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Research article

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

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Our goal was to interrogate the idea that “mountain passes are higher in the tropics” by investigating ecological and biogeographic drivers of elevational range-sizes patterns among equatorial flora. We used herbarium records for 60 species-rich plant families, representing 18 535 species total, 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). We then evaluated how family-level ERR slopes correlated with each metric individually, as well as when using multivariate techniques to reduce dimensionality. We hypothesized that if long term climate stability over millions of years promotes habitat specialization, then among taxa with longer-term tropical affiliations, we would expect smaller range-sizes within lowland forests, with greater range-size expansion towards higher elevations, expressed as a positive ERR slope. Conversely, variation in growing conditions should promote larger, relatively consistent, range-sizes at all sections of an elevational gradient, expressed as a neutral ERR slope. Our results support this corollary because of the dichotomy of ERR slopes observed in relation to the elevational distribution of richness and historical biogeographic positioning. We found that 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, as did clades with temperate origins. Families with Wallacea affiliation, broader latitudinal or elevational distributions, cosmopolitanism, greater richness, or older evolutionary age had mixed results. We conclude that the relative steepness of an ERR slope is an indicator of a taxonomic group’s tolerance of habitat variation and vulnerability to contemporary climate change.

Keywords: elevational range-sizes, island biogeography, macroecology, Malesia (Indo-Australian Archipelago), Rapoport’s rule, tropical mountains



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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, produces 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 occurrence requires quantification of underlying factors that determine how richness is distributed or why it is restricted, with consideration of migration barriers (Janzen 1967, Rehm and Feeley 2015, Whitman et al. 2021, Ashton et al. 2022) and biogeographic history (McCain and Grytnes 2010, Freeman et al. 2018, Pálincás 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, diurnal temperature range, geographic area or land-mass positioning, and metrics of species richness (Morueta-Holme et al. 2013, Sheth et al. 2020, Sundaram and Leslie 2021, Guo et al. 2022, Gallou et al. 2023), as well as intrinsic factors such as species' response to competition, dispersal ability, life-history strategies, ecophysiological limits, 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, Sizling et al. 2009). However, despite the influence of historical factors on diversity, relatively few studies have examined variation in ERR slopes with respect to biogeographic history, with replication of statistical analyses across highly diverse families.

Tropical mountains offer unique locations to further test tradeoffs between climate stability and range-size breadth. A notable hypothesis is that "mountain passes are higher in the tropics" (Janzen 1967), which, when applied to macroecological range-size patterns, means that a greater shift in species' ecological niche space is required to occupy each incremental increase in elevation (Stevens 1992, Sheldon et al. 2018). This hypothesis rests on two assumptions. First, evolutionary adaptations to consistent environmental conditions 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 (Dobzhansky 1950). Tropical mountains also display greater floristic and structural elevational zonation than temperate mountain counterparts (Ashton et al. 2022), meaning that equatorial species' range-sizes are mediated by more than just temperature (Zhou et al. 2019, Whitman et al. 2021). Taxon-specific characteristics (e.g. edaphic specialization, methods of dispersal) may further contract or expand the boundaries of occurrence, thus leading to divergence, rather than uniformity, of predicted range-size trends for different lineages along a shared gradient.

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. Surprisingly little research on ERR has been conducted within Malesia, except for localized studies (Whitman et al. 2021). Malesia is an exceptional study system to investigate potential correlates of variation in ERR slopes because it is a biodiversity hotspot that encompasses a $\sim 2\,000\,000\text{ km}^2$ area, collectively representing the largest archipelago on Earth, spanning from the Malay Peninsula to New Guinea (Myers et al. 2000). Even though Malesia straddles the equator, mountains including Mt Kinabalu (4095 m a.s.l.), Mt Wilhelm (4509 m a.s.l.), and Puncak Jaya (4884 m a.s.l.) are subject to freezing events (Hope 1976). Within Malesia, delineation of biogeographic regions is a point of ongoing investigation (van Welzen et al. 2011, Webb and Ree 2012, Kooyman et al. 2019, Joyce et al. 2021), with boundaries often based on Wallace's line, named after Alfred E. Wallace and his observations of islands with highly dissimilar terrestrial vertebrate composition (Wallace 1863, Richardson et al. 2012). 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, such as drought (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 to 45 Mya), Sundaland and portions of Wallacea (mainly the Philippines) straddled the equator, whereas Sahul (New Guinea) was partially submerged and positioned $\sim 20^\circ$ southwards in latitude (Hall 1998, Zhang et al. 2023). 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).

