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

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ABSTRACT

Aims To examine species-richness patterns in Papua New Guinea's terrestrial vertebrates and test for geographical congruence between the four classes, and between lizard and snake subgroups. To assess the environmental correlates of Papua New Guinean terrestrial vertebrate richness, and contrast effects of varying analytical resolution and correction for spatial autocorrelation. We predict congruence in the bird, mammal and to a lesser extent amphibian richness, with weak congruence or incongruence between reptiles and the other taxonomic groups. We further predict these patterns will stem from relative or in the case of reptiles dissimilar, correlative trends with environmental predictors such as elevation and temperature.

Location Papua New Guinea

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

Results Papua New Guinean amphibian, bird and mammal species richness are spatially congruent, a trend which strengthens with decreasing spatial resolution. Reptiles and the lizard and snake subgroups reveal remarkably different spatial richness trends. Elevational predictors, particularly elevational range at coarse

resolutions, provide the strongest correlates of species richness. Whereas terrestrial vertebrate richness increases with elevation, reptile richness decreases.

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

INTRODUCTION

Tropical regions hold the greatest species richness on the planet (Fine, 2015). Species-richness patterns and drivers within tropical regions, however, remain largely overlooked (Tuomisto *et al.*, 2014). Analyses at continental and global scales can mask regional correlations between species richness and 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, colonisation 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). Tropical regions have the highest rates of net primary productivity (npp; Gillman *et al.*, 2014); a factor thought to cause a trophic cascade of resource abundance, resulting in diversity peaks (Currie, 1991; O'Brien, 1998).

Environmental and topographic heterogeneity (i.e., elevational range) are purported to be among the most important factors influencing species richness (Stein *et al.*, 2014), especially at medium to fine spatial scales (Field *et al.,* 2009). Topographic heterogeneity is thought to increase the number of habitat types and resources available, which in turn increases the potential niche space allowing more species to co-exist (Stein *et al.*, 2014). Topographically heterogeneous regions are thought to be particularly important for narrowly ranging endemics by acting as both cradles and museums of biodiversity (Fjeldså *et al.*, 2012). The cradle hypothesis posits that increased range in topography and climate will create greater potential for speciation by isolation and divergent adaptation. According to the museum hypothesis, refuge potential in elevationally diverse regions is greater during periods of climatic fluctuation, increasing species persistence (Currie, 1991; Tews *et al.*, 2004). Topography is suggested to influence richness most in regions experiencing the greatest climatic stability over the longest period of time, such as those in the tropics (Fine, 2015).

Indeed, broad-scale studies have often highlighted the significance of tropical montane regions for species diversity (Orme *et al*., 2005; Cadena *et al.,* 2011). At large spatial scales species turnover in montane regions, caused by environmental heterogeneity and niche availability absent in homogenous landscapes, inflates species richness (McCain & Beck, 2016).

New Guinea is among the most biologically diverse regions on the planet (Brooks *et al*., 2006). The exceedingly rich vertebrate assemblage (~5% of the world's terrestrial vertebrate species on less than 0.2% of the Earths land surface) is thought to be the product of the island's large size (785,753 km^2), tropical climate, complex geological history and extensive mountain ranges (Allison, 2009; Shearman and Bryan, 2011). New Guinea has a remarkable degree of tectonic complexity (Baldwin *et al*., 2012), resulting in extensive mountain uplift (over 31% of its mainland area is above 1,000 m, Allison, 2009). These extensive and often isolated mountain ranges produce high levels of range-restricted species. The climate of much of New Guinea is weakly seasonal, with temperature variation largely influenced by elevation, although the savannah areas have a distinct dry season and reduced precipitation overall (~1000-1500 mm annual rainfall; Allison, 2009). Roughly, two-thirds of the island is covered in broadleaf forests, mostly rain forest, which receive from 2000 to more than 10,000 mm of rainfall annually and lack a pronounced dry season. As the fauna on the eastern side of New Guinea, in the country of Papua New Guinea (PNG), has been more thoroughly surveyed (Heads, 2002), we restrict our study on the terrestrial vertebrates in the country of PNG. The many offshore islands that also comprise a significant portion of PNG are not included in our analyses, so it should be understood henceforth that our use of "PNG" refers only to the mainland New Guinea portion of that country.

We assess species richness, cross-taxon congruence and environmental correlates of PNG's terrestrial vertebrates. To determine the effect of spatial scale on these relationships, we conduct analyses at three spatial resolutions. We predict that the aseasonal tropical climate will result in the highest terrestrial-vertebrate richness predominantly in montane regions. Sharp climatic clines coupled with decreasing connectivity at higher altitudes, are expected to promote species' elevational segregation

(Janzen, 1967; Ghalambor *et al*., 2006) and increase the number of high-elevation range-restricted local endemics. This trend will be most evident in taxa with comparatively poor dispersal ability, such as amphibians. We further predict that PNG amphibian richness will be less constrained by water availability than observed in other, more water-limited, regions (Buckley & Jetz, 2007). While amphibians' physiological and ecological requirements for water (Feder & Burggren, 1992) will remain fundamentally the same, the extremely high degree of precipitation across most of PNG will reduce its level of constraint across the region. We predict that PNG bird and mammal species richness will be strongly positively correlated, exhibiting concordant trends to the environmental predictors due to the equivalent physiology and energetic requirements of endotherms (Grenyer *et al*., 2006). We predict that PNG reptiles will show the greatest degree of disparity in richness patterns. Reptiles are strongly constrained by temperature due to their physiology and they fundamentally differ from amphibians in their ability to control water loss with dry and scaly skin (Adolph & Porter, 1993). We predict reptile richness will peak in warm lowland regions, thus the ectothermic groups should display incongruent species-richness patterns compared with congruent endothermic richness.

MATERIALS AND METHODS

Species geographical range data

We compiled geographical range data for all 232 PNG native mainland reptile species using ArcGIS 10.0, following the taxonomy of Uetz and Hošek (2015), but including three lizards (*Cryptoblepharus novaeguineae*, *Gehyra baliola*, and *Sphenomorphus anotus*) considered valid by the IUCN Melanesian Reptile Working Group, 2014 (see Appendix S1 and S2 in Supporting Information). We obtained reptile range maps from the Bishop Museum Pacific Biological Survey Project and during the IUCN Melanesian Reptile Redlist Project (July, 2014). We converted all point-locality data to polygons using a 10 km^2 buffer (radius = 1.72 km), in accordance with IUCN mapping standards (http://www.amphibians.org/wp-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-ranges 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:

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

where $_j$ represents the total gridded domain of PNG, and $_i$ a given cell within the grid. E_i represents the mean elevation in cell $_i$, and E_{jmid} is half the difference between the maximum and minimum mean elevation recorded in grid $_j$.

