

INSIGHTS ON ECOLOGICAL DIVERSITY INFORMED BY FLORA OF TROPICAL
MOUNTAINS OF SOUTHEAST ASIA

by

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Rules are meant to be tested, and the discipline of ecology is no exception. For my dissertation I focused on testing ecological rules as applied to flora along tropical elevation gradients. One controversial rule is Rapoport's rule, which predicts that species' range-sizes increase across elevational and latitudinal gradients, for diverse taxa and habitat types. First, I tested Rapoport's rule, for 54 plant families of tropical Southeast Asia. I found that the strength and significance of Rapoport's rule varied relative to the elevation where richness peaked, and by elevation distribution breadth, for each family. Next, I focused on richness and range-size trends at a smaller spatial scale, at Mt. Kinabalu. Using model selection, replicated for three soil association categories, I found more support for piece-wise regression models that incorporated vegetation zone boundaries. In addition, flora associated with ultramafic soil had distinct richness and range-size patterns. Next, I examined if it is possible to maintain a single ecological strategy along an elevation gradient, indicated by a suite of functional traits that remain relatively unchanged across different contexts, while still adhering to universal life history trade-offs. To do this, I used 169 species from the genus, *Rhododendron*, noted as having a "stress-tolerant" ecological strategy, with species occurring from sea-level to

mountain summits. I found that the genus was able to maintain their stress-tolerant strategy, and a narrow set of associated traits, which is in contrast to the assumption that functional traits must change with elevation. The ability of *Rhododendron* species to occur across a wide elevation gradient, including expanding into resource-rich areas at lower elevations where they have reduced competitive ability, was most likely facilitated by species occupying new niches (transitioning from terrestrial to epiphytic growth forms) or by specializing in extremely stressful habitat types with reduced biotic filtering (ultramafic soil). I propose the "stable stress, novel niche" hypothesis as the explanation for how *Rhododendron* species can occur at different elevations. Overall this dissertation demonstrates that the exceptions to ecological norms offer an interesting perspective on the parameters which define rules regarding species range-size, richness, and functional traits along elevation gradients.

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DEDICATION

In loving memory of my dad, DeWitt



Le Népenthés.

Le Népenthés. *Les merveilles de la végétation.* 1866.

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*You ask me why I dwell in the green mountain;
I smile and make no reply for my heart is free of care.
As the peach-blossom flows down stream and is gone into the unknown,
I have a world apart that is not among men.*

- GREEN MOUNTAIN, BY LI BAI (701-762).



Rhododendron. *Dictionary of words and things*. 1895.

PREFACE

How did I choose topics for my dissertation? This is a point of reflection that I have mulled over for quite some time. I think it all began after a meeting with my advisor during my first year of study when she suggested that I narrow my plethora of interests and focus on something that is achievable within the span of a PhD. She politely reminded me that I cannot possibly study the all the flora of Borneo, an area of remarkably high biodiversity, so please, just focus on a single genus. I was advised to consult the literature on various notable taxonomic groups for the region, such as *Macaranga*, *Ficus*, or *Shorea*. Her own genus of choice for her dissertation was *Virola*, commonly known as nutmeg, dispersed by monkeys of the Peruvian Amazon. Given my botanical interests, the advice was to dive into knowing a genus well and an assortment of research questions were sure to follow.

Reading through botanical descriptions of tropical Southeast Asia, I noted the genus *Rhododendron* was mentioned multiple times. Odd I thought, I had always regarded *Rhododendron* as a temperate genus; the species *R. macrophyllum* was the official flower of my home state of Washington after all. I put *Rhododendron* species on the back burner of my mind and continued with my review of literature about functional traits, elevation gradients, and ecological theory for how plant communities are shaped.

One day I was feeling curious and decided to download a selection of herbarium record coordinates for flora of Malaysia from the Global Biodiversity Information Faculty. My intent was mostly to practice R code for plotting species richness, but soon that led down the path of thinking about what determines the elevation minimum and

maximum for each species, what are the boundaries that limit where species do or don't occur? Via experimentation with the data I felt a growing appreciation of the relationship between species richness, range-size, and patterns of species turnover across gradients.