A lingering unknown is whether the contemporary species interchange between Malesian biogeographic regions may homogenize macroecological range-size patterns, or if older artifacts of geographic separation, tectonic events, or paleoclimatic conditions continue to shape species' distributions and tolerance to climatic variability. The most recent interchange of species (< 5 Mya) has been facilitated by the relatively closer positioning of landmasses and the emergence of islands which act as stepping-stones for range expansion (Hall 1998, Ashton 2014, Morley 2018, Zhang et al. 2023). Mountaintops act as 'sky islands' to facilitate migration 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). Widespread establishment of perhumid conditions also promotes species interchange via similarity of climate conditions across islands (Morley 2018).

Despite movement of species across the archipelago (Yap et al. 2018), plant clades of Sundaland have historically had tropical association, with greater interchange with the mainland Indochina (Kooyman et al. 2019, Zhang et al. 2023). Conversely, plant clades on the Sahul continental shelf often have greater Australasian associations, especially for flora specific to mountain ranges that have remained above sea-level for longer, or that establish before the current positioning of the archipelago (Culmsee and Leuschner 2013, Morley 2018, Brambach et al. 2020, Trethowan et al. 2023b, Wilf and Kooyman 2023). Wallacea is centrally located, potentially mediating a greater interchange with neighboring areas, and is comprised of smaller, younger, or recently uplifted islands with relatively shorter mountains and less lowland habitat (Ashton 2014, Hamilton et al. 2019). However, Wallacea can also represent an interchange barrier, with habitat filtering due to localized seasonality, greater aridity, fire disturbance, and edaphic stressors such as ultramafic soil (Hamilton et al. 2019, Trethowan 2021). The oldest Gondwanan clades can occur on both western and eastern sides of Malesia (Hall 1998, Richardson et al. 2012, Wilf and Kooyman 2023), as can taxa with long-distance or stochastic seed dispersal abilities (Baker and Couvreur 2012, Webb and Ree 2012). Species with larger fruit or seeds tend to have limited distribution ranges if reliant on animal-mediated dispersal, especially within aseasonal wet habitats relative to other biomes (Ashton and Lee 2022, Trethowan et al. 2023a). Even if habitat conditions are suitable, taxa originating from outside a given region can have limited establishment success if communities are already saturated (Yap et al. 2018).

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 18 535 species) to estimate occurrences across a 4500 m elevational gradient and by biogeographic regions. For each family, we estimated the change in average range-sizes with increasing elevation (ERR slope) and 15 metrics that reflect the ecology, evolution, and biogeography of each family, including descriptions of 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. We hypothesized a relationship between long-term climate stability and elevational range-sizes, integrating concepts from Janzen (1967) and Ashton et al. (2022). Thus, we predicted steeply positive ERR slopes for families that evolved within biogeographic regions with consistent proximity to the equator over millions of years (e.g. Sundaland endemics) and for smaller islands with maritime buffering of temperature extremes (e.g. Wallacea endemics). However, for taxa on larger landmasses that moved towards the equator (e.g. Sahul endemics), 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 clades with montane or temperate origins. Second, we anticipated that the way richness is spatially distributed would also affect these predictions, based on both ecological mechanisms and geometric constraints. For families with relatively 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. For a subset of communities adjacent to mountain summits, we predicted negative ERR slopes. For widespread families with fewer barriers for expansion (e.g. overlapping multiple regions or displaying cosmopolitanism; dispersed richness, broad familial extent), we predicted shallower or neutral ERR slopes.

Material and methods

Query of herbarium records for elevational distributions of species-rich plant families

For herbarium data, we queried the Global Biodiversity Information Facility (Derived Dataset) and a Mt Kinabalu regional dataset (Whitman et al. 2022). 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. We

also examined alternate biogeographic delineations which produced comparable results (Supporting information).

Change in average range-sizes 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 changes with increasing elevation (ERR) we used a novel approach based on quantile binning (rather than even-increment bins), 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. 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, similar to Stevens 1992. For each family, we used ordinary least squares regression (OLS) to test and quantify ERR slopes, which we then used as the response variable for across-family analyses. For extended methods, see the Supporting information.

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 ('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 (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 angiosperm data by Hawkins et al. (2011).