Simulation models

Richness patterns are typically investigated through curve-fitting analysis (Rahbek *et al.*, 2007) and as such cannot model species ranges directly or generate quantitative predictions of species richness (Gotelli *et al.*, 2009). Spreading-dye models (termed "Geometric constraint models" in Jetz and Rahbek, 2001) were developed as an alternative method for assessing richness gradients in heterogeneous landscapes. These spatially explicit models can simulate speciation, dispersal and extinction of species in heterogeneous landscapes (Gotelli *et al.*, 2009). Spreading-dye models reconstruct distributions by assigning cells to a species' range within the gridded domain. After the initial cell has been selected the range is allowed to expand to adjacent cells, with the cell number in each species' predicted range equivalent to its observed range. The initial grid cell and subsequent adjacent cell selection can either occur stochastically, with all grid cells equal in selection probability, or be weighted according to underlying environmental predictor values across the gridded domain (Storch *et al.*, 2006; Rahbek *et al.*, 2007; Szabo *et al.*, 2009).

To simulate species richness according to our predictors, we used spreading-dye models at a quarter-, half- and one-degree grid scale (Jetz & Rahbek, 2001; Storch *et al.,* 2006). For each terrestrial vertebrate group we developed nine species-richness simulation models, eight simulation models derived from

environmental predictors and one null model. The null model specifies a single geographic origin for each species, and allows each range to spread cohesively and randomly within the gridded domain (Gotelli *et al*., 2009). Simulations were modified to assess the role of environmental gradients on species richness by weighting cells according to the predictor values (Storch *et al*., 2006; Rahbek *et al*., 2007; Szabo *et al*., 2009). The gridded predictors: mean elevation, elevational range, mean annual npp, mean annual temperature, annual temperature range, mean annual precipitation and annual precipitation range were rescaled to between 0 and 1, using minimum and maximum values for each predictor. This ensured that a given proportional change resulted in an equivalent change in cell selection probability across all environmental predictors (Rangel *et al*., 2007). The relative probability of initial cell and subsequent adjacent cell selection was determined by variation in the environmental predictor values. Thus environmental determinism per cell ranged from completely random ($_i$ = 0) to strongly deterministic ($_i$ = 1). Simulated terrestrial-vertebrate species richness, derived from the nine predictors at three spatial resolutions, was carried out 999 times for each group, and the gridded mean species richness calculated from all models.

Statistical analysis

All statistical analyses were carried out in R 3.3.0 (R Development Core Team, 2016). Cross-taxon congruence among PNG terrestrial-vertebrate group richness was initially assessed using Pearson's correlation coefficient; however, non-independence in the spatial data was detected using Moran's *I* (see Appendix S6). Spatial autocorrelation arises when neighbouring locality values in spatial data are more similar than expected by chance (Legendre, 1993), leading to increased type-1 error rates and incorrect parameter estimates (Lennon, 2000). To account for spatial autocorrelation we used Dutilleul's modified *t*-test (Dutilleul *et al*., 1993), provided in the package SpatialPack (Osorio & Vallejos, 2014).

To identify the strongest environmental correlates of each PNG terrestrial vertebrate group, we regressed observed species richness against richness simulated by the eight environmental predictors and the single stochastic predictor. We initially conducted ordinary least squares (OLS) regression, then

accounted for spatial autocorrelation in model residuals by using simultaneous autoregressive (SAR) models (Kissling & Carl, 2008), provided in the package spdep (Bivand & Piras, 2015). The spatial structure was specified as the eight nearest neighbours to each cell, and neighbour cells were weighted according to the row-standardized coding scheme. We assessed the relative explanatory power in the OLS and SAR models using Akaike's Information Criterion (AIC$_c$).

RESULTS

Species richness

PNG bird and mammal richness have generally concordant patterns at the quarter-degree grid scale, whereas amphibian and reptile richness patterns are distinct from these and from each other (Fig. 1). Amphibian richness (13 - 55 species per grid cell, mean 27 ± 8 SD; Fig. 1) peaks within the Central Highlands and northwestern Bewani and Torricelli mountain ranges, with less pronounced peaks on the southeastern Owen Stanley mountain range. Lowest amphibian richness occurs in the southwestern Trans-Fly, northwestern Sepik, and coastal lowland areas. Bird richness reveals a strong affinity to the Papuan peninsula, with greatest richness bordering the Owen Stanley mountain ranges and lowest within the interior of the Central Highlands, southwestern Trans-Fly and northwestern Sepik lowlands (133 - 411 species per grid cell, mean: 289 ± 47; Fig. 1). Mammal richness peaks trace the Central and southern Owen Stanley Mountains periphery, with lowest richness in the Trans-Fly and Sepik lowlands (35 - 118 species per grid cell, mean: 76 ± 21). Reptile richness peaks occur within the lowlands of the Trans-Fly, Huon Gulf and south-central Papuan Peninsula, with richness decreasing towards the major mountain range interiors (11 - 89 species per grid cell, mean 56 ± 15; Fig. 1). Dividing PNG reptiles into lizards (*n* = 150) and snakes (*n* = 68) reveals strikingly different richness peaks (Fig. 1). Lizard richness peaks in northern lowland areas along the Huon Gulf and northwest West Sepik Province, whereas snake richness peaks in the lowlands of the Trans-Fly and south-central Papuan Peninsula.

Cross-taxon congruence

Cross-taxon congruence between PNG amphibian, bird and mammal species richness is positive irrespective of spatial autocorrelation or resolution (Table 1). Mammal richness exhibits the strongest degree of congruence with amphibian and bird richness, across the three spatial resolutions (Pearson's r = 0.61 - 0.87, P <0.01). In contrast, once corrected for spatial autocorrelation, reptile richness is not significantly correlated with amphibian, bird or mammal richness at any of the spatial resolutions. Lizard and snake richness largely exhibit no correlation with the other three terrestrial vertebrate groups. Lizard and bird richness are positively correlated at the quarter-degree resolution (Pearson's r = 0.39, P <0.01), however, this relationship becomes insignificant at the coarser resolutions. A positive correlation between lizard and snake richness, also diminishes with decreasing spatial resolution (Pearson's r = 0.69 [P <0.01], 0.54 [P <0.01] and 0.36 [P 0.02] at the quarter-degree, half-degree and one-degree resolutions).

