

# Competition poorly correlates with morphological niche partitioning in a radiation of tropical lizards

Alex Slavenko<sup>1</sup>, Allen Allison<sup>2</sup>, and Shai Meiri<sup>3</sup>

<sup>1</sup>The University of Sheffield

<sup>2</sup>Bishop Museum

<sup>3</sup>Tel Aviv University

May 5, 2020

## Abstract

Morphology is expected to represent species' ecological niches, based on microhabitat and ecological selection pressures dictating morphological adaptations for efficient performance. However, the presence of competitor species is predicted to cause niches to contract. Therefore, an increase in species richness is expected to lead to narrower niches, and reduced overlap and distances between niches of different species. We tested these predictions on the skink fauna of New Guinea, the world's largest tropical island. We show that, while some morphospace metrics change predictably with species richness, elevation is a stronger predictor of morphospace occupancy. As elevation increases niches become narrower and closer to each other, and overall morphospace occupancy decreases. Highland skinks are, on average, smaller, thinner, and with shorter limbs than lowland species. We hypothesize that harsh climates in highland habitats impose strong selection on skinks to occupy specific areas of morphospace that facilitate efficient thermoregulation in sub-optimal thermal conditions.

## Competition poorly correlates with morphological niche partitioning in a radiation of tropical lizards

Alex Slavenko<sup>1,2\*</sup>, Allen Allison<sup>3</sup>, Shai Meiri<sup>2,4</sup>

1 – Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

2 – School of Zoology, Tel Aviv University, Tel Aviv, Israel

3 – Bernice P. Bishop Museum, Honolulu, USA

4 – The Steinhardt Museum of Natural History, Tel Aviv, Israel

\* – Corresponding author; a.slavenko@sheffield.ac.uk

**Article type:** Letters

**Short running title:** Morphospace partitioning of tropical lizards

**Statement of Authorship:**

AS collected data and designed and performed the statistical analyses. AA and SM both contributed to acquisition of funds, supervision of the project, and conceptual design. AS wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

**Data Availability:**

All data used in the study and code to run the analyses are packaged as an R project and included in Appendix S1.

**Keywords:** Scincidae, tropical ecology, Papua New Guinea, character displacement, competitive exclusion

**Words in abstract:** 150

**Words in text:** 4425

**References:** 88

**Figures:** 5

**Tables:** 1

## Abstract

Morphology is expected to represent species' ecological niches, based on microhabitat and ecological selection pressures dictating morphological adaptations for efficient performance. However, the presence of competitor species is predicted to cause niches to contract. Therefore, an increase in species richness is expected to lead to narrower niches, and reduced overlap and distances between niches of different species. We tested these predictions on the skink fauna of New Guinea, the world's largest tropical island. We show that, while some morphospace metrics change predictably with species richness, elevation is a stronger predictor of morphospace occupancy. As elevation increases niches become narrower and closer to each other, and overall morphospace occupancy decreases. Highland skinks are, on average, smaller, thinner, and with shorter limbs than lowland species. We hypothesize that harsh climates in highland habitats impose strong selection on skinks to occupy specific areas of morphospace that facilitate efficient thermoregulation in sub-optimal thermal conditions.

## Introduction

Niche partitioning is among the most fundamental processes in ecology, and is a major force generating phenotypic diversity. Ecological opportunity promotes diversification and partitioning of the niche space among species (Schoener 1974; Rainey & Travisano 1998; Losos 2010). Competing species are thought to be unable to co-occur if they are too similar (Gause 1934; Hardin 1960). Competition is thus reduced between closely-related taxa occupying similar niches via partitioning of microhabitat use, activity times and diet – all of which are thought to manifest in morphological adaptation (Brown & Wilson 1956; Pianka 1974; Slatkin 1980; Grant & Grant 2006). That said, such community-wide character displacement is not always manifest (Simberloff & Boecklen 1981; Meiri *et al.* 2011; Stuart & Losos 2013).

Trait divergence leading to niche partitioning can occur for many different traits. Some of the most classic examples of divergence leading to niche partitioning are of morphological traits. Morphological variation underlies some of the most impressive cases of adaptive radiations, such as trophic morphology evolution in African cichlids (Sturmbauer 1998; Rüber *et al.* 1999; Rüber & Adams 2001), adaptation to benthic or pelagic microhabitats in threespine sticklebacks (Lavin & McPhail 1985, 1986; McKinnon & Rundle 2002; McGee *et al.* 2013), bill evolution of Hawaiian honeycreepers (Freed *et al.* 1987; Lovette *et al.* 2002; Reding *et al.* 2008; Lerner *et al.* 2011) and Darwin's finches (Lack 1947; Grant 1999; Abzhanov *et al.* 2004; Herrel *et al.* 2005), shape and size differentiation of Greater Antilles anoles (Schoener 1974; Losos 1990, 2008; Losos & Ricklefs 2009), limb reduction and loss in Australian skinks (Greer 1989; Rabosky *et al.* 2007; Wiens 2009; Skinner 2010), and many more.

We examined patterns of morphospace occupancy and partitioning in the skink fauna of Papua New Guinea (PNG). Skinks occur in almost all habitats on the island and display much variation in morphology, microhabitat use, diel activity, reproductive biology and diet (Allison 1982; Allison & Greer 1986; Allison

2007, 2009; Meiri 2018). We used morphological measurements from 1860 specimens of PNG skinks (Fig. 1a), comprising 79 species out of 110 currently recognized in PNG, to test the following hypotheses:

1. As skink richness increases, niches will become narrower (*i.e.*, individual species will occupy a smaller area of morphospace; Fig. 1b).
2. The overall size of the morphospace will not vary greatly with richness, but the relative distances and overlaps between various species will. That is, the size of the proverbial morphological “pie” remains the same, but the size of the “slices” that the “pie” is partitioned into will change (Fig. 1c).
3. As skink richness increases, distances between species will decrease as the morphospace becomes more saturated (Fig. 1d).
4. As skink richness increases, niche overlap between species will decrease due to diffuse competition reducing overlap between closely competing species in species-rich areas (Pianka 1972, 1974) (Fig. 1e).
5. Competitive exclusion (Gause 1934; Elton 1946; Hardin 1960) and limiting similarity (MacArthur & Levins 1967) will prevent similar species from co-occurring. Therefore, the mean distances between morphology of a focal species and sympatric species will be longer than the distance of its morphology and those of allopatric species (Fig. 1f), and species morphology will overlap more with that of allopatric relatives than with sympatric ones (Fig. 1g). Alternatively, habitat filtering and phylogenetic relatedness of spatially proximate species may create the opposite pattern, whereby sympatric species’ morphology is more similar than expected by chance.

We show here that morphospace occupation metrics poorly correlate with richness, and sympatric and allopatric species occupy similar areas of morphospace. Competition was therefore likely not a strong driver of niche partitioning in PNG skinks. We also show that morphospace occupancy changes strongly with elevation, with highland assemblages occupying both a reduced, and a distinct, area of morphospace compared to lowland assemblages, suggesting a strong role for changing habitats and environmental conditions in shaping niche partitioning in this large radiation of lizards.

## Methods

### Data collection

We measured 1860 specimens of PNG skinks, comprising 79 currently recognized species, in natural history collections. From each specimen we recorded 16 morphometric measurements to quantify variation in body size and shape (Fig. 1a). Measurements of limbs were all taken from the left side of the body, barring cases where the left limbs were damaged (*e.g.* missing digits), in which case all measurements for that specimen were taken from the right side of the body instead. All measurements were taken using a digital caliper to the nearest 0.1 mm.

We obtained distribution maps from Roll *et al.* (2017) for all the species included in the study. We overlaid the maps onto a 25\*25 km equal-area Berhmann projection grid of PNG (*sensu* Tallowin *et al.* 2017), comprising 620 cells, excluding cells with < 50% land cover to prevent edge effects. For each cell, we tallied the total skink species richness, and recorded which species occur in it.

We obtained elevation data from the Papua New Guinea Resource Information System (3<sup>rd</sup> Edition; Bryan & Shearman 2008). We then calculated mean elevation (in m a.s.l.) for each cell and assigned cells to either “highland” (mean elevation [?] 1000 m a.s.l.) or “lowland” (mean elevation < 1000 m a.s.l), based on habitat categorizations in Bryan & Shearman (2015), who define lower montane forest from *ca.* 1000 m and above. Similarly, we averaged mean elevation per cell (in m a.s.l.) across the distribution of each species and assigned species to either “highland” or “lowland” using the same categorization scheme.

All the analyses were performed in R v3.6.1 (R Core Team 2019) and R code is available in Appendix S1.

## Morphometric analyses

We performed size adjustment on all morphometric measurements (apart from SVL) by dividing them by SVL. Therefore, we had one non-transformed measurement, SVL (in mm), and 15 size-adjusted measurements (as proportion from each individual's SVL). We reduced dimensionality in the morphometric data by performing a PCA using the 'prcomp' function from the *stats* package in R, and we used the "broken stick" method (Jackson 1993) to select only those PC axes which explained a statistically significant portion of variance for downstream analyses. These PCs were used to define the morphospace of PNG skinks. We used the *hypervolume* package (Blonder & Harris 2018) to calculate the volume of morphospace occupied by each species (using the 'hypervolume\_gaussian' function), measured as a Gaussian 95% kernel density (a method to estimate the probability density function) estimate around the coordinates of individuals of each species in morphospace.

## Spatial analyses of morphospace

We calculated four morphospace metrics for each cell, based on the morphospace volumes of the different species (Fig. 1b-e): (a) the mean volume of morphospace occupied by all species in the cell; (b) the total volume of morphospace occupied by all species in the cell, defined as the Gaussian 95% kernel density estimate around the coordinates of individuals of all species occurring in the cell; (c) the mean pairwise distance between all species pairs in the cell, defined as the Euclidean distance between the centroids of the volumes of each pair of species (using the 'hypervolume\_distance' function); and (d) the mean pairwise overlap between all species pairs in the cell, defined as the Jaccard similarity index (ranging from 0 to 1) of the volumes of each pair of species (using the 'hypervolume\_overlap\_statistics' function).

We then ran multiple linear regression models for each metric, with mean elevation and species richness as predictor variables (they do not co-vary strongly, Variance Inflation Factor  $< 2$ ). We compared models that had either both predictors (full model), one of them (mean elevation or richness), or none (the null model) using AICc scores, selecting the model with the lowest AICc score. If the best model was the full model, we compared relative variable importance by decomposing the contribution to  $R^2$  of each predictor averaged over different orderings (*i.e.*, adding each predictor to the model in different orderings [first, second, last, *etc.*], measuring the addition to model  $R^2$  in each ordering, and then averaging across all different orderings) as implemented in the 'calc.relimp' function from the *relaimp* package (Gromping 2006).

We further calculated the centroid of PC scores for each cell, which we used as a metric to quantify the commonest area of morphospace occupied in each cell. We compared highland to lowland cells by performing a PERMANOVA analysis with the 'adonis' function from the *vegan* package (Oksanen *et al.* 2019), testing to examine if there's a shift in the PC centroids between lowland and highland cells. Furthermore, we generated histograms of the PC scores on each PC for each cell and examined changes in the distributions of PC scores with elevation by fitting linear regression models of mean elevation against the standard deviation, skewness and kurtosis of PC scores in each cell.