In the quiet space of looking at matrices of species presence and absence with my practice dataset from Malaysia, I vaguely remembered the *Rhododendron* genus. How many *Rhododendron* species in the tropics were there again? A basic query and a few plots later I found myself looking at a very odd peak in richness. Rather than residing with all the other plants in lower elevations, I discovered that *Rhododendron* species were plants of the mountain tops, with a distribution pattern that set them apart from the trends of the majority. I then recalled reading about Rapoport's rule, a broad scale phenomenon that in many ways was the inverse of species richness trends. In examples where richness was highest at lower elevations, range-size would tend to increase with elevation. So, I did the next logical step, which was to test if Rapoport's rule applied to *Rhododendron*. To my surprise *Rhododendron* showed a flat line, no significant relationship, a slope that was indistinguishable from zero!? In a slight panic I checked, did I do the calculations wrong? No. Other species-rich genera, behaved as predicted from the literature, they were proper representatives of the a-priori paradigm, displaying nice positive slopes in support of Rapoport's rule. I had just stumbled across yet another instance of *Rhododendron* being the odd taxa out.

Months later, via serendipitous means, I learned that *Rhododendron* species were the third most popular plant to collect in the Victorian era (after orchids and tulips) and it just so happened that largest public collection of *Rhododendron* in North America was

just south of my family's home, and an even larger collection existed in Edinburgh, Scotland. Greenhouses devoted to growing wild collected species in a *de facto* common garden, all the possible leaf traits to measure as an indication of adaptive variation? Tempting...and so I found myself sampling an assortment of *Rhododendron* species from around the globe. I started with one the most studied functional traits, specific leaf area (SLA), a strong indicator of life history strategy and response to environment. Yet again, I found that *Rhododendron* proved to be an enigmatic muse. There was no change in SLA based on mean elevation. The results left me scratching my head and wondering why yet again. My response was simple: I decided I must sample more species. I needed to know if my initial inconclusive results were attributed to low sample size, or if *Rhododendron* were trying to drop the hint that they simply play by a different set of ecological rules.

As you might guess by now, *Rhododendron* had emerged victorious as my model taxa of choice for pondering ecological mechanisms and how plants respond to their environment. *Rhododendron* seem to defy all of my preconceived notions of trends that I should expect along an elevation gradient, yet paradoxically the same genus adhered to known trade-offs in terms of functional trait correlations. I could not shake the feeling that the *Rhododendron* genus were somehow taunting me. Daring me. Come, be curious, explore bigger datasets and ask bigger questions. True that my research route has been different and more challenging than I originally envisioned... but the process continues to be interesting. I may not have all the answers to *Rhododendron*'s ways, but at least I have a model taxonomic group that never fails to have me asking new questions.

INTRODUCTION

A central dilemma in ecology is whether or not there are universal laws, or rules, that establish a sense of order applicable across different spatial scales, periods of times, or taxonomic units of interest (Stevens 1989, Lawton 1999, West et al. 1999, Wright et al. 2004, Hubbell 2005). For instance, it has been observed that the variation in species richness corresponds with latitude, with higher species richness nearest the equator and declining towards the polar regions (Reid 1998, Hawkins et al. 2003, Ricklefs 2004, Nogués-bravo and Araújo 2006), which raises the question as to whether this richness gradient is universal. The underlying mechanisms that shape species patterns of richness may also be linked to the distribution and overlap of species' range-sizes (Whittaker et al. 1973, Colwell and Hurtt 1994, Morin and Chuine 2006, Swenson et al. 2011a). Similarly, another large scale ecological rule that is the subject of debate is Rapoport's rule. According to Rapoport's rule species' geographic ranges vary across environmental gradients, and is the observation that species' range-size tends to expand with increasing elevation or latitude (Stevens 1989, 1992, Sanders 2002, Lear et al. 2017).

There are universal trade-offs with regards to the physical characteristics, or functional traits, of species based on constraints of available resources, how energy or liquids move through a system, metabolic rates, and principles of scaling applied to the limits of growth or size of an organism (Reich et al. 1999, West et al. 1999, Niklas and Enquist 2003, DeLong 2012). A common mechanism behind physiologically oriented rules is that growth or maintenance of an organ, or abundance of organisms within a community if the principle is applied at a larger scale, cannot exceed the resources

needed to produce or sustain those entities (Givnish 1988, Hawkins et al. 2003). When rules describing life history trade-offs are applied towards how organisms interact with each other or their environment, it can help with identification of the benefits and costs of various ecological strategies (Grime 1977, Tilman 1982).