Simulated environmental predictors

Our analyses reveal that elevation provides the best predictor of PNG terrestrial-vertebrate richness (Table 2 and see Appendix S7). Correcting for spatial autocorrelation affected the variance explained by each predictor model. This altered the best-fit predictor models for amphibian and mammal richness at the finest resolutions and for birds at the two coarser resolutions. Spatial resolution similarly affects the best-fit predictor models, primarily between the quarter- and half degree for all terrestrial vertebrates except reptiles. PNG reptile richness exhibits a distinct, negative correlation with mean elevation at quarter-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 = 0.25, P <0.01; SAR Naglekerke r^2 = 0.49, P <0.01). At the quarter-degree resolution, PNG bird richness is strongly correlated with the mid-elevation richness model (OLS r^2 = 0.20, P <0.01; SAR Naglekerke r^2 = 0.63, P <0.01). Variance in amphibian richness is best explained by temperature range (OLS r^2 = 0.42, P <0.01; SAR Naglekerke r^2 = 0.80, P <0.01), and mammal richness by elevational range (OLS r^2 = 0.76, P <0.01; SAR Naglekerke r^2 = 0.88, P <0.01). Further, elevational range best explains the variance in amphibian, bird and mammal richness at both the half- and one-degree resolution, following correction for spatial autocorrelation. The stochastic

spreading-dye and net-primary-productivity richness models consistently provide the worst predictors of PNG terrestrial vertebrate species richness.

DISCUSSION

This study provides a comprehensive assessment of the biogeographical patterns of species richness for terrestrial-vertebrates in Papua New Guinea, a remarkably diverse but understudied region. Our analyses reveal congruent richness patterns in all Papua New Guinea terrestrial vertebrates except for reptiles and the constituent lizard and snake groups. Our findings are generally consistent with the cross-taxon congruence observed in most groups at the global scale (Grenyer *et al.*, 2006; Qian & Ricklefs, 2008), and reptiles being outliers within regions such as Australia (Powney *et al.*, 2010), and Africa (Lewin *et al.*, 2016). As in previous studies (Grenyer *et al.*, 2006; Belmaker & Jetz, 2011) spatial resolution influenced the degree of congruence among richness patterns for PNG amphibians, birds and mammals, but had no effect on reptile incongruence. These congruent versus contrasting patterns are evidently linked to the underlying abiotic and biotic factors governing each species' distribution, a trend increasingly apparent at finer spatial scales.

Climatic variables are frequently considered to provide the strongest predictors of broad-scale species richness (Hawkins *et al.*, 2003; Field *et al.*, 2009), while other studies have suggested topographic heterogeneity measures may strongly regulate species richness gradients, especially at small spatial scales (Kerr & Packer, 1997; Whittaker *et al.*, 2001; Ricklefs, 2006; Rahbek *et al.*, 2007; Stein *et al.*, 2014). Belmaker & Jetz (2011) noted that measures of global amphibian, bird and mammal richness patterns display contrasting relationships with climate, but similar relationships with topographical heterogeneity. The primacy of topographical heterogeneity in predicting species richness is particularly evident in high-energy regions such as the tropics (Orme *et al.*, 2005; Grenyer *et al.*, 2006; Davies *et al.*, 2007; Kreft & Jetz, 2007; Thomas *et al.*, 2008; Qian, 2010). Our analyses reveal that elevational range strongly correlates with PNG amphibian, bird and mammal richness at coarser spatial resolutions. Furthermore, in accordance with

Belmaker & Jetz (2011), we show that all terrestrial vertebrates, except reptiles, display similar topographical-heterogeneity-richness slopes (Table 2). We thus provide evidence for the existence of elevational-based mechanisms promoting species richness through high levels of persistence and speciation in PNG amphibian, bird and mammal groups. In contrast, reptile richness is strongly constrained by elevation, with peaks in the warmer lowlands, suggesting that these are central regions for reptile diversification and persistence.

Our analyses reveal PNG reptile species richness is strongly constrained by elevation and, as predicted, is positively correlated with temperature (Currie, 2001; Whittaker *et al.*, 2007; Qian, 2010), probably through direct effects on life-history traits (Meiri *et al.*, 2013). Adaptation to survive in water-limited regions has enabled reptiles to persist in the southern Trans-Fly and Port Moresby savannah areas. Richness peaks in these areas likely reflects the accumulation of numerous Australian reptile species, largely wide-ranging snakes, during the land connections of the last series of glaciations. Except for reptiles, vertebrate species richness in savannah is generally lower than in closed-canopy wet forest, suggesting decreased competition and predation pressure may also enable a greater diversity of reptiles to exist in these areas (Sweet & Pianka, 2007). The northern reptile richness peaks, dominated by lizards, likely represent important transition zones between once-geographically distinct assemblages and thus contain a high degree of phylogenetic diversity.

Although elevation *per se* is unlikely to cause species-richness gradients, topographic heterogeneity likely acts as a surrogate for precise local climatic conditions, such as temperature and precipitation, purportedly strong determinants of species richness (Qian, 2010). Interplay among factors such as slope and aspect will increase the range of climatic conditions in geographically proximate mountains, thus increasing diversity in taxa with slightly different climatic envelopes. Climatic stratification along tropical elevational gradients purportedly limits the elevational extent to which any particular species' physiological profile can function (Janzen, 1967; Ghalambor *et al.*, 2006). Turnover in elevational plant communities led to elevational range being commonly used as a proxy for habitat heterogeneity, with this inferred increased habitat

diversity purported to allow for increased sampling of habitat specialists (Rahbek & Graves, 2001; Davies *et al.*, 2007, but see Hortal *et al.*, 2013). It is likely that these processes have been highly influential in promoting amphibian, bird and mammal diversity in PNG's topographically complex regions. Whereas, reptile richness may be limited along mountain slopes by factors such as restricted access to solar radiation caused by increased humidity, vegetation and cloud cover (McCain, 2010).

Climatic predictors such as temperature, precipitation and primary productivity, are frequently reported as strong correlates of broad-scale vertebrate richness patterns (Jetz & Rahbek 2002; Currie *et al.*, 2004; but see Adler *et al.*, 2011). However, these predictors consistently had lower effects sizes on PNG terrestrial vertebrate richness, compared with the topographic predictors (Table 2). In particular, npp performed poorly across all taxonomic groups and analytical resolutions. This indicates that these climatic predictors do not constrain species richness to the same degree as in higher-latitude regions. The 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 savannah, 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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BIOSKETCH

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

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SUPPORTING INFORMATION

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

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

Appendix S3 – Species range maps digitized for this study.

Appendix S4 – Gridded Papua New Guinean vertebrate species richness.

Appendix S5 – Papua New Guinea environmental predictors.

Appendix S6 – Morans *I* correlograms.

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

Appendix S8 – Terrestrial vertebrate species richness in New Guinea.