Similar to the previously described analyses, we also examined if the overall morphospace occupied per cell shifted between species in the highlands and lowlands. After assigning each species to either "highland" or "lowland" (as described in the "data collection" section), we used a PERMANOVA analysis to compare morphospace occupancy between highland and lowland species.

Finally, we tested for signals of competition between species sharing similar areas of morphospace in their distributions (Fig. 1f-g). We did this by tallying for each species which cells are within its range, and which cells are outside its range. We then calculated the mean distance and overlap from the focal species for each cell (*i.e.* the average of all distances or overlaps between each species in the cell and the focal species), and calculated the mean distances from the focal species across all cells within its range, and outside its range. We then performed two tests: (a) t-tests comparing, for each species, the mean distances and overlaps between cells within the focal species' range and outside the focal species' range, and (b) a linear regression through the origin with mean distance/overlap within the focal species' range on the x axis, and mean

distance/overlap outside the focal species' range on the y axis. In the linear regression we tested whether the slope differed significantly from 1 (a slope of 1 meaning no difference in distances or overlaps within and outside focal species' ranges), our null hypothesis with no signal of competitive exclusion or limiting similarity. The alternative hypotheses we examined are a slope shallower than 1 for mean distances (meaning distances between species are higher within focal species' ranges), and a slope steeper than 1 for mean overlap (meaning overlap between species is lower within focal species' ranges), which we interpret as indicative of competition.

## Results

The broken stick test determined that only the first two PCs explained a statistically significant portion of variance (Fig. S1). Cumulatively, these PCs explain 78.1% of the variance (PC1 61%, PC2 17.1%; Fig. S2). PC1 mainly captures variation in limb lengths and head length (long limbs and heads relative to body length, vs. short limbs and heads; Fig. 2), whereas PC2 mainly captures variation in body length (SVL) and depth, and head depth, and to a lesser extent width (large and thick-bodied vs. small and thin; Fig. 2).

None of the four morphospace metrics is congruent with skink richness, which peaks along the northern coast of PNG (Fig. 3). All four measures, however, vary systematically with mean cell elevation (Fig. 3). Mean pairwise distance and total volume mostly peak at low elevations along the coasts, and decrease in the high elevation regions in the Central Cordillera and the Papuan Peninsula (Fig. 3a,d). Mean niche volume peaks along the southern coast of Papua New Guinea and is lower in the Central Cordillera and along the northern coast (Fig. 3c). Mean pairwise overlap shows the most complex pattern, mostly peaking in mid-elevations on the slopes of the Central Cordillera and the Owen Stanley Mts in the Papuan Peninsula (Fig. 3b).

Multiple linear regression models for all morphospace metrics have variation in all metrics explained by both skink richness and mean elevation (Table 1). Model  $R^2$  values range between 16.2% (for mean pairwise overlap) to 64.2% (for total volume). Mean morphospace volume, total morphospace volume, and mean pairwise distance all decrease with mean elevation, whereas mean pairwise overlap increases with mean elevation. Mean morphospace volume, and mean pairwise overlap, decrease with skink richness – whereas total morphospace volume and mean pairwise distance increase with increasing richness. Mean elevation is 2.4 to 17.7 times more important than skink richness for mean volume, total volume, and mean pairwise distance (Table 1). Only for mean pairwise overlap is species richness nearly as important as mean elevation.

Based on t-tests to compare mean pairwise distances and overlaps between each species and species occurring in either sympatry or allopatry, 40 of 77 species (51.9%) have significantly higher distances from species within their ranges than outside their ranges, and 30 of 77 species (39%) have significantly lower overlap with species within their ranges than outside their ranges. However, only 24 species (31.2%) have both higher distances and lower overlap with species within their ranges than outside their ranges (Table S1). This suggests that few species significantly differ in morphospace occupancy from sympatric species.

We then ran linear regressions through the origin, with mean distance/overlap within the focal species' range on the x axis, and mean distance/overlap outside the focal species' range on the y axis (Fig. 1f-g). The regression slopes for both mean pairwise distance and mean pairwise overlap, when the parameters within the focal species' range are compared against the parameters outside the focal species' range, do not differ significantly from 1 ( $0.99 \pm 0.01$  and  $0.98 \pm 0.02$ , respectively;  $p_{\text{distance}} = 0.26, p_{\text{overlap}} = 0.34$ ). That is, the mean distances and overlap between each species and other species within their ranges do not differ from those of species outside their ranges (Fig. 4), suggesting that on average, species occupy similar positions in morphospace as either sympatric or allopatric species.

On average, as elevation increases, the average area of morphospace occupied by species decreases (mean volume), the total area of morphospace occupied by assemblages decreases (total volume), the average distance between species in morphospace decreases (mean pairwise distance), and the average overlap between species in morphospace increases (mean pairwise overlap). Total volume changes the most with elevation, whereas mean pairwise overlap changes the least, as signified by the differences in standardized regression

coefficients for the different metrics (Table 1). Furthermore, the 95% CI ellipsoid encompassing species from lowland cells is roughly 1.5 times as large as the 95% CI ellipsoid encompassing species from highland cells (area of ellipsoids: 106.11 for lowland species, 72.01 for highland species). This means that species from the lowlands of PNG occupy a larger area of morphospace than species from the highlands (Fig. S3).

Highland cells occupy a significantly different area of morphospace from lowland cells (PERMANOVA based on 999 permutations,  $p = 0.001, R^2 = 0.17$ ; Fig. 5). Centroids of highland cells have, on average, higher PC1 scores and lower PC2 scores than lowland cells, meaning highland cells have, on average, smaller and thinner skinks with shorter limbs. As elevation increases, the skewness and kurtosis of PC1 and the standard deviation, skewness and kurtosis of PC2 increase. The distributions of centroids in the cells thus become more right-skewed and more centered around the modal values (Fig. 5b-c; Table S2; Fig. S5). There is also a pronounced shift in the modal values, with the centroids of PC1 increasing and the centroids of PC2 decreasing with an increase in elevation (Fig. 5b-c; Table S2; Fig. S5). Similarly, species from lowland and highland cells occupy distinct areas of morphospace (PERMANOVA based on 999 permutations,  $p = 0.001, R^2 = 0.027$ ; Fig. S3), albeit the difference is much smaller than the assemblage-level comparison and the model has very low explanatory power.

## Discussion

### Little evidence of competition-driven niche partitioning

Classic ecological theory predicts that, as the number of competitors increases, species morphology will adapt to reduce similarity due to the effects of diffuse competition (Hutchinson 1957; Pianka 1974). However, we found little evidence of competition-driven ecological niche partitioning in PNG skinks. Morphospace occupancy appears to be more strongly influenced by elevation, a proxy for environmental conditions and habitat type, than it is by species richness, a metric for interspecific competition (Fig. 3; Table 1). Furthermore, there is little evidence of competitive exclusion or limiting similarity having driven assemblage structure (Fig. 4 & Table S1). Therefore, in PNG skinks, similar to what has been described in several other cases (*e.g.*, Meiri *et al.* 2011; Stuart & Losos 2013), the effects of competition on shaping niche partitioning appear weak. There are several possible explanations for the weak effect of competition.

First, there may be other axes of niche space that are not captured by the morphometric measurements used here. For instance, several species of skinks from the genera *Prasinochaema* and *Lipinia* have developed subdigital lamellae, likely in association with their arboreal habits (Greer 1974). Traits such as these, which have well documented impacts on locomotory performance (Irschick *et al.* 1996; Glossip & Losos 1997; Macrini *et al.* 2003; Elstrott & Irschick 2004), are likely important in microhabitat niche partitioning, and competition may affect some axes of trait space more strongly than others.

Second, the method we employed here assumes that all species that occur within a 25\*25 km cell are sympatric and syntopic, an assumption that is not here tested and very likely isn't true for all cells in PNG. For instance, skink species on Mt Kiandi are separated by microhabitat and elevation (Allison 1982), meaning that despite all co-occurring in the same cell, few of them interact ecologically with one another. The extent to which species in the same cell interact with each other across PNG, and therefore experience competition, and whether patterns of co-occurrence change spatially and with elevation, need to be determined.

Third, taxonomic diversity of Papua New Guinea skinks is potentially greatly underestimated (*e.g.*, Slavenko *et al.* 2020). Therefore, patterns of morphospace occupancy could potentially change as new species are described. However, if taxonomic changes will be of splitting wide-ranging complexes of cryptic species into mostly allopatric and morphologically similar species (*e.g.*, *Papuascincus* spp.; Slavenko *et al.* 2020), then the overall spatial patterns of species richness and morphospace occupancy are not likely to change greatly.

## The size of occupied morphospace changes with elevation

We found that highland species occupy a smaller portion of morphospace than do lowland species (Figs. 3d,h & S3). Indeed, many of the most morphologically distinct skinks in Papua New Guinea, which occupy the margins of the morphospace, are lowland species – these include the semi-aquatic and unusually long-limbed *Foija bumui* (Greer & Simon 1982), the extremely large *Tiliqua gigas* (on average 4.7 times longer, and 290 times heavier, than other Papua New Guinea skinks; mass data from Slavenko *et al.* 2016), or several species of large-headed *Tribolonotus*, noted for their strongly keeled scales and bony protrusions (Austin *et al.* 2010).

The larger morphological diversity in lowlands might be explained by the “area effect” – larger areas providing more opportunities for diversification, and therefore the potential to occupy novel areas of the adaptive landscape (Gavrilets & Vose 2005; Kisel & Barraclough 2010; Mahler *et al.* 2013). The lowlands in PNG are indeed more extensive in area than the highlands, roughly a ratio of 2/1 between areas below and above 1000 m (Allison 2009). Additionally, higher primary productivity in the lowlands may also enable wider, more diverse niche space there than in the less productive highlands.

This “area effect” originally ascribes to island systems and attempts to explain differences in morphological diversity between small and large (Mahler *et al.* 2013). While this may be the case for some systems such as Caribbean anoles, where unique morphologies evolve only on large islands (Gavrilets & Vose 2005; Mahler *et al.* 2013), it is unclear if this scenario applies to New Guinea. Since phylogenetic affinities of most New Guinea skinks are unresolved, and the number of transitions between lowland and highland taxa remain unknown, is it difficult to ascertain if the lowlands and highlands form distinct landmasses for separate events of radiation. There is evidence, though, to suggest this is not the case. For instance, *Foija bumui*, as well as several *Lipinia* spp. and two species of *Prasinohaema* (*P. virens* and *P. semoni*), are nested within a clade of mostly montane skinks (*Lobulia*, *Papuascincus* and highland *Prasinohaema*; Rodriguez *et al.* 2018). Several other highland skink species likely also represent independent colonisations from lowland origins – for instance highland *Sphenomorphus* and *Emoia* species (phylogenetic positions of *Sphenomorphus* and *Emoia* from Skinner *et al.* 2011; Pyron & Wiens 2013). It seems likely therefore that the highlands of New Guinea are an extension of the same radiation of skinks as the lowlands, and not a distinct radiation in themselves, and have both been colonised and provided sources for shifts back to lowland distribution several times in the past.