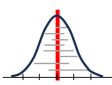
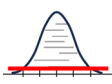
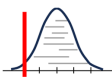
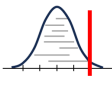
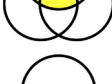
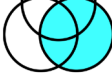
Metrics of species' distributions across biogeographical regions of Malesia

For the second series of predictor variables, we quantified species' distribution within and across the three bioregions of Malesia using a Venn diagram approach ('predictor' and 'symbol' column Table 1, Fig. 1). 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 ($A \cap B \cap C$), indicating the number of species occurring across the entirety of Malesia (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 a 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, 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 performed a set of across-family univariate analyses of ERR slopes as a function of each variable (Table 1), as well as the first two principal components at the family level (15 factors in total), using linear regression (shown in black) and phylogenetic independent contrasts (PIC) with the slope shown in red and summarized in Table 1. We transformed all values into z-scores to facilitate comparisons of factors at different scales, meaning results are consistent (adjusted R^2 , F-statistic and p-values), but the intercept becomes zero and relationships can be described as positive (slope of 1), negative (slope of -1), or neutral (0). Note, we did not use scaling when reporting individual family ERR slopes (Supporting information), or for visual representation of scatterplot axes. Second, to visualize similarities and differences between families and to reduce the dimensionality of multiple (potentially covarying) factors, we used phylogenetic principal components analysis (pPCA) with scaling to ordinate and derive two orthogonal variables. The pPCA included a dozen factors (we excluded biogeographic overlap metrics to reduce complexity), further restricted to families with data for all factors. The first two components were then individually tested as predictors of ERR slope, similar to the univariate methods stated earlier.

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, conducted separately for each variable using phylogenetic independent contrasts (PIC). Values shown represent z-scaling with intercepts set to zero. The response variable (ERR slopes) represents the change in average range-sizes with elevation. Predictor variables include metrics of species richness; familial distribution and boundaries along elevational or latitudinal gradients; evolutionary age; and biogeographical affiliation.

Fig.	Predictor	df	r ²	F-stat.	p-value	Slope	Symbol
3a	Malesian richness $\gamma = \sum_{i=1}^n \text{Species Within Malesia}$	58	0.01	1.4	NS	-0.16	γ
	Localized richness ratio $\beta = \frac{\alpha = \text{Bin richness}}{\gamma = \text{Malesian richness}}$	58	0.49	57.4	< 0.001	0.67	β
	Elevation with peak in richness (highest point of distribution curve)	58	0.71	145.1	< 0.001	-0.88	
	Familial elevational extent (breadth of distribution curve)	58	0.32	29.0	< 0.001	-0.58	
	Avg. lower elevation limit $\frac{\sum i = \text{Elevation Min.}}{n = \text{Richness}}$	58	0.80	232.2	< 0.001	-0.86	
3b	Avg. higher elevation limit $\frac{\sum i = \text{Elevation Max.}}{n = \text{Richness}}$	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 Abs.(N.lat.deg. - S.lat.deg.)	47	-0.02	0.2	NS	-0.02	
3c	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	
	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	
	Sahul endemism $C \cap (A \cap B)'$	58	0.34	31.8	< 0.001	-0.55	
3d	Sahul overlap C	58	0.11	8.3	0.005	-0.34	
	Cosmopolitanism $(A \cap B \cap C)$	58	0.05	3.9	NS	0.28	