However, the universal applicability of any rule must be questioned. Does lack of universal applicability imply that its underlying concept is essentially flawed, or does that simply provide a point of context for the parameters which define it? For instance, by extension, elevation has often been used as a proxy for latitude, based on similarities in temperature decline along each gradient, yet where richness peaks can differ between mountains, and vary within a given area depending on the growth form or taxonomic group examined (Whittaker 1960, McCain and Grytnes 2010, Lee et al. 2013).

Inconsistencies have also been found with regards to the applicability of Rapoport's rule (Lyons and Willig 1997, Ruggiero and Werenkraut 2007, McCain and Bracy Knight 2013), leading to questions about the processes behind observed trends and to what degree patterns are based on chance alone. Scaling rules, such as growth-size relationships (Russo et al. 2007a) or size-abundance relationships (Russo et al. 2003), can also differ substantially between species, life-history strategy, or trophic level. The applicability of ecological laws or rules may become especially obscured at intermediate spatial or temporal scales (Lawton 1999), where multiple environmental factors interact and cause divergence from predicted outcomes.

One point of uncertainty with Rapoport's rule is whether the variation in its significance can be attributed to the characteristics of the model group examined, with

consideration of the role of ecological, taxonomic, and biogeographic history for the pool of species examined. To disentangle possible factors contributing to the strength of Rapoport's rule, with strength being the correlation coefficient of range-size and elevation, I tested fifty four plant families of tropical Southeast Asia. I found not only differences in the strength of Rapoport's rule based on growth form and taxonomy, but more importantly by looking at results across families I put into context when Rapoport's rule did, or did not, apply. In instances where richness peaked at lower elevation, or when the distribution breadth for the family was more restricted, Rapoport's rule tended to apply especially for arborescent growth forms. However, in instances where family richness peaked at higher elevations, or when a family had a more expansive or cosmopolitan distribution breadth, then Rapoport's rule tended to not apply.

A different question that is relevant for the study of ecology is whether macroecological rules (trends or predictions applicable to large geographic areas) can be applied to assemblages of species within a region, and whether distinct combinations of environmental factors emerge as important at this spatial scale. For instance, on a global scale temperature is often assumed to be a major determinant of species distribution patterns, but at the local scale nutrients, or moisture availability, may be stronger factors for defining where species occur or the limits for their range-size (Harrison 1997, Hawkins et al. 2003, Harrison and Grace 2007, Laurance et al. 2010). In Chapter 2, I examined how edaphic association, and vegetation zones, influenced plant species range-sizes along elevation gradients of Mt. Kinabalu, Borneo. I found that even though piece-wise regression models were more complex, they better represented range-size trends

along an elevation gradient as compared to simpler linear regression models that are more commonly used to test Rapoport's rule. Species that specialized in, or tolerate, ultramafic soil also displayed distinct richness and range-size trends compared species associated with other soil types. Chapter 2 illustrates that other environmental factors (*e.g.*, soil fertility, position relative to the cloud layer), besides the dominate one defining the gradient (*e.g.* temperature), can affect whether patterns predicted under a rule are universally applicable along that gradient.

The study of universal trade-offs governing why plant functional traits vary creates an expectation that there is a spectrum of possible responses for how plants respond to biotic pressures or habitat conditions. Ironically, when these traits are then examined along environmental gradients there tends to be uniform change in mean values combined with a narrowing variance as abiotic stressors increase, which suggests that the ecological strategy that is optimal may also change depending on location. Many studies on functional trait trends along gradients sample a diverse pool of species that are distantly related, and thus are likely to also represent a broad suite of possible ecological strategies. However, by focusing on species from within the same genus it may be possible to examine a single ecological strategy as applied to many different contexts.