Another important caveat is that the species in this study are not phylogenetically independent, and failing to account for phylogeny may impact results of such morphological analyses (Revell 2009). If phylogenetic niche conservatism (Blomberg *et al.* 2003; Wiens & Graham 2005) occurs in PNG skinks, the low morphospace occupancy in high elevations may simply be explained by the close phylogenetic affinities of many highland species (Rodriguez *et al.* 2018). Unfortunately, genetic data are not available for most PNG skink species, rendering a phylogenetic correction for these analyses currently impossible. However, the extent to which phylogenetic niche conservatism occurs in this radiation of skinks is unknown, and we have no reason to assume *a priori* that it exists. For instance, *Foija bumui*, an extremely morphologically and ecologically distinct lowlands species (Greer & Simon 1982) is phylogenetically closely related to morphologically very dissimilar highland species such as *Papuascincus* spp. and *Prasinohaema* spp. (Rodriguez *et al.* 2018) (Fig. S4).

## Lowland and highland species occupy distinct areas of morphospace

As well as occupying a smaller portion of morphospace in general, highland cells also occupy a distinct area of morphospace compared to lowland cells (Fig. 5). Such differences in morphospace could arise in several distinct mechanisms. For instance, environmental differences could lead to different selection regimes driving morphological evolution (Pinto *et al.* 2008). Similarly, ecological opportunity (Losos 2010; Wagner *et al.* 2012) and the evolution of key innovations (Baum & Larson 1991; Heard & Hauser 1995) might lead to colonisations of novel areas of the adaptive landscape. However, highland species in PNG do not so much represent a distinct area of morphospace, but rather a diminished subset of the morphologies found in the lowlands (Fig. S4). Therefore, the differences between lowland and highland assemblages are derived from

a shift in the distributions and modal values of morphologies in the assemblages (Fig. 5b,c), rather than the presence of unique morphologies in highland assemblages.

As elevation increases, temperatures drop, patterns of rainfall shift, and the habitat changes drastically, particularly with reduced stratification as canopy height decreases and eventually disappears entirely above the tree line (Bryan & Shearman 2015). Skinks from highland cells are, on average, smaller, thinner and with shorter limbs (Figs. 2 & 5). Relative limb length is related to locomotory performance, and therefore to microhabitat use (Garland Jr & Losos 1994). Longer limbs are typically associated with faster sprinting speeds and enhanced jumping capability (Pianka 1969; Melville & Swain 2000; Irschick *et al.* 2005). Therefore, species occupying open habitats tend to have longer limbs (Melville & Swain 2000; Goodman *et al.* 2008; but see *e.g.*, Schulte II *et al.* 2004). Conversely, arboreal and ground-dwelling species in leaf litter and dense vegetation tend to be smaller and shorter limbed (Melville & Swain 2000). Many of the highland Papua New Guinea skinks occur in alpine grasslands, shrublands and tree-fall gaps (Allison & Greer 1986; Greer *et al.* 2005), but some, such as *Papuascincus* spp., also inhabit rocky substrates (Allison & Greer 1986). Locomotion in dense grasslands might provide selective pressure for short relative limb length in these skinks.

Another possible avenue for selection on body size and shape in highland skinks is climate. The lapse rate in PNG is roughly 0.5-0.6degC for every 100 m gained in altitude (Bourke 2010), meaning that montane regions of New Guinea are typified by extremely cold temperatures with occasional frosts, with mean temperatures dropping as low as 5-6degC (Allison 2009), and nightly temperatures reaching freezing levels (Sarmiento 1986). These harsh climates are far from ideal for ectotherms such as lizards, and indeed species richness of reptiles decreases with elevation in PNG (Tallowin *et al.* 2017). Many montane species exhibit adaptations for cold climate such as ovoviviparity (Greer *et al.* 2005). A relationship between body size and climate has long been contented, although evidence for such a relationship in reptiles is dubious (Slavenko *et al.* 2019). The driving mechanism behind this change is purported to be thermoregulation – small body sizes lead to increased surface area-to-volume ratios, which in ectotherms such as lizards may improve heat gain in cold climates (Carothers *et al.* 1997). Thermoregulation may be extremely difficult in montane habitats (Monasterio *et al.* 2009; Zamora-Camacho *et al.* 2014), and therefore needs to be especially efficient (Ortega *et al.* 2016). In high elevations, low ambient temperatures lead to short windows available for activity. Therefore, ectotherms require sunbathing to achieve optimal temperatures, and the more efficient and faster heat gain is, the more effective the use of this window for activity. We suggest that the harsh climatic conditions of montane habitats in PNG drive morphological evolution. Morphologies that are suboptimal for thermoregulation may be adequate in the mild climates of the lowlands, but lead to reduced performance in harsh highland climates, particularly in intraspecific interactions such as competition for limited food resources or mating opportunities (Irschick *et al.* 1996; Macrini *et al.* 2003; Pinto *et al.* 2008). This hypothesis could be tested by comparing the thermoregulatory efficiency of species with different morphologies, or even using inert models to compare passive rates of heat acquisition and retention.

## Conclusions

Competition is classically considered to be a foremost driver of niche partitioning (Hutchinson 1957; Pianka 1974), and ecological theory predicts that competitors cannot co-exist in the same niche (Brown & Wilson 1956; Hardin 1960; Pianka 1974; Slatkin 1980; Grant & Grant 2006). However, evidence suggests that competition is not always the strongest driver of niche partitioning (*e.g.* Meiri *et al.* 2011; Stuart & Losos 2013). Our results support the latter conclusion, and that, at least for PNG skinks, selective pressures due to harsh environmental conditions may be more important. We strongly recommend that competition not be taken to be a strong driver of community assembly and niche partitioning *a priori*, and that its effects should always be quantified and clearly tested.

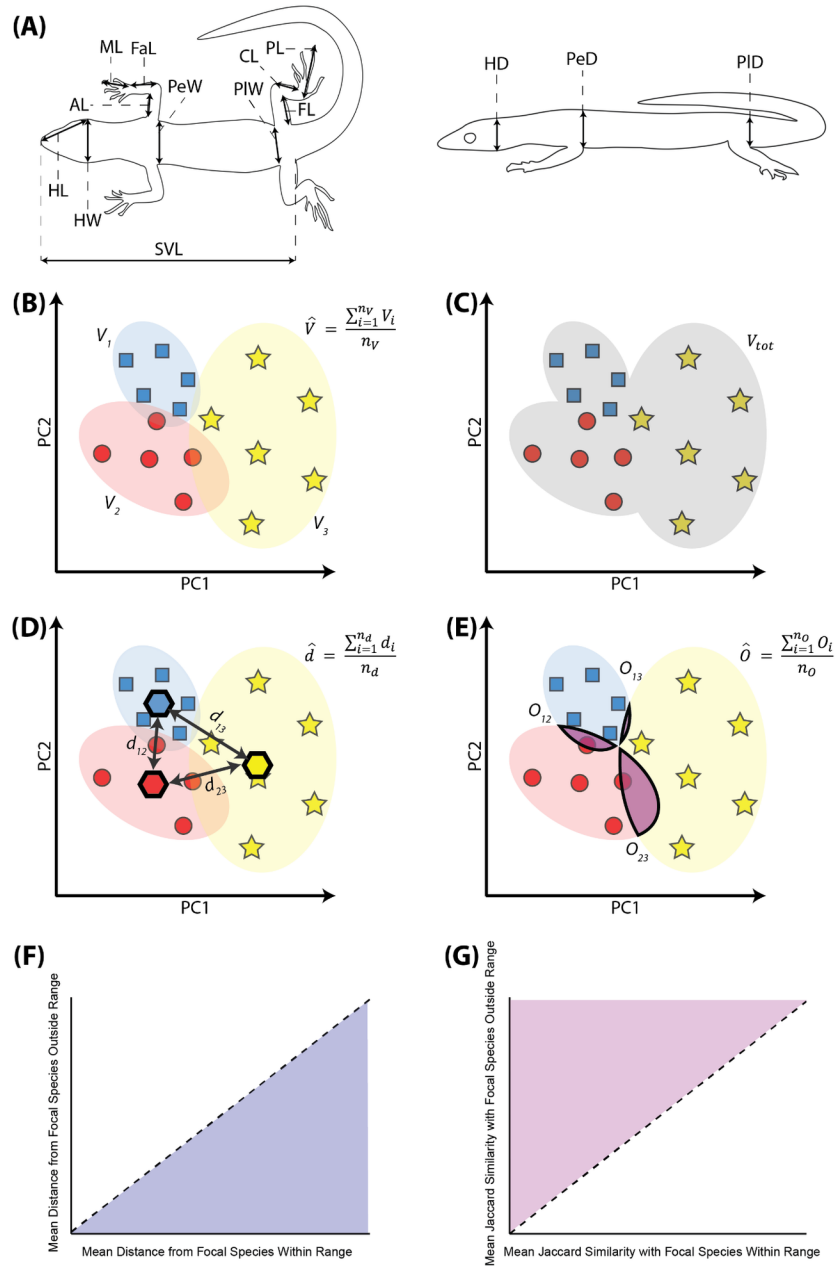
## Acknowledgements

We thank Molly Hagemann (Bernice P. Bishop Museum), Chris Austin and Seth Parker (Louisiana State University Museum of Zoology), and Jose Rosado (Museum of Comparative Zoology) for facilitating accesses

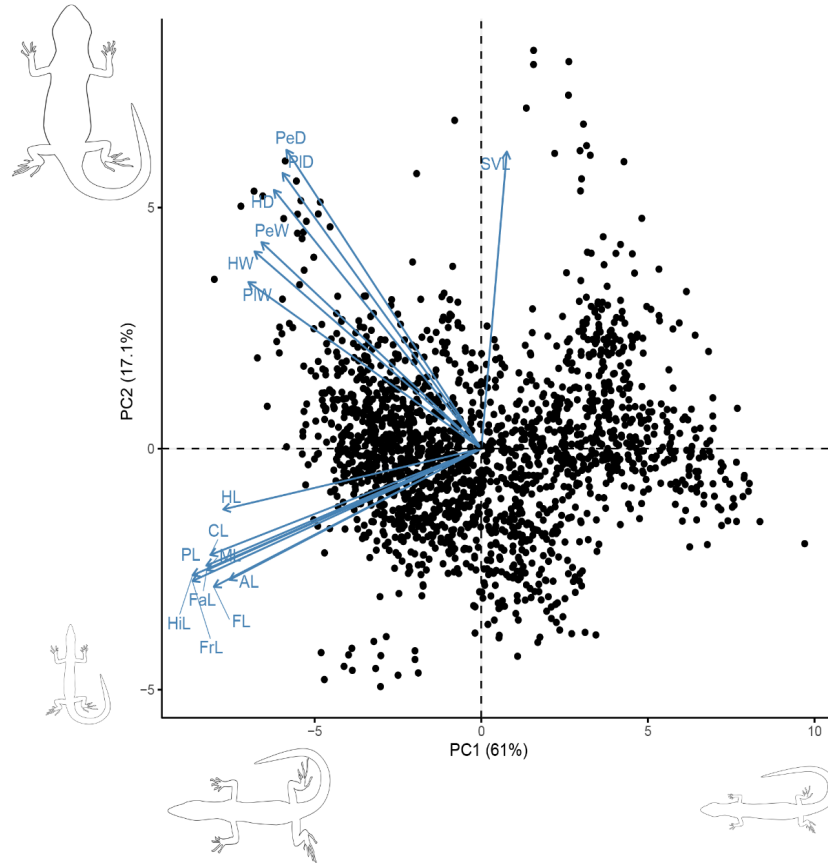


to their collections and permitting measurements of the specimens used in this study. This research was funded by BSF grant no. 2012143 to S.M. and A.A., and BSF grant no. 00020309000 to A.S. Finally, the collections of all specimens used in this study was only accomplished through the gracious collaboration throughout the years of provincial governments, the PNG National Research Institute, the PNG Conservation and Environment Protection Authority, and countless local communities in Papua New Guinea who provided access to their ancestral lands.

