

Biogeographic affiliation and centers of richness as predictors of elevational range-size patterns for Malesian flora

Melissa Whitman¹ and Sabrina E. Russo¹

¹University of Nebraska-Lincoln

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Abstract

Our goal was to interrogate Janzen’s idea that “mountain passes are higher in the tropics” by investigating putative ecological and biogeographic drivers of patterns of elevational range-sizes among equatorial plant families. We used herbarium records for sixty species-rich plant families, representing a total of 18535 species, to estimate distributions over a 4500 m elevational gradient. For each family, we estimated the change in average range-sizes with increasing elevation (i.e. Rapoport’s rule, abbreviated as ERR) and quantified 15 metrics of familial richness distribution, evolutionary age, and biogeographic affiliation. We visualized covariation across families using phylogenetic principal components analysis (pPCA), with color illustrating endemism. We then evaluated how family-level ERR slopes correlated with each metric individually, and the first two pPCA components, using phylogenetic independent contrasts. Families with greater Sundaland endemism, or richness that was restricted to tropical lowland forests, had positive ERR slopes. Families with stronger Sahul affiliation, or montane centered richness, had shallower, neutral, or negative ERR slopes. Families with Wallacea affiliation, broader latitudinal or elevational distributions, cosmopolitanism, or older evolutionary age had mixed results. Our findings support Janzen’s hypothesis that “mountain passes are higher in the tropics.” If long term climate stability over millions of years promotes habitat specialization, then among taxa with long-term tropical affiliations, we would expect smaller range-sizes within lowland forests, with range-size expansion towards higher elevations, expressed as a positive ERR slope. Conversely, variation in growing conditions should promote larger, relatively consistent, range-sizes expressed as a neutral ERR slope. Our results support this corollary because of the dichotomy of ERR slopes observed in relation to elevational and historical biogeographic positioning, which may be an indicator of vulnerability of these plant groups to contemporary climate change.

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Introduction

Macroscale changes in landscapes, such as the creation of islands or movement of continents, as well as the stability of habitats and climate over various intervals of time, produce the template upon which assembly processes play out (Currie and Paquin 1987, Brown et al. 1996, Ricklefs 2004, Mittelbach et al. 2007, Morley 2018). Investigation of the drivers of present day species' distributions must therefore account for both contemporary and historical processes, especially because climate change is affecting the distributions of diversity on earth, including along elevational gradients (Rahbek et al. 2019, Feeley et al. 2020). However, evaluating climate change's effects on species' elevational distributions requires quantification of underlying factors that determine how richness is distributed or why it is restricted, with consideration of biogeographic history (McCain and Grytnes 2010, Rehm and Feeley 2015, Pálinkás 2018, Freeman et al. 2018).

The distribution of diversity across a landscape is a function of range-sizes of the species present (Rapoport 1982). Species' elevational distributions often exhibit asymmetry of average range-sizes for communities at either end of the gradient (e.g. smaller elevational range-sizes at lowland habitats as compared to montane areas), which is commonly referred to as Rapoport's rule (Rapoport 1982, Stevens 1992) or abbreviated as ERR (Zhou et al. 2019). Variation in range-sizes across environmental gradients has been attributed to extrinsic factors such as climate and paleoclimate, habitat stability, geographic area or landmass positioning, and metrics of species richness (Morueta-Holme et al. 2013, Sheth et al. 2020, Sundaram and Leslie 2021, Guo et al. 2022), as well as intrinsic factors such as species' response to competition, dispersal ability, life-history strategies, edaphic specialization, and growth forms (Morin and Lechowicz 2013, Grossenbacher et al. 2015, Xu et al. 2018, Saupe et al. 2019, Whitman et al. 2021, Freeman et al. 2022). Stochastic processes or geometric constraints add complexity when differentiating biological versus non-biological causes of observed range-size patterns (Colwell and Hurtt 1994, Lyons and Willig 1997, Šizling et al. 2009). However, despite the influence of historical factors on diversity, relatively few studies have examined variation in ERR slopes with respect to higher-level taxonomy or biogeography.

Among plants, a study in Nepal found stronger ERR support for species with tropical compared to temperate origins, especially within sections of the gradient without natural barriers that can limit range-size potential (Feng et al. 2016). Within the tropics, a study on Mt Kenya found that variation in richness and rangesizes was attributed to rates of endemism and growth form (Zhou et al. 2019). A study on Mt. Kinabalu reinforced the complexity of species' distributions on equatorial mountains, finding that stress-tolerant species had larger and relatively consistent range-sizes, whereas most tropical species had smaller range-sizes with pronounced variation in ERR slopes that coincided with vegetation zone boundaries (Whitman et al. 2021). Tests of macroecological hypotheses are most robust when there is sufficient replication of analyses, often encompassing different geographic areas or taxonomic groups (Ruggiero and Wrenkraud 2007, Hawkins et al. 2011, McCain and Bracy Knight 2013, Sheth et al. 2020, Guo et al. 2022). Thus, equatorial habitats with high biodiversity offer a unique opportunity to test drivers of species range-sizes.

The goal of this study was to quantify variation in elevational range-sizes and distributions of major Malesian plant families, and to investigate ecological and biogeographical drivers of these patterns. Malesia is a biodiversity hotspot that encompasses a 2,000,000 km² area and collectively represents the largest archipelago on Earth, straddling the equator and spanning from the Malay Peninsula in the west to New Guinea in the east (Myers et al. 2000). Malesia includes a vast elevational gradient with mountain summits that are subject to freezing events (Hope 1976). Notable Malesian mountains include Mt. Kinabalu (4,095 m a.s.l.), Mt. Wilhelm (4,509 m a.s.l.), and Puncak Jaya (4,884 m a.s.l.). Surprisingly little research on ERR has been conducted within Malesia, except for localized studies (Whitman et al. 2021). There is growing evidence that equatorial mountains represent a unique environment type, with distinct richness and altitudinal zonation

patterns governed by more than just temperature (Ashton et al. 2022). For these reasons, Malesia offers an exceptional study system to investigate potential correlates of variation in ERR slopes.

Delineation of biogeographic boundaries for plants is a point of ongoing investigation (van Welzen et al. 2011, Webb and Ree 2012, Kooyman et al. 2019, Joyce et al. 2021). Biogeographic boundaries within Malesia are often based on Wallace’s line, named after Alfred E. Wallace and his observations of islands with highly dissimilar terrestrial vertebrate composition (Richardson et al. 2012). However for plants, Malesia can be divided into three sections (i.e. Sundaland, Wallacea, and Sahul) in reference to geological history and major waterways (Richardson et al. 2012) as well as consideration of differences in species’ response to environmental characteristics (van Welzen et al. 2011).

Millions of years ago (Mya), major landmasses of Malesia were positioned farther apart as compared to current day orientations (Hall 1998, Morley 2018). During the Eocene (~ 49 – 45 Mya), Sundaland and portions of Wallacea (mainly the Philippines) straddled the equator, whereas Sahul (New Guinea) was partially submerged and positioned ~20 degrees southwards in latitude (Hall 1998, Zhang et al. 2022). During this time period the Indian Plate collided with Asia, changing regional patterns of sediment flow and climate within SE Asia as well as introducing Gondwanan flora to the western portion of Malesia (Hall 1998, Morley 2018). The Australian shelf, which Sahul represents the leading edge of, broke apart from Antarctica and began drifting northwards and upwards (Hall 1998). During the Miocene (~ 15 Mya) the mountains of Borneo became wider and higher and the adjacent Philippine Sea Plate began rotating closer to mainland Asia, with volcanic activity creating new islands (Hall 1998). Sahul began rising higher above sea-level, while simultaneously increasing the area of lowland habitats. The Pliocene (~ 5 Mya) was marked by the collision of Sundaland and Australian plates, with landforms positioned in a similar orientation as today (Hall 1998).