Table 1 Cross-taxon congruence in PNG terrestrial vertebrate species richness at the 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)	

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

Table 2 Ordinary least squares (OLS) regression and simultaneous autoregressive models (SAR) of observed species richness against simulated species richness in the four Papua New Guinea terrestrial vertebrate 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

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

Figure Legends

Figure 1. Species richness for Papua New Guinea (a) amphibians, (b) birds, (c) mammals, (d) reptiles, (e) lizards and (f) snakes at a quarter-degree resolution using an equal-area Behrmann projection. Note that richness of endotherms and amphibians is correlated with elevation and steep environmental gradients, whereas that of reptiles is confined to the lowlands. Richness is plotted in a 32-quantile spectrum from highest in red to lowest in blue. The legend indicates maximum, median and minimum gridded species richness values.
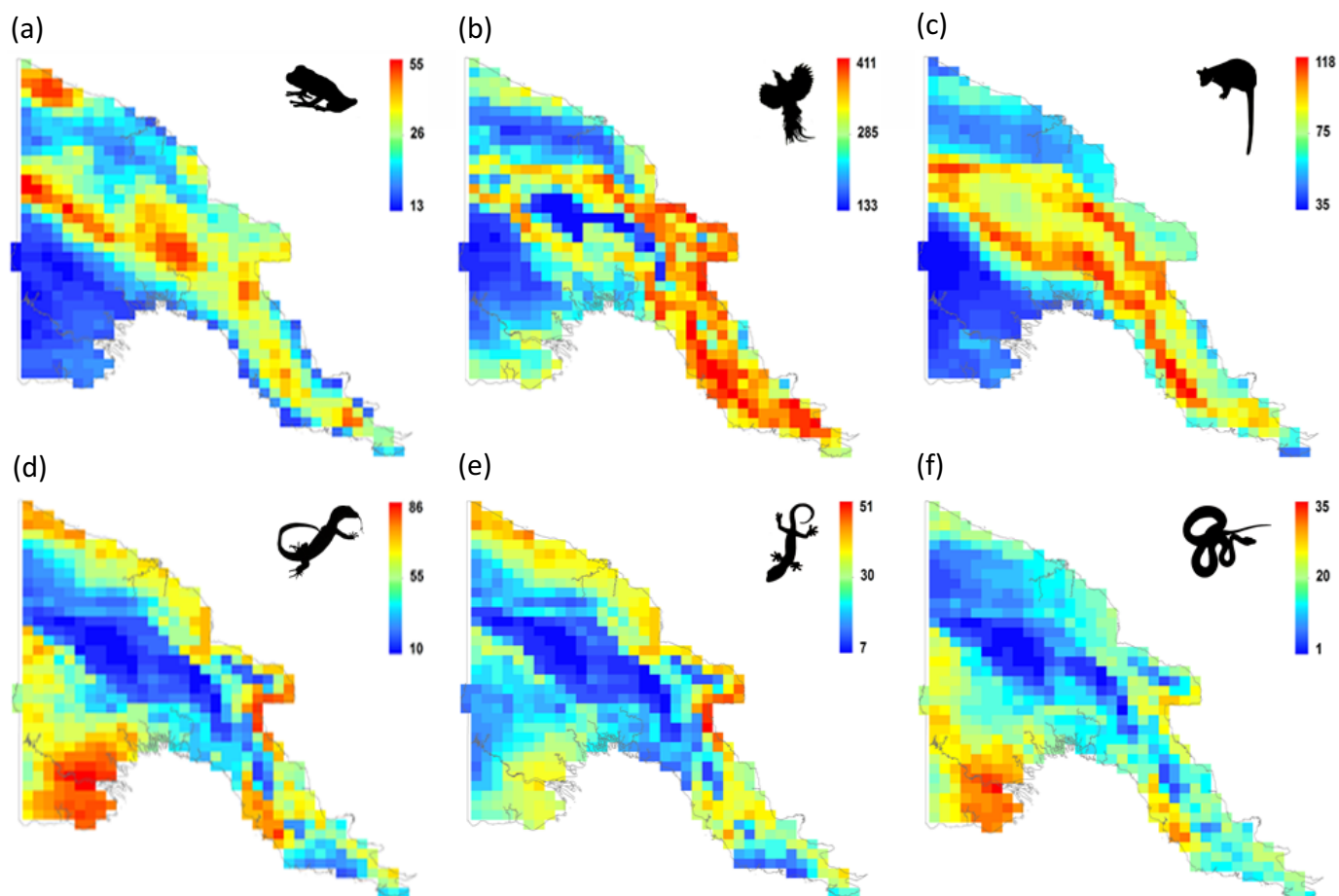
SUPPORTING INFORMATION

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

Oliver J.S. Tallowin[1*], Allen Allison[2], Adam C. Algar[3], Fred Kraus[4] and Shai Meiri[1]

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

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

Appendix S3 – Species range maps digitized for this study.

Appendix S4 – Gridded Papua New Guinean vertebrate species richness.

Appendix S5 – Papua New Guinea environmental predictors.

Appendix S6 – Morans *I* correlograms.

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

Appendix S8 – Terrestrial vertebrate species richness in New Guinea.