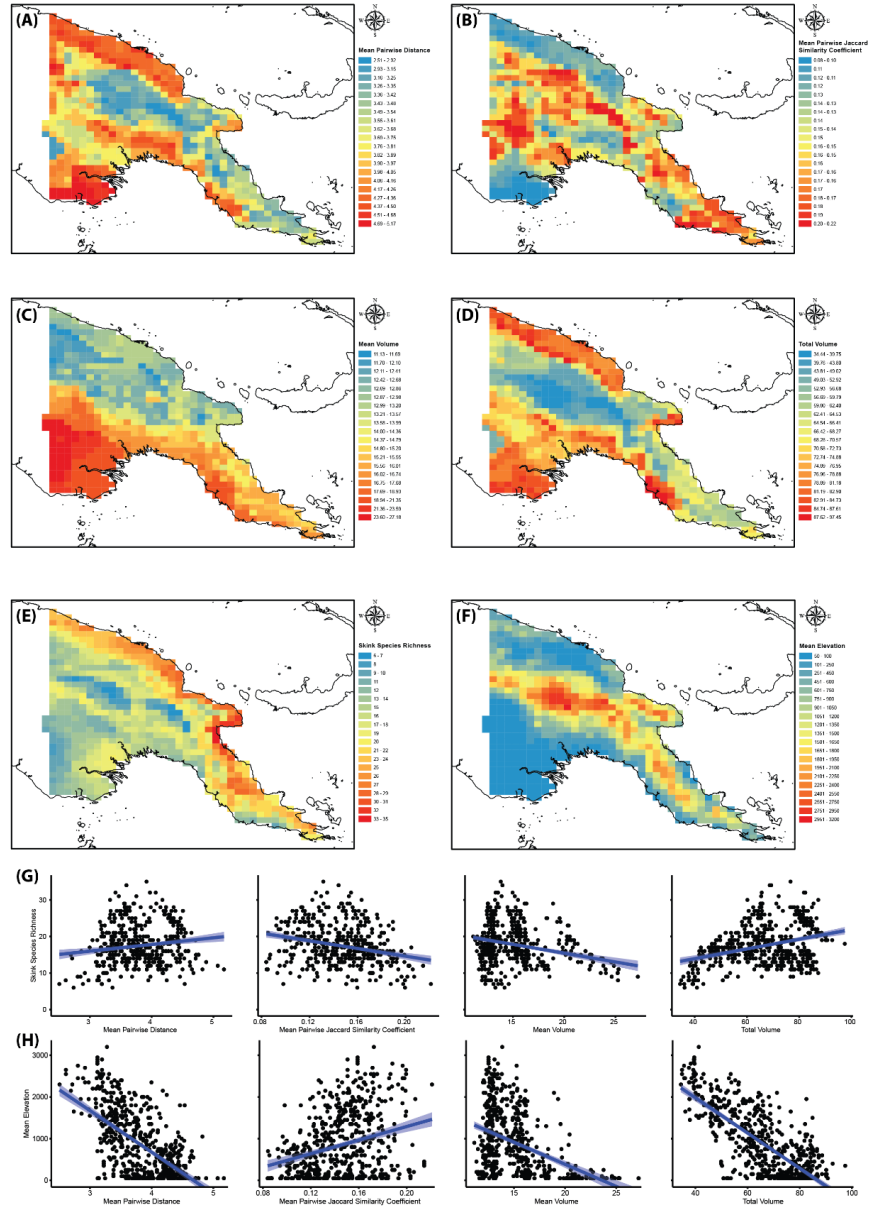
**Figure 1.** (a) A schematic representation of a skink with 14 morphometric measurements marked on it. The measurements are: SVL – snout-vent-length; HL – head length (from anterior edge of ear opening to snout); HW – head width (at the widest point); HD – head depth (at the deepest point); PeW – pectoral girdle width; PeD – pectoral girdle depth; PIW – pelvic girdle width; PID – pelvic girdle depth; AL – arm length (shoulder to elbow); FaL – forearm length (elbow to wrist); ML – manus length (wrist to tip of longest digit); FL – femur length (from pelvis to knee); CL – crus length (from knee to heel); PL – pes length (from heel to tip of longest digit). Two additional measurements not displayed here are: FrL – length of front limb (sum of AL, FaL and ML); HiL – length of hind limb (sum of FL, CL and PL). (b-e) Schematic representations of the morphospace of a hypothetical assemblage of three skink species, denoted by blue squares, red circles and yellow stars, each representing a different species. (b) Mean volume is calculated as the mean of all individual species’ volumes of morphospace in the assemblage, represented here by coloured ellipses. (c) Total volume is calculated as the volume of morphospace occupied by individuals from all species in the assemblage, represented here by the grey shape. (d) Mean pairwise distance is calculated as the mean of all distances between centroids of all pairs of species in the assemblage, the centroids represented here by hexagons. (e) Mean overlap is calculated as the mean of all overlaps between all pairs of species in the assemblage, represented here as purple shaded polygons with dark outlines. (f-g) Hypotheses tested for the comparison of mean distance from and mean overlap with the focal species within and outside their ranges. The dashed line represents the null regression with an intercept of 0 and a slope of 1. (f) The blue shaded area represents mean distances from the focal species that are higher within the focal species’ range, *i.e.* regression slope shallower than 1. (g) The purple shaded area represents mean overlaps with the focal species that are lower within the focal species’ range, *i.e.* regression slope steeper than 1. Thus these shaded areas represent the expectations of the ecological competition paradigm.



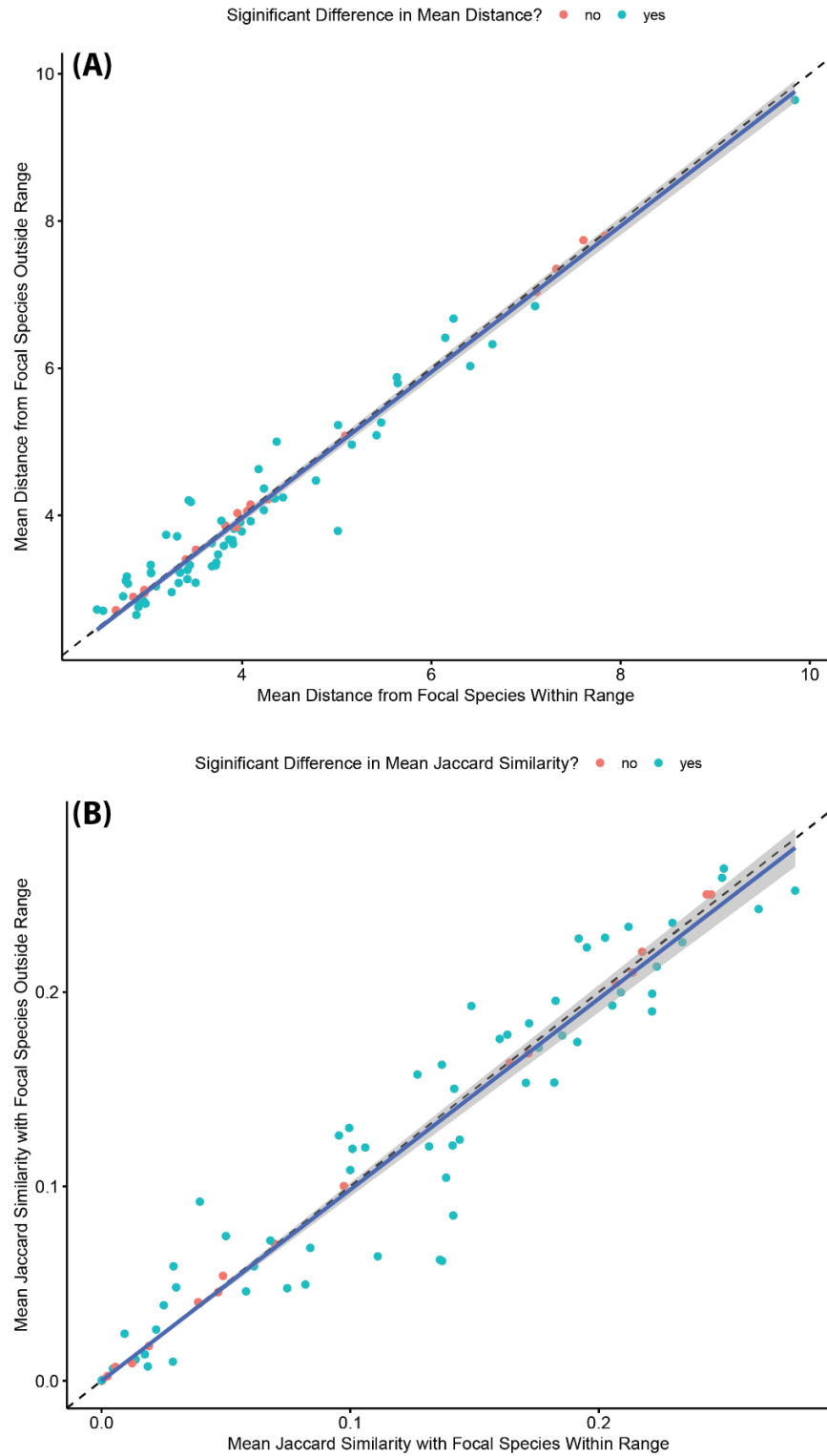
**Figure 2.** Morphospace of Papua New Guinea skinks. The blue arrows show the loadings of the various morphometric measurements on the PC axes. On the edges of each axis are schematic representations of skinks visualizing how morphology changes along each axis.



**Figure 3.** (a-f) Maps showing spatial distributions of (a) mean pairwise distance per cell, (b) mean pairwise Jaccard similarity coefficient per cell, (c) mean volume per cell; (d) total volume per cell; (e) skink species richness per cell, and (f) mean elevation per cell. Cooler colours represent lower values, whereas warmer colours represent higher values. (g) Scatterplots showing the relationship between each of the four metrics from maps a-d (left to right) and skink species richness. (h) Scatterplots showing the relationship between each of the four metrics from maps a-d (left to right) and mean elevation.