Plant families of Malesia have established across the archipelago at different intervals of time based on a complex history of speciation, local extinctions, and migration (Webb and Ree 2012, Richardson et al. 2012, Ashton 2014, Kooyman et al. 2019, Xia et al. 2022), with most families originating elsewhere (Morley 2018). Plant clades of Sundaland have historically had tropical association, with greater interchange with the mainland Indochina (Kooyman et al. 2019, Zhang et al. 2022). Conversely, plant clades positioned eastwards on the Sahul continental shelf have greater Australasian associations, especially for montane flora specific to mountain ranges that have remained above sea-level for extended periods of time (Morley 2018, Brambach et al. 2020). Wallacea is centrally located, likely mediating a greater interchange with neighboring areas (Ashton 2014), and is comprised of many smaller, younger, or recently uplifted islands with relatively shorter mountains. The oldest Gondwanan clades can occur on both western and eastern sides of Malesia (Hall 1998, Richardson et al. 2012), as can taxa with long-distance or stochastic seed dispersal abilities (Webb and Ree 2012, Baker and Couvreur 2012).

Present day species’ distributions within Malesia are heavily influenced by the last 1-15 million years of tectonic events (Hall 1998, Ashton 2014, Morley 2018, Zhang et al. 2022). The recent interchange of species (< 5 Mya) is facilitated by landmasses that are positioned closer together and the emergence of islands which act as stepping-stones for range expansion (Webb and Ree 2012, Ashton 2014). Volcanos and mountaintops further act as “sky islands” to facilitate speciation and the interchange of montane flora restricted to cooler conditions (Webb and Ree 2012, Culmsee and Leuschner 2013, Morley 2018). Land bridges, which are ephemeral under changing sea-levels, act as pathways for land-animal dispersed species (Ashton 2014, Morley 2018). Climate stability further promotes species interchange, with asymmetrical migrations in favor of tropical Asian routes as compared to Australian pathways (Ashton 2014, Zhang et al. 2022). Variation in regional conditions, such as seasonally dry periods, coincided with glacial periods before widespread establishment of perhumid conditions towards the end of the Oligocene (Morley 2018). A lingering unknown is whether the contemporary species interchange may homogenize macroecological range-size patterns (e.g. Rapoport’s rule) between biogeographic areas, or if older artifacts of geographic separation and paleoclimatic conditions continue to shape species distributions.

In order to investigate potential mechanisms underlying variation in plant elevational range-sizes, we used a database of herbarium records for 60 of the most species-rich plant families in Malesia (representing a total

of 1799 genera and 18535 species) to estimate species occurrence across a 4500 m elevational gradient and by biogeographic regions. For each family, we estimated the change in average elevational range-sizes with increasing elevation (ERR slope). We evaluated the correlation between family-level ERR slopes and 15 metrics that reflect the ecology, evolution, and biogeography of each family, including richness; evolutionary age; latitudinal or elevational extent; biogeographical distribution with respect to Sundaland, Sahul, and Wallacea; degree of endemism versus cosmopolitanism; and inferred habitat specialization versus generalization.

Our predictions are rooted in the concept that “mountain passes are higher in the tropics” (Janzen 1967). When applied to determinants of species’ elevational range-sizes (Stevens 1992), this statement means that a greater shift in species’ ecological niche space is required to occupy each incremental increase in elevation. Janzen’s statement rests on at least two assumptions. First, evolutionary adaptations to reduced environmental variation promotes specialization and a reduction of species’ physiological tolerances, as well as an increase in interspecific biotic competition that leads to narrower niches, both of which would be associated with smaller elevational range-sizes. Second, evolutionary adaptations to variation in growing conditions, from factors such as higher diurnal temperature fluctuations or seasonality, would result in larger range-sizes, similar to the climate variability hypothesis (Dobzhansky 1950).

As applied to families that evolved within biogeographic regions with longer-term climate stability, based on proximity to the equator over millions of years, we would predict more positive ERR slopes. However, for taxa on landmasses that moved towards the equator, or that were newly created or uplifted, we predicted weakly positive, or neutral, ERR slopes, with the same prediction for evolutionarily younger families, recent colonizers, or those with montane or temperate origins. We anticipated that the way richness is spatially distributed would also affect these predictions. For families with more restricted distributions (e.g., narrower familial extent; concentrated centers of richness; higher endemism; adjacency to physical boundaries such as sea-level) we predicted steeper positive ERR slopes based on a combination of ecological factors and geometric constraints. For a subset of communities nearest mountain summits, we would predict negative ERR slopes. For widespread families with fewer barriers for expansion (e.g., cosmopolitanism; dispersed richness, broad familial extent) we predicted shallower or neutral ERR slopes.

Materials and methods

Query of herbarium records for elevation and location of species-rich plant families

For herbarium data, we queried the Global Biodiversity Information Facility; Naturalis Biodiversity Center; and a Mt Kinabalu regional dataset. We defined species-rich families as ≥ 75 species with two or more herbarium records, making an exception for Podocarpaceae as the sole Gymnosperm. We defined species occurrence by biogeographic regions within Malesia, based on van Welzen *et al.*, 2011, with Sundaland representing Sumatra, Malay Peninsula, and Borneo; Wallacea as Java, Sulawesi, Maluku, the Lesser Sunda Isles, and the Philippines; and Sahul as New Guinea, excluding the Bismarck Archipelago or Australia. Alternate biogeographic delineations were also examined (e.g. affiliation for Java, Palawan, Bali), producing comparable results (see Supporting information).

Methods to calculate how range-size averages change with elevation (ERR)

For each species we calculated the average point of elevational occurrence (referred to as midpoint) and range-size, defined as maximum minus minimum elevation. To quantify how average range-sizes change with increasing elevation (ERR) we used a novel approach based on quantile binning (rather than even increments), which better reflects non-normal data distributions or variation in sampling efforts. We assessed four other ERR methods (Stevens 1992, Rohde *et al.* 1993, Vetaas and Grytnes 2002, Feng *et al.* 2016) and found comparable results, thus we selected the quantile binning method because it produced the most linear relationships, less skewed by outliers (see Supporting information). Species’ midpoint values were divided equally into twenty bins (ventiles), each bin representing 5% of each families’ Malesian richness. We then interpolated species’ presence between all points of observation (meaning potential presence within multiple bins) and distribution overlap to estimate species-richness curves, followed by calculating within-bin

richness and average range-sizes. For each family, we used ordinary least squares regression (OLS) to test and quantify ERR slopes which then were used as the response variable for across-family analyses.

Metrics of family-level species richness, evolutionary age, and spatial distributions

We estimated metrics of the distribution of richness, evolutionary age, and boundaries of occurrence on elevational and latitudinal gradients at the family level (see “predictor” and “symbol” column in Table 1). Our metrics are as follows: 1) *Malesian richness* ; is defined as the total number of species (gamma diversity or γ) of a given family occurring within Malesia, also referred to as the union (rather than intersection) of three biogeographic regions ($A \cup B \cup C$). Note, *Malesian richness* may have fewer species than expected from literature because of our [?] 2 record criteria, thus excluding rare species. 2) *Localized richness ratio* ; is a proportional metric calculated as richness within a single elevation bin (α) divided by *Malesian richness* (γ); comparable to beta-diversity. 3) *Elevation with peak in richness* ; is based on distribution curves for each family (see Supporting information) using polynomial regression to predict richness in one meter increments; used to infer the habitat optimum or point of origin. Metrics 4), 5), and 6) are the elevational boundaries of familial distribution. 4) *Familial elevational extent* ; was calculated as the maximum upper-most limit minus the minimum lower-most limit of any species within a given family; used to infer familial expansion across habitat types. 5) *Average lower elevation limit* and 6) *Average higher elevation limit* were calculated separately using species’ average lower or upper most elevation of occurrence. We regarded *average lower elevation limits* as an indicator of biotic competition based boundaries, whereas *average upper elevation limits* as indicative of tolerance to abiotic stressors. Metrics 7) *evolutionary age* and 8) *latitudinal extent* , are based on data by Hawkins *et al.* , 2011.