To determine how ecological strategy influences trait variation along environmental gradients, in Chapter 3 I used one of the most species-rich genera of the Malay Archipelago, *Rhododendron*. The genus is commonly described as having a "stress-tolerant" ecological strategy, with *Rhododendron* species often associated with habitat types with low productivity. I sampled functional traits from 169 *Rhododendron*

species growing in botanical garden greenhouses under comparable conditions, thus traits were a reflection the adaptive variation of each species, and elevation was based on the mean location of species occurrence. I found that *Rhododendron* species followed functional trait trade-offs as predicted from the leaf economic spectrum, however, they deviated from standard expectations for tropical woody species for how mean traits values change along elevation gradients. Functional traits associated with ecological strategy and defense, and thus inferred speed of growth, investment or retention time of leaves (*e.g.*, specific leaf area, lamina density) remained constant regardless of location, whereas traits that are influenced more by environment, rather than biotic pressures, had values that corresponded with elevation gradients (*e.g.*, leaf size). In addition, multivariate metrics of functional trait dispersion and centroid position did differ between plants associated with extremely stressful habitat types (ultramafic association compared to other soil associations; epiphytic as compared to terrestrial growth forms), indicating that while *Rhododendron* may be very consistent in trait variance, they are very fluid, or opportunistic, in terms of habitat niche. This study demonstrates that it is possible to adhere to universal functional trait trade-offs, while at the same time displaying a distinct trend in trait variance along elevation gradients via having an ecological strategy that differs from the majority.

Overall, my dissertation research centers around understanding and testing ecological rules as applied to flora along tropical elevation gradients. My main findings include 1) that species range-size along an elevation gradient depends upon a multitude of factors, including specialization on unique soil types or position relative to soft

ecological boundaries such as the transition between vegetation zones, and may be influenced by the context of where richness peaks, and distribution breadth, of the family that they originate, and 2) it is possible to maintain a very specific suite of traits with narrow dispersion of values, while also adhering to a single ecological strategy based on stress-tolerance, regardless of position along an elevation gradient if those species are flexible in habitat associations and the serendipitous exploitation of novel niches.



Végétation tropicale. *Les merveilles de la végétation*. 1866.

CHAPTER 1

The exceptions to the Rule: taxonomic variation in the strength of Rapoport's rule with elevation in the Southeast Asian flora

1.1 Introduction

Rapoport's rule, named after Eduardo H. Rapoport, is the observation that species latitudinal range-sizes (maximum minus minimum latitude) tended to be smaller near the equator and larger at higher latitudes (Stevens 1989). Analogous patterns in range-size distributions have also been observed along other environmental gradients, such as elevation or sea depth (Stevens 1992, 1996). Hence, a positive relationship between species' range-size and either elevation or latitude is taken as support for Rapoport's rule. However, the ecological mechanisms behind Rapoport's rule remain enigmatic (Gaston et al. 1998, Šizling et al. 2009, McCain and Bracy Knight 2013). The determinants of elevational or latitudinal variation in range-size are important to understand because they also affect patterns of species richness along these gradients, since the more species' ranges that overlap at a location, the greater the species richness occurring there. Thus,

patterns of range-size and species diversity distributions along gradients are intimately linked and may be determined by similar mechanisms.

Possible mechanisms explaining species range-size and richness distributions are both biological and non-biological. A common explanation for Rapoport's rule is that range-size reflects the amount of variation in climatic conditions that species experiences. The rationale is that greater seasonality or diurnal variability in the environment selects for the ability to tolerate and plastically respond to a wide range of environmental conditions, whereas stable conditions promote specialization and thus smaller range-sizes (Janzen 1967, Stevens 1989, Morueta-Holme et al. 2013). Different evolutionary processes can facilitate the ability of species to tolerate greater environmental variation. Species originating in temperate or montane regions are expected to have evolved under conditions of greater climatic variation than species originating in tropical regions, and so may have physiological adaptations that allow them to tolerate a wider range of environmental conditions. Similarly, habitat productivity also may affect patterns of range-size, with the prediction being that locations with higher resource availability can support more organisms within a smaller geographic area, which can allow for narrower niches that could be associated with distribution ranges (Whittaker et al. 1973, May 1974, Ricklefs 2004, Morin and Lechowicz 2013). Along latitudinal gradients, differential extinction has also been cited for why larger-ranged species tended to occur in boreal to temperate regions, with disproportionate elimination of small-ranged species during glaciation events (Brown 1984).

