ECOGRAPHY

Research

Edaphic specialization and vegetation zones define elevational range-sizes for Mt Kinabalu regional flora

Q1 **Melissa Whitman, Reed S. Beaman, Rimi Repin, Kanehiro Kitayama, Shin-Ichiro Aiba and Sabrina E. Russo**

M. Whitman (https://orcid.org/0000-0002-5947-0774) ✉ (islandevolution@gmail.com) and S. E. Russo, School of Biological Sciences, Univ. of Nebraska – Lincoln, Lincoln, NE, USA. – R. S. Beaman, Division of Biological Infrastructure, National Science Foundation, Alexandria, VA, USA. – R. Repin, Research and Education Division, Sabah Parks, Kota Kinabalu, Malaysia. – K. Kitayama, Graduate School of Agriculture, Kyoto Univ., Kitashirakawa Oiwake-cho, Kyoto, Japan. – S. Aiba, Faculty of Environmental Earth Science, Hokkaido Univ., Sapporo, Japan. SER also at: Center for Plant Science Innovation, Univ. of Nebraska – Lincoln, Lincoln, NE, USA.

Ecography
44: 1–12, 2021
doi: 10.1111/ecog.05873

Subject Editor: John-Arvid Grytnes
Editor-in-Chief: Miguel Araújo
Accepted 28 July 2021

Identifying physical and ecological boundaries that limit where species can occur is important for predicting how those species will respond to global change. The island of Borneo encompasses a wide range of habitats that support some of the highest richness on Earth, making it an ideal location for investigating ecological mechanisms underlying broad patterns of species distribution. We tested variation in richness and range-size in relation to edaphic specialization and vegetation zone boundaries using 3060 plant species from 193 families centered around the elevational gradient of Mt Kinabalu, Borneo. Across species, average range-size increased with elevation, consistent with Rapoport's rule. However, plants associated with ultramafic soil, which is low in nutrient and water availability and often has high concentrations of heavy metals, had larger range-sizes and greater richness than expected along the elevational gradient, as compared to a null model with randomization of edaphic association. In contrast, non-ultramafic species had smaller range-sizes and lower richness than expected. These results suggest that tolerance of resource limitation may be associated with wider rangesizes, whereas species intolerant of edaphic stress may have narrower range-sizes, possibly owing to more intense competition in favorable soil types. Using elevation as a predictor of average range-sizes, we found that piece-wise models with break-points at vegetation zone transitions explained species distributions better than models that did not incorporate ecological boundaries. The greatest relative increases in range-size with respect to elevation occurred mid-elevation, within the montane cloud forest vegetation zone. Expansion of average range-size across an area without physical boundaries may indicate a shift in ecological strategy and importance of biotic versus abiotic stressors. Our results indicate that elevational range-size patterns are structured by ecological constraints such as species' edaphic association, which may limit the ability of species to migrate up or down mountains in response to climate change.

Keywords: edaphic specialization, elevational range-size, Rapoport's rule, tropical mountains, ultramafic soil, vegetation zones

NORDIC SOCIETY OIKOS

www.ecography.org

Introduction

In an era of global change, shifting environmental conditions are affecting plant species' geographic and habitat distributions (Allen and Breshears 1998, Morueta-Holme et al. 2013, Tito et al. 2020). Therefore, it is imperative to understand the macroecological drivers of species' range-sizes as a means to anticipate how patterns of richness may also change (Pither 2003, Morin and Lechowicz 2013). Species' distribution patterns are not only affected by biogeographic and evolutionary history (MacArthur 1965, Janzen 1967, Lomolino 2001, Mittelbach et al. 2007), but also by their life history characteristics, such as pollen and seed dispersal modes, competitive strategy and degree of niche specialization (Klopfer and MacArthur 1961, Whittaker et al. 1973, May 1974, Hillebrand 2004, Morin and Chuine 2006, Russo et al. 2007, Morin and Lechowicz 2013). Greater stability of resource rich environmental conditions promotes survival of species with narrower ecological niches (Klopfer 1959, Janzen 1967, Slatyer et al. 2013), often indicated by smaller range-sizes. However as a tradeoff, smaller-ranged species may be more sensitive to climate change (Morin and Chuine 2006). Conversely, larger range-sizes require greater tolerance of environmental variation, including thermal limits and seasonal extremes (Pither 2003, Morin and Lechowicz 2013, Slatyer et al. 2013, Subedi et al. 2020).

A contentious empirical pattern observed at the macroscale is the monotonic increase in average range-size for species assemblages with increasing elevation and latitude for terrestrial ecosystems, or deeper water-depths for oceanic ecosystems, referred to as 'Rapoport's rule' (Stevens 1989, 1992, 1996), noted across a wide array of taxonomic groups (Lee et al. 2013, Tedersoo et al. 2014) and plant growth forms (Pither 2003, Zhou et al. 2019, Subedi et al. 2020) However there is considerable debate as to whether range-size trends are universal or indicative of underlying ecological mechanisms (Colwell and Hurtt 1994, Lyons and Willig 1997, Gaston et al. 1998, Weiser et al. 2007, Šizling et al. 2009, McCain and Bracy Knight 2013, Tomašových et al. 2016). Differences in average range-size at opposite ends of an environmental gradient are thought to arise because of species' adaptive responses to variation in habitat conditions. Species at the poleward portions of a latitudinal gradient experience pronounced seasonality, whereas species near equatorial areas experience greater stability of energy input and annual temperature (Francis and Currie 2003, Hawkins et al. 2003, Pither 2003). Analogously, on any given mountain, species observed nearest the summit are often subject to greater diurnal temperature variation as compared to species closer to sea level (Janzen 1967, Stevens 1992), but with differences possible between mountains (Grubb 1971, Tanner 1977, Kitayama 1992a). Range-size truncation can also be the result of species' position relative to physical boundaries (i.e. 'hard' boundaries), which makes occurrence beyond impossible, such as at sea-level (Colwell and Hurtt 1994, Šizling et al. 2009). Limits on range-size can also reflect ecological boundaries (i.e. 'soft' boundaries), which are transitions where significant habitat filtering occurs between adjacent areas or ecological systems (Gosz 1993), with locations that can fluctuate in time or space (Allen and Breshears 1998, Fiorentino et al. 2018).

While some factors affecting species' distributions on environmental gradients display smooth, continuous variation (e.g. a linear decline in mean daily temperature with increasing elevation), other factors can shift in an abrupt or non-continuous manner (e.g. soil nutrients), which adds complexity in the identification of ecological boundaries (Proctor et al. 1988, Fisher et al. 2013, van der Ent et al. 2016, Tito et al. 2020). Vegetation zones often corresponds with temperature and position of orographically generated persistent cloud layers that form at particular elevations (von Humboldt 1849, Holdridge et al. 1971, Gentry 1988, Kitayama 1992b, Bruijnzeel et al. 1993, Juvik and Nullet 1995, Jarvis and Mulligan 2011), or indicate changes in the underlying geological substrate (Cain 1944, Whittaker et al. 1973, Tanner 1977, Aiba and Kitayama 1999, van der Ent et al. 2016). On tropical mountains, the lowest elevation vegetation zones often experience intermittent rainfall, whereas middle-elevation vegetation zones have more consistent fog immersion, and the highest elevation vegetation zones experience infrequent moisture from mist (Vogelmann 1973, Kitayama 1992b, Juvik and Nullet 1995, Kudo and Suzuki 2004, Rehm and Feeley 2015). The tree-line is an ecological boundary since key physiological adaptations (e.g. freezing tolerance) are needed for species to occur above that threshold (Stevens and Fox 1991, Körner 1998, Rehm and Feeley 2015). Similarly, the minimum elevation for occurrence can reflect a species' thermal tolerance (Pither 2003, Feeley et al. 2020), with rising temperatures under climate change further truncating montane species distribution if upper elevation limits are fixed.