Species distributions across biogeographical regions of Malesia

For the second series of predictor variables, we quantified species’ distribution within and across the three bioregions of Malesia using a Venn diagram approach (see “predictor” and “symbol” column Table 1, Fig. 1; see Supporting information). For each family we estimated: 1) *regional endemism*, which we defined as species occurring strictly within one biogeographic region ($A \cap (B \cap C)'$), and 2) *regional overlap* as being a non-exclusive term for species within a given region, expressed as (A), (B) or (C), with any given species having the potential to also occur within neighboring regions. Lastly, 3) A metric of *cosmopolitanism*, which we defined as species with distributions intersecting all three bioregions ($A \cap B \cap C$), which is the number of species shared by multiple regions (zeta-diversity or ζ). For each biogeographical metric, we divided the number of species matching said criteria by familial *Malesian richness* ($A \cup B \cup C$), being union of all bioregions, resulting in proportional values ranging from 0 - 1. We translated these metrics into colors, creating a unique CMYK hex code for each family, which we used for all figures. Color saturation was determined by the endemism metric (magenta – Sundaland; yellow – Wallacea; cyan - Sahul) and cosmopolitanism (black), adjusted to 25% transparency.

Analyses across plant families

First, we used phylogenetic principal components analysis (pPCA) with scaling to ordinate and derive two orthogonal variables, accounting for the most variation among them (Fig. 2, see Supporting information). We then fit linear models of ERR slopes as a function of each variable (Table 1), as well as the first two principal components at the family level, using phylogenetic independent contrasts (PIC). For across-family analyses, all variables were transformed into z-scores to facilitate comparisons of factors at different scales (reported in Table 1), meaning results remain consistent (adj. R^2 , F -statistic, and P -values), but the intercept becomes zero and slopes of said relationships can be described as positive (slope of 1), negative (slope of -1), or neutral (0). Note, we did not use scaling for reporting individual family ERR slopes, or for visual representation of scatterplot axes. For extended methods, see Supporting information.

Results

Variation in ERR slopes and metrics of richness and distribution among families

When grouping all species together, richness was highest within lowland tropical forests and average range-sizes increased with elevation (i.e. in support of Rapoport’s rule), with differences emerging when comparing individual families. Average elevational range-sizes significantly corresponded with elevation (ERR) for 56 out of the 60 plant families examined (see Supporting information). Observed ERR slope values (without scaling) for individual families were mostly positive, averaging 0.28 across families, but ranged from negative (- 0.13 Asteraceae) to positive (0.62 Celastraceae). Among families, there was considerable variation in the predictive metrics explored (see Supporting information). For *Malesian richness*, the number of species ranged from 66 (Podocarpaceae) to 3015 (Orchidaceae), with differences in the skew and shape of richness distribution curves across the elevational gradient.

Families with a high *localized richness ratio* were mostly affiliated with lowland tropical forests, with the exception of Fagaceae and Podocarpaceae. Low *localized richness ratio* families included Begoniaceae and Gesneriaceae. Values for the metric *elevational extent* were comparable to those for the *localized richness ratio* in that families with restricted distributions tended to have concentrated richness, but differed in that *elevational extent* identified families which span the majority of the elevation gradient, such as Asteraceae with an *elevational extent* of ~ 4500 m. Families with *peaks in richness* near sea-level included trees or shrubs (Anacardiaceae, Burseraceae, Calophyllaceae, Dipterocarpaceae, Ebenaceae, Myristicaceae, Myrtaceae, Sapindaceae), palms (Arecaceae), and mixed growth forms (Acanthaceae, Apocynaceae, Celastraceae, Euphorbiaceae, Fabaceae, Malvaceae, Pandanaceae, Polygalaceae, Sapotaceae). Families with peaks in richness towards the middle of the elevational gradient, transitioning from premontane to lower montane cloud forests, included Fagaceae, Cyatheaceae, and Orchidaceae. Families with the highest elevation *peaks in richness*, often in habitats ranging from upper montane cloud forests to subalpine thickets, included woody growth forms (Ericaceae, Podocarpaceae, Rosaceae), ferns (Polypodiaceae, Aspleniaceae) and mosses, all of which also had the highest (*lower or upper*) *average elevational limits*.

Each family had at least one endemic species per biogeographical region, but endemism proportions differed among families and locations (Figs. 1; see Supporting information). Families with the highest *Sundaland endemism* ($> 50\%$ of species) included Dipterocarpaceae, Fagaceae, Polygalaceae, Calophyllaceae, Annonaceae, Ebenaceae, Anacardiaceae, Gesneriaceae, Zingiberaceae, and Arecaceae. Using the same threshold for *Sahul endemism*, notable families included Ericaceae and Solanaceae. Wallacea had fewer endemics, with maximum endemism values of 26.5% for Acanthaceae. Higher *cosmopolitanism* values were noted for ferns (Hymenophyllaceae), Podocarpaceae, and taxonomic groups not included in cross-family analyses, such as Bryophytes, grasses (Poaceae) and sedges (Cyperaceae).

For the pPCA analysis using a dozen factors (we excluded metric of overlap), we found that the first two loadings explained 62% of the data variance (Table 1, Fig. 2, see Supporting information), with pPC1 accounting for $\sim 43\%$ and PC2 $\sim 19\%$. Lower pPC1 scores were associated with greater *Sundaland endemism* (represented by magenta), or high *localized richness ratio* values. At the other end of the spectrum included montane affiliated families, based on locations of richness peaks, the lower or upper limits of occurrence, and *Sahul endemism* (represented by cyan). When the components were plotted (Fig. 2), this created a spectrum of colors across the horizontal axis, with Dipterocarpaceae and Anacardiaceae having the lowest pPC1 scores and Ericaceae and Asteraceae having the highest pPC1 values. Positive pPC2 values were ambiguous (associated with age, richness, or *Wallacea endemism*) with less distinction between families. However, negative pPC2 values included metrics of *cosmopolitanism* and broad *latitudinal extent*. Families with strongly negative pPC2 values included Fabaceae, Convolvulaceae, Lamiaceae, Vitaceae, and Moraceae, which are families noted for global agriculture use, including sweet potato, legumes, grapes, breadfruit, and aromatics.

As a post-hoc investigation of the interplay between factors we examined correlations between *Sundaland endemism* and *latitudinal extent* ($r = - 0.44$, $P < 0.0017$), with the negative relationship reinforcing species’ tropical affiliation within this biogeographic region. In contrast, we found positive correlations between *latitudinal extent* and *Wallacea overlap* ($r = 0.54$, $P < 0.001$), as well as *cosmopolitanism* ($r = 0.57$, $P < 0.001$), with the latter two factors also correlated to each other ($r = 0.83$, $P < 0.001$) suggesting a broad

tropical-subtropical species interchange within this centrally positioned biogeographical region. *Latitudinal extent* and *familial elevational extent* also had a positive relationship ($r = 0.49$, $P < 0.001$; see Supporting information), reinforcing our prediction that larger range-sizes are indicative of tolerance to variations habitat conditions.

Across-family analyses of ERR Slopes with respect to ecological, evolutionary, and biogeographic correlates

