the existence of

296   elevational based mechanisms promoting species richness through high levels of persistence and

297   speciation in PNG amphibian, bird and mammal groups. In contrast, reptile richness is strongly constrained

298   by elevation, with peaks in the warmer lowlands, suggesting that these are central regions for reptile

299   diversification and persistence.

300 Our analyses reveal PNG reptile species richness is strongly constrained by elevation and, as

301 predicted, is positively correlated with temperature (Currie, 2001; Whittaker *et al*., 2007; Qian, 2010),

302 probably through direct effects on life-history traits (Meiri *et al.*, 2013). Adaptation to survive in water-

303 limited regions has enabled reptiles to persist in the southern Trans-Fly and Port Moresby savanna areas.

304 Richness peaks in these areas likely reflects the accumulation of numerous Australian reptile species,

305 largely wide-ranging snakes, during the land connections of the last series of glaciations. Except for reptiles,

306 vertebrate species richness in savanna is generally lower than in closed-canopy wet forest, suggesting

307 decreased competition and predation pressure may also enable a greater diversity of reptiles to exist in

308 these areas (Sweet & Pianka, 2007). The northern reptile richness peaks, dominated by lizards, likely

309 represent important transition zones between once-geographically distinct assemblages and thus contain a

310 high degree of phylogenetic diversity.

311 Although elevation *per se* is unlikely to cause species richness gradients, topographic heterogeneity

312 likely acts as a surrogate for precise local climatic conditions, such as temperature and precipitation,

313 purportedly strong determinants of species richness (Qian, 2010). Interplay among factors such as slope

314 and aspect will increase the range of climatic conditions in geographically proximate mountains, thus

315 increasing diversity in taxa with slightly different climatic envelopes. Climatic stratification along tropical

316 elevational gradients purportedly limits the elevational extent to which any particular species'

317 physiological profile can function (Janzen, 1967; Ghalambor *et al.*, 2006). Turnover in elevational plant

318 communities led to elevational range being commonly used as a proxy for habitat heterogeneity, with this

319 inferred increased habitat diversity purported to allow for increased sampling of habitat specialists

320 (Rahbek & Graves, 2001; Davies *et al.,* 2007, but see Hortal *et al.*, 2013). It is likely that these processes

321 have been highly influential in promoting amphibian, bird and mammal diversity in PNG's topographically

322 complex regions. Whereas, reptile richness may be limited along mountain slopes by factors such as

323 restricted access to solar radiation caused by increased humidity, vegetation and cloud cover (McCain,

324 2010).

325 Climatic predictors such as temperature, precipitation and primary productivity, are frequently

326 reported as strong correlates of broad-scale vertebrate richness patterns (Jetz & Rahbek 2002; Currie *et al*.,

327 2004; but see Adler *et al.*, 2011). However, these predictors consistently had lower effects sizes on PNG

328 terrestrial vertebrate richness, compared with the topographic predictors (Table 2). In particular, npp

329 performed poorly across all taxonomic groups and analytical resolutions. This indicates that these climatic

330 predictors do not constrain species richness to the same degree as in higher latitude regions. The

331 stochastic spreading-dye model, essentially equivalent to a mid-domain effect which predicts higher

richness at the centre of an island or continent (Gotelli *et al.*, 2009), also performed poorly for all taxa, except for reptiles where it was reversed (reptiles being rich at coastal lowland areas), probably reflecting the effects of temperature. Cross-scale variation in predictor primacy and the effect of spatial autocorrelation, highlight the need for careful examination of broad-scale biogeographical data. Failure to do so can affect the study inferences, as illustrated in this study (Table 1 - 2).

Environmental predictor effect sizes, in both the OLS and SAR models, for PNG terrestrial vertebrates were lowest in reptiles at the one-degree resolution (Table 2). This indicates that extraneous factors, such as differing affinities to geological terranes, may be influencing reptile richness patterns in PNG. New Guinea's complex geotectonic history and major mountain-building events are purported to be a crucial factor shaping the regions biotic diversity (Georges *et al.*, 2014; Toussaint *et al.*, 2014). In particular, environmental change during orogenesis is likely to have driven diversification in New Guinea (Toussaint *et al.*, 2014). This may explain the high alpha- and beta-diversity of amphibians, birds and mammals in the montane regions (see Appendix S8). Once-isolated terranes that are now accreted along New Guinea's northern coast have also been important allopatric speciation centres, especially for amphibians and reptiles.