A less well examined ecological boundary is driven by variation in lithology, which creates edaphic conditions that influence plant species composition (Whittaker 1954, Kitayama et al. 1998, Kruckeberg 2002, Davies et al. 2005, Russo et al. 2005, van der Ent et al. 2016). For edaphically specialized species, the insular distribution of suitable soil patches can act as barriers for establishment. Patchy distribution of edaphic habitats not only leads to high rates of species turnover and endemism (Whittaker 1954, Harrison 1997, Kruckeberg 2002, Proctor 2003, Rajakaruna 2004, Isnard et al. 2016, van der Ent et al. 2016), but may also exacerbate the effects of climate change (Damschen et al. 2011, Rajakaruna 2018, Corlett and Tomlinson 2020). Soil type can even be a stronger predictor of habitat suitability than climate for the distribution of plants that specialize on very infertile soils (Harrison 1997, Fernandez-Going et al. 2012). Even within a given soil type, smaller-scale spatial variation in soil chemistry can further shape plant species composition (Proctor et al. 1988, 1998, van der Ent et al. 2014, 2016, 2018a). Edaphic specialization on infertile soils may be associated with tradeoffs in traits that enable tolerance of environmental stressors while reducing competitive ability within resource rich habitats (Grime 1977, Kazakou et al. 2008, Russo et al. 2008, Rajakaruna 2018).

Ultramafic soils are an example of highly infertile environments recognized globally for distinct plant communities with high rates of endemism (Proctor et al. 1988, 1998, Anacker 2011, Isnard et al. 2016, van der Ent et al. 2016, Galey et al. 2017). The term ultramafic soil is sometimes synonymous with ultrabasic (Proctor et al. 1988, Aiba and Kitayama 1999) or serpentine soil (Kruckeberg 2002, Proctor 2003, Brady et al. 2005) based on similarity of rock type from which they are derived, or grouped with unusual substrates with 'extreme edaphic' conditions (Rajakaruna 2004, 2018, Damschen et al. 2011, Corlett and Tomlinson 2020). Tropical ultramafic ecosystems differ from temperate counterparts based on degree of weathering from rain and temperature, elemental composition and organic matter (Galey et al. 2017, van der Ent et al. 2018b). Ultramafic soils are challenging to plant growth, as they tend to have reduced water retention, high deposits of heavy metals (e.g. nickel) and nutrients that are either limited (e.g. nitrogen or phosphorous), or in such excess (e.g. magnesium), that they require specialized physiological adaptations (Jenny 1980, Kruckeberg 2002, Proctor 2003, van der Ent et al. 2016). Vegetation on ultramafic soil is often reduced in stature, with plants exhibiting 'serpentine-syndrome' marked by stunted growth and reduced productivity (Jenny 1980, Aiba and Kitayama 1999, Kruckeberg 2002, Brady et al. 2005, van der Ent et al. 2016). However, there can be similarities of biomass or foliar characteristics of ultramafic and non-ultramafic communities in areas with compounding of abiotic stressors, or when the severity of edaphic stressors is mitigated via either greater resource efficiency or by other habitat characteristics that synthesize to help offset soil associated limitations (Grubb 1977, Aiba and Kitayama 1999, Kitayama and Aiba 2002, Isnard et al. 2016, van der Ent et al. 2016, Galey et al. 2017). Further ecological filtering can occur within areas of sparse vegetation which leads to elevated soil temperatures, high exposure stress, erosion and low soil moisture (Kruckeberg 2002, Brady et al. 2005, Ivalú Cacho and Strauss 2014). Adaptations to ultramafic soil may facilitate expansion into other ecological niches with very limited resource availability, such as former mining sites (van der Ent and Edraki 2018) or granite massifs (Kudo and Suzuki 2004).

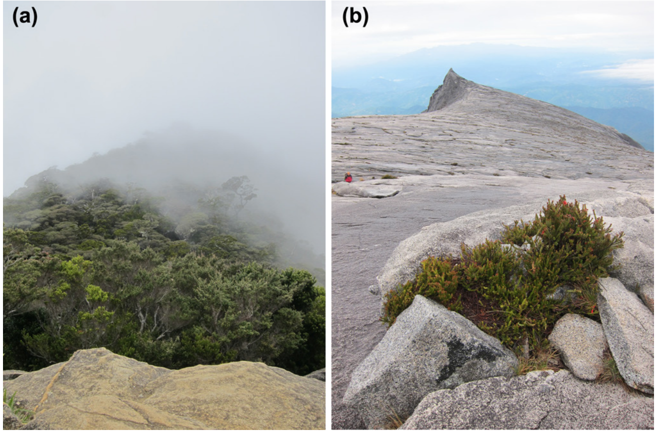
The goal of our study was to investigate how elevational patterns of species richness and range-size in the northern Bornean flora are structured by ecological boundaries defined by vegetation zonation and edaphic association. The study region included the tallest mountain in Southeast Asia, Mt Kinabalu (4095 m a.s.l.), a center of botanical research for more than a century (Stapf 1894, Meijer 1963, Steenis 1964, Cockburn 1978, Beaman and Beaman 1990, Kitayama 1992b, Kudo and Suzuki 2004, Beaman 2005, Grytnes and Beaman 2006, Argent et al. 2007, Aiba et al. 2015, van der Ent et al. 2016). While there is extensive knowledge about plant diversity of Mt Kinabalu (Beaman and Beaman 1990, Grytnes and Beaman 2006), especially for communities associated with ultramafic soil, how vegetation zonation and edaphic specialization shapes macroecological patterns of species richness and range-size is less explored. We assembled a dataset of 3060 vascular plant species from 193 families and compiled their elevational occurrences and edaphic associations, based on information from botanical monographs, scientific literature and comprehensive herbarium databases. We used model selection and null models to test whether vegetation zone boundaries and species' edaphic associations were important determinants of elevation-driven patterns in species richness and elevational range-size.

Material and methods

Database of species elevational distributions and edaphic associations

We assembled a database of all vascular plant species (trees, forbs, grasses, orchids and ferns) occurring in an area encompassing Mt Kinabalu, Mt Tomboyukon and the Crocker Range, within the Sabah region of northern Borneo (Malaysia). Northern Borneo is a global center of biodiversity (Barthlott et al. 1996, Galey et al. 2017), estimated to support over 8000 species, of which more than 5000 species occur within Mt Kinabalu Park (Beaman 2005, van der Ent et al. 2014, 2015, 2016). Ultramafic soil within Sabah totals 3500 km^2, or 4.6% of the regional landmass (Proctor et al. 1988), with discontinuous distribution from 400 to 2950 m a.s.l. (van der Ent et al. 2014, 2015, 2018a). Species preferring ultramafic soil (2854 species; van der Ent et al. 2016) may represent more than half of the plant richness of Mt Kinabalu Park, but this estimate may reflect more intensive sampling of atypical environments (McCain and Grytnes 2010). Species restricted to ultramafic soils include *Nepenthes rajah* (Nepenthaceae), *Rinorea bengalensis* (Violaceae) and *Phyllanthus balgooyi* (Phyllanthaceae), with the latter two having physiological means to hyperaccumilate heavy metals at levels toxic to most plants (Proctor 2003, van der Ent et al. 2014, 2016, 2018a). Other ultramafic associated flora associated include *Rhododendron*, podocarps, ferns and orchids (Aiba and Kitayama 1999, Argent 2006, Kitayama et al. 2011, van der Ent et al. 2014, Aiba et al. 2015). Some species, such as *Rhododendron ericoides* (Ericaceae), are restricted to ultramafic soil within mid-elevation shrublands, or exposed granite near the summit (Argent 2006), yet absent from non-ultramafic soil positioned between these two areas (Fig. 1a–b).