For across-family analyses using phylogenetic independent contrasts (PIC), we found that *Malesian richness* was not associated with ERR slopes (Table 1). However, clustering of richness, based on the *localized richness ratio*, was positively associated with ERR slopes (Table 1, Fig. 3a). Families with high *localized richness ratio* metrics and steeply positive ERR slopes included Dipterocarpaceae (ratio of 0.82 and ERR slope of 0.53) and Anacardiaceae (ratio of 0.84 and slope of 0.45). In contrast, families with *low localized richness ratio* metrics and weaker positive ERR slopes included Begoniaceae (ratio of 0.34 and slope of 0.24) and Gesneriaceae (ratio of 0.35 and slope of 0.14). Similarly, the *elevation with peak in richness* had a negative relationship with ERR slopes, with higher ERR slopes when richness peaked at low elevations as compared to high elevations (Table 1, Fig. 3b). For instance, the first quartile of families (15 total) with low elevation peaks in richness (< 200 m a.s.l.) had an ERR slope average of 0.48, whereas those with peaks within the last elevation peak quartile (avg. 1295 m a.s.l.) had an ERR slope average of 0.09. *Familial elevational extent* also had a negative relationship with ERR slopes (Table 1, Fig. 3c). Families restricted to a narrow section of the gradient, either from ecological specialization or geometric constraints (e.g. Burseraceae, familial extent of ~ 2000 m and ERR slope of 0.55), had steeper ERR slopes as compared to families with broad elevational occurrence (e.g. Asteraceae, familial extent of ~ 4500 m and ERR slope of -0.13). *Average lower elevation limit* and *average higher elevation limit* metrics both had negative relationships with ERR slopes (Table 1, Fig. 3d), with higher ERR slopes for families with occurrence boundaries constrained to lower elevations. Counter to our predictions, neither *evolutionary age* nor *latitudinal extent* had a direct relationship with ERR slopes (results insignificant). Consistent with our predictions, biogeographical affiliation strongly influenced ERR slopes. Families with greater westwardly skewed species occurrence (towards Sundaland) displayed a strongly positive relationship with ERR slopes, whereas a negative relationship emerged eastwardly (towards Sahul), with ERR slopes becoming shallower, neutral, or negative (Table 1, Fig. 4a-d). The spatially intermediate location, Wallacea, had mixed results when comparing metrics of *endemism* or *overlap* (Table 1). *Cosmopolitanism* did not directly influence ERR slopes (Table 1, Fig. 4d). The first pPCA component (pPC1, representing 43% of the variance) had a positive relationship with ERR slopes ($d.f. = 47$, F-statistic = 141.8, Adj. $R^2 = 0.75$, P -value < 0.001 , Fig. 5). The observed dichotomy of range-size trends for lowland Sundaland flora with concentrated centers of richness, with low pPC1 scores and strongly positive ERR slopes, compared to montane Sahul flora with distributed richness, with high pPC1 scores and weaker ERR slopes (Table 1; see Supporting information). The second component (pPC2, 19% of the variance) was non-significant.

Discussion

Does elevational range-size (ERR) slope inform the idea that mountain passes are higher in the tropics?

Long-term stability of environmental conditions, inferred via adjacency to the equator as well as location along an elevational gradient, facilitates not only ecological niche specialization but also determines relative shifts in average range-sizes. Our results support the idea that “mountain passes are higher in the tropics” as indicated by differences in ERR slopes for species-rich families with greater affiliation to lowland tropical of Sundaland, as compared to places with either contemporary, or historic, variability of conditions, such as for flora noted with either montane or Sahul affiliation.

Lowland, consistently tropical, families

For lowland tropical flora, a notable family is Dipterocarpaceae with high endemism to Sundaland and one of the steepest positive ERR slopes (0.53), which we have labeled as “1” on all scatterplots. Dipterocarpaceae

are described as having one-seeded fruits with reduced dormancy ability (Ashton 1988), with limited dispersal because of reduced wind flow beneath the forest canopy. The migration ability of Dipterocarpaceae is further limited by intermittent masting, narrow elevational distributions, and exclusive occurrence within mature forests, often with specialized soil associations (Ashton 1988, Davies et al. 2005). The genus *Shorea* (Dipterocarpaceae) is sometimes compared to *Syzygium* (Myrtaceae) based on similarities in intraspecific morphological variation and endemism (Ashton and Lee 2022) and both taxonomic groups having peaks in richness within tropical lowland habitats (< 400 m). However, Myrtaceae has higher endemism within Sahul relative to Sundaland, and *Syzygium* species are regarded as well-dispersed via animals (Ashton and Lee 2022). As a post-hoc analysis of this study (see Supporting information), we found that *Shorea* has an ERR slope of 0.54 whereas *Syzygium* had 0.37, and Myrtaceae as a whole 0.38. Despite the tropical lowland affiliation of Myrtaceae, the family has broader latitudinal occurrence, extending southward into temperate latitudes with seasonality (Hawkins et al. 2011).

Our study reinforces the concept that taxa occupying environments with prolonged periods of climate stability are associated with steeper positive ERR slopes. Under a climate change scenario where temperature increases, lowland tropical species have the benefit of being able to shift upwards in elevation. However, migration to maintain a narrow temperature window may be futile if these species lack resilience to increasing variability of habitat conditions, or if they rely on specific secondary factors such as edaphic conditions or essential services provided by another species with limited geographic span. A potential practical application of this finding is that ERR slopes may provide a broad-scale quantitative metric of a taxonomic groups' potential response to climate change, which could be used to focus limited resources for more intensive investigations on particularly vulnerable species.

Montane, or temperate, families

Flat, or negative, ERR slopes are also informative if regarded as indicators of ecological strategy (stress-tolerance) or resiliency to variation in environmental conditions. Relatively neutral ERR slopes may also reflect richness that is predominantly distributed mid-gradient, farthest from physical boundaries which may artificially truncate potential range-sizes, or for flora with ranges that are not limited by soft ecological boundaries (e.g. distributions that traverse vegetation zones or habitat types) (Whitman et al. 2021). One of the oldest families in our study, Podocarpaceae, had a shallow ERR slope (0.13), with species' distributions that are constrained by competitive exclusion within contemporary plant communities, rather than climate, with species that are restricted to habitat refugia in montane areas or soils with extreme nutrient limitation (e.g. ultramafic soils) (Coomes and Bellingham 2011). Upper montane forests are often noted for Gymnosperms from the Southern Hemisphere, with clades that are believed to have evolved and established before the current positioning of the archipelago (Culmsee and Leuschner 2013). Another outlier of our study is Ericaceae, with a flat ERR slope (-0.001), which we have labeled as "2" on all scatterplots. Counter to most tropical clades, the species-rich genus *Rhododendron* (Ericaceae) migrated into Malesia from temperate areas of the Himalayas, with Borneo as a distribution hub followed by rapid speciation across New Guinea as recently as 6 million years ago (Webb and Ree 2012, Soza et al. 2022). *Rhododendron* likely colonized montane areas first, with downward elevational expansion facilitated by exploitation of novel ecological niches and epiphytic growth forms (Whitman 2018). As a post-hoc analysis (see Supporting information), we found that the *Rhododendron* had centers of richness at some of the highest elevations (est. 2142 m a.s.l.) and a negative ERR slope (-0.04). To further test the idea that temperate origins are affiliated with reduced ERR slopes, we ran a secondary post-hoc analysis of families not included in the main study, grouping together species from Hamamelidaceae, Juglandaceae, Magnoliaceae, and Nyssaceae ($n = 63$) and found that the combined families had a weak ERR slope of 0.17 (adj. $R^2 = 0.70$, P -value < 0.001). Our findings suggest that montane-temperate association or point of origin is a stronger factor for determining ERR slopes than evolutionary age or richness. A broader question worth investigating is whether directionality of expansion (e.g. into the tropics versus out of the tropics) influences how range-sizes shift over a gradient, and whether ecological strategies also remain constant. If montane species can tolerate a wider span of abiotic conditions and habitat types, a different unknown is whether biotic competition is instead the most limiting factor for downward expansion. Rising temperatures, combined with upward migration of competition, may place

future constraints on montane species' range-sizes.

Conclusion

By comparing distribution patterns for plants families of Malesia, this study offers valuable insights on the mechanisms underlying elevational range-sizes of flora on tropical mountains and their potential response to changing environments. The synthesis of our findings is that long-term climate stability, in the sense of both centers of richness within lowland tropical forests as well as the consistently equatorial position of landmasses over millions of years, is linked to how much average range-sizes increase with elevation (ERR slope). Positive ERR slopes may indicate changes in ecological strategies, such as a shift from communities driven by biotic competition at lower elevations to ones that are more tolerant of abiotic stressors with increasing elevation. In contrast neutral, or even negative, ERR slopes may indicate directional expansion out of habitats with high abiotic variation, such as transitioning downward from montane habitats into lowland forests, or tectonic movement of landmasses towards the equator. Our findings indicate that lowland endemics of landmasses with consistent positioning near the equator (e.g. Sundaland) may be disproportionately at a higher risk of extinction as environmental conditions change and become more variable.

Table 1. Elevational range-size (ERR) slopes regressed against metrics of familial distributions across Malesia.