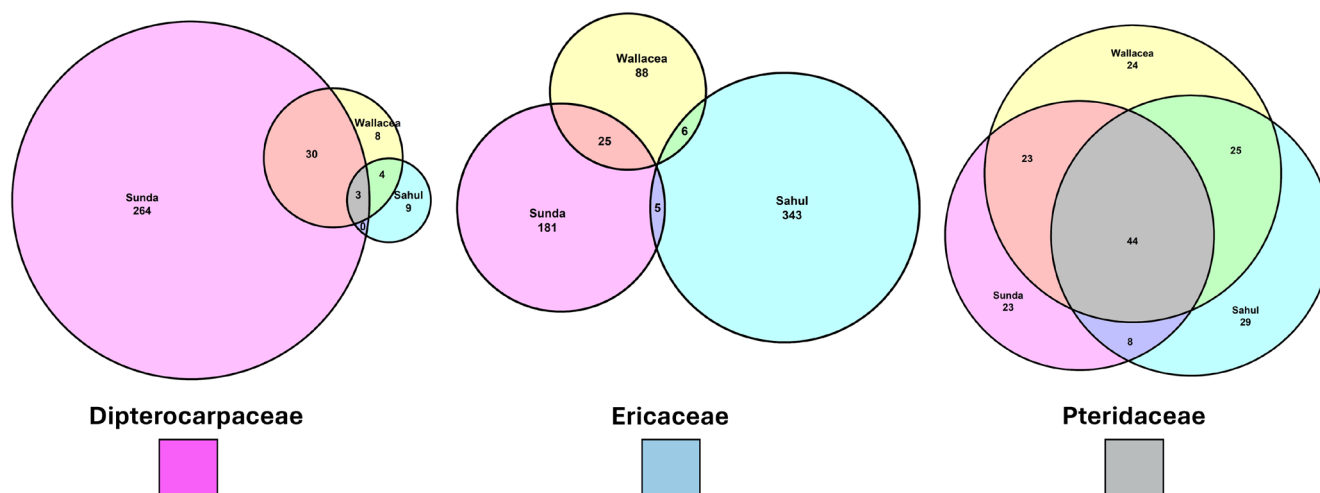


Figure 1. Venn diagram examples of three species-rich families and their biogeographical distribution across Malesia. The size of each circle is proportionate to the number of species present matching our inclusion criteria. The Venn diagram indicates spatial exclusivity, which is used to calculate biogeographical 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 single color (CYMK hex code) with Sundaland as magenta, Wallacea as yellow, and Sahul as cyan; Cosmopolitanism as black; all with 25% transparency. These three families are labeled on all scatterplots as 1) Dipterocarpaceae, 2) Ericaceae, 3) Pteridaceae.

Results

Individual metrics of biogeographic affiliation and distribution of richness

Among the 60 species-rich families, there was considerable variation in the predictive metrics explored (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 typically affiliated with lowland tropical forests, with the exception of Fagaceae and Podocarpaceae. Low localized richness ratio families included Begoniaceae and Gesneriaceae. Elevational extent values were comparable to the localized richness ratio metric 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 (e.g. Asteraceae). 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 proportional metrics for overlap and endemism differed among families and locations. 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), conifers (Podocarpaceae), Bryophytes, grasses (Poaceae) and sedges (Cyperaceae).

Variation in the steepness of ERR slopes, with respect to ecological, evolutionary, and biogeographic correlates across-families

When grouping all Malesian plant species together, richness was highest within lowland tropical forests and average range-sizes increased with elevation (i.e. in support of Rapoport's rule). For 56 out of the 60 plant families examined, average elevational range-sizes significantly (positively or negatively) corresponded with elevation (ERR); see the Supporting information. Observed ERR slope values (without scaling) were mostly positive, averaging 0.28 across families, ranging from -0.13 (Asteraceae) to 0.62 (Celastraceae).

For across-family analyses to infer the mechanisms underlying observed elevational range-size trends, we found that most, but not all, results matched our predictions (Table 1, Fig. 2a–d). First, Malesian richness was not associated with ERR slopes. However, clustering of richness, based on