We suspect that comparable environmental conditions and biotic diversity across New Guinea will result in equivalent cross-taxon congruence and environmental-richness correlates to those observed by us in PNG. Although the New Guinean biota remains poorly known compared to many other parts of the world, the overall patterns of biotic distribution and richness, particularly within Papua New Guinea, are reasonably well known and are unlikely to change appreciably as new species are discovered and named (Allison & Tallowin, 2015). We minimised distributional errors in PNG species by using expert-drawn range maps, combining both observation and speculative data. Expert-drawn maps are less susceptible to underestimation of true range size compared with point-observation data and do not grossly overestimate a species' range and elevational limits, as seen in extent-of-occurrence range maps (Hulbert & Jetz, 2007; Rocchini *et al.*, 2011). Over-estimation of species ranges is particularly influential in narrow ranging species found in low tropical latitudes (Jetz *et al.*, 2008).

The congruent spatial-richness patterns identified among PNG amphibian, bird and mammal species, and the incongruent reptile richness patterns, have important implications for regional conservation. Protected areas targeted towards high species richness in a single taxon are likely to provide coverage for a range of terrestrial vertebrate species. However, such protected areas would fail to capture areas of high reptile richness. Disparity in reptile species richness, caused by their divergent environmental requirements, suggest that reptile-specific conservation approaches will provide the most effective

method for preserving their regional centres of diversity. As reptile diversification centres correspond to important biogeographical regions, such as the Trans-Fly and Port Moresby savanna, conservation efforts targeting reptile hotspots will also have the added benefit of preserving these unique regions. Effective conservation strategies in PNG will ultimately require additional assessment of congruence patterns for range-restricted and threatened-species combined with a geographical understanding of the major threats to terrestrial vertebrates (Shearman & Bryan, 2010). However, these assessments will greatly benefit from further research addressing the taxonomic and distribution shortfalls particularly evident in groups, such as amphibians (Allison, 2009), and reptiles (Meiri, 2016). By revealing the spatial species richness patterns in PNG's terrestrial vertebrates and identifying their strongest environmental correlates, we provide baseline information, which may contribute to conservation planning in PNG.

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569

570 **BIOSKETCH**

571 **Oliver Tallowin** is a PhD student at the University of Tel Aviv with a broad interest in understanding biogeographical
572 and macroecological patterns of diversity. His PhD focuses on the ecology and evolution of terrestrial vertebrate
573 diversity in Papua New Guinea.

574

575 Author contributions: O.J.S.T. and S.M. conceived the ideas; O.J.S.T. and A.A. compiled and digitised the PNG
576 vertebrate range maps; A.C.A. provided the spreading-dye R script; O.J.S.T. analysed the data and led the writing.

577 Editor: Walter Jetz

578

579 **SUPPORTING INFORMATION**

580 **Appendix S1** – Papua New Guinean vertebrate species list with references.

581 **Appendix S2** – Reptile species distributions at quarter degree grid scale.

582 **Appendix S3** – Species range maps digitized for this study.

583   **Appendix S4** – Gridded Papua New Guinean vertebrate species richness.

584   **Appendix S5** – Papua New Guinea environmental predictors.

585   **Appendix S6** – Morans *I* correlograms.

586   **Appendix S7** – Richness predictors at half-degree and one-degree resolution.

587   **Appendix S8** – Terrestrial vertebrate species richness in New Guinea.

588 **Table 1** Cross-taxon congruence in Papua New Guinea (PNG) terrestrial vertebrate species richness at the
589 quarter-, half- and one-degree spatial resolution.

	Amphibian	Bird	Mammal	Reptile	Lizard	Snake
Quarter-degree						
Amphibian		**0.41**	**0.76**	-0.37	-0.10	-0.38
Bird	**0.01 (<0.01)**		**0.61**	0.25	**0.39**	0.28
Mammal	**<0.01 (<0.01)**	**<0.01 (<0.01)**		-0.43	-0.21	-0.36
Reptile	0.04 (<0.01)	0.07 (<0.01)	0.03 (<0.01)		**0.88**	**0.93**
Lizard	0.53 (0.01)	**<0.01 (<0.01)**	0.22 (<0.01)	**<0.01 (<0.01)**		**0.69**
Snake	0.05 (<0.01)	0.11 (<0.01)	0.10 (<0.01)	**<0.01 (<0.01)**	**<0.01 (<0.01)**	
Half-degree						
Amphibian		**0.63**	**0.82**	-0.20	0.16	-0.27
Bird	**<0.01 (<0.01)**		**0.80**	0.20	0.46	0.17
Mammal	**<0.01 (<0.01)**	**<0.01 (<0.01)**		-0.20	0.10	-0.20
Reptile	0.33 (0.01)	0.26 (<0.01)	0.36 (0.01)		**0.81**	**0.90**
Lizard	0.16 (0.04)	0.02 (<0.01)	0.60 (0.19)	**<0.01 (<0.01)**		**0.54**
Snake	0.26 (<0.01)	0.48 (0.04)	0.43 (0.01)	**<0.01 (<0.01)**	**<0.01 (<0.01)**	
One-degree						
Amphibian		**0.68**	**0.85**	0.04	0.45	-0.19
Bird	**<0.01 (<0.01)**		**0.87**	0.44	0.68	0.23
Mammal	**<0.01 (<0.01)**	**<0.01 (<0.01)**		0.18	0.47	<0.01
Reptile	0.85 (0.79)	0.09 (<0.01)	0.46 (0.27)		**0.78**	**0.82**
Lizard	0.04 (<0.01)	0.01 (<0.01)	0.05 (<0.01)	**<0.01 (<0.01)**		0.36
Snake	0.52 (0.23)	0.47 (0.14)	0.97 (0.97)	**<0.01 (<0.01)**	0.16 (0.02)	