Table of variable definitions and results from across-family analyses using phylogenetic independent contrasts (PIC). To facilitate interpretation of findings and slope comparisons, values shown represent z-scaling of all variables and setting intercepts to zero. The response variable used in each model is abbreviated as ERR, which represents the change in average elevational range-size with elevation (slope), replicated for each species-rich plant family. Predictor variables consisted of metrics of species richness; familial distribution and boundaries along elevational gradients; evolutionary age; latitudinal extent; and biogeographical metrics of overlap, endemism, or cosmopolitanism within Malesia. Analyses were conducted separately for each variable because of covariation among them.

FIG.	PREDICTOR	df.	R ²	F-STAT.	P-VALUE	SLOPE	SYMBOL
	Malesian richness $\gamma = \sum_{i=1}^n \text{species within Malesia}$	58	0.01	1.4	NS	- 0.16	γ
3a	Localized richness ratio $\beta = \frac{\alpha = \text{bin richness}}{\gamma = \text{Malesian richness}}$	58	0.49	57.4	< 0.001	0.67	β
3b	Elevation with peak in richness (highest point of distribution curve)	58	0.71	145.1	< 0.001	- 0.88	
3c	Familial elevational extent (breadth of distribution curve)	58	0.32	29.0	< 0.001	- 0.58	
	Avg. lower elevation limit $\frac{\sum i = \text{Elevation Min.}}{n = \gamma \text{ richness}}$	58	0.80	232.2	< 0.001	- 0.86	
3d	Avg. higher elevation limit $\frac{\sum i = \text{Elevation Max.}}{n = \gamma \text{ richness}}$	58	0.71	142.2	< 0.001	- 0.87	
	Evolutionary age (millions of years)	47	- 0.02	0.0	NS	0.06	
	Familial latitudinal extent <i>Abs. (N. lat. deg - S. lat. deg.)</i>	47	- 0.02	0.2	NS	- 0.02	
4a	Sundaland endemism $A \cap (B \cap C)'$	58	0.13	9.7	0.003	0.38	
	Sundaland overlap A	58	0.31	27.4	< 0.001	0.52	
4b	Wallacea endemism $B \cap (A \cap C)'$	58	0.10	7.2	0.009	- 0.35	
	Wallacea overlap B	58	0.0	1.0	NS	0.15	
4c	Sahul endemism $C \cap (A \cap B)'$	58	0.34	31.8	< 0.001	- 0.55	
	Sahul overlap C	58	0.11	8.3	0.005	- 0.34	
4d	Cosmopolitanism $(A \cap B \cap C)$	58	0.05	3.9	NS	0.28	

Figure 1. Venn diagram examples of three species-rich families and their biographical distribution across Malesia.

The size of each circle is proportionate to the number of species present matching our inclusion criteria. The Venn diagram indicates spatial exclusivity, which is used to calculate biogeographical distribution metrics of *endemism*, *overlap*, or *cosmopolitanism*. For example, in our Malesian dataset there are 318 Dipterocarpaceae, thus Sundaland *endemism* is calculated as $264/318 = 0.83$; Sundaland *overlap* as $(264+30+0+3)/318 = 0.93$; and *cosmopolitanism* as $3/318 = 0.01$. The endemism metrics are translated into a CYMK hex code, with Sundaland as magenta, Wallacea as yellow, and Sahul as cyan; *Cosmopolitanism* as black. These three families are labeled on all scatterplots as 1) Dipterocarpaceae, 2) Ericaceae, 3) Pteridaceae.

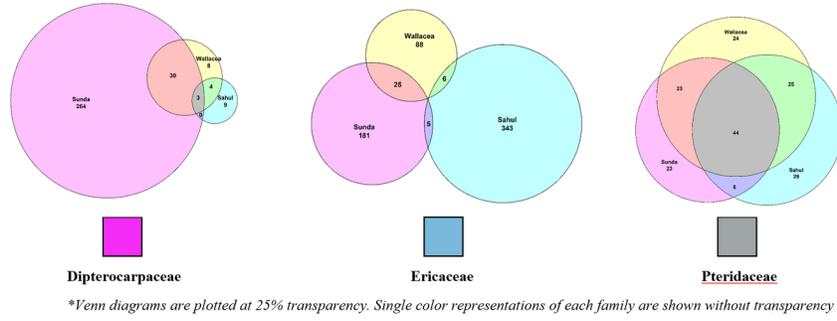


Figure 2. Principal components analysis (pPCA) of major species-rich plant families.

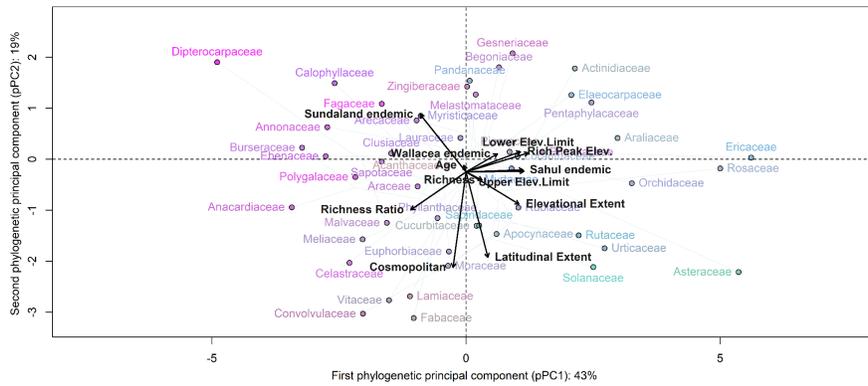
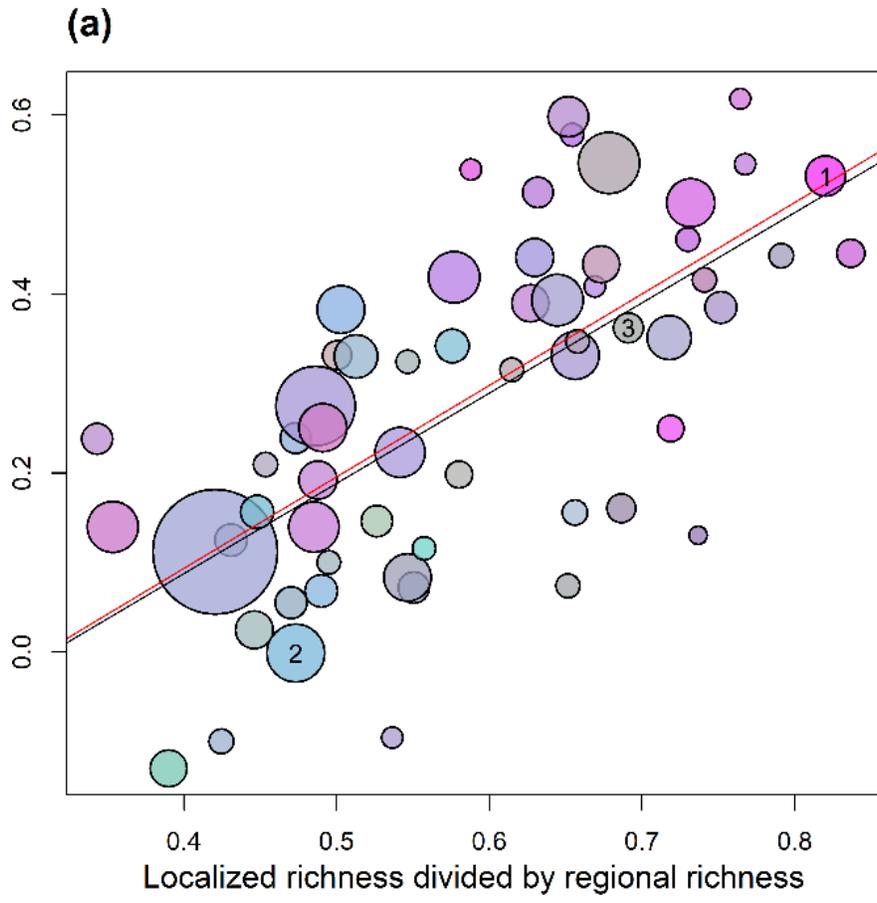
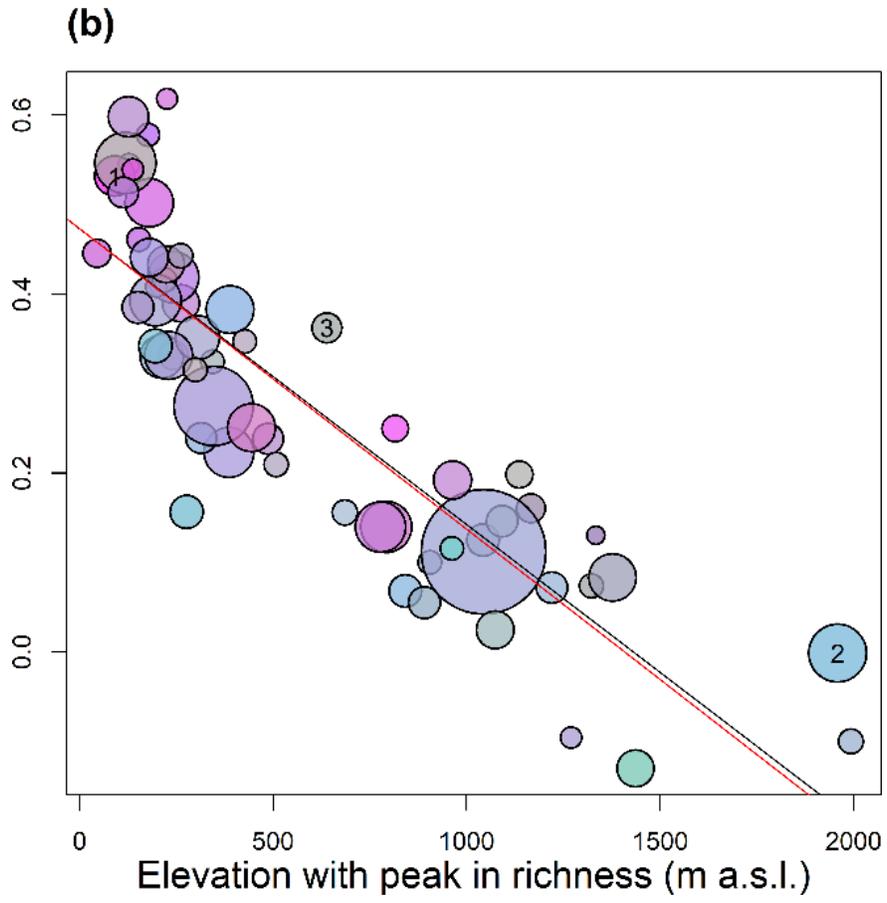