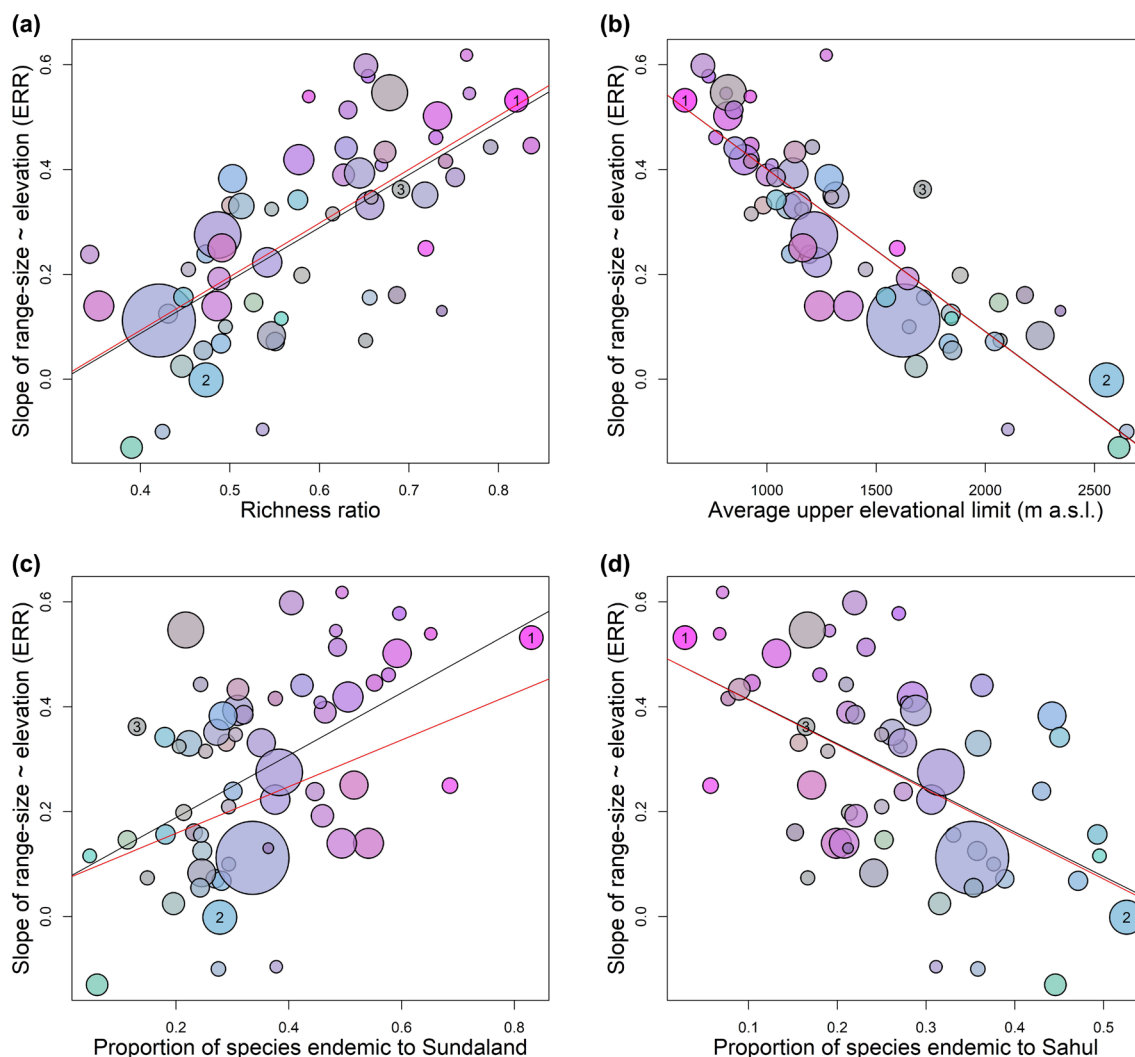


Figure 2. (a–d) Metrics of biogeographic endemism and familial richness distributions along elevational gradients, used to test mechanisms shaping the slope of ERR via cross-family analyses. Example of four metrics (out of a total of 15 examined) that have a strong positive, or negative, relationship with ERR slopes. Each point represents a species-rich plant family ($n=60$), with size of point representative of Malasian richness. Three families labeled as examples for comparisons between scatterplots: 1) Dipterocarpaceae, 2) Ericaceae, 3) Pteridaceae. On the y-axis, the response variable (abbreviated as ERR), representing the slope of average elevational range-size (m) as a function of position along an elevational gradient (m a.s.l.). On the x-axis, the predictor variable(s), representing familial metrics of biogeographical endemism and elevational distribution of richness. Plots include metrics of: (a) richness ratio, (b) average upper elevational limit, (c) Sundaland endemism and (d) Sahul endemism. Linear regression results shown as a black slope, phylogenetic independent contrasts as a red slope, both plotted without scaling. 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, and plots of the other individual metrics examined, included in the Supporting information.

the localized richness ratio, was positively associated with ERR slopes (Fig. 2a). 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 elevational peak in richness had a negative relationship with ERR slopes, with higher ERR slopes when richness peaked at lower elevations as compared to

higher elevations. For instance, the first quartile of families (15 total) with peaks in richness < 200 m a.s.l. had an ERR slope average of 0.48, whereas those with peaks within the last elevation quartile (1295 m a.s.l.) had an average ERR slope of 0.09. Familial elevational extent also had a negative relationship with ERR slopes. Families restricted to a narrow section of the gradient, either from ecological specialization or geometric constraints, had steeper ERR slopes as compared to families with broad elevational occurrence (e.g. Burseraceae, familial extent of ~ 2000 m and ERR slope of 0.55, versus Asteraceae, familial extent of ~ 4500 m and

ERR slope of -0.13). Average lower (and higher) elevation limit metrics both had negative relationships with ERR slopes (Fig. 2b), with steeper ERR slopes in instances where boundaries are constrained to lower elevations. Neither evolutionary age nor latitudinal extent had a direct relationship with ERR slopes. 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 (Fig. 2c), whereas a negative relationship emerged eastwardly (e.g. towards Sahul, Fig. 2d), with ERR slopes becoming shallower, neutral, or negative. Wallacea had mixed results when comparing metrics of endemism and overlap. Cosmopolitanism did not directly influence ERR slopes.