590 Cross-taxon congruence using Pearson's r values above the diagonal, with P-values, corrected and uncorrected in parenthesis,
591 below the diagonal. Boldface represents significant Pearson's r values, corrected for spatial autocorrelation. Regular font
592 represents significant Pearson's r values, uncorrected for spatial autocorrelation. Grey script represents insignificant Pearson's r
593 values. Degrees of freedom equate to 618 at the quarter-degree, 118 at the half-degree, and 39 at the one-degree spatial
594 resolution.

595 **Table 2** Ordinary least squares (OLS) regression and simultaneous autoregressive models (SAR) of observed
596 species richness against simulated species richness in the four Papua New Guinea terrestrial vertebrate
597 taxa at the one-degree resolution.

Predictor	OLS				SAR			
	Intercept	Slope ± s.e.	r^2	AIC$_c$	Intercept	Slope ± s.e.	Naglekerke r^2	AIC$_c$
Amphibian								
Stochastic spreading-dye	24.877	0.855 ± 0.556	0.03	343	28.311	0.723 ± 0.572	0.26	335
Mean elevation	28.166	0.707 ± 0.080	0.66	301	28.742	0.687 ± 0.084	0.69	300
Elevational range	**22.565**	**0.967 ± 0.096**	**0.72**	**293**	**22.556**	**0.967 ± 0.093**	**0.72**	**295**
Mid-elevation	26.531	0.781 ± 0.081	0.69	296	26.949	0.765 ± 0.084	0.71	297
Net Primary Productivity	56.204	-0.596 ± 0.247	0.11	340	52.007	-0.479 ± 0.228	0.31	333
Temperature (mean annual)	60.804	-0.809 ± 0.095	0.64	303	59.739	-0.794 ± 0.102	0.67	302
Temperature (annual range)	22.088	0.986 ± 0.116	0.64	303	22.476	0.973 ± 0.120	0.65	305
Precipitation (mean annual)	33.857	0.439 ± 0.208	0.08	341	34.759	0.414 ± 0.220	0.29	334
Precipitation (annual range)	22.816	0.954 ± 0.181	0.4	324	25.593	0.837 ± 0.185	0.47	322
Bird								
Stochastic spreading-dye	421.717	-0.201 ± 0.193	<0.01	455	423.952	-0.201 ± 0.197	0.27	445
Mean elevation	320.574	0.303 ± 0.057	0.41	433	329.402	0.281 ± 0.061	0.49	431
Elevational range	305.78	0.377 ± 0.061	0.48	428	**309.936**	**0.402 ± 0.066**	**0.61**	**420**
Mid-elevation	314.594	0.333 ± 0.057	0.45	430	322.867	0.312 ± 0.062	0.52	428
Net Primary Productivity	447.296	-0.329 ± 0.105	0.18	447	421.091	-0.198 ± 0.103	0.30	443
Temperature (mean annual)	**457.999**	**-0.382 ± 0.056**	**0.53**	**424**	454.04	-0.363 ± 0.058	0.55	426
Temperature (annual range)	306.742	0.372 ± 0.072	0.39	435	313.929	0.386 ± 0.078	0.53	427
Precipitation (mean annual)	390.953	-0.048 ± 0.105	<0.01	456	380.57	0.040 ± 0.107	0.25	446
Precipitation (annual range)	321.577	0.298 ± 0.106	0.15	449	335.423	0.281 ± 0.101	0.37	439
Mammal								