Appendix S5 – (a) mean elevation (m), (b) elevation range (m), (c) mid-elevation peak, (d) net primary productivity ($\log_{10}(gC\ yr^{-1})$), (e) mean annual precipitation (mm), (f) mean annual precipitation range (mm), (g) mean annual temperature (^{o}C) (h) mean annual temperature range (^{o}C) at quarter-degree grid resolution using a Behrmann equal-area projection.
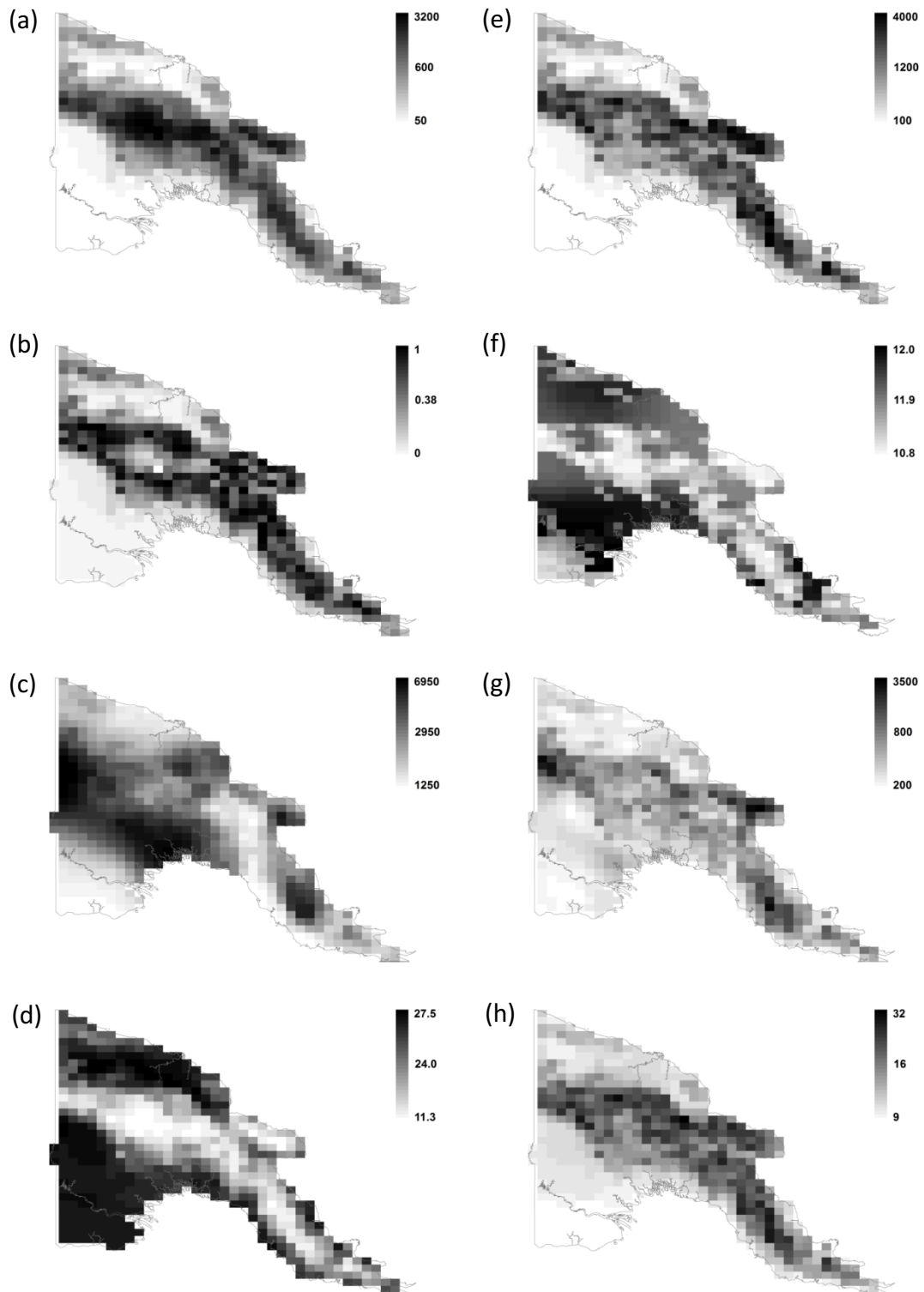
Appendix S6 - Moran's *I* correlogram showing spatial autocorrelation in PNG (a) amphibian, (b) bird, (c) mammal, (d) reptile, (e) lizard and (f) snake richness and the quarter-, half-, and one-degree spatial resolution. Correlation units on y-axis and distance (mean-of-class) on x-axis.
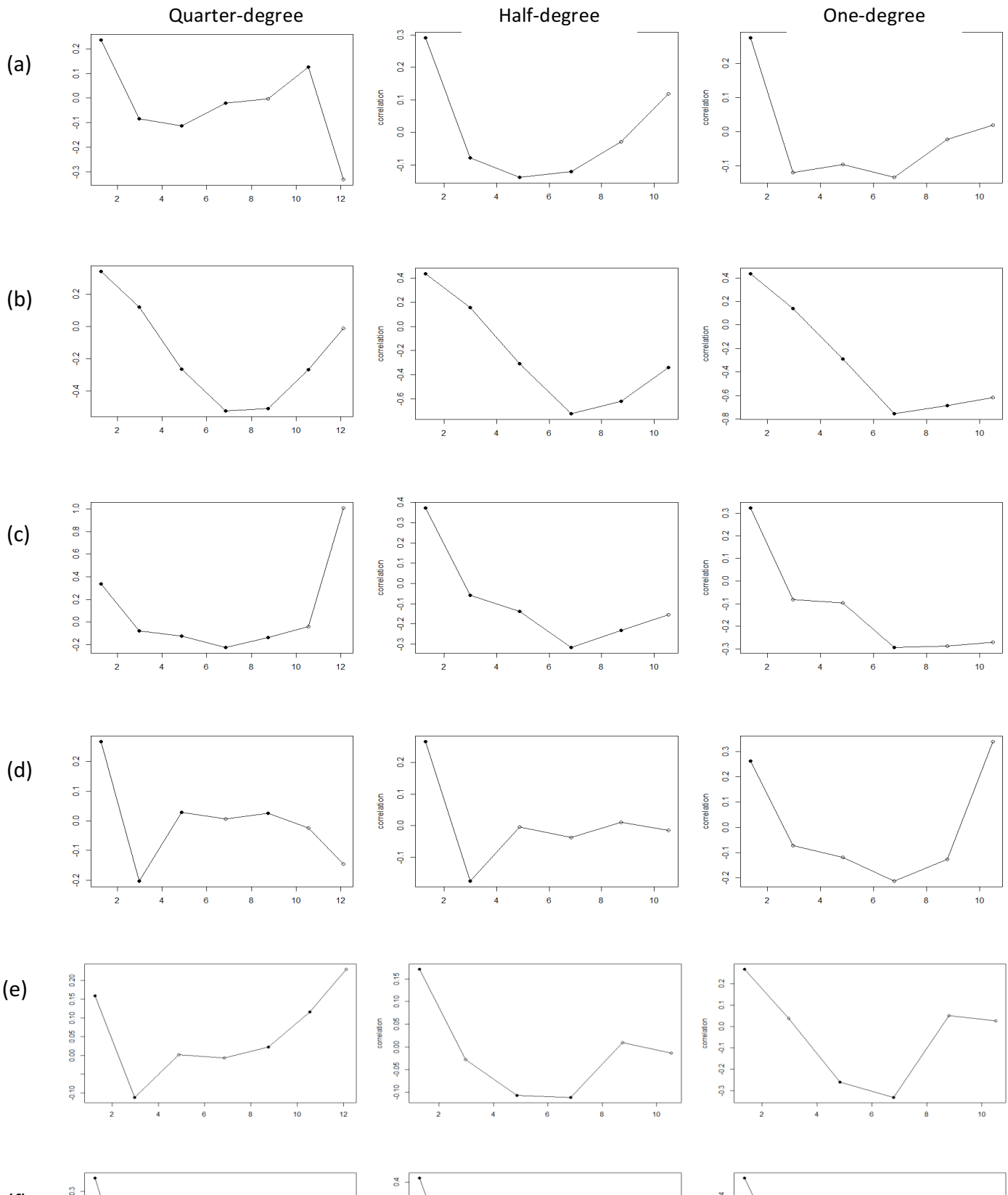
Appendix S7 - Ordinary least squares regression (OLS) and simultaneous autoregressive models (SAR) of observed richness against simulated species richness in six Papua New Guinea terrestrial vertebrate taxa at the (a) quarter-degree, (b) half-degree (c) and lizards and snakes at the one-degree resolution. Models at quarter-, half- and one-degree have 618, 158 and 39 degrees of freedom, respectively. The best model in every set (lowest AIC$_c$) is shown in boldface.