For species' elevational range-size we used the Sabah Parks herbarium database (Beaman 2005), which included 21 861 notes on elevation out of > 100 000 occurrence records queried. We also used 15 764 records from the Global Biodiversity Information Faculty (GBIF) for Malaysia, subsetted to match the Sabah Parks species list (<www.GBIF.org> (27 January 2018) GBIF Occurrence Download <https://doi.org/10.15468/dl.j7dfvv>), which helped represent species occurrence beyond the park boundaries. Information on elevation was also gathered from literature (Meijer 1963, Argent et al. 2007, van der Ent et al. 2014). The geographic area of this



Q2 Figure 1. Examples of vegetation of Mt Kinabalu. The first image (a) is of mid-elevation stunted forest and shrublands on ultramafic soil (~ 3000 m), and (b) is exposed granite with limited vegetation near the summit (~ 4000 m). Both sites shown support *Rhododendron ericoides*, a species absent from more nutrient rich soils positioned between these two sites.

study encompasses the greater Mt Kinabalu region, but it is possible that some species were sampled from adjacent areas.

To ensure data quality we excluded occurrence records that were: 1) without elevation, 2) were not identified to the species level or 3) potentially duplicated. Records flagged as extreme outliers, or with elevation noted as a rough estimate, were manually evaluated. Nomenclature errors were corrected using the Taxonomic Name Resolution Service (Boyle et al. 2013). For each species with at least two occurrences, we summarized elevation minimum and maximum as meters above sea level (m a.s.l.). We also excluded species with a single elevation record, as two observations are needed to calculate range-size, and species with a range-size of zero, because this can indicate under-sampling or possible nomenclature error. The final dataset accounting for elevation included 34 148 records with an average of 11 records (range of 2–126) per species.

For edaphic association, we categorized species as: 1) ultramafic specialists, 2) ultramafic tolerant species and 3) species with no association with ultramafic soil. First, we queried occurrence record descriptions using string matching of the term 'ultramafic', 'ultrabasic' or 'serpentine.' Next, we made a qualitative distinction between ultramafic specialists and tolerant species, based on summaries within the Sabah Parks database (Beaman 2005), which corresponded with 'The Plants of Mount Kinabalu' v1:5 monograph series (Parris et al. 1992, Wood et al. 1993, Beaman and Beaman 1998, Beaman et al. 2001, Beaman and Anderson 2004), and notes from other literature (Stapf 1894, Meijer 1963, Aiba and Kitayama 1999, Argent et al. 2007, van der Ent et al. 2014, 2018b, Aiba et al. 2015). We defined 'ultramafic specialists' as species that predominately or exclusively occur on ultramafic soils; analogous to ultramafic 'obligate association' or 'preferential' by van der Ent et al. (2014). We also referred to specialist keywords including 'indicator species,' 'hyperaccumulators', 'extreme,' or 'especially' or 'often' on ultramafic soil. It is possible for outlier ultramafic specialists to occur on other infertile soil types or high elevation areas where ultramafic soil is absent (> 3000 m a.s.l.). We defined 'ultramafic tolerant' as species that occasionally, but not predominantly, occur on ultramafic soil; analogous to 'facultative' species by van der Ent et al. (2014), or by keywords 'sometimes,' 'probably,' or 'possibly' occurring on ultramafic soil. Ultramafic tolerant species may have an opportunistic or ruderal life history strategy (Grime 1977), occurring at sites with natural or anthropogenic disturbance (e.g. edges of roads, mudslides, post-fire areas). 'Non-ultramafic association' was defined as species that are edaphic generalists with no known soil affiliation, that are repelled by ultramafic soil, or that are associated with other soil types.

Our final dataset included 3060 species, from 879 genera and 193 families (available on Dryad). Q3 Most species were categorized as having a non ultramafic edaphic association, representing 1895 species (62% of the total richness), followed by 641 (21%) ultramafic tolerant species, and 524 (17%) ultramafic specialist species (Supporting information). Taxonomic distribution at the family level was relatively even, in that most families had at least one species represented within each edaphic association category (Supporting information). As we limited the dataset to species with at least two records to reduce bias, as described above, our analyses do not necessarily capture rare nor under-collected species.

Species richness and elevation range-size patterns with respect to ecological boundaries

Following Stevens (1992), elevational range-size (extent) was calculated as the difference between maximum and minimum elevations for each species (without rounding), assuming species occurred continuously between those two points. We partitioned the elevational gradient (0 – 4095 m a.s.l.) into 100 m bins, for a total of 41 elevation bins. Within each bin, individual species were either present (1) or absent (0), with the sum representing species richness. Average range-size in each bin was calculated as the sum of range-size values for species present, divided by richness. Across the gradient, we estimated the peak in richness as the bin with the greatest number of species.

To evaluate whether elevational richness and range-size patterns of species differed by edaphic associations, we used a null model. Species' edaphic association was randomly shuffled 1000 times without replacement, and species richness and range-size in each bin were calculated at each iteration to produce null distributions. The total number of species in each edaphic association was kept constant, as were the paired values for species' elevation minimum and maximum. Whether the species richness or range-size was significantly smaller or larger than expected by chance was determined based on the rank of the observed value for richness or range-size relative to the lower 2.5% and upper 97.5% confidence intervals of the null distribution of values for that bin.

The elevational gradient of Mt Kinabalu includes multiple vegetation zones (at least three) but with inconsistent descriptions of their boundaries (Stapf 1894, Meijer 1963, Cockburn 1978, Kitayama 1992b, van der Ent et al. 2016). The first vegetation zone at low-elevations encompasses lowland dipterocarp and hill forests, with oxisol soils and tropical climate (Kitayama 1992b). The second vegetation zone at mid-elevations groups together lower montane and upper montane forests, with spodosol/histosol soils and warm (comparable to temperate climate in terms of annual thermal index) climate in an area overlapping the cloud belt (Kitayama 1992b). Mid-elevation habitat is sometimes subdivided; however, we opted to merge lower/upper montane habitats because the transition is gradual. The third vegetation zone at high-elevations includes subalpine and alpine scrublands, with inceptisol to entisol soils underlain by granitic rock, with cool (comparable to polar climate) marked by occasional freezing events (Kitayama 1992b).

To quantify how vegetation zonation and edaphic specialization affected variation in elevational range-sizes as a function of elevation, we fit a series of linear regression and piece-wise models separately for each edaphic association (non-ultramafic, ultramafic tolerant, ultramafic specialists). The first model ('no boundaries model') was the simplest, using linear regression with elevation as the predictor and no vegetation zonation. The no boundaries model was also fit using all 3060 species for comparison to other studies on Rapoport's rule. The second model ('fixed boundaries model') allowed for comparisons of slope by piece-wise section, with the assumption of identical vegetation zone boundaries across edaphic associations.

With started with natural history observations of vegetation zone transitions at ~ 1200 and 2800 m a.s.l. by Kitayama (1992b), but with a search of possible breakpoints nearby. We fit piece-wise regressions separately for each edaphic association and compared models with low and high elevation breakpoints, chosen among possible values every 100 m from 900 to 1500 m a.s.l. and from 2500 to 3100 m a.s.l. The most supported breakpoints for each transition were averaged, with the final fixed boundaries model breakpoints placed at 1500 and 2700 m a.s.l. The third model, the 'fluid boundaries model,' allowed the data to determine the position of vegetation zone boundaries for each edaphic association. We identified the best fit breakpoints for each edaphic association using the R package strucchange (Zeileis et al. 2001). The fluid boundaries model had no predetermined number or position of breakpoints, but we required that each vegetation zone span at least 600 m. For each edaphic association we used Akaike's information criterion (AIC) to select the best model (Akaike 1974).