For the pPCA analysis ($n=49$), we found that the first two loadings explained 62% of the data variance (Table 2, Fig. 3), with pPC1 accounting for $\sim 43\%$ and PC2 $\sim 19\%$. Negative pPC1 loadings were associated with greater Sundaland endemism (represented by magenta), or high richness ratio values. Loadings with minimal weight i.e. values close to zero (visualized via shorter arrows) included metrics that were also insignificant within individual regression analyses (Table 1–2). Positive pPC1 loadings encompassed montane affiliation, with peak in richness, lower or upper limits of occurrence at higher elevations, and greater Sahul endemism (represented by cyan). When individual pPCA scores were plotted (Fig. 3), with each point representing a family, a spectrum of colors emerged across the horizontal axis. The first pPCA component had a negative relationship with ERR slopes ($df=47$, F-statistic = 141.8, Adj. $R^2=0.75$, p-value < 0.001 , Fig. 4), with low pPC1 scores and strongly positive ERR slopes for families with greater Sundaland endemism or

constrained richness (e.g. Dipterocarpaceae, labeled as no. 1 on Fig. 4), compared to high pPC1 scores and weaker ERR slopes for families with montane affiliation, distributed richness or greater Sahul endemism (e.g. Ericaceae, labeled as no. 2 on Fig. 4). The second pPC2 axis was ambiguous, with less distinction between families. Loadings with the greatest pPC2 absolute values included metrics of cosmopolitanism and latitudinal extent, with outlier families (Fabaceae, Convolvulaceae, Lamiaceae, Vitaceae, and Moraceae) often used for agriculture, including sweet potato, legumes, grapes, breadfruit, and herbal aromatics. However, the second component was non-significant with regards to ERR slopes.

Discussion

Our study supports the idea that long-term stability of environmental conditions, inferred via adjacency to the equator and affinity to lower-elevation habitats, facilitates ecological niche specialization and promotes narrower elevational range-sizes. Specifically, elevational range-sizes increased with elevation (positive ERR slopes) for flora with greater affiliation to lowland tropical regions of Sundaland, a location with consistent equatorial positioning over millions of years. In contrast, elevational range-sizes did not vary significantly, or declined with elevation, for flora associated with locations having greater historic variability of environmental conditions, that is, encompassing montane habitats or Sahul affiliation (a continental shelf with tectonic movement towards the equator). Other factors, such as cosmopolitanism or affiliation with centralized landmasses (e.g. islands of Wallacea), can obfuscate this ERR slope dichotomy.

Biogeographic evidence for why mountain passes are higher in the tropics

For lowland tropical families, a notable example is Dipterocarpaceae with high endemism to Sundaland and one of the steepest positive ERR slopes (0.53). Dipterocarpaceae are described as having one-seeded fruits with reduced dormancy ability (Ashton and Kettle 2012), with limited dispersal due to 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 (Davies et al. 2005, Ashton and Kettle 2012). 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 genera 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, Low et al. 2022). Myrtaceae also has broader latitudinal occurrence, extending southward into temperate areas with seasonality (Hawkins et al. 2011, Low et al. 2022). As a post hoc analysis

Table 2. Loadings from a phylogenetic principal components analysis (pPCA) of richness, elevational and latitudinal distribution, age, and biogeographical affiliation for 49 plant families. Table of phylogenetic principal components analysis (pPCA) loadings, representing a dozen factors listed in descending order. Loadings with very negative (e.g. localized richness ratio) or very positive (e.g. average lower elevational limit) values were regarded as having the most weight or importance; loading values close to zero as having less weight (e.g. evolutionary age). Results based on a subset of species-rich plant families with complete data for all factors and phylogenetic information available (restricted to just angiosperms). To reduce model complexity metrics of biogeographic overlap were excluded.

Factors	pPC1 43%	pPC2 19%
Localized richness ratio	-0.36	-0.25
Sundaland endemism	-0.30	0.38
Cosmopolitanism	-0.09	-0.62
Evolutionary age	-0.02	0.04
Malesian richness	0.10	-0.05
Latitudinal extent	0.14	-0.56
Wallacea endemism	0.21	0.12
Elevational extent	0.35	-0.21
Elevation with peak in richness	0.36	0.13
Sahul endemism	0.37	0.01
Average upper elevational limit	0.38	0.01
Average lower elevational limit	0.41	0.12