Non-biological explanations for Rapoport's rule involve geometric constraints, specifically that ranges are necessarily truncated when approaching hard boundaries, such as sea-level or the tops of mountains (Colwell and Hurtt 1994, Šizling et al. 2009). Such hard boundaries limit the range-sizes of species at the ends, compared to the middle, of a gradient, and so can produce a mid-domain peak in species richness purely as a result of the random arrangement of range-sizes along a gradient. If geometric constraints are the dominant mechanism underling range-size patterns, then when only the lower portion of the gradient is examined, range-size can appear to increase along the gradient, since any declines in range-size at the upper boundary are not captured (Colwell and Hurtt 1994).

Comparative studies of Rapoport's rule have been made between latitudinal and elevation gradients, and across geographic regions (*e.g.*, range-size of species in North America as compared to South America), as well as at smaller scales between individual study sites or mountains (Weiser et al. 2007, McCain and Bracy Knight 2013). Most studies on Rapoport's rule tend to be centered in the New World, with a smaller proportion in Europe or Australia (Gaston et al. 1998), and minimal research has been conducted in Africa or Asia, with the exception of elevational studies in the Himalayas (Bhattarai and Vetaas 2006, Feng et al. 2016). In general, more support for Rapoport's rule has been found in temperate rather than tropical regions (Gaston et al. 1998, Ruggiero and Werenkraut 2007) or when higher elevations have been excluded from the analysis (Feng et al. 2016). However, relatively few studies have examined range-size distribution patterns in tropical portions of Southeast Asia, especially of land plant species.

A greater understanding of the mechanisms that shape patterns of species distributions may be possible via the integration of ecological, taxonomic, and biogeographic paradigms (Ashton 1988), as well as by consideration of differences in where species richness peaks based on growth form (Whittaker et al. 1973). Studies examining taxonomic variation in Rapoport's rule generally focus on broad groupings, such as contrasting studies of birds and amphibians (Stevens 1992, McCain and Bracy Knight 2013), or all woody plants (Weiser et al. 2007), with analyses conducted from a more taxon-specific perspective being the exception (Letcher and Harvey 1994, Sanders 2002). However, comparisons at lower taxonomic levels, such as among families occurring in a large geographic region, may provide insights on how ecological and evolutionary factors, such as the family's biogeographic origin or age, may influence patterns of range-size along gradients.

Often studies that examine multiple taxonomic groups or geographic locations quantify support for Rapoport's rule in terms of the proportion of groups or location for which the slope of the relationship between average range-size and the environmental gradient is significantly positive (Stevens 1996, Rohde 1999, Weiser et al. 2007, McCain and Bracy Knight 2013). However, given that many different environmental factors, including climate and soils, vary simultaneously along latitudinal or elevational gradients, range-size can be viewed as a proxy for a species' ecological niche breadth. Hence, the steepness of the positive slope of the range-size versus elevation relationship (*i.e.*, the strength of Rapoport's rule) can be taken to represent the amount of asymmetry in range-sizes of species at either ends the gradient. For instance, such asymmetry could develop

when a subset of the species in a group expands into novel habitat types at one end of the gradient, potentially facilitated by key adaptations, which may expand the range of the gradient that these subset of species could occupy.

Analogously at the family-level, the overall breadth of distribution can also be an indication of a taxon's biogeographic or evolutionary history. For instance, a family with narrow distribution breadth suggests that the majority of the species may be more specialized to a particular habitat type (*e.g.*, wet tropical lowland forest) or that the group is dispersal limited. However, a wide distribution breadth could arise when the family has a more cosmopolitan affiliation with many different habitat types, and thus is tolerant of multiple stressors. Evolutionarily older families might also have a wider distribution breadth owing to longer time for expansion and establishment into wider or more distant geographic areas. The location of where species richness peaks also can indicate either the geographic point of origin for a group, or the conditions that are most optimal for survival or speciation.