Results

Across 3060 vascular plant species, the peak in species richness was in the 1200 m a.s.l. elevation bin, where 1811 species (59%) occurred (Fig. 2). Species from both non-ultramafic and ultramafic tolerant edaphic associations also displayed a peak in richness at 1200 m a.s.l. (Fig. 3), with 1065 non-ultramafic species (56%) and 414 of the ultramafic tolerant species (65%) occurring there. For ultramafic species, the peak in richness was at a higher elevation, 1500 m a.s.l. (Fig. 3), with 360 species (69%).

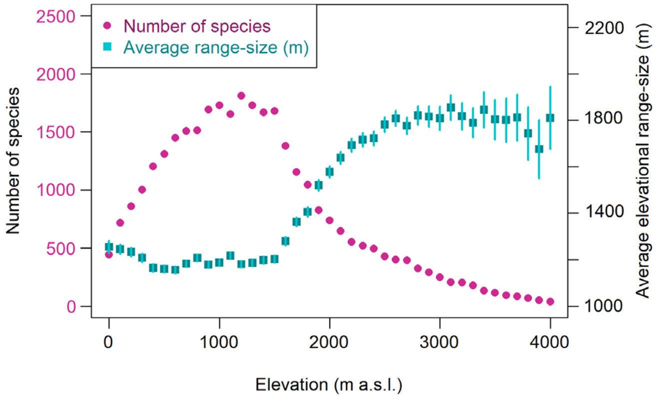


Figure 2. Variation in species richness (left ordinate) and elevation range-size in meters (right ordinate) of 3060 plant species with elevation on the island of Borneo. Range-size values represent the mean (point) and ± one standard error (bar) across species for each 100 m elevation bin.

Within an elevation bin, richness for non-ultramafic species was significantly lower than predicted by the null model (Fig. 3). In contrast, ultramafic tolerant and specialist species displayed greater richness than expected (Fig. 3) across most of the gradient. Non-ultramafic species had significantly smaller range-sizes than null model expectations in every elevation bin (Fig. 4a), whereas ultramafic tolerant and specialist species tended to have larger range-sizes across the gradient (Fig. 4b–c).

Across all 3060 species, average range-size was 962.3 ± 617.7 m (min = 5 m, max = 3690 m), but with deviation

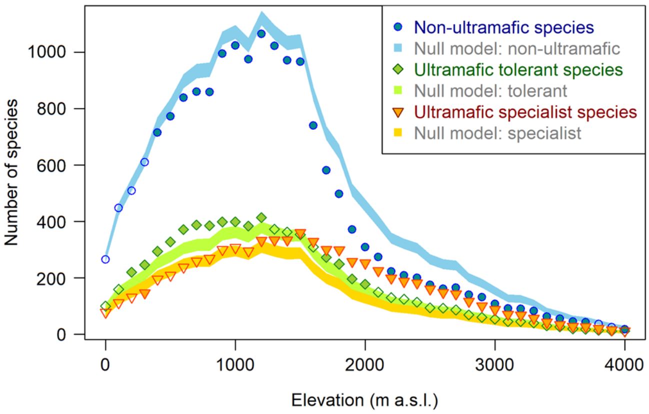


Figure 3. Variation in species richness of vascular plants along an elevation gradient on the island of Borneo, for species categorized in three edaphic associations. Observed values are shown as points, and ribbons, represent 95% confidence intervals based on a null model that randomized edaphic associations. Filled and unfilled points indicate observed values that differed and did not differ significantly from null model predictions, respectively.

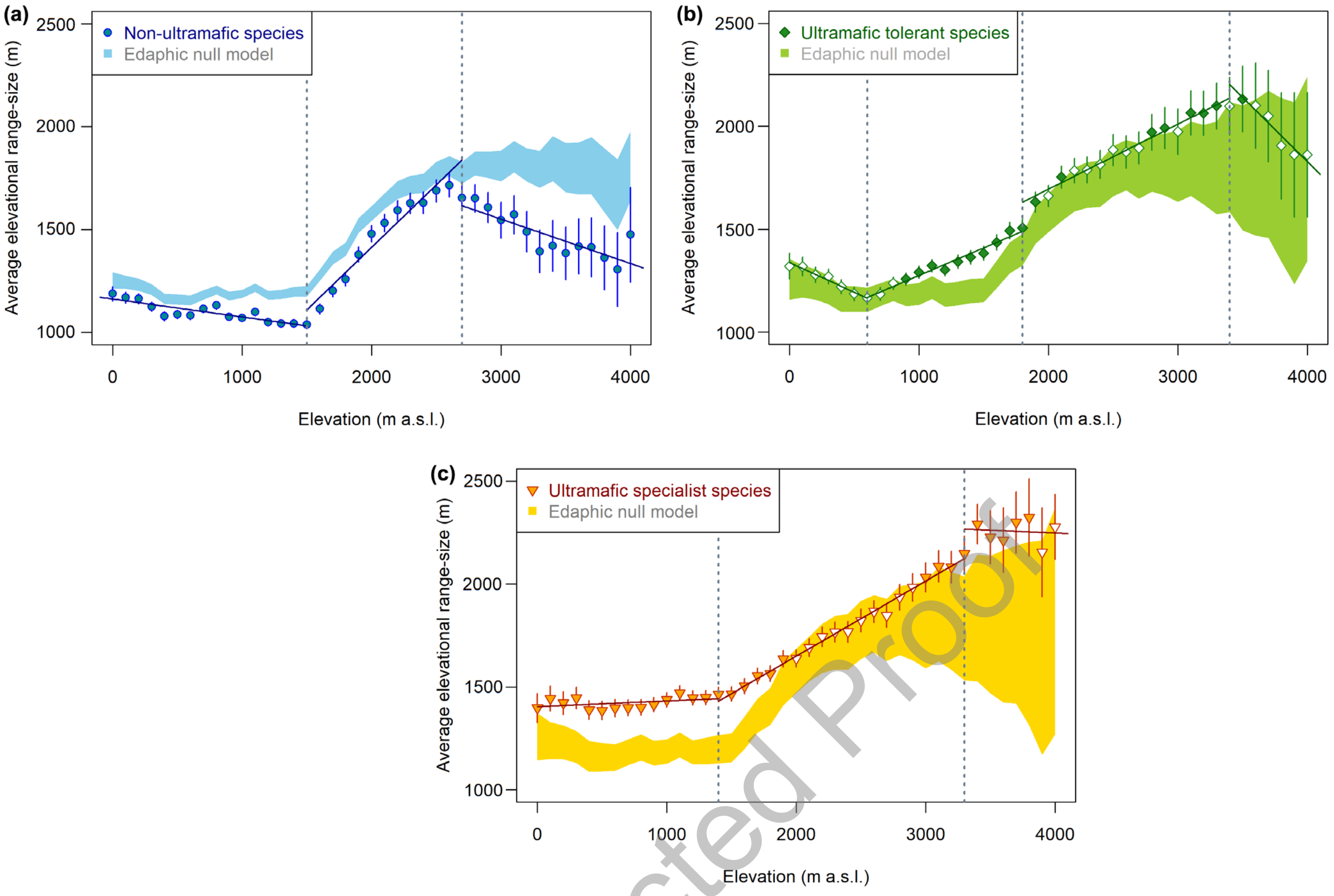


Figure 4. Variation in the average elevation range-size along a Bornean elevation gradient for vascular plant species in three edaphic associations (a) non-ultramafic, (b), ultramafic tolerant and (c) ultramafic specialist species. Elevation breakpoints along the x-axis indicate the most-supported model for each edaphic specialization category (Table 1) and indicate transitions between vegetation zones. Ribbons represent 95% confidence intervals based on a null model randomizing species edaphic association 1000 times, while keeping richness constant. Points represent observed values; filled versus unfilled points show whether the observed value was significantly different or not from the null model.

from the mean most apparent at opposite ends of the elevation gradient. Species positioned near sea-level had smaller range-sizes whereas species towards the summit of Mt Kinabalu had larger range-sizes, thus lending general support for Rapoport's rule (linear regression, $F = 177.6$, $df = 39$, adjusted $R^2 = 0.82$, $p < 0.001$). Across the gradient, the pattern of range-size variation was relatively consistent at lower elevations (slope near zero), followed by a rapid increase in average range-sizes starting at ∼ 1600 m a.s.l. (steep positive slope), and then values plateauing at higher elevations (Fig. 2).