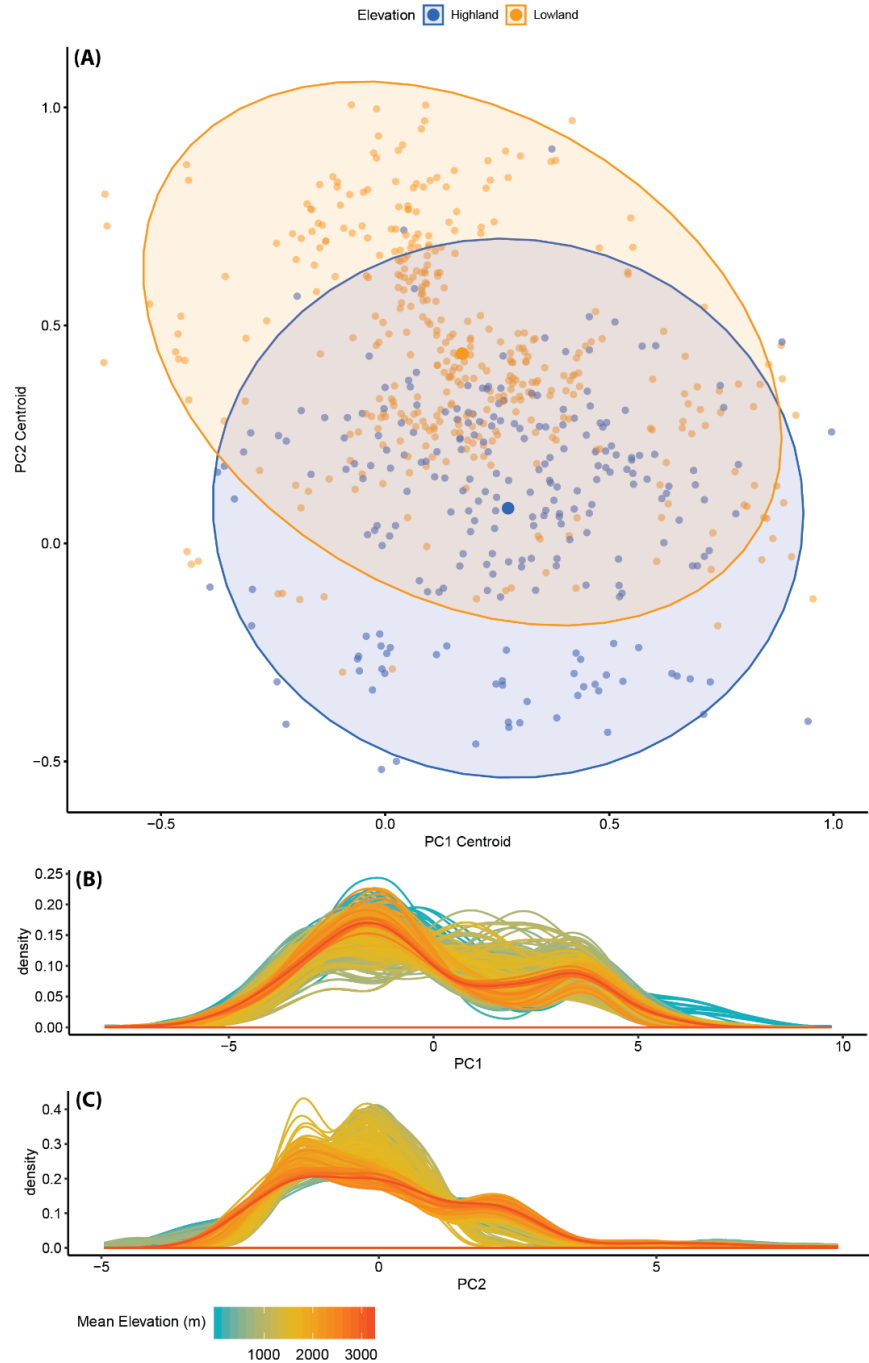


**Figure 4.** Comparisons of (a) mean distance from and (b) mean overlap with the focal species within and outside their ranges. The dashed line represents the null regression slope of 1. Each dot is coloured based on the significance of t-tests comparing the metric within and outside the focal species' range – turquoise for significant difference between ranges, and pink for no significant difference between ranges.



**Figure 5.** (a) Scatterplot showing the coordinates of the centroids of PCs 1 & 2 per cell. Highland cells

(elevation > 1000 m) are coloured blue, and lowland cells (elevation < 1000 m) are coloured teal. The ellipses encompass 95% of observations for each group. (b-c) Density histograms showing the distribution of PC scores within each cell (each histogram is the distribution of an individual cell). Colours represent the mean elevation of the cell, with cooler colours representing lower elevations and warmer colours representing higher elevations.



**Table 1.** Results of the best models for each morphospace metric. Standardized regression coefficients are written for each predictor (all predictors are significant;  $p < 0.001$ ). The two right-most columns are the relative importance calculated for both predictors in each model.

Model	Skink Richness	Mean Elevation	$R^2$	Richness	Relative Importance	Elevation
Mean Volume	-0.33	-0.5	0.35	0.29		0.71
Total Volume	0.31	-0.75	0.67	0.15		0.85
Mean Pairwise Distance	0.13	-0.61	0.39	0.05		0.95
Mean Pairwise Overlap	-0.26	0.29	0.16	0.44		0.56

## References

- Abzhanov A., Protas M., Grant B.R., Grant P.R. & Tabin C.J. (2004). *Bmp4* and morphological variation of beaks in Darwin's finches. *Science* , 305, 1462-1465.
- Allison A. (1982). Distribution and ecology of New Guinea lizards. In: *Biogeography and ecology of New Guinea* (ed. Gressitt JL). Springer The Hague, Netherlands, pp. 803-813.
- Allison A. (2007). Section 4.6. Herpetofauna of Papua. In: *The Ecology of Papua, Part One* (eds. Marshall AJ & Beehler BM). Periplus Editions Singapore, pp. 564-616.
- Allison A. (2009). New Guinea, Biology. In: *Encyclopedia of islands* (eds. Gillespie RG & Clague DA). University of California Press Berkley and Los Angeles, California, pp. 652-658.
- Allison A. & Greer A.E. (1986). Egg shells with pustulate surface structures: basis for a new genus of New Guinea skinks (Lacertilia: Scincidae). *Journal of Herpetology* , 20, 116-119.
- Austin C.C., Rittmeyer E.N., Richards S.J. & Zug G.R. (2010). Phylogeny, historical biogeography and body size evolution in Pacific Island Crocodile skinks *Tribolonotus* (Squamata; Scincidae). *Molecular Phylogenetics and Evolution* , 57, 227-236.
- Baum D.A. & Larson A. (1991). Adaptation reviewed: a phylogenetic methodology for studying character macroevolution. *Systematic Zoology* , 40, 1-18.
- Blomberg S.P., Garland Jr. T. & Ives A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* , 57, 717-745.
- Blonder B. & Harris D.J. (2018). hypervolume: High dimensional geometry and set operations using kernel density estimation, support vector machines, and convex hulls. In: <https://CRAN.R-project.org/package=hypervolume>.
- Bourke R.M. (2010). Altitudinal limits of 230 economic crop species in Papua New Guinea. In: *Altered Ecologies: Fire, Climate and Human Influence on Terrestrial Landscapes* (eds. Haberle S, Stevenson J & Prebble M). ANU Press Canberra, pp. 473-512.
- Brown W.L. & Wilson E.O. (1956). Character Displacement. *Systematic Zoology* , 5, 49-64.
- Bryan J.E. & Shearman P. (2008). *Papua New Guinea resource information handbook* . 3rd edn. University of Papua New Guinea, Port Moresby, Papua New Guinea.
- Bryan J.E. & Shearman P.L. (2015). *The state of the forests of Papua New Guinea 2014: measuring change over the period 2002-2014* . University of Papua New Guinea, Port Moresby, Papua New Guinea.
- Carothers J.H., Fox S.F., Marquet P.A. & Jaksic F.M. (1997). Thermal characteristics of ten Andean lizards of the genus *Liolaemus* in central Chile. *Revista Chilena de Historia Natural* , 70, 297-309.

- Elstrott J. & Irschick D.J. (2004). Evolutionary correlations among morphology, habitat use and clinging performance in Caribbean *Anolis* lizards. *Biological Journal of the Linnean Society* , 83, 389-398.
- Elton C.S. (1946). Competition and the structure of ecological communities. *Journal of Animal Ecology* , 15, 54-68.
- Freed L.A., Conant S. & Fleischer R.C. (1987). Evolutionary ecology and radiation of Hawaiian passerine birds. *Trends in Ecology & Evolution* , 2, 196-203.
- Garland Jr T. & Losos J.B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In: *Ecological morphology: integrative organismal biology* (eds. Wainwright PC & Reilly SM). University of Chicago Press Chicago, IL, pp. 240-302.
- Gause G.F. (1934). *The struggle for existence* . Williams and Wilkins, Baltimore, MD.
- Gavrilets S. & Vose A. (2005). Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences* , 102, 18040-18045.
- Glossip D. & Losos J.B. (1997). Ecological correlates of number of subdigital lamellae in anoles. *Herpetologica* , 53, 192-199.
- Goodman B.A., Miles D.B. & Schwarzkopf L. (2008). Life on the rocks: habitat use drives morphological and performance evolution in lizards. *Ecology* , 89, 3462-3471.
- Grant P.R. (1999). *Ecology and evolution of Darwin's finches* . Princeton University Press, Princeton, New Jersey.
- Grant P.R. & Grant B.R. (2006). Evolution of character displacement in Darwin's finches. *Science* , 313, 224-226.
- Greer A.E. (1974). The generic relationships of the scincid lizard genus *Leiopisma* and its relatives. *Australian Journal of Zoology Supplementary Series* , 22, 1-67.
- Greer A.E. (1989). *The biology and evolution of Australian lizards* . Surrey Beatty and Sons, Chipping Norton, NSW.
- Greer A.E., Allison A. & Cogger H.G. (2005). Four new species of *Lobulia* (Lacertilia: Scincidae) from high altitude in New Guinea. *Herpetological Monographs* , 19, 153-179.
- Greer A.E. & Simon M. (1982). *Fojia bumui* , an unusual new genus and species of scincid lizard from New Guinea. *Journal of Herpetology* , 16, 131-139.
- Grömping U. (2006). Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software* , 17, 1-27.
- Hardin G. (1960). The competitive exclusion principle. *Science* , 131, 1292-1297.
- Heard S.B. & Hauser D.L. (1995). Key evolutionary innovations and their ecological mechanisms. *Historical Biology: An International Journal of Paleobiology* , 10, 151-173.
- Herrel A., Podos J., Huber S.K. & Hendry A.P. (2005). Evolution of bite force in Darwin's finches: a key role for head width. *Journal of Evolutionary Biology* , 18, 669-675.
- Hutchinson G.E. (1957). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* , 93, 145-159.
- Irschick D.J., Austin C.C., Petren K., Fisher R.N., Losos J.B. & Ellers O. (1996). A comparative analysis of clinging ability among pad-bearing lizards. *Biological Journal of the Linnean Society* , 59, 21-35.
- Irschick D.J., Carlisle E., Elstrott J., Ramos M., Buckley C., Vanhooydonck B., Meyers J.A.Y. & Herrel A. (2005). A comparison of habitat use, morphology, clinging performance and escape behaviour among two



divergent green anole lizard (*Anolis carolinensis*) populations. *Biological Journal of the Linnean Society* , 85, 223-234.