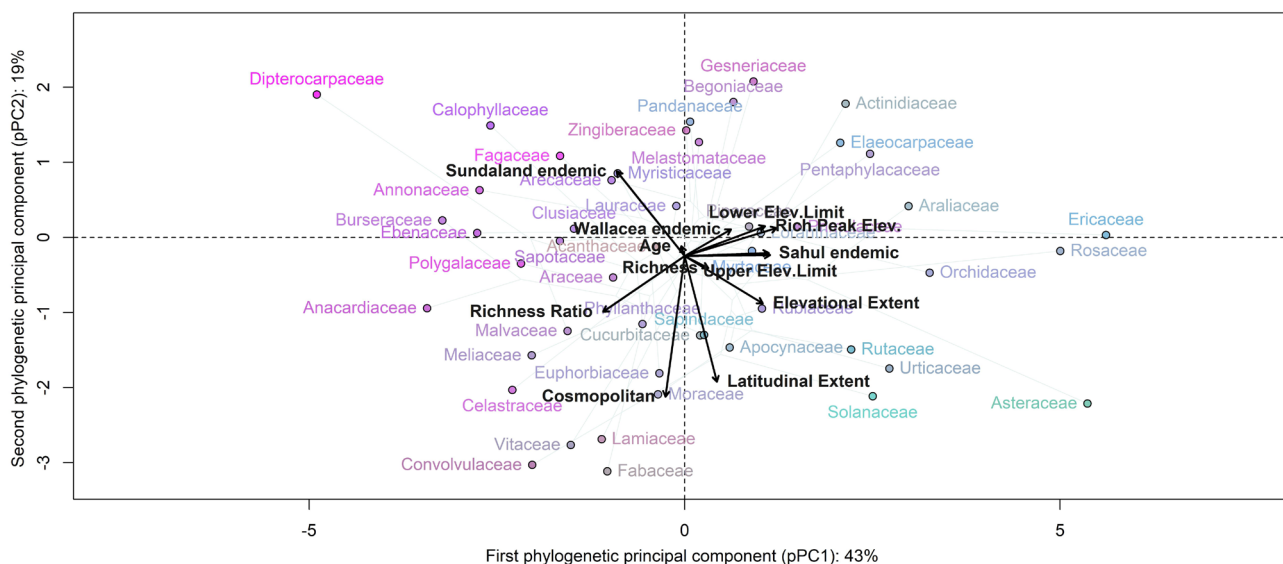


Figure 3. Phylogenetic principal components analysis (pPCA) of major species-rich plant families. Figure of pPCA includes metrics we compiled for richness, elevational or biogeographical distributions of each family ($n = 49$), as well as latitudinal range and evolutionary age as estimated by Hawkins 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 loadings.

of this study, we found that *Shorea* had an ERR slope of 0.54 whereas *Syzygium* had 0.37 (Supporting information), illustrating the differences between flora within low elevation areas based on biogeographic affiliation and life history characteristics. Other studies have noted differences in the distribution of richness and range-sizes for endemic and non-endemic flora (Zhou et al. 2019), but our study adds the novel nuance that taxa occupying environments with prolonged periods of climate stability have 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, with temperatures exceeding critical photosynthetic thresholds, or if they rely on specific secondary factors (e.g. edaphic conditions) or essential services (e.g. seed dispersal) provided by another species with limited geographic distributions (Russo et al. 2007, Doughty et al. 2023, Trethowan et al. 2023a). 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 conservation of particularly vulnerable species.

Exceptions to the (Rapoport's) rule: stress-tolerant families

Flat, or negative, ERR slopes are informative if regarded as indicators of ecological strategy (stress-tolerance) or resiliency to changing conditions. Other studies have noted that the most stress-tolerant species (e.g. endemic to ultramafic soil) are

widely distributed across Malesian islands (Trethowan et al. 2022) and less adherent to vegetation zone boundaries as compared to other tropical flora (Whitman et al. 2021). One of the oldest families in our study, Podocarpaceae, had a shallow ERR slope (0.13), with species' distributions within contemporary time periods constrained by competitive exclusion, rather than climate. Podocarpaceae species are typically restricted to habitat refugia in montane areas or soils with extreme nutrient limitation (Coomes and Bellingham 2011, Wilf and Kooyman 2023). At the other end of the evolutionary-age spectrum, *Rhododendron* (Ericaceae) is one of the youngest clades within Malesia, migrating into the tropics from temperate areas ~ 6 Mya (Webb and Ree 2012, Soza et al. 2022) and most likely colonizing montane or edaphically extreme habitats first, with leaf traits indicating stress-tolerance (Whitman 2018). Post hoc, we noted that *Rhododendron* had a richness peak at 2142 m a.s.l., ERR slope of -0.04 , but it is unclear if ecological strategy or point of origin is the stronger underlying mechanism. Other studies have noted differences in ERR support for flora with temperate, as compared to tropical, origins (Feng et al. 2016), especially within mid-elevation areas without physical barriers that can truncate potential range-sizes (Colwell and Lees 2000). For further post hoc insights on the importance of temperate origins, we grouped together species from families Hamamelidaceae, Juglandaceae, Magnoliaceae and Nyssaceae, and found that they also had a weak ERR slope of 0.17. A lingering question is how directionality of expansion (e.g. into the tropics versus out of the tropics) influences ERR trends and whether ecological strategies, such as stress-tolerance, also remain constant. If montane species can tolerate a wider span of abiotic conditions, a different unknown is