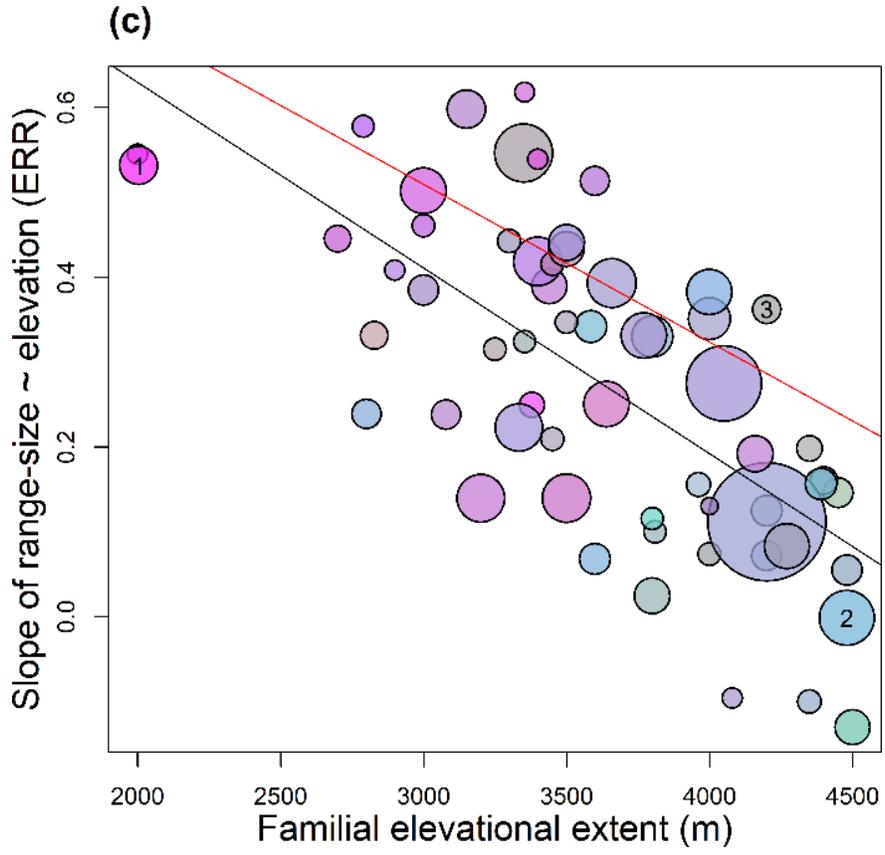
Figure of pPCA includes metrics we compiled for richness, elevational or biogeographical distributions of each family ($n = 49$), as well as latitudinal range and evolutionary age as estimated by Hawkins et al. 2011. CYMK colors of each family represent endemism to a given biogeographic region and proportion of species shared by all locations (cyan – Sahul, yellow – Wallacea, magenta – Sundaland, black – cosmopolitanism). Length and direction of arrows proportionate to loading significance.

Figures 3a-d. Metrics of familial distributions along elevational gradients, used to test mechanisms shaping the slope of ERR via cross-family analyses.

Each point represents a species-rich plant family ($n = 60$), with size of point representative of *Malesian richness*. Three families labeled as examples for comparisons between scatterplots: 1) Dipterocarpaceae, 2) Ericaceae, 3) Pteridaceae. On the y-axis, slope of average elevational range-size (m), abbreviated as ERR, as a function of position along an elevational gradient (m a.s.l.). On the x-axis, familial metrics of richness and elevational distribution. Plots include a) the *localized richness ratio*, which is defined as the greatest richness observed at any section of the elevation gradient, divided by total family richness across all of Malesia; b) *elevation with peak in richness* (highest point of the predicted richness curve); c) *familial elevational extent* (breadth of the richness curve), calculated as the highest elevation minus the lowest elevation values for any species within a family; d) *the average upper elevational limit* for species occurrence. Other metrics not shown include e) *Malesian richness* and f) *average lower elevational limit*. Linear regression results shown as a black slope, phylogenetic independent contrasts as a red slope, both plotted without scaling; dashed lined represent non-significance. Point colors (CMYK model) represent the combined metrics of biogeographic association of each family, with endemism to Sundaland represented as magenta tones, Wallacea as yellow, Sahul as cyan, and cosmopolitan as black, with 25% transparency. Full color legend for the 60 families in Supporting information.