Jackson D.A. (1993). Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* , 74, 2204-2214.

Kisel Y. & Barraclough T.G. (2010). Speciation has a spatial scale that depends on gene flow. *The American Naturalist* , 175, 316-334.

Lack D. (1947). *Darwin's finches* . Cambridge University Press, Cambridge, UK.

Lavin P.A. & McPhail J.D. (1985). The evolution of freshwater diversity in the threespine stickleback (*Gasterosteus aculeatus*): site-specific differentiation of trophic morphology. *Canadian Journal of Zoology* , 63, 2632-2638.

Lavin P.A. & McPhail J.D. (1986). Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*). *Canadian Journal of Fisheries and Aquatic Sciences* , 43, 2455-2463.

Lerner H.R.L., Meyer M., James H.F., Hofreiter M. & Fleischer R.C. (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Current Biology* , 21, 1838-1844.

Losos J.B. (1990). Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* , 60, 369-388.

Losos J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* , 11, 995-1003.

Losos J.B. (2010). Adaptive radiation, ecological opportunity, and evolutionary determinism. *The American Naturalist* , 175, 623-639.

Losos J.B. & Ricklefs R.E. (2009). Adaptation and diversification on islands. *Nature* , 457, 830-836.

Lovette I.J., Bermingham E. & Ricklefs R.E. (2002). Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proceedings of the Royal Society of London B: Biological Sciences* , 269, 37-42.

MacArthur R.H. & Levins R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* , 101, 377-385.

Macrini T.E., Irschick D.J. & Losos J.B. (2003). Ecomorphological differences in toepad characteristics between mainland and island anoles. *Journal of Herpetology* , 37, 52-58.

Mahler D.L., Ingram T., Revell L.J. & Losos J.B. (2013). Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science* , 341, 292-295.

McGee M.D., Schluter D. & Wainwright P.C. (2013). Functional basis of ecological divergence in sympatric stickleback. *BMC Evolutionary Biology* , 13, 277.

McKinnon J.S. & Rundle H.D. (2002). Speciation in nature: the threespine stickleback model systems. *Trends in Ecology & Evolution* , 17, 480-488.

Meiri S. (2018). Traits of the lizards of the world: variation around a successful evolutionary design. *Global Ecology and Biogeography* , 27, 1168-1172.

Meiri S., Simberloff D. & Dayan T. (2011). Community-wide character displacement in the presence of clines: a test of Holarctic weasel guilds. *Journal of Animal Ecology* , 80, 824-834.

Melville J. & Swain R.O.Y. (2000). Evolutionary relationships between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scincidae: Lygosominae). *Biological Journal of the Linnean Society* , 70, 667-683.

Monasterio C., Salvador A., Iraeta P. & Díaz J.A. (2009). The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. *Journal of Biogeography* , 36, 1673-1684.

Oksanen J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E. & Wagner H. (2019). vegan: community ecology package. R package version 2.5-6. In. <https://CRAN.R-project.org/package=vegan>.

Ortega Z., Mencía A. & Pérez-Mellado V. (2016). The peak of thermoregulation effectiveness: thermal biology of the Pyrenean rock lizard, *Iberolacerta bonnali* (Squamata, Lacertidae). *Journal of Thermal Biology* , 56, 77-83.

Pianka E.R. (1969). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology* , 50, 1012-1030.

Pianka E.R. (1972). *r* and *K* selection or *b* and *d* selection? *The American Naturalist* , 106, 581-588.

Pianka E.R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences* , 71, 2141-2145.

Pinto G., Mahler D.L., Harmon L.J. & Losos J.B. (2008). Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proceedings of the Royal Society B: Biological Sciences* , 275, 2749-2757.

Pyron R.A. & Wiens J.J. (2013). Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. In: *Proceedings of the Royal Society B: Biological Sciences* .

R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rabosky D.L., Donnellan S.C., Talaba A.L. & Lovette I.J. (2007). Exceptional among-lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proceedings of the Royal Society of London B: Biological Sciences* , 274, 2915-2923.

Rainey P.B. & Travisano M. (1998). Adaptive radiation in a heterogeneous environment. *Nature* , 394, 69.

Reding D.M., Foster J.T., James H.F., Pratt H.D. & Fleischer R.C. (2008). Convergent evolution of 'creepers' in the Hawaiian honeycreeper radiation. *Biology Letters* , 5, 221-224.

Revell L.J. (2009). Size-correction and principal components for interspecific comparative studies. *Evolution* , 63, 3258-3268.

Rodriguez Z.B., Perkins S.L. & Austin C.C. (2018). Multiple origins of green blood in New Guinea lizards. *Science Advances* , 4, eaao5017.

Roll U., Feldman A., Novosolov M., Allison A., Bauer A., Bernard R., Bohm M., Chirio L., Collen B., Colli G.R., Dabul L., Das I., Doan T.M., Grismer L.L., Herrera F.C., Hoogmoed M.S., Itescu Y., Kraus F., LeBreton M., Lewin A., Martins M., Maza E., Meirte D., Nagy Z.T., Nogueira C., Pauwels O.S.A., Pincheira-Donoso D., Powney G.D., Sindaco R., Tallowin O., Torres-Caravajal O., Trape J.-F., Uetz P., Vidan E., Wagner P., Wang Y., Orme C.D.L., Grenyer R. & Meiri S. (2017). The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution* , 1, 1677-1682.

Ruber L. & Adams D.C. (2001). Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. *Journal of Evolutionary Biology* , 14, 325-332.

Ruber L., Verheyen E. & Meyer A. (1999). Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika. *Proceedings of the National Academy of Sciences* , 96, 10230-10235.

Sarmiento G. (1986). Ecological features of climate in high tropical mountains. In: *High altitude tropical biogeography* (eds. Vuilleumier F & Monasterio M). Oxford University Press Oxford, UK, pp. 11-45.

Schoener T.W. (1974). Resource partitioning in ecological communities. *Science* , 185, 27-39.

Schulte II J.A., Losos J.B., Cruz F.B. & Nunez H. (2004). The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae\*: Liolaemini). *Journal of Evolutionary Biology* , 17, 408-420.

Simberloff D. & Boecklen W. (1981). Santa Rosalia reconsidered: size ratios and competition. *Evolution* , 35, 1206-1228.

Skinner A. (2010). Rate heterogeneity, ancestral character state reconstruction, and the evolution of limb morphology in *Lerista* (Scincidae, Squamata). *Systematic Biology* , 59, 723-740.

Skinner A., Hugall A.F. & Hutchinson M.N. (2011). Lygosomine phylogeny and the origins of Australian scincid lizards. *Journal of Biogeography* , 38, 1044-1058.

Slatkin M. (1980). Ecological character displacement. *Ecology* , 61, 163-177.

Slavenko A., Feldman A., Allison A., Bauer A.M., Bohm M., Chirio L., Colli G.R., Das I., Doan T.M., LeBreton M., Martins M., Meirte D., Nagy Z.T., Nogueira C., Pauwels O.S.A., Pincheira-Donoso D., Roll U., Wagner P., Wang Y. & Meiri S. (2019). Global patterns of body size evolution in squamate reptiles are not driven by climate. *Global Ecology and Biogeography* , 28, 471-483.

Slavenko A., Tallowin O.J.S., Itescu Y., Raia P. & Meiri S. (2016). Late Quaternary reptile extinctions: size matters, insularity dominates. *Global Ecology and Biogeography* , 25, 1308-1320.

Slavenko A., Tamar K., Tallowin O.J.S., Allison A., Kraus F., Carranza S. & Meiri S. (2020). Cryptic diversity and non-adaptive radiation of montane New Guinea skinks (*Papuascincus* ; Scincidae). *Molecular Phylogenetics and Evolution* , 146, 106749.

Stuart Y.E. & Losos J.B. (2013). Ecological character displacement: glass half full or half empty? *Trends in Ecology & Evolution* , 28, 402-408.

Sturmbauer C. (1998). Explosive speciation in cichlid fishes of the African Great Lakes: a dynamic model of adaptive radiation. *Journal of Fish Biology* , 53, 18-36.

Tallowin O., Allison A., Algar A.C., Kraus F. & Meiri S. (2017). Papua New Guinea terrestrial-vertebrate richness: elevation matters most for all except reptiles. *Journal of Biogeography* , 44, 1734-1744.

Wagner C.E., Harmon L.J. & Seehausen O. (2012). Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* , 487, 366-369.

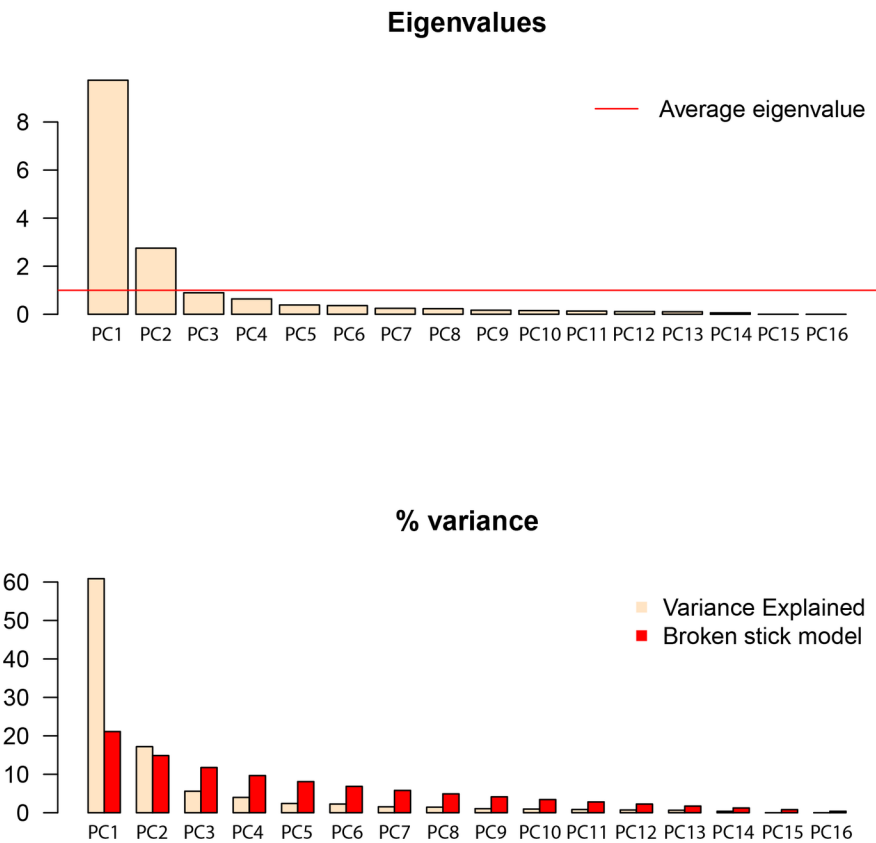
Wiens J.J. (2009). Estimating rates and patterns of morphological evolution from phylogenies: lessons in limb lability from Australian *Lerista* lizards. *Journal of Biology* , 8, 19.