Piece-wise models that accounted for vegetation zones (fixed boundaries model, fluid boundaries model) were always more supported than the model that did not account for vegetation zones (no boundaries model), regardless of edaphic association. However, the best fit models differed in the quantity and position of breakpoints representing vegetation zone boundaries (Table 1, Fig. 4a–c; Supporting information). For non-ultramafic species, the fixed boundaries model had the most support, with pre-assigned breakpoints at 1500 and 2700 m a.s.l. (Table 1, Fig. 4a, Supporting information). For ultramafic tolerant species, the fluid boundaries model was selected, with fitted breakpoints at 600, 1800 and 3400 m a.s.l. (Table 1, Fig. 4b, Supporting information). For ultramafic specialists, the fluid boundaries mModel was also selected, but with breakpoints at 1400 and 3300 m a.s.l. (Table 1, Fig. 4c, Supporting information). Overall, non-ultramafic species tended to have smaller range-sizes, with abrupt changes in slope across different portions of the elevation gradient (slope of −0.09 across low-elevations, 0.61 middle-elevations, −0.22 high-elevations), shown in Fig. 4a and in the Supporting information. In contrast, species associated with ultramafic soil tended to have larger range-sizes with less variation in size, leading to more subtle changes in slope between vegetation zones (Fig. 4b–c, Supporting information).

Discussion

Identifying ecological constraints on where species can occur is fundamental to understanding the drivers of large-scale

Table 1. Model selection using Akaike information criterion (AIC) comparing three different types of models for each edaphic association category. The first model is based on linear regression; the second model is using piece-wise regression with forced breakpoints based on observations of vegetation zone boundaries; the third model is also based on piece-wise regression, but with non-forced breakpoints that reflect points of dramatic change in the data trends. Deltas with the lowest value indicate the top model selected (shown in black); rejected models shown in grey.

	AIC	*K*	Deltas
Non-ultramafic models			
Linear model[1]	538.6	3	96.4
Piece-wise, fixed breakpoints (1500, 2700 m)*[2]	**442.2**	**9**	**0**
Piece-wise, fitted breakpoints(1400, 2000, 2600, 3200 m)[3]	451.2	13	9.0
Ultramafic tolerant models			
Linear model[1]	514.8	3	125.3
Piece-wise, fixed breakpoints (1500, 2700 m)[2]	471.0	9	81.5
Piece-wise, fitted breakpoints (600, 1800, 3400 m)*[3]	**389.5**	**11**	**0**
Ultramafic specialists models			
Linear model[1]	494.4	3	82.1
Piece-wise, fixed breakpoints (1500, 2700 m)[2]	435.8	9	23.4
Piece-wise, fitted breakpoints (1400, 3300 m)*[3]	**412.3**	**9**	**0**

**Best model.*
[1] Referred to as ‘no boundaries model’.
[2] Referred to as the ‘fixed boundaries model’.
[3] Referred to as the ‘fluid boundaries model’.

patterns of species diversity. Using a dataset of the occurrence of 3060 vascular plant species in Borneo, here we demonstrated that edaphic specialization and vegetation zonation structures elevational range-sizes and richness along an elevation gradient, ultimately shaping elevational patterns in vascular plant richness. In addition, we found greater similarity in range-size patterns between ultramafic specialists and tolerant species, compared to non-ultramafic species, possibly illustrating tradeoffs of different life history strategies and responses to environmental stressors or competition. The varying lithological and climatic conditions, along with the extremely high species richness of our study region, provides a powerful system in which to investigate how physical and ecological boundaries affect species' distributions. Our study highlights the importance of considering such constraints, as they may limit the ability of species to migrate in response to global change.

Differences in distribution of richness and range-size by edaphic association

In this study, species richness was highest at ~ 1200 m a.s.l., a result that is comparable to prior studies on vascular plants for Mt Kinabalu (Grytnes and Beaman 2006) despite differences in methods used. A mid-elevation peak in richness is a relatively common observation, however there are conflicting explanations for it (Terborgh 1977, Sanders 2002, Vetaas and Grytnes 2002, Rahbek 2004, Grytnes et al. 2008, McCain and Grytnes 2010, van der Ent et al. 2016). The mid-domain effect states that a richness peak at mid-elevations arises because random range-sizes and distributions have higher chances of overlapping towards the center of the gradient (Colwell and Lees 2000, Grytnes et al. 2008). Geometric constrains (i.e. physical boundaries) can also shift how richness is distributed via truncation of potential range-sizes when approaching each end of the gradient (Colwell and Lees 2000, Grytnes et al. 2008). A mid-elevation richness peak may also arise as a result of species–area relationships (Sanders 2002).

There are also ecological drivers of mid-elevation peaks in species richness. Mid-elevation areas may be a transition zone that supports species from multiple ecological niches or habitat types (Klopfer and MacArthur 1961). In the instance of Mt Kinabalu, mid-elevation areas may support co-occurrence for species from both tropical lowland and lower montane forests (Kitayama 1992b). A reduction of species richness at lower elevations might also indicate disproportionate levels of anthropogenic disturbance, such as deforestation beyond the Mt Kinabalu Park boundaries (Phua et al. 2008). The non-linear or discontinuous distribution of a key resource (e.g. fog mist, essential elements) may support higher species richness within an atypical portion of the gradient. For species ultramafic soil specialists, we found the peak in richness to be positioned at a higher elevation (~ 1500 m a.s.l.), which may represent the mid-point of where most ultramafic outcrops occur. The 1500 m a.s.l. area is also approximately where tree species richness declines and non-woody richness increases for orchids, pteridophytes, grasses and herbaceous plants (Grytnes and Beaman 2006, van der Ent et al. 2016). As ultramafic specialist species are generally shorter-statured (Jenny 1980, Aiba et al. 2015), higher elevation areas may be where they are at less of a competitive disadvantage in terms of light interception.

Elevational range-size may be an indicator of species' ecological niche breadth or of sensitivity to variation in environmental conditions (Morin and Chuine 2006, Essl et al. 2009, Morin and Lechowicz 2013). Smaller range-sizes are associated with specialization in a narrow set of habitat conditions and can reflect distribution limitations across ecological barriers, as in the hypothesis that the ‘mountain passes are higher in the tropics’ (Janzen 1967), and may facilitate higher rates of endemism (Essl et al. 2009). Narrow niches can also be generated via interspecific competition (Hutchinson 1959, Levin 1970, MacArthur 1972, Whittaker et al. 1973, Stevens 1992, Morin and Chuine 2006) and is a hypothesis for high diversity observed in tropical regions (Orians 1969, Vázquez and Stevens 2004). We found that even though non-ultramafic species accounted for the greatest number of total species across the gradient as a whole, this group had both lower than expected richness and average range-size within any given elevation bin, compared null expectations. In contrast, species associated with ultramafic soil (specialists and tolerant species) had larger than expected range-sizes, and thus higher richness within any given elevation bin. These observations are consistent with the hypothesis that adaptations for tolerance of soil infertility may make species more able to tolerate other stressors, such as those caused by climatic variation, producing wider niches, whereas species associated with more fertile soils may be more competitive, but less stress tolerant, producing narrower niches (Grime 1977). Distribution patterns of ultramafic associated species may also reflect non-climate based factors such as seed dispersal distance (Morin and Chuine 2006). Our finding of larger range-sizes for ultramafic associated species was counter to expectations from other studies on serpentine endemics in Austria that found these species had the smallest ranges of any vegetation group examined (Essl et al. 2009). One explanation is that there is a divergence between the size of the 'fundamental niche' of ultramafic species at the macroscale, which includes tolerance of multiple climate and edaphic stressors, versus the size of their 'realized niche' at the local scale where populations are restricted to patches of nutrient or moisture limited soil via competitive exclusion from adjacent resource-rich areas (Vetaas 2002, Wright et al. 2006).