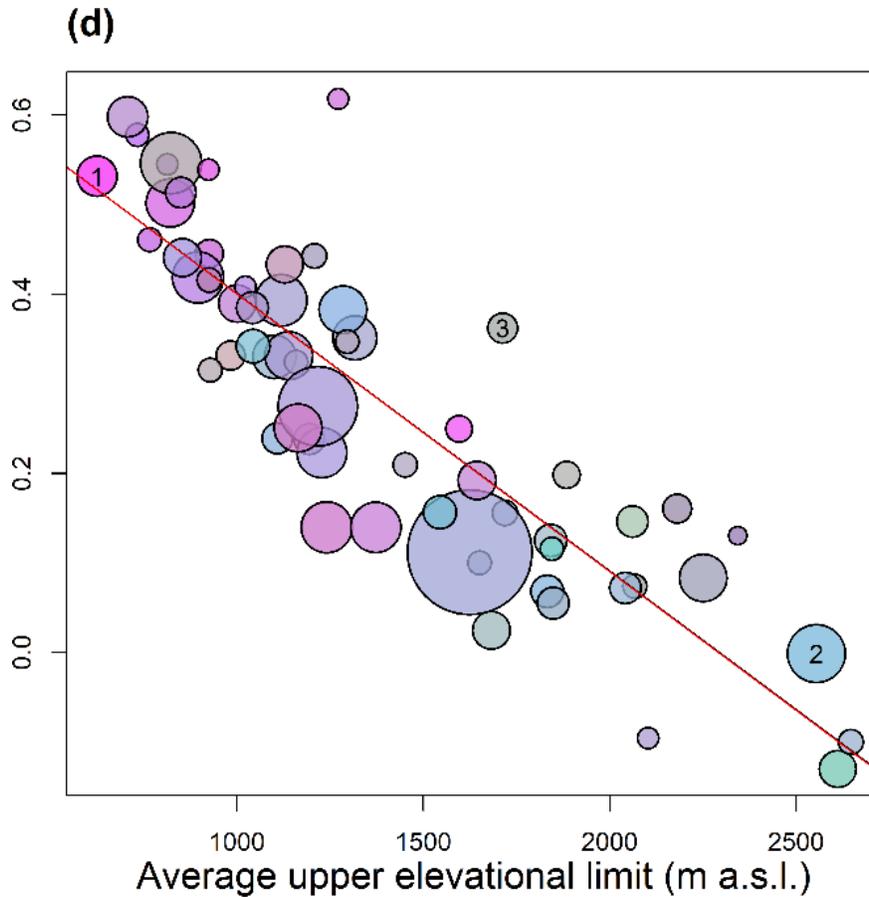
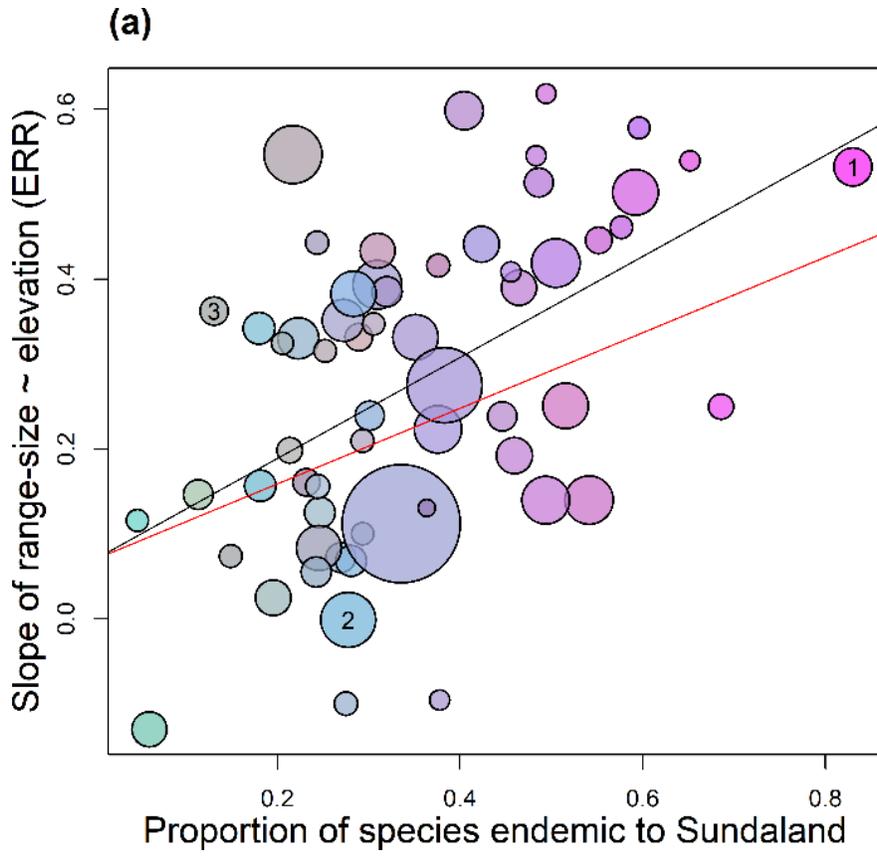
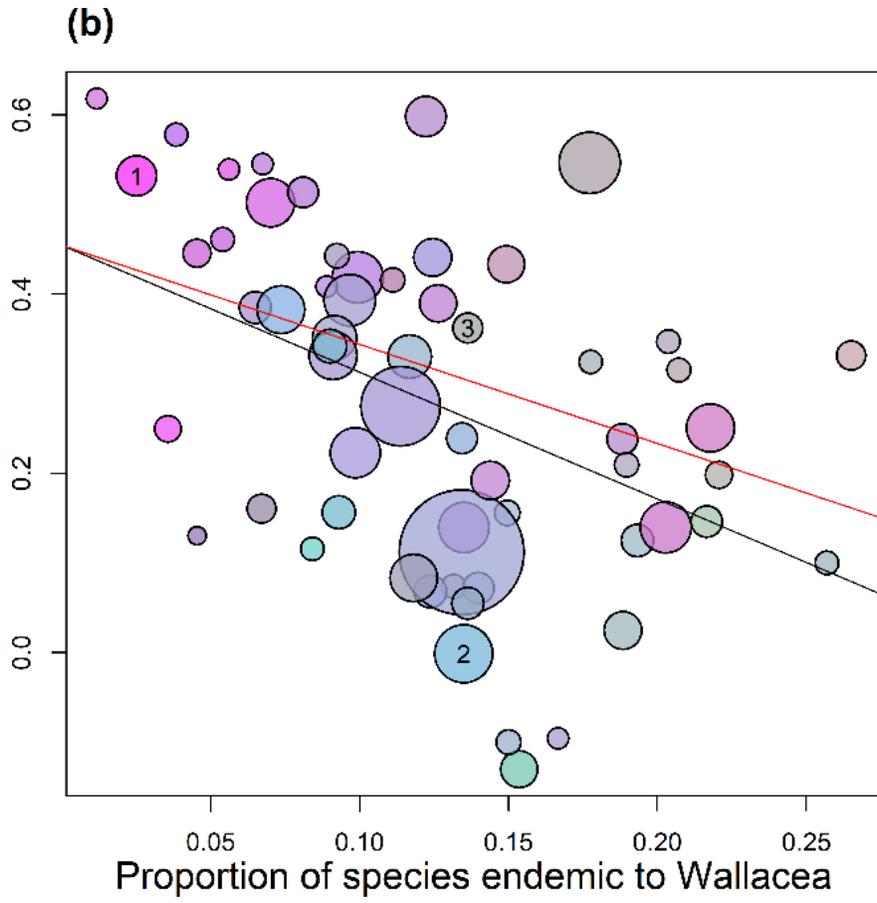
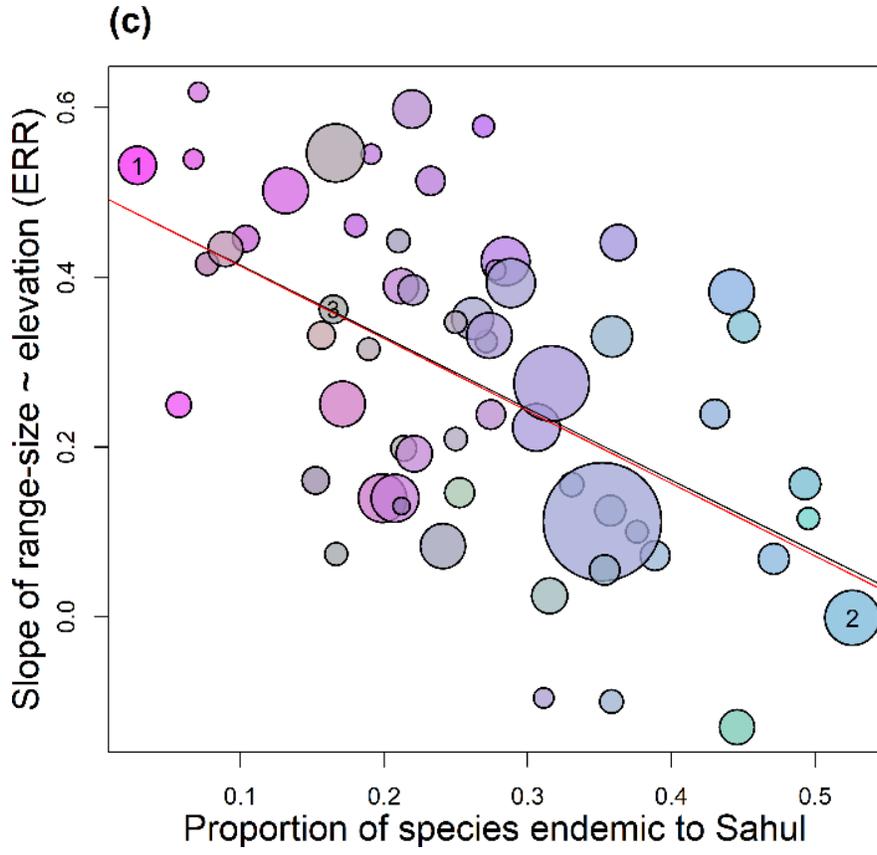


Figure 4a-d. Metrics of biogeographical overlap and endemism, used for across-family analyses on the mechanisms shaping the slope of ERR.