Wiens J.J. & Graham C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* , 36, 519-539.

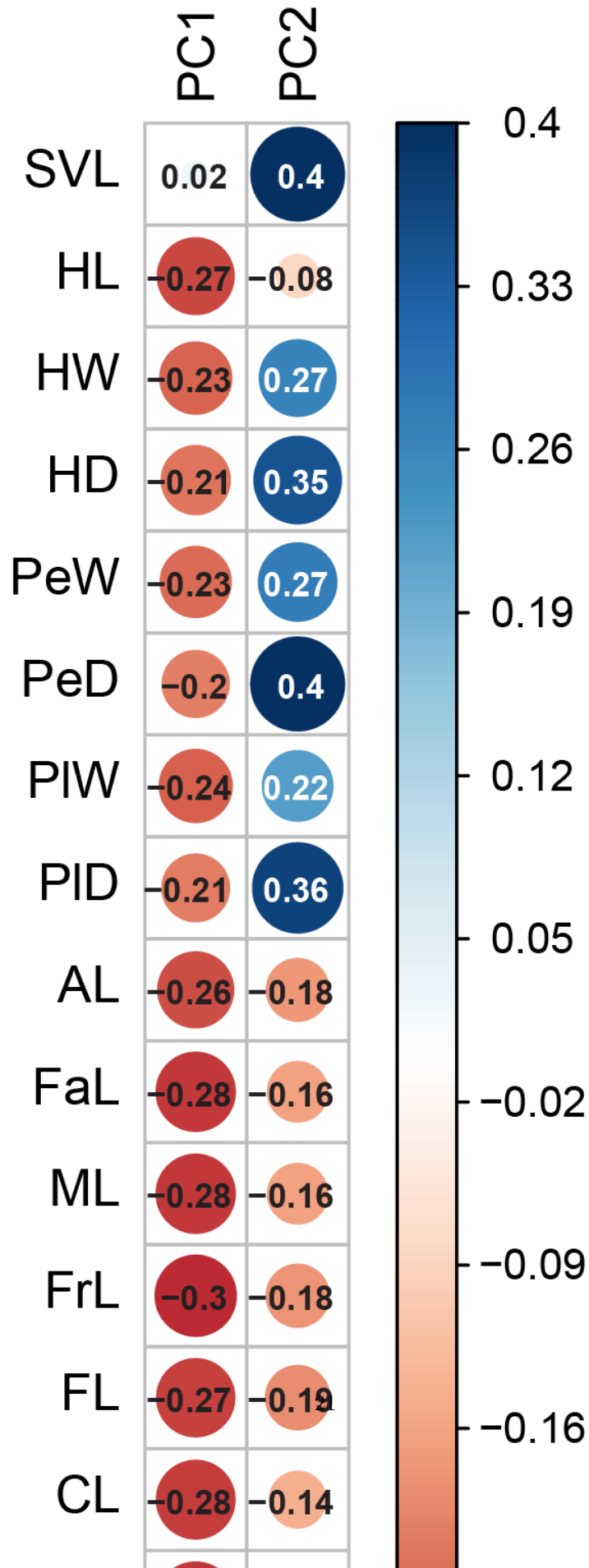
Zamora-Camacho F.J., Reguera S. & Moreno-Rueda G. (2014). Bergmann's Rule rules body size in an ectotherm: heat conservation in a lizard along a 2200-metre elevational gradient. *Journal of Evolutionary Biology* , 27, 2820-2828.

**Appendix S1.** All data and code required to run the analyses packaged as an R project.

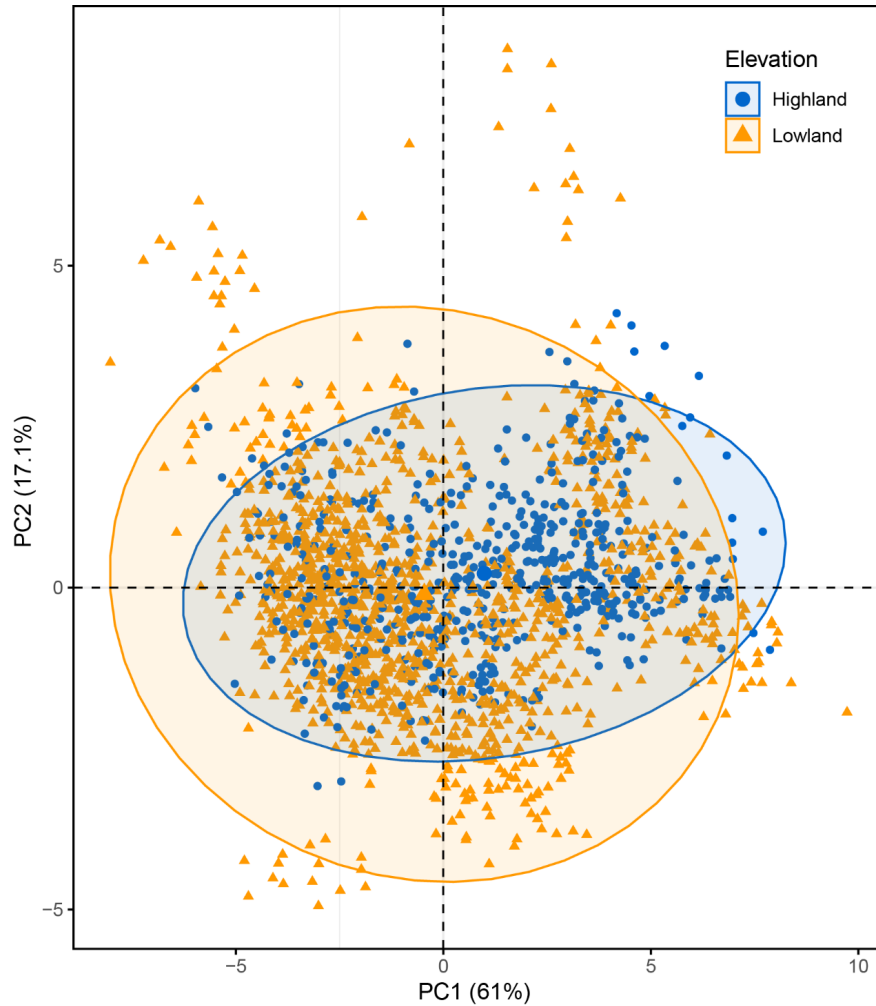
**Figure S1.** Results of a "broken stick" analysis indicating which PCs explain a statistically significant portion of variance. In the top panel, values above the red line (average eigenvalue) are PCs that explain a statistically significant portion of variance. In the bottom panel, the same PCs are the ones where the variance explained (yellow bars) is higher than the expectation under a "broken stick" model (red bars).



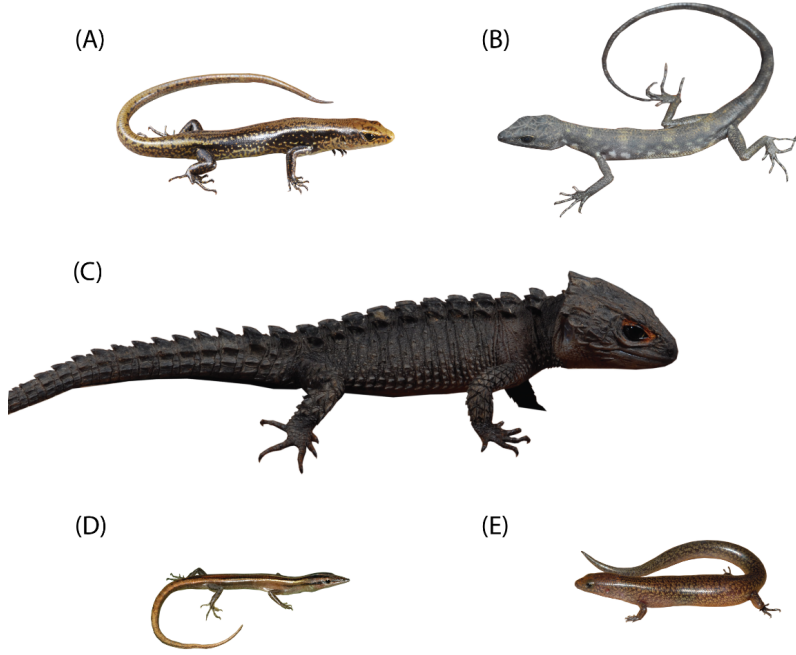
**Figure S2.** Variable loadings for each of the morphometric measurements on the two first PCs. Red colours are for negative loadings, and blue colours are for positive loadings. The hue and the size of the circle are correlated with the absolute value of the loading, such that higher loadings (in either direction) are represented by deeper colours and larger circles.

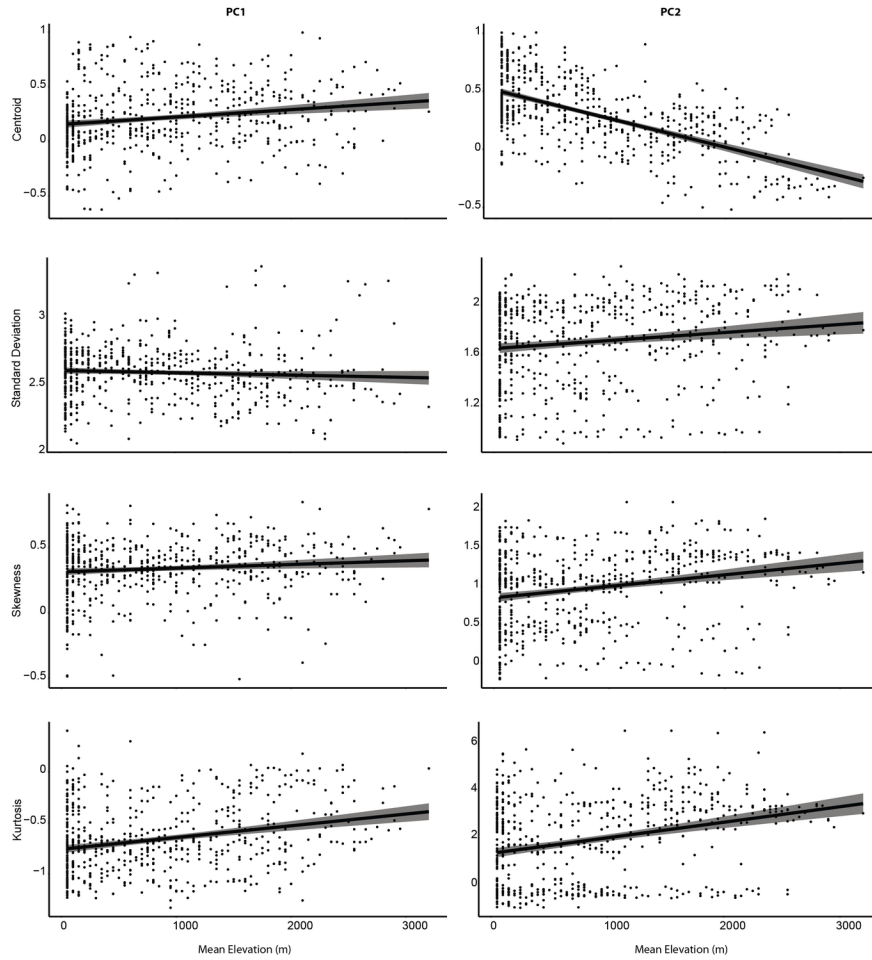


**Figure S3.** Morphospace of Papua New Guinea skinks (same loadings as Figure 2), with individuals coloured based on the elevational distribution of the species – blue circles for highland (> 1000 m) and teal triangles for lowland (< 1000 m). The ellipses encompass 95% of observations for each group.