(a) – quarter-degree resolution

	OLS				SAR			
Predictor	Intercept	Slope ± s.e.	r^2	AICc	Intercept	Slope ± s.e.	Naglekerke r^2	AICc
Amphibian								
Stochastic spreading-dye	21.57	0.25 ± 0.06	0.03	4360	14.177	0.59 ± 0.09	0.73	3562
Mean elevation	19.83	0.34 ± 0.01	0.47	3978	19.031	0.36 ± 0.03	0.79	3405
Elevational range	18.87	0.38 ± 0.02	0.50	3946	**18.622**	**0.38 ± 0.02**	**0.80**	**3391**
Mid-elevation	**18.46**	**0.40 ± 0.02**	**0.50**	**3943**	18.647	0.38 ± 0.02	0.79	3400
Net Primary Productivity	32.13	-0.28 ± 0.04	0.06	4335	24.511	0.04 ± 0.03	0.72	3599
Temperature (mean annual)	38.82	-0.61 ± 0.04	0.27	4177	30.300	-0.25 ± 0.06	0.72	3587
Temperature (annual range)	19.08	0.37 ± 0.04	0.42	4038	17.796	0.43 ± 0.03	0.80	3381
Precipitation (mean annual)	23.96	0.13 ± 0.04	0.02	4366	18.260	0.38 ± 0.07	0.73	3569
Precipitation (annual range)	17.19	0.47 ± 0.03	0.36	4100	17.290	0.43 ± 0.04	0.77	3466
Bird								
Stochastic spreading-dye	344.98	-0.25 ± 0.03	0.10	6463	336.110	-0.21 ± 0.05	0.58	5999
Mean elevation	261.92	0.13 ± 0.01	0.12	6450	260.116	0.14 ± 0.02	0.60	5970
Elevational range	252.99	0.17 ± 0.01	0.19	6396	237.677	0.24 ± 0.03	0.62	5932
Mid-elevation	**250.11**	**0.178 ± 0.01**	**0.20**	**6388**	**244.613**	**0.22 ± 0.02**	**0.63**	**5916**
Net Primary Productivity	347.06	-0.26 ± 0.02	0.17	6414	306.513	-0.08 ± 0.03	0.57	6007
Temperature (mean annual)	343.24	-0.24 ± 0.03	0.12	6449	275.273	0.07 ± 0.04	0.57	6013
Temperature (annual range)	263.25	0.12 ± 0.02	0.09	6474	254.930	0.17 ± 0.02	0.60	5965
Precipitation (mean annual)	335.67	-0.21 ± 0.02	0.13	6446	326.823	-0.17 ± 0.04	0.58	5997
Precipitation (annual range)	265.12	0.11 ± 0.02	0.05	6501	260.236	0.14 ± 0.03	0.58	5994

Mammal								
Stochastic spreading-dye	50.69	0.39 ± 0.06	0.07	5501	33.029	0.65 ± 0.09	0.79	4593
Mean elevation	49.98	0.81 ± 0.02	0.70	4803	49.164	0.82 ± 0.03	0.86	4311
Elevational range	40.27	0.56 ± 0.01	0.76	4673	**40.780**	**0.55 ± 0.02**	**0.88**	**4248**
Mid-elevation	**38.30**	**0.59 ± 0.01**	**0.77**	**4648**	40.290	0.55 ± 0.02	0.88	4255
Net Primary Productivity	85.78	-0.16 ± 0.05	0.02	5538	66.276	0.09 ± 0.03	0.77	4357
Temperature (mean annual)	107.51	-0.50 ± 0.05	0.16	5441	64.583	0.11 ± 0.06	0.77	4645
Temperature (annual range)	40.45	0.56 ± 0.02	0.66	4874	38.625	0.59 ± 0.02	0.87	4267
Precipitation (mean annual)	63.10	0.20 ± 0.04	0.04	5527	45.305	0.45 ± 0.07	0.78	4604
Precipitation (annual range)	33.94	0.66 ± 0.02	0.56	5046	35.886	0.62 ± 0.04	0.84	4431
Reptile								
Stochastic spreading-dye	78.13	-0.62 ± 0.04	0.24	4943	74.518	-0.54 ± 0.07	0.69	4390
Mean elevation	65.85	-0.33 ± 0.01	0.48	4715	63.287	-0.27 ± 0.02	0.71	4351
Elevational range	65.84	-0.26 ± 0.01	0.35	4848	59.115	-0.12 ± 0.02	0.68	4417
Mid-elevation	65.08	-0.31 ± 0.02	0.32	4879	55.359	-0.05 ± 0.03	0.67	4432
Net Primary Productivity	53.51	-0.02 ± 0.04	<0.01	5117	52.711	0.03 ± 0.04	0.67	4433
Temperature (mean annual)	38.65	0.36 ± 0.04	0.11	5045	32.704	0.56 ± 0.06	0.71	4353
Temperature (annual range)	66.76	-0.36 ± 0.02	0.40	4798	60.751	-0.20 ± 0.03	0.68	4409
Precipitation (mean annual)	68.03	-0.39 ± 0.03	0.18	4991	66.979	-0.36 ± 0.06	0.69	4397
Precipitation (annual range)	70.54	-0.45 ± 0.02	0.36	4835	64.856	-0.31 ± 0.04	0.69	4387
Lizard								
Stochastic spreading-dye	44.876	**-0.690 ± 0.046**	**0.27**	4172	42.737	**-0.601 ± 0.075**	**0.62**	**3771**
Mean elevation	34.603	-0.218 ± 0.016	0.24	4200	33.383	-0.163 ± 0.025	0.61	3789
Elevational range	33.713	-0.178 ± 0.019	0.13	4282	30.723	-0.034 ± 0.029	0.59	3821
Mid-elevation	33.741	-0.179 ± 0.020	0.12	4289	29.336	0.036 ± 0.030	0.59	3822
Net Primary Productivity	33.214	-0.155 ± 0.039	0.02	4352	30.469	-0.021 ± 0.039	0.59	3822
Temperature (mean annual)	27.778	0.095 ± 0.043	0.01	4363	22.687	0.348 ± 0.064	0.60	3795
Temperature (annual range)	34.754	-0.226 ± 0.019	0.18	4241	31.769	-0.086 ± 0.031	0.59	3817
Precipitation (mean annual)	38.658	-0.405 ± 0.031	0.22	4216	37.654	-0.364 ± 0.053	0.61	3782