Each point represents a species-rich plant family ($n=60$), with size of point representative of family richness. Three families labeled as examples for comparisons between scatterplots: 1) Dipterocarpaceae, 2) Ericaceae, 3) Pteridaceae. On the y-axis, slope of average elevation range-size (m), abbreviated as ERR, as a function of position along an elevational gradient (m a.s.l.). On the x-axis, familial metrics of distribution by Malesian biogeographical region (Sundaland, Wallacea, or Sahul), with values ranging from 0 - 1. Plots 4a-c represent *endemism*, defined as the proportion of species that exclusively occur within a single biogeographical region. Plot 4d represents *cosmopolitanism*, defined as the proportion of species that occur in all three biogeographical regions. Not shown is the *overlap* metric, defined as the proportion of species occurring within a given biogeographical region and with the potential to occur elsewhere, summarized in Table 1. Linear regression results shown as a black slope, phylogenetic independent contrasts as a red slope, both plotted without scaling; dashed lined represent non-significance. Point colors (CMYK model) represent the combined metrics of biogeographic association of each family, with endemism to Sundaland represented as magenta tones, Wallacea as yellow, Sahul as cyan, and cosmopolitan as black, with 25% transparency. Full color legend for the 60 families in Supporting information.







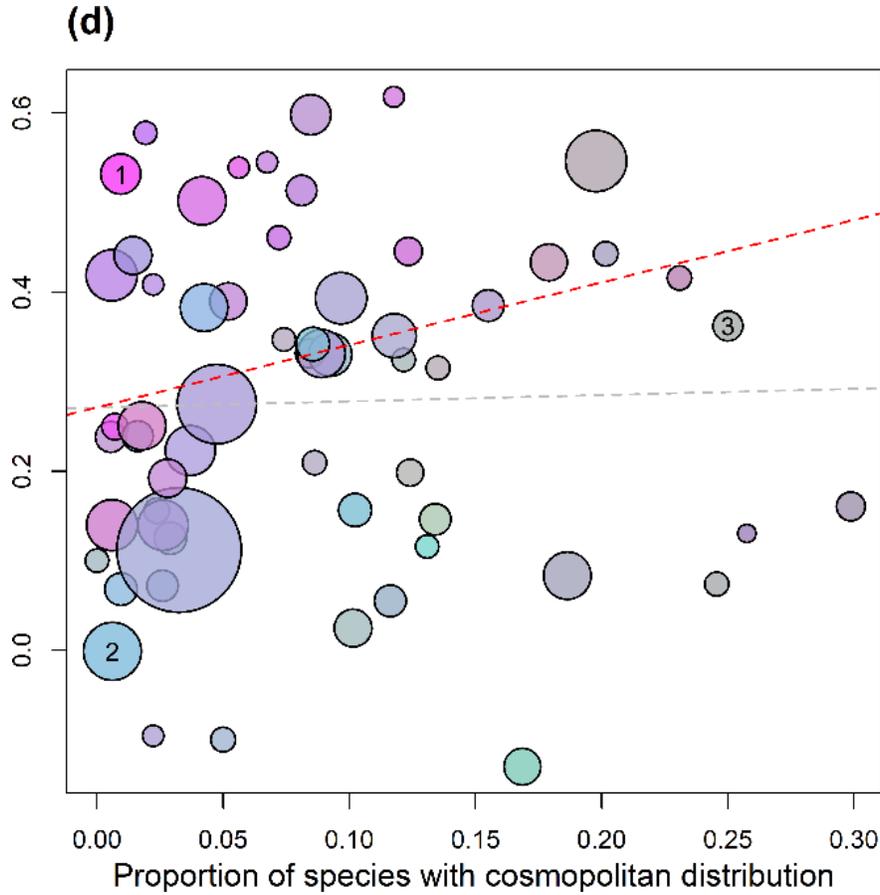
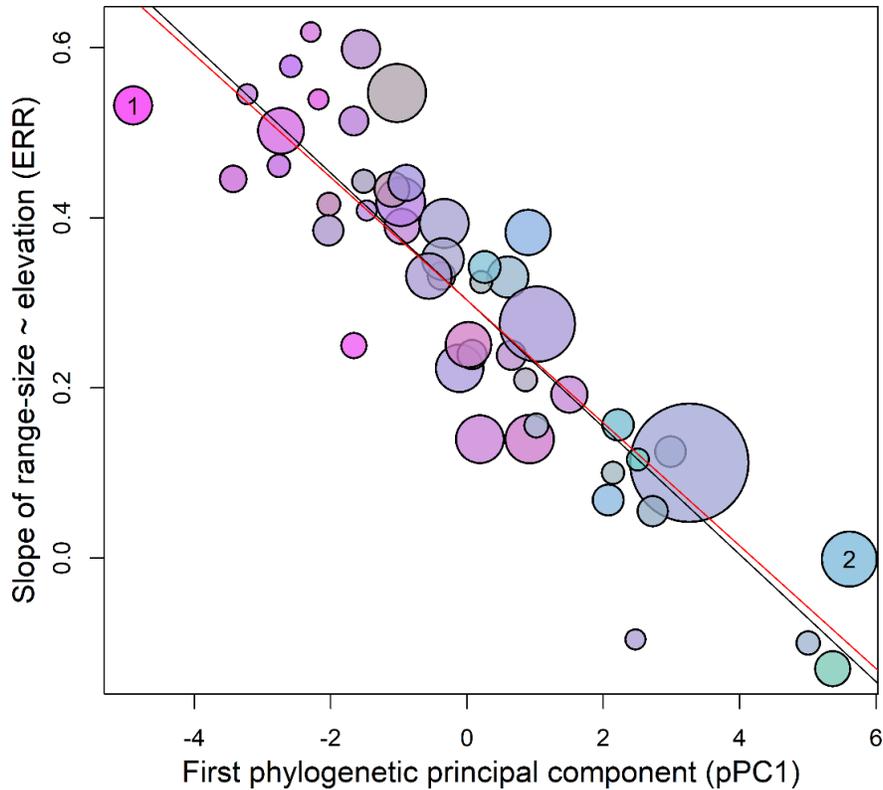


Figure 5. Linear regression of ERR slopes as a function of the first phylogenetic principal components (pPC1). Each point represents a species-rich plant family ($n=49$), with size of point representative of *Malesian richness*. Two families labeled as examples for comparisons between plots: 1) Dipterocarpaceae and 2) Ericaceae. Negative pPC1 scores represent stronger *Sundaland endemism* (represented by magenta tones) or *overlap*, as well as higher *richness ratio*, which is proportion of Malesian richness concentrated within a single 100 m elevational band. Positive pPC1 scores represent *Sahul endemism* (cyan tones) or greater montane affiliation based on *lower* or *upper average elevational limits* for occurrence, *peak in richness* at higher elevations, or broader *familial elevational extent* of occurrence. Results using linear regression with slope shown in black, phylogenetic independent contrasts slope in red.



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*Additional references for data sources, nomenclature websites, statistical/mathematical programs or methods, biogeographic boundaries, or other secondary sources of note are included in Supporting information

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