Elevation range-size depends on more than just elevation

A general paradigm in macroecology is that species occurring at lower elevations will have smaller elevational range-sizes, whereas those at higher elevations will have larger range-sizes (i.e. Rapoport's rule). Based on all vascular plant species occurring on Mt Kinabalu and neighboring areas, we found support for Rapoport's rule. However, this overall relationship does not tell the full story, since the best fit models were those that incorporated disjunctions caused by ecological dynamics, such as vegetation zonation and edaphic specialization. Interestingly, the mid-elevation section of the gradient had the strongest asymmetry in range-sizes for all edaphic associations (i.e. steepest positive slope), which is notable because it is also furthest from hard physical boundaries of sea level and mountain top. One interpretation is that for non-ultramafic species within the mid-elevation segment, the relatively steeper positive slope may be due to a shift in ecological strategy from competition driven dynamics at lower elevations (reflected by narrower range-sizes) towards a more stress tolerant strategy with increasing elevation (reflected by broader range-sizes). In contrast, species associated with ultramafic soil had less variation in range-sizes, and thus similarity of piece-wise slopes across gradient sections examined, suggesting a more consistent ecological strategy based on stress tolerance regardless of position along the elevation gradient. Future use of piece-wise regression or other nonlinear analyses may be useful as a means to compare vegetation zone boundaries, using metrics such as atmospheric moisture content (Cockburn 1978, Kitayama 1992a, Juvik and Nullet 1995) or soil chemistry (van der Ent et al. 2016) rather than elevation, with consideration of the Massenerhebung effect (Schröter et al. 1908, Grubb 1971, Proctor et al. 1988, Bruijnzeel et al. 1993). To generalize our findings, exploration of latitudinal range-size trends for other types of edaphic specialists would also be informative, including comparisons between Mediterranean serpentine ecosystems and tropical ultramafic sites (Damschen et al. 2011, Galey et al. 2017, Rajakaruna 2018), or other habitat types (e.g. granite inselbergs, karsts, white sand) with extreme edaphic stress (Prance 1996, Porembski and Barthlott 2000, Whitman et al. 2011, Rajakaruna 2018).

Concluding remarks

Accounting for ecologically distinct plant communities, whether defined by vegetation zones or edaphic association, is critical for understanding macroecological patterns of species richness and elevational range-size. Limitations on where species occur, or can migrate to, may indicate tradeoffs in ecological strategy or response to climate change. At the species level, a larger elevational range-size implies tolerance of a wider suite of environmental conditions. Paradoxically for ultramafic associated species, adaptations for extreme edaphic stressors may facilitate expansion into novel nutrient limited habitat types, potentially mitigating risks from climate change. However, an upward shift in vegetation zones can still threaten ultramafic species, to the extent that it results in taller vegetation stature that could cause competitive exclusion. Range truncation may also occur for species with strong fidelity to a single soil type if that soil type is not available at elevations that become more climatically suitable. Conversely, narrower range-sizes implies specificity of habitat requirements that may lead to greater sensitivity to climate change. Research on how tolerance of environmental variation trades off with traits that influence the migratory ability of plants, such as fecundity, seed dispersal and seed survival, is necessary, as such tradeoffs may constrain species' long-term resilience to climate change.

Acknowledgements – We thank all the people that have contributed to the rich botanic knowledge of the Sabah region of Borneo; expansive herbarium records have enabled studies such as this to explore macroscale questions. In memoriam of John H. Beaman and George Argent for their contributions to our knowledge of the flora of Mt Kinabalu. Additional thanks to John-Arvid Grytnes, Antony van der Ent, John Delong, Ken Feeley, Sheri Fritz, Diana Pilson and Dave Wedin.

Funding – MW was supported by funds from National Science Foundation Graduate Research Fellowship Program, as well as the University of Nebraska School of Biological Sciences Special Fund, associated with the Gretchen Beghtol Lee Fund, Myrle M. Burk Botany Memorial Fund and the Amanda H. Heppner Fellowship Fund.

Author contributions

Melissa Whitman: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead). **Reed S. Beaman**: Data curation (equal); Resources (equal). **Rimi Repin**: Data curation (equal); Resources (equal). **Shin-Ichiro Aiba**: Conceptualization (supporting); Writing – review and editing (supporting). **Kanehiro Kitayama**: Conceptualization (supporting); Writing – review and editing (supporting). **Sabrina E. Russo**: Supervision (lead); Writing – review and editing (lead). Q4

Transparent Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.05873>.

Q5 Data availability statement

Q6 Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.XXXXX> (Whitman et al. 2021).

References

Aiba, S. and Kitayama, K. 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. – Plant Ecol. 140: 139–157.

Aiba, S. et al. 2015. Structure, floristics and diversity of tropical montane rain forests over ultramafic soils on Mount Kinabalu (Borneo) compared with those on non-ultramafic soils. – Aust. J. Bot. 63: 191.

Akaike, H. 1974. A new look at the statistical model identification. – IEEE Trans. Autom. Control 19: 716–723.

Allen, C. D. and Breshears, D. D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. – Proc. Natl Acad. Sci. USA 95: 14839–14842.

Anacker, B. L. 2011. Phylogenetic patterns of endemism and diversity. – In: Harrison, S. P. and Rajakaruna, N. (eds), Serpentine: the evolution and ecology of a model system. Univ. of California Press, pp. 49–70.

Argent, G. 2006. Rhododendrons of the subgenus Vireya. – R. Hort. Soc., London, UK.

Argent, G. et al. 2007. The rhododendrons of Sabah, Malaysian Borneo. – Natural History Publications (Borneo), Kota Kinabalu.

Barthlott, W. et al. 1996. Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. – Erdkunde 50: 317–327.

Beaman, J. H. 2005. Mount Kinabalu: hotspot of plant diversity in Borneo. – In: Friis, I. and Balsley, H. (eds), Plant diversity and complexity patterns: local, regional and global dimensions. Proc. Int. Symp. held at the R. Danish Acad. Sci. and Letters in Copenhagen, Denmark, May, 2003. Det Kongelige Danske Videnskabernes Selskab, Copenhagen, pp. 103–127.

Beaman, J. H. and Anderson, C. 2004. The plants of Mount Kinabalu. v5. Dicotyledon families Magnoliaceae to Winteraceae. – Natural History Publications (Borneo), Kota Kinabalu, in association with Royal Botanical Gardens, Kew, Kota Kinabalu.

Beaman, J. H. and Beaman, R. S. 1990. Diversity and distribution patterns in the flora of Mount Kinabalu. – In: Baas, P. et al. (eds), The plant diversity of Malesia. Springer, pp. 147–160.

Beaman, J. H. and Beaman, R. S. 1998. The plants of Mount Kinabalu. v3. Gymnosperms and non-orchid monocotyledons. – Natural History Publications (Borneo), Kota Kinabalu, in association with R. Bot. Gard.Kew.

Beaman, J. H. et al. 2001. The plants of Mount Kinabalu. v4. Dicotyledon families Acanthaceae to Lythraceae. – Natural History Publications (Borneo), Kota Kinabalu, in association with R. Bot. Gard.Kew, Kota Kinabalu.