Predictor	Intercept	Slope ± s.e.	r^2	AIC$_c$	Intercept	Slope ± s.e.	Naglekerke r^2	AIC$_c$
Precipitation (annual range)	36.634	-0.312 ± 0.026	0.19	4235	34.183	-0.200 ± 0.039	0.60	3801
Snake								
Stochastic spreading-dye	28.990	-0.609 ± 0.054	0.17	3935	28.396	-0.570 ± 0.089	0.70	3303
Mean elevation	25.547	**-0.379 ± 0.019**	**0.39**	**3745**	24.181	-0.283 ± 0.030	0.71	3278
Elevational range	25.140	-0.351 ± 0.022	0.29	3835	22.576	-0.166 ± 0.033	0.69	3321
Mid-elevation	25.147	-0.352 ± 0.023	0.27	3860	21.505	-0.087 ± 0.035	0.69	3335
Net Primary Productivity	20.044	-0.009 ± 0.047	0.01	4053	20.130	0.018 ± 0.040	0.68	3339
Temperature (mean annual)	13.790	0.409 ± 0.049	0.10	3986	11.865	**0.588 ± 0.066**	**0.72**	**3265**
Temperature (annual range)	25.969	-0.407 ± 0.023	0.35	3790	23.444	-0.232 ± 0.035	0.70	3311
Precipitation (mean annual)	25.838	-0.398 ± 0.040	0.14	3959	25.292	-0.354 ± 0.067	0.70	3314
Precipitation (annual range)	27.066	-0.480 ± 0.031	0.28	3848	24.798	-0.322 ± 0.047	0.70	3303

(b) – half-degree resolution

	OLS				SAR			
Predictor	Intercept	Slope ± s.e.	r^2	AIC$_c$	Intercept	Slope ± s.e.	Naglekerke r^2	AIC$_c$
Amphibian								
Stochastic spreading-dye	25.32	0.337 ± 0.171	0.02	1212	23.356	0.426 ± 0.204	0.51	1105
Mean elevation	23.272	0.439 ± 0.171	0.53	1092	23.446	0.434 ± 0.040	0.70	1027
Elevational range	**20.262**	**0.591 ± 0.037**	**0.62**	**1062**	**20.284**	**0.599 ± 0.048**	**0.73**	**1009**
Mid-elevation	22.15	0.496 ± 0.034	0.58	1077	22.74	0.474 ± 0.041	0.71	1019
Net Primary Productivity	43.579	-0.581 ± 0.104	0.16	1187	37.249	-0.347 ± 0.096	0.53	1097
Temperature (mean annual)	50.415	-0.923 ± 0.078	0.47	1114	47.042	-0.815 ± 0.100	0.63	1061
Temperature (annual range)	20.295	0.589 ± 0.043	0.54	1090	20.35	0.608 ± 0.056	0.70	1025
Precipitation (mean annual)	28.404	0.182 ± 0.075	0.03	1210	26.972	0.233 ± 0.102	0.51	1104
Precipitation (annual range)	19.38	0.634 ± 0.058	0.42	1128	21.109	0.554 ± 0.073	0.62	1063
Bird								
Stochastic spreading-dye	386.444	-0.278 ± 0.074	0.08	1719	369.826	-0.209 ± 0.092	0.53	1615
Mean elevation	279.782	0.220 ± 0.027	0.29	1677	288.735	0.203 ± 0.033	0.60	1587
Elevational range	266.446	0.282 ± 0.028	0.39	1654	**271.42**	**0.286 ± 0.036**	**0.65**	**1567**
Mid-elevation	272.755	0.253 ± 0.027	0.35	1663	280.879	0.244 ± 0.033	0.64	1573
Net Primary Productivity	411.161	-0.394 ± 0.051	0.27	1682	361.287	-0.165 ± 0.051	0.54	1611

Temperature (mean annual)	**427.196**	**-0.469 ± 0.045**	**0.40**	**1650**	384.683	-0.274 ± 0.058	0.55	1607
Temperature (annual range)	272.992	0.251 ± 0.033	0.27	1683	280.696	0.248 ± 0.042	0.60	1589
Precipitation (mean annual)	353.467	-0.124 ± 0.044	0.04	1725	340.04	-0.058 ± 0.056	0.52	1619
Precipitation (annual range)	273.896	0.247 ± 0.041	0.18	1700	291.896	0.187 ± 0.049	0.55	1607
Mammal								
Stochastic spreading-dye	65.266	0.317 ± 0.134	0.03	1475	66.049	0.300 ± 0.157	0.58	1343
Mean elevation	51.263	0.546 ± 0.030	0.68	1299	54.133	0.510 ± 0.038	0.78	1242
Elevational range	**44.29**	**0.660 ± 0.031**	**0.74**	**1263**	**45.095**	**0.661 ± 0.041**	**0.82**	**1206**
Mid-elevation	48.025	0.600 ± 0.030	0.73	1269	50.658	0.570 ± 0.036	0.81	1215
Net Primary Productivity	107.039	-0.366 ± 0.100	0.07	1468	83.296	-0.022 ± 0.080	0.57	1347
Temperature (mean annual)	128.461	-0.717 ± 0.084	0.31	1420	102.48	-0.346 ± 0.098	0.60	1337
Temperature (annual range)	44.727	0.653 ± 0.037	0.66	1308	46.282	0.651 ± 0.050	0.78	1241
Precipitation (mean annual)	74.183	0.275 ± 0.093	0.05	1472	71.192	0.347 ± 0.122	0.59	1339
Precipitation (annual range)	41.595	0.704 ± 0.052	0.53	1358	48.916	0.595 ± 0.066	0.70	1293
Reptile								
Stochastic spreading-dye	83.22	-0.570 ± 0.092	0.19	1247	78.532	-0.461 ± 0.120	0.48	1180
Mean elevation	**69.63**	**-0.212 ± 0.028**	**0.25**	**1234**	**67.906**	**-0.167 ± 0.036**	**0.49**	**1176**
Elevational range	69.482	-0.208 ± 0.037	0.16	1252	65.617	-0.100 ± 0.048	0.44	1190
Mid-elevation	68.557	-0.184 ± 0.032	0.16	1252	65.785	-0.107 ± 0.040	0.45	1187
Net Primary Productivity	63.493	-0.051 ± 0.074	<0.01	1281	65.358	-0.089 ± 0.069	0.44	1191
Temperature (mean annual)	53.968	0.199 ± 0.069	0.04	1273	55.406	0.189 ± 0.084	0.45	1188
Temperature (annual range)	70.825	-0.244 ± 0.038	0.20	1244	67.355	-0.152 ± 0.050	0.46	1186
Precipitation (mean annual)	70.523	-0.235 ± 0.047	0.13	1258	68.402	-0.181 ± 0.066	0.46	1186
Precipitation (annual range)	70.214	-0.228 ± 0.049	0.12	1261	66.992	-0.139 ± 0.060	0.449	1188
Lizard								
Stochastic spreading-dye	**46.588**	**-0.547 ± 0.103**	**0.15**	**1090**	**43.847**	**-0.435 ± 0.132**	**0.41**	**1033**
Mean elevation	36.771	-0.084 ± 0.033	0.03	1110	36.071	-0.049 ± 0.041	0.38	1041
Elevational range	35.326	-0.016 ± 0.042	0.01	1116	33.681	0.076 ± 0.054	0.38	1041
Mid-elevation	35.840	-0.040 ± 0.037	0.01	1115	34.674	0.024 ± 0.044	0.38	1042
Net Primary Productivity	39.325	-0.205 ± 0.077	0.04	1109	38.296	-0.161 ± 0.076	0.39	1038