The goal of this study was to investigate variation in Rapoport's rule along elevation gradients among land plant families of Southeast Asia and to explore possible mechanisms underlying this variation by describing its ecological, evolutionary, and biogeographic correlates. Specifically, I asked the following questions: 1) Is there variation among land plant families in their strength of support for Rapoport's rule? 2) If so, are there correlates of this variation related to growth form, the elevation where richness peaks, or the breadth of the elevational distribution of the family? To answer these questions, I used a data set of more than 300,000 observations of the distributions

of land plants from lowlands to mountaintops in Southeast Asia for 54 families of angiosperms, gymnosperms, bryophytes, and pteridophytes. Information on the global distribution, latitudinal range, growth form, evolutionary age, and habitat associations of these families was also gathered from literature. First, for each plant family I calculated the slope of the relationship between species average elevation range-size versus elevation as a metric of the strength of support for Rapoport's rule. Second, I estimated the elevation where richness peaks, and distribution curve (elevation breadth), for each family along an elevation gradient. I then tested for a correlation between the slope of Rapoport's rule and 1) the elevation of highest richness and 2) the elevation breadth for each family, which I defined as summation of consecutive 100 m elevation bins with thirty or more species within a family. Differences in where richness peaked, in elevation breadth, and in the strength of Rapoport's rule also were examined based on growth form (arborescent vs. herbaceous). For a broader scale perspective, I also tested for a correlation between latitudinal and elevation range-sizes across families.

I predicted that families with weak support for Rapoport's rule should be geographically widespread, have biogeographic origins within temperate regions or montane habitats, have an herbaceous growth form, or be distributed across areas without geometric constraints (non-adjacent to either sea-level or mountain summit boundaries). Species with weak support for Rapoport's rule also would be expected to have greater tolerance of abiotic stressors and be able to occupy a wider suite of possible habitats along an elevation gradient, thus leading to range-sizes that are similar across the gradient and with distributions that are limited by factors other than climate variability. In

contrast, I predicted families with strong support for Rapoport's rule to be more geographically restricted, have highest richness in tropical habitats or areas with relatively stable climatic conditions, predominately have arborescent growth forms, or subject to geometric constraints on potential range-sizes towards the ends of an environmental gradient.

1.2 Methods

1.2.1 Study region

The study region encompasses the Malay Archipelago and Papua New Guinea (Fig. 1.1), an area that is approximately 2,000,000 km² in size, consisting of thousands of islands that collectively represent the largest archipelago on Earth. This region is centered around the equator and is regarded as one of Earth's biodiversity hotspots (Myers et al. 2000, De Bruyn et al. 2014). The majority of islands occur within an area spanning from 55'E to 155'W longitude, and -13'S to 21'N latitude. Notable mountains, such as Mt. Kinabalu (Borneo, 4,095 m), Mt. Wilhelm (Bismarck Range, 4,509 m), and Puncak Jaya (Western Sudirman, 4,884 m) are tall enough to have summits that are subject to freezing events (Hope 1976).

1.2.2 Herbarium records

I queried the Global Biodiversity Information Facility (GBIF) herbarium records from the countries of Indonesia, Malaysia, Brunei, Singapore, Philippines, East Timor, and Papua New Guinea (downloaded from gbif.org, initial query February 2013; updated December 2017, Fig. 1.2). In addition, I also added more than 1,000 species to the overall dataset from the Mt. Kinabalu herbarium database, which are not included in GBIF. While geographic coordinates of the records could have been used to extract elevation data, I elected not to do this because of concerns that the spatial resolution of the data would be too coarse to adequately estimate elevation values for species from higher elevation areas with relatively minimal area compared to lowland sites. Instances where GBIF records flagged as possibly erroneous, such as coordinates out of range or occurring at an elevation higher than the tallest known peak, were excluded. The Taxonomic Name Resolution Service (TNRS) was used with partial matching (use of fuzzy logic) to check for synonyms or nomenclature changes at the species level. Subspecies and varieties were collated to the species level. I then used the R package “taxonlookup” (Pennell et al. 2016) to assign taxonomic groups and family names to genera. I manually filled in missing information for newly discovered species or genera whenever possible. Species with nomenclature errors, TNRS warning flags, or a high degree of uncertainty (*e.g.* low TNRS score) were excluded. For the final dataset I retained species with two or more herbarium records containing elevation data. I examined other thresholds to establish the minimum number of records, however higher cut-offs resulted in a dramatic decline in the total number of species used in analyses (*e.g.* approximately half of the species were

excluded if criteria was changed to a minimum of three records) and caused disproportionate elimination of rare species. My final dataset contained 20,484 terrestrial plant species from 389 