Boyle, B. et al. 2013. The taxonomic name resolution service: an online tool for automated standardization of plant names. – BMC Bioinf. 14. Q7

Brady, K. U. et al. 2005. Evolutionary ecology of plant adaptation to serpentine soils. – Annu. Rev. Ecol. Evol. Syst. 36: 243–266.

Bruijnzeel, L. A. et al. 1993. Hydrological observations in montane rain forests on Gunung Silam, Sabah, Malaysia, with special reference to the 'Massenerhebung' effect. – J. Ecol. 81: 145–167.

Cain, S. A. 1944. Foundations of plant geography. – Harper and Brothers, New York, NY, USA.

Cockburn, P. F. 1978. The flora. – In: Kinabalu, Summit of Borneo. Sabah Society Monographs, Kota Kinabalu, pp. 179–190.

Colwell, R. K. and Hurtt, G. C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. – Am. Nat. 144: 570–595.

Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. – Trends Ecol. Evol. 15: 70–76.

Corlett, R. T. and Tomlinson, K. W. 2020. Climate change and edaphic specialists: irresistible force meets immovable object? – Trends Ecol. Evol. 35: 367–376.

Damschen, E. I. et al. 2011. Climate change and plant communities on unusual soils. – In: Harrison, S. P. and Rajakaruna, N. (eds), Serpentine: the evolution and ecology of a model system. Univ. of California Press, pp. 359–382.

Davies, S. J. et al. 2005. Soil-related floristic variation in a hyperdiverse dipterocarp forest. – In: Pollination ecology and the rain forest. Springer, pp. 22–34.

Essl, F. et al. 2009. Distribution patterns, range size and niche breadth of Austrian endemic plants. – Biol. Conserv. 142: 2547–2558.

Feeley, K. et al. 2020. The thermal tolerances, distributions and performances of tropical montane tree species. – Front. For. Global Change 3: 25.

Fernandez-Going, B. M. et al. 2012. Temporal variability in California grasslands: soil type and species functional traits mediate response to precipitation. – Ecology 93: 2104–2114.

Fiorentino, D. et al. 2018. On the art of classification in spatial ecology: fuzziness as an alternative for mapping uncertainty. – Front. Ecol. Evol. 6: 231.

Fisher, J. B. et al. 2013. Nutrient limitation in rainforests and cloud forests along a 3000-m elevation gradient in the Peruvian Andes. – Oecologia 172: 889–902.

Francis, A. P. and Currie, D. J. 2003. A globally consistent richness–climate relationship for angiosperms. – Am. Nat. 161: 523–536.

Galey, M. L. et al. 2017. Ultramafic geoecology of South and Southeast Asia. – Bot. Stud. 58: 1–28.

Gaston, K. J. et al. 1998. Rapoport's rule: time for an epitaph? – Trends Ecol. Evol. 13: 70–74.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. – Ann. Miss. Bot. Gard. 75: 1–34.

Gosz, J. R. 1993. Ecotone hierarchies. – Ecol. Appl. 3: 369–376.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – Am. Nat. 111: 1169–1194.

Grubb, P. J. 1971. Interpretation of the 'Massenerhebung' effect on tropical mountains. – Nature 229: 44–45.

Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. – Annu. Rev. Ecol. Syst. 8: 83–107.

Grytnes, J. A. and Beaman, J. H. 2006. Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. – J. Biogeogr. 33: 1838–1849.

Grytnes, J.-A. et al. 2008. The mid-domain effect matters: simulation analyses of range-size distribution data from Mount Kinabalu, Borneo. – J. Biogeogr. 35: 2138–2147.

Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. – Ecology 78: 1898–1906.

Hawkins, B. A. et al. 2003. Energy, water and broad-scale geographic patterns of species richness. – Ecology 84: 3105–3117.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. – Am. Nat. 163: 192–211.

Holdridge, L. R. et al. 1971. Forest environments in tropical life zones: a pilot study. – Pergamon Press.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? – Am. Nat. 93: 145–159.

Isnard, S. et al. 2016. How did the ultramafic soils shape the flora of the New Caledonian hotspot? – Plant Soil 403: 53–76.

Ivalú Cacho, N. and Strauss, S. Y. 2014. Occupation of bare habitats, an evolutionary precursor to soil specialization in plants. – Proc. Natl Acad. Sci. USA 111: 15132 151 7.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – Am. Nat. 101: 233–249.

Jarvis, A. and Mulligan, M. 2011. The climate of cloud forests. – Hydrol. Processes 25: 327–343

Jenny, H. 1980. State factor parent material. – In: Ecological studies 37. The soil resource: origin and behavior. Springer, pp. 246–275.

Juvik, J. O. and Nullet, D. 1995. Relationships between rainfall, cloud-water interception and canopy throughfall in a Hawaiian montane forest. – In: Tropical montane cloud forests. Ecological studies (analysis and synthesis), vol. 110. Springer, pp. 165–182.

Kazakou, E. et al. 2008. Hypotheses, mechanisms and tradeoffs of tolerance and adaptation to serpentine soils: from species to ecosystem level. – Biol. Rev. 83: 495–508.

Kitayama, K. 1992a. Comparative vegetation analysis on the wet slopes of two tropical mountains: Mt Haleakala, Hawaii and Mt Kinabalu, Borneo. – PhD thesis, Univ. of Hawaii.

Kitayama, K. 1992b. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. – Vegetatio 102: 149–171.

Kitayama, K. and Aiba, S. I. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. – J. Ecol. 90: 37–51.

Kitayama, K. et al. 1998. Soil nitrogen mineralization rates of rainforests in a matrix of elevations and geological substrates on Mount Kinabalu, Borneo. – Ecol. Res. 13: 301–312.

Kitayama, K. et al. 2011. The ecology of podocarps in tropical montane forests of Borneo: distribution, population dynamics and soil nutrient acquisition. – Ecol. Podocarpaceae Trop. For. 95: 101–117.

Klopfer, P. H. 1959. Environmental determinants of faunal diversity. – Am. Nat. 93: 337–342.

Klopfer, P. H. and MacArthur, R. H. 1961. On the causes of tropical species diversity: niche overlap. – Am. Nat. 95: 223–226.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Q8

Kruckeberg, A. R. 2002. Geology and plant life. – Univ. of Washington Press, Seattle.

Kudo, G. and Suzuki, S. 200 Flowering phenology of tropical-alpine dwarf trees on Mount Kinabalu, Borneo. – J. Trop. Ecol. 20: 563–571.

Lee, C.-B. B. et al. 2013 Altitudinal patterns of plant species richness on the Baekdudaegan Mountains, South Korea: mid-domain effect, area, climate and Rapoport's rule. – Ecol. Res. 28: 67–79.

Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. – Am. Nat. 104: 413–423.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. – Global Ecol. Biogeogr. 10: 3–13.

Lyons, S. K. and Willig, M. R. 1997. Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. – Oikos 79: 568–580.

MacArthur, R. H. 1965. Patterns of species diversity. – Biol. Rev. 40: 510–533.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. – Harper and Rowe, NY, USA.

May, R. M. 1974. On the theory of niche overlap. – Theor. Popul. Biol. 5: 297–333.

McCain, C. M. and Bracy Knight, K. 2013. Elevational Rapoport's rule is not pervasive on mountains. – Global Ecol. Biogeogr. 22: 750–759.

McCain, C. M. and Grytnes, J.-A. 2010. Elevational gradients in species richness. – Encyclopedia of Life Sciences, pp. 1–10.

Meijer, W. 1963. A botanical guide to the flora of Mount Kinabalu. – In: Symosium on ecological research on humid tropical vegetation (Kuching). UNESCO and Government of Sarawak, Kuching, pp. 325–366.

Mittelbach, G. G. et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. – Wiley.

Morin, X. and Chuine, I. 2006. Niche breadth, competitive strength and range size of tree species: a tradeoff based framework to understand species distribution. – Ecol. Lett. 9: 185–195.