Predictor	Intercept	Slope ± s.e.	r^2	AIC$_c$	Intercept	Slope ± s.e.	Nagelkerke r^2	AIC$_c$
Temperature (mean annual)	37.130	-0.101 ± 0.073	0.01	1114	35.485	-0.017 ± 0.091	0.38	1042
Temperature (annual range)	36.203	-0.057 ± 0.044	0.01	1115	34.510	-0.033 ± 0.058	0.38	1042
Precipitation (mean annual)	39.909	-0.232 ± 0.050	0.11	1096	38.584	-0.176 ± 0.069	0.40	1037
Precipitation (annual range)	36.382	-0.066 ± 0.054	0.01	1115	35.287	-0.008 ± 0.066	0.38	1042
Snake								
Stochastic spreading-dye	30.982	-0.579 ± 0.107	0.15	987	**30.550**	**-0.548 ± 0.135**	**0.53**	**895**
Mean elevation	**26.320**	**-0.256 ± 0.038**	**0.22**	**973**	**25.756**	**-0.196 ± 0.046**	**0.53**	**895**
Elevational range	26.721	-0.284 ± 0.044	0.20	977	25.452	-0.172 ± 0.057	0.51	903
Mid-elevation	25.965	-0.231 ± 0.041	0.16	985	25.011	-0.138 ± 0.050	0.51	904
Net Primary Productivity	23.252	-0.044 ± 0.087	0.01	1014	24.436	-0.081 ± 0.079	0.49	909
Temperature (mean annual)	19.374	-0.224 ± 0.082	0.04	1007	20.842	0.184 ± 0.096	0.50	906
Temperature (annual range)	**27.216**	**-0.318 ± 0.047**	**0.22**	**973**	26.154	-0.228 ± 0.060	0.52	899
Precipitation (mean annual)	26.784	-0.288 ± 0.058	0.13	991	26.443	-0.247 ± 0.078	0.51	901
Precipitation (annual range)	26.462	-0.266 ± 0.060	0.11	995	25.734	-0.188 ± 0.072	0.51	904

(c) – one-degree resolution

	OLS				SAR			
Predictor	Intercept	Slope ± s.e.	r^2	AIC$_c$	Intercept	Slope ± s.e.	Nagelkerke r^2	AIC$_c$
Lizard								
Stochastic spreading-dye	50.857	-0.319 ± 0.251	0.02	289	47.782	-0.178 ± 0.263	0.22	283
Mean elevation	42.760	0.077 ± 0.075	0.01	290	43.770	0.030 ± 0.077	0.21	283
Elevational range	40.204	0.202 ± 0.092	0.09	286	40.486	0.197 ± 0.097	0.28	279
Mid-elevation	41.526	0.138 ± 0.078	0.05	288	42.254	0.108 ± 0.080	0.24	282
Net Primary Productivity	48.882	-0.221 ± 0.135	0.04	288	45.044	-0.037 ± 0.130	0.21	283
Temperature (mean annual)	**48.804**	**-0.217 ± 0.082**	**0.13**	**284**	**47.583**	**-0.166 ± 0.086**	**0.27**	**280**
Temperature (annual range)	40.703	0.178 ± 0.100	0.05	288	**40.900**	**0.179 ± 0.106**	**0.26**	**280**
Precipitation (mean annual)	46.509	-0.106 ± 0.115	0.01	290	44.374	0.513 ± 0.122	0.21	283
Precipitation (annual range)	39.858	0.219 ± 0.127	0.05	288	**39.634**	**0.244 ± 0.124**	**0.28**	**280**
Snake								
Stochastic spreading-dye	**36.372**	**-0.690 ± 0.233**	**0.16**	**250**	34.730	-0.599 ± 0.228	0.49	233

Mean elevation	29.160	-0.163 ± 0.083	0.07	255	29.365	-0.141 ± 0.077	0.45	236
Elevational range	30.079	-0.230 ± 0.099	0.10	253	29.300	-0.137 ± 0.097	0.43	237
Mid-elevation	28.732	-0.132 ± 0.089	0.03	256	28.799	-0.095 ± 0.083	0.43	238
Net Primary Productivity	27.846	-0.067 ± 0.147	0.01	258	27.601	-0.003 ± 0.119	0.41	239
Temperature (mean annual)	26.364	0.041 ± 0.099	0.01	258	27.122	-0.046 ± 0.088	0.41	239
Temperature (annual range)	30.443	-0.256 ± 0.105	0.11	253	29.755	-0.177 ± 0.104	0.44	236
Precipitation (mean annual)	30.999	-0.298 ± 0.117	0.12	252	29.745	-0.191 ± 0.116	0.44	237
Precipitation (annual range)	28.350	-0.105 ± 0.143	0.01	258	28.226	-0.050 ± 0.121	0.41	239

Appendix S8 – The geographic distribution of (a) amphibian (b) bird (c) mammal (d) reptile (e) lizard and (f) snake species richness in New Guinea (as opposed to PNG, Fig. 1) at a quarter-degree grid resolution using a Behrmann equal-area projection. Richness plotted in 32-quantile spectrum from highest in red to lowest in blue. Legend values indicate maximum, median and minimum gridded species richness.