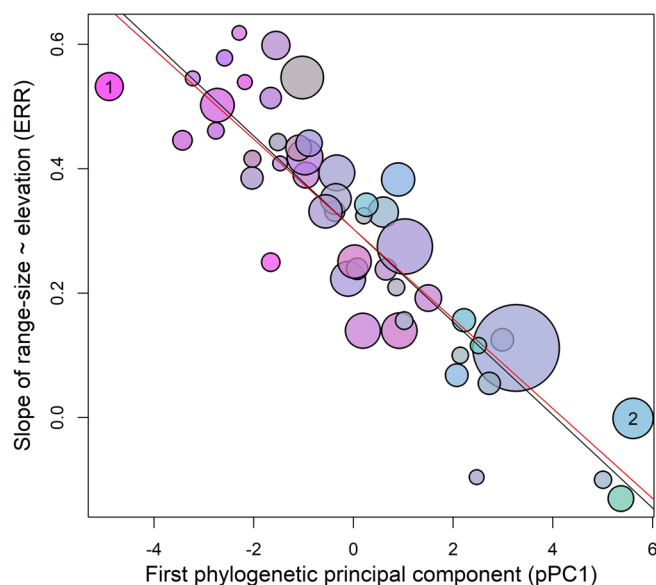


Figure 4. Linear regression of ERR slopes as a function of the first phylogenetic principal components (pPC1). Each point represents a species-rich plant family ($n = 49$), with size of point representative of Malesian richness. Two families labeled as examples for comparisons between plots: 1) Dipterocarpaceae and 2) Ericaceae. Negative pPC1 scores represent stronger Sundaland endemism (represented by magenta tones), as well as higher richness ratio, which is proportion of Malesian richness concentrated within a given 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.

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 (Rehm and Feeley 2015, Trethowan et al. 2023b, Wilf and Kooyman 2023).

Biogeographic complexities

Some of our results were unexpected and illustrate the complex ways that biogeographic affiliations and correlates influence elevational range-sizes. Wallacea *endemism* had a negative relationship with ERR slopes, whereas the overlap metric was positive (Table 1). Counter-intuitive results may have occurred because Wallacea is more centralized in terms of species interchange, yet is relatively dissimilar to Sundaland and Sahul when considering geologic history, climate, topography, and disturbances, with greater stressors such as fire disturbance and localized climatic conditions (aridity) contributing to habitat filtering (van Welzen et al. 2011, Hamilton et al. 2019, Trethowan 2021). Another surprise result was that species richness was non-significant with regards to ERR slopes across-families, which is counter to ubiquitous observations on the inverse relationship between richness and range-sizes (Sheldon et al. 2018, Guo et al. 2022). However, recent studies

have found no relationship between Rapoport's rule and rates of species diversification (Smyčka et al. 2023). Evolutionary age or latitudinal extent was also non-significant, but the potential nuances of seasonality response and inferred range-size breadth might be untangled via consideration of migration pathways and point of origin for a given clade. Further insights on the strengths and weaknesses of various factors could emerge via replication of analyses across Afrotropical, Neotropical, and Far Eastern tropical mountains, with each continent offering distinct biogeographic histories, degrees of monsoon seasonality, and species-level assemblages, but with unifying points of similarity at the family-level.

Conclusion

By comparing elevational distribution patterns for plants families of Malesia, this study offers insights on ecological mechanisms underlying elevational range-sizes and potential responses to changing environments. We found that lineages that have centers of richness in habitats and regions with long-term climatic stability, such as lowland forest or consistently equatorial landmasses, display average range-sizes that increase with elevation (positive ERR slopes, in support of Rapoport's rule). These 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 downwards 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.

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Melissa Whitman: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead);

Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Sabrina E. Russo**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.866t1g1x9> (Whitman and Russo 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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