Stochastic spreading-dye	70.726	0.497 ± 0.320	0.03	388	76.037	0.422 ± 0.328	0.28	379
Mean elevation	63.28	0.623 ± 0.065	0.69	341	63.576	0.619 ± 0.066	0.7	343
Elevational range	**55.197**	**0.760 ± 0.068**	**0.75**	**332**	**53.995**	**0.786 ± 0.076**	**0.78**	**330**
Mid-elevation	60.165	0.676 ± 0.064	0.73	335	60.067	0.677 ± 0.062	0.74	337
Net Primary Productivity	113.923	-0.237 ± 0.188	0.01	389	101.996	-0.060 ± 0.173	0.25	381
Temperature (mean annual)	134.772	-0.591 ± 0.097	0.48	363	131.02	-0.544 ± 0.101	0.50	364
Temperature (annual range)	53.055	0.796 ± 0.080	0.71	339	52.818	0.811 ± 0.088	0.74	337
Precipitation (mean annual)	78.686	0.362 ± 0.160	0.09	385	77.426	0.409 ± 0.163	0.35	375
Precipitation (annual range)	51.887	0.818 ± 0.134	0.48	363	57.613	0.734 ± 0.137	0.54	361
Reptile								
Stochastic spreading-dye	**93.482**	**-0.469 ± 0.196**	**0.11**	**317**	**88.481**	**-0.345 ± 0.207**	**0.22**	**314**
Mean elevation	79.259	-0.079 ± 0.064	0.01	321	**79.567**	**-0.091 ± 0.067**	**0.21**	**315**
Elevational range	78.367	-0.055 ± 0.082	<0.01	322	77.109	-0.020 ± 0.087	0.17	317
Mid-elevation	77.77	-0.038 ± 0.069	<0.01	322	77.681	-0.037 ± 0.072	0.18	317
Net Primary Productivity	78.374	-0.055 ± 0.118	<0.01	322	74.749	-0.050 ± 0.113	0.17	317
Temperature (mean annual)	76.436	-0.002 ± 0.118	<0.01	323	75.612	0.023 ± 0.079	0.17	317
Temperature (annual range)	79.215	-0.078 ± 0.086	<0.01	322	77.913	-0.043 ± 0.092	0.18	317
Precipitation (mean annual)	82.102	-0.157 ± 0.095	0.04	320	79.115	-0.079 ± 0.102	0.18	316
Precipitation (annual range)	74.742	0.044 ± 0.110	<0.01	322	73.337	0.088 ± 0.109	0.18	316

598 All models have 39 degrees of freedom. The best model in every set (lowest AIC_c) shown in boldface.
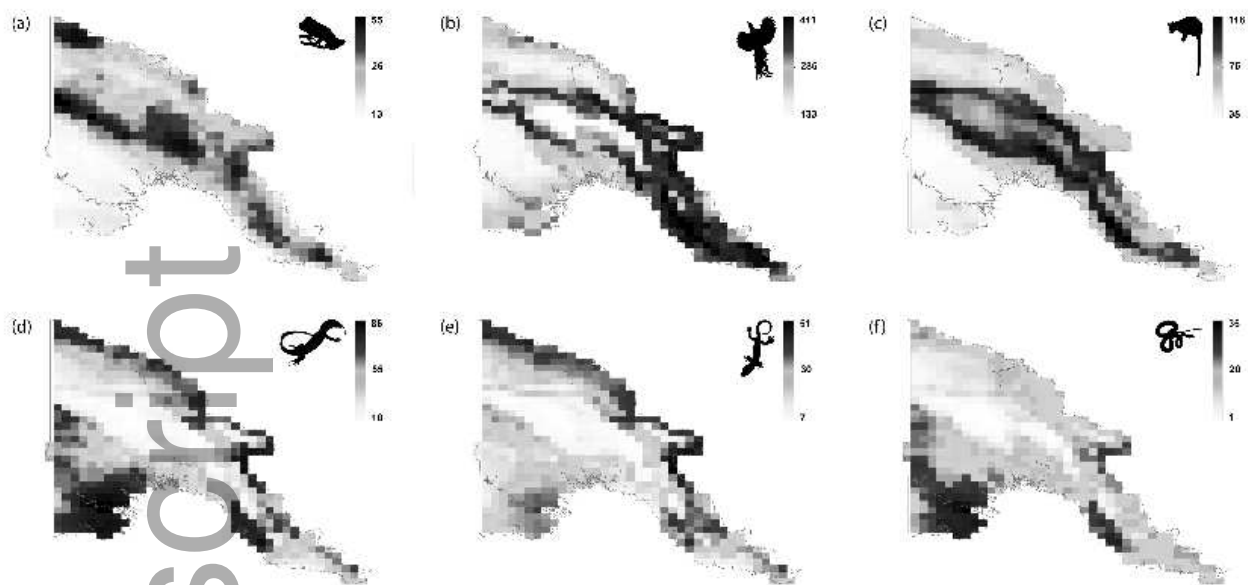
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