**Figure S4.** Examples of some Papua New Guinea skinks and their various morphologies. (A) *Papuascincus stanleyanus* sensu lato; (B) *Fojia bumui* ; (C) *Tribolonotus gracilis* ; (D) *Lipinia longiceps* ; (E) *Sphenomorphus forbesi* .





**Figure S5.** Scatterplots showing regressions on mean elevation of (top to bottom) centroid, standard deviation, skewness and kurtosis per cell for PC1 (left column) and PC2 (right column).

**Table S1.** Results of  $t$ -tests comparing mean distances from and mean Jaccard overlap with each species within and outside its range. Written are the means and the  $p$  values of the  $t$ -tests, as well as the elevation of each species (highland:  $> 1000$  m; lowland:  $< 1000$  m). Significant  $p$  values ( $< 0.05$ ) are marked bold. For both distance and Jaccard similarity, the larger of the two values (either within or outside the focal species' range) is marked bold. Comparisons that fit the predictions of the competitive exclusion hypothesis, *i.e.* larger distances within focal species' ranges or smaller Jaccard similarity within focal species' ranges, are shaded grey.

Species	Mean Distance Within Range	Mean Distance Outside Range	$p$ value for Distance	M
<i>Carlia aenigma</i>	3.82	<b>3.86</b>	0.42	0
<i>Carlia aramia</i>	3.51	<b>3.53</b>	0.62	0
<i>Carlia bicarinata</i>	<b>3.42</b>	3.13	<b>0.001</b>	0
<i>Carlia eohen</i>	3.78	<b>3.93</b>	<b>0.03</b>	0
<i>Carlia luctuosa</i>	<b>5.16</b>	4.96	<b>0.045</b>	0
<i>Carlia mysi</i>	<b>3.404</b>	3.401	0.89	0
<i>Carlia pulla</i>	<b>3.9</b>	3.67	<b>&lt; 0.001</b>	0
<i>Cryptoblepharus novaeguineae</i>	<b>4.43</b>	4.24	<b>&lt; 0.001</b>	0



Species	Mean Distance Within Range	Mean Distance Outside Range	<i>p</i> value for Distance	N
<i>Cryptoblepharus virgatus</i>	<b>4.78</b>	4.47	< <b>0.001</b>	0
<i>Cryptoblepharus yulensis</i>	<b>4.34</b>	4.23	<b>0.02</b>	0
<i>Ctenotus spaldingi</i>	<b>3.73</b>	3.36	< <b>0.001</b>	0
<i>Emoia aenea</i>	3.03	<b>3.33</b>	< <b>0.001</b>	0
<i>Emoia atrocostata</i>	<b>2.9</b>	2.75	< <b>0.001</b>	0
<i>Emoia aurulenta</i>	3.03	<b>3.22</b>	< <b>0.001</b>	0
<i>Emoia battersbyi</i>	<b>3.98</b>	3.9	<b>0.02</b>	0
<i>Emoia brongersmai</i>	4.05	<b>4.06</b>	0.97	0
<i>Emoia caeruleocauda</i>	<b>2.98</b>	2.8	< <b>0.001</b>	0
<i>Emoia guttata</i>	<b>3.93</b>	3.84	0.38	0
<i>Emoia jakati</i>	2.97	<b>2.99</b>	0.45	0
<i>Emoia kordoana</i>	<b>3.25</b>	2.96	< <b>0.001</b>	0
<i>Emoia longicauda</i>	<b>2.88</b>	2.65	< <b>0.001</b>	0
<i>Emoia loveridgei</i>	2.66	<b>2.71</b>	0.06	0
<i>Emoia maxima</i>	<b>3.9</b>	3.61	< <b>0.001</b>	0
<i>Emoia montana</i>	4.09	<b>4.15</b>	0.23	0
<i>Emoia obscura</i>	2.85	<b>2.89</b>	0.09	0
<i>Emoia oribata</i>	3.95	<b>4.03</b>	0.38	0
<i>Emoia pallidiceps</i>	<b>2.97</b>	2.94	0.52	0
<i>Emoia physicae</i>	<b>3.92</b>	3.82	<b>0.01</b>	0
<i>Emoia physicina</i>	<b>3.34</b>	3.22	< <b>0.001</b>	0
<i>Emoia popei</i>	<b>3.45</b>	3.32	< <b>0.001</b>	0
<i>Emoia pseudopallidiceps</i>	<b>3.33</b>	3.08	< <b>0.001</b>	0
<i>Emoia submetallica</i>	<b>2.96</b>	2.83	<b>0.02</b>	0
<i>Emoia tropidolepis</i>	4.23	<b>4.36</b>	<b>0.01</b>	0
<i>Emoia veracunda</i>	<b>2.9</b>	2.83	<b>0.004</b>	0
<i>Eugongylus rufescens</i>	<b>5.01</b>	3.79	< <b>0.001</b>	0
<i>Fojia bumui</i>	5.63	<b>5.88</b>	< <b>0.001</b>	1
<i>Glaphyromorphus crassicaudus</i>	<b>9.84</b>	9.64	< <b>0.001</b>	4
<i>Glaphyromorphus nigricaudis</i>	<b>3.74</b>	3.47	< <b>0.001</b>	0
<i>Lamprolepis smaragdina</i>	<b>3.91</b>	3.82	< <b>0.001</b>	0
<i>Lipinia longiceps</i>	5.01	<b>5.23</b>	< <b>0.001</b>	0
<i>Lipinia noctua</i>	<b>3.8</b>	3.58	< <b>0.001</b>	0
<i>Lipinia pulchra</i>	<b>4.23</b>	4.07	< <b>0.001</b>	0
<i>Lobulia brongersmai</i>	3.86	<b>3.67</b>	< <b>0.001</b>	0
<i>Lobulia elegans</i>	<b>3.42</b>	3.26	< <b>0.001</b>	0
<i>Lobulia subalpina</i>	2.46	<b>2.72</b>	< <b>0.001</b>	0
<i>Lygisaurus curtus</i>	2.74	<b>2.9</b>	< <b>0.001</b>	0
<i>Lygisaurus macfarlani</i>	<b>3.72</b>	3.32	< <b>0.001</b>	0
<i>Papuascincus morokanus</i>	2.78	<b>3.17</b>	< <b>0.001</b>	0
<i>Papuascincus stanleyanus</i>	2.79	<b>3.07</b>	< <b>0.001</b>	0
<i>Prasinochaema flavipes</i>	2.77	<b>3.11</b>	< <b>0.001</b>	0
<i>Prasinochaema prehensicauda</i>	3.46	<b>4.18</b>	< <b>0.001</b>	0
<i>Prasinochaema semoni</i>	<b>3.09</b>	3.04	<b>0.04</b>	0
<i>Prasinochaema virens</i>	<b>3.33</b>	3.24	< <b>0.001</b>	0
<i>Sphenomorphus aruensis</i>	<b>3.51</b>	3.08	< <b>0.001</b>	0
<i>Sphenomorphus brunneus</i>	4.36	<b>5</b>	< <b>0.001</b>	0
<i>Sphenomorphus cinereus</i>	3.31	<b>3.71</b>	< <b>0.001</b>	0
<i>Sphenomorphus darlingtoni</i>	3.2	<b>3.74</b>	< <b>0.001</b>	0
<i>Sphenomorphus derooyae</i>	<b>4.09</b>	3.92	< <b>0.001</b>	0

Species	Mean Distance Within Range	Mean Distance Outside Range	<i>p</i> value for Distance	<i>R</i> <sup>2</sup>
<i>Sphenomorphus forbesi</i>	6.23	<b>6.67</b>	<b>0.004</b>	0
<i>Sphenomorphus fragilis</i>	<b>7.11</b>	7.04	0.35	0
<i>Sphenomorphus granulatus</i>	2.53	<b>2.7</b>	< <b>0.001</b>	0
<i>Sphenomorphus jobiensis</i>	<b>3.68</b>	3.62	<b>0.003</b>	0
<i>Sphenomorphus latifasciatus</i>	<b>6.41</b>	6.03	< <b>0.001</b>	2
<i>Sphenomorphus leptofasciatus</i>	3.43	<b>4.2</b>	< <b>0.001</b>	0
<i>Sphenomorphus microtympanus</i>	<b>7.61</b>	7.74	0.28	0
<i>Sphenomorphus minutus</i>	<b>4</b>	3.78	< <b>0.001</b>	0
<i>Sphenomorphus neuhaussi</i>	<b>6.64</b>	6.32	< <b>0.001</b>	0
<i>Sphenomorphus nigriventris</i>	6.15	<b>6.41</b>	<b>0.007</b>	0
<i>Sphenomorphus nigrolineatus</i>	<b>5.09</b>	5.08	0.87	0
<i>Sphenomorphus oligolepis</i>	5.64	<b>5.8</b>	<b>0.01</b>	0
<i>Sphenomorphus papuae</i>	3.04	<b>3.21</b>	< <b>0.001</b>	0
<i>Sphenomorphus pratti</i>	<b>5.47</b>	5.26	< <b>0.001</b>	0
<i>Sphenomorphus schultzei</i>	4.17	<b>4.63</b>	< <b>0.001</b>	0
<i>Sphenomorphus simus</i>	<b>4.27</b>	4.22	0.2	0
<i>Sphenomorphus solomonis</i>	<b>5.42</b>	5.09	< <b>0.001</b>	0
<i>Sphenomorphus undulatus</i>	<b>3.68</b>	3.31	< <b>0.001</b>	0
<i>Tiliqua gigas</i>	<b>7.1</b>	6.84	< <b>0.001</b>	4
<i>Tribolonotus gracilis</i>	<b>7.83</b>	7.8	0.15	5
<i>Tribolonotus novaeguineae</i>	7.32	<b>7.35</b>	0.1	0

**Table S2.** Model summaries of linear regressions of parameters of distributions of PC scores per cell against mean elevation (m). The parameters are the centroid, standard deviation, skewness and kurtosis of the distributions. Listed are the standardized regression coefficients, *p* values of the regression, and *R*<sup>2</sup> of the model.

<i>R</i> <sup>2</sup>	<i>p</i>	Standardized Coefficient	Model
0.03	<0.001	0.05	PC1 Centroid
0.004	0.1	-0.01	PC1 Standard Deviation
0.01	0.01	0.02	PC1 Skewness
0.07	<0.001	0.09	PC1 Kurtosis
0.39	<0.001	-0.19	PC2 Centroid
0.02	<0.001	0.05	PC2 Standard Deviation
0.06	<0.001	0.12	PC2 Skewness
0.08	<0.001	0.51	PC2 Kurtosis