Morin, X. and Lechowicz, M. J. 2013. Niche breadth and range area in North American trees. – Ecography 36: 300–312.

Morueta-Holme, N. et al. 2013. Habitat area and climate stability determine geographical variation in plant species range sizes. – Ecol. Lett. 16: 1446–1454.

Orians, G. H. 1969. The number of bird species in some tropical forests. – Ecology 50: 783–801.

Parris, B. S. et al. 1992. The plants of Mount Kinabalu. v1. Ferns and fern allies. – R. Bot. Gard.Kew.

Phua, M. H. et al. 2008. Detecting deforestation with a spectral change detection approach using multitemporal Landsat data: a case study of Kinabalu Park, Sabah, Malaysia. – J. Environ. Manage. 88: 784–795.

Pither, J. 2003. Climate tolerance and interspecific variation in geographic range size. – Proc. R. Soc. B 270: 475–481.

Porembski, S. and Barthlott, W. 2000. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. – Plant Ecol. 151: 19–28.

Prance, G. T. 1996. Islands in Amazonia. – Phil. Trans. R. Soc. B 351: 823–833.

Proctor, J. 2003. Vegetation and soil and plant chemistry on ultramafic rocks in the tropical Far East. – Perspect. Plant Ecol. Evol. Syst. 6: 105–124.

Proctor, J. et al. 1988. Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. – J. Ecol. 76: 320.

Proctor, J. et al. 1998. Forests of the ultramafic Mount Giting-Giting, Sibuyan Island, the Philippines. – Edinb. J. Bot. 55: 295–316.

Rahbek, C. 2004. The role of spatial scale and the perception of large-scale species–richness patterns. – Ecol. Lett. 8: 224–239.

Rajakaruna, N. 2004. The edaphic factor in the origin of plant species. – Int. Geol. Rev. 46: 471–478.

Rajakaruna, N. 2018. Lessons on evolution from the study of edaphic specialization. – Bot. Rev. 84: 39–78.

Rehm, E. M. and Feeley, K. J. 2015. The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. – Ecography 38: 1167–1175.

Russo, S. E. et al. 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. – J. Ecol. 93: 879–889.

Russo, S. E. et al. 2007. Determinants of tree species distributions: comparing the roles of dispersal, seed size and soil specialization in a Bornean rain forest. – In: Dennis, A. J. et al. (eds), Seed dispersal: theory and its application in a changing world. CAB Int., pp. 499–518.

Russo, S. E. et al. 2008. Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. – J. Ecol. 96: 192–203.

Sanders, N. J. 2002. Elevational gradients in ant species richness: area, geometry and Rapoport's rule. – Ecography 25: 25–32.

Schröter, C. et al. 1908. Das Pflanzenleben der Alpen. Eine Schilderung der Hochgebirgsflora. – Zurich. Q9

Šizling, A. L. et al. 2009. Rapoport's rule, species tolerances and the latitudinal diversity gradient: geometric considerations. – Ecology 90: 3575–3586.

Slatyer, R. A. et al. 2013. Niche breadth predicts geographical range size: a general ecological pattern. – Ecol. Lett. 16: 1104–1114.

Stapf, O. 1894. On the flora of Mount Kinabalu in Northern Borneo. – Trans. Linn. Soc. Lond..

Steenis, C. Van. 1964. Plant geography of the mountain flora of Mt Kinabalu. – Proc. R. Soc. B 161: 7–38.

Stevens, G. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. – Am. Nat. 140: 893–911.

Stevens, G. 1996. Extending Rapoport's rule to Pacific marine fishes. – J. Biogeogr. 23: 149–154.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. – Am. Nat. 133: 240–256.

Stevens, G. C. and Fox, J. F. 1991. The causes of treeline. – Annu. Rev. Ecol. Syst. 22: 177–191.

Subedi, S. C. et al. 2020. Gymnosperm species richness patterns along the elevational gradient and its comparison with other plant taxonomic groups in the himalayas. – Front. Biogeogr. 12: 1–14.

Tanner, E. V. J. 1977. Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. – J. Ecol. 65: 883.

Tedersoo, L. et al. 2014. Global diversity and geography of soil fungi. – Science 346: 1256688.

Terborgh, J. 1977. Bird diversity on an Anndean elevational gradient. – Ecology: 1007–1019. Q10

Tito, R. et al. 2020. Mountain ecosystems as natural laboratories for climate change experiments. – Front. For. Global Change 3: 38.

Tomašových, A. et al. 2016. Unifying latitudinal gradients in range size and richness across marine and terrestrial systems. – Proc. R. Soc. B 283: 1–9.

van der Ent, A. and Edraki, M. 2018. Environmental geochemistry of the abandoned Mamut Copper Mine (Sabah) Malaysia. – Environ. Geochem. Health 40: 189–207.

van der Ent, A. et al. 2014. The ultramafic flora of Sabah: an introduction to the plant diversity on ultramafic soils. – Natural History Publications (Borneo), Sabah Parks.

van der Ent, A. et al. 2015. Plant diversity and ecology of ultramafic outcrops in Sabah (Malaysia). – Aust. J. Bot. 63: 204–215.

van der Ent, A. et al. 2016. Vegetation on ultramafic edaphic 'islands' in Kinabalu Park (Sabah, Malaysia) in relation to soil chemistry and elevation. – Plant Soil 403: 77–101.

van der Ent, A. et al. 2018a. Ecological implications of pedogenesis and geochemistry of ultramafic soils in Kinabalu Park (Malaysia). – Catena 160: 154–169.

van der Ent, A. et al. 2018b. Foliar elemental profiles in the ultramafic flora of Kinabalu Park (Sabah, Malaysia). – Ecol. Res. 33: 659–674.

Vázquez, D. P. and Stevens, R. D. 2004. The latitudinal gradient in niche breadth: concepts and evidence. – Am. Nat. 164: E1–E19.

Vetaas, O. R. 2002. Realized and potential climate niches: a comparison of four *Rhododendron* tree species. – J. Biogeogr. 29: 545–554.

Vetaas, O. R. and Grytnes, J. A. 2002. Distribution of vascular plant species richness and endemic richness along Himalayan elevation gradient in Nepal. – Global Ecol. Biogeogr. 11: 291–301.

Vogelmann, H. W. 1973. Fog precipitation in the cloud forests of eastern Mexico. – BioScience 23: 96–100.

von Humboldt, A. 1849. Aspects of nature, in different lands and different climates; with scientific elucidations. – Lea and Blanchard, Philadephia.

Weiser, M. D. et al. 2007. Latitudinal patterns of range size and species richness of New World woody plants. – Global Ecol. Biogeogr. 16: 679–688.

Whitman, M. et al. 2011. Conservation of Madagascar's granite outcrop orchids: the influence of fire and moisture. – Lankesteriana 11: 55–67.

Whitman, M. et al. 2021. Data from: Edaphic specialization and vegetation zones define elevational range-sizes for Mt. Kinabalu regional flora. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.XXXXX>. Q11

Whittaker, R. H. 1954. The ecology of serpentine soils. – Ecology 35: 258–288.

Whittaker, R. H. et al. 1973. Niche, habitat and ecotope. – Am. Nat. 107: 321–338.

Wood, J. J. et al. 1993. The plants of Mount Kinabalu. v2. Orchids. – R. Bot. Gard.Kew.

Wright, J. W. et al. 2006. Experimental verification of ecological niche modeling in a heterogeneous environment. – Ecology 87: 2433–2439.

Zeileis, A. et al. 2001. strucchange: an R package for testing for structural change in linear regression models. Q12

Zhou, Y. et al. 2019. The species richness pattern of vascular plants along a tropical elevational gradient and the test of elevational Rapoport's rule depend on different life-forms and phytogeographic affinities. – Ecol. Evol. 9: 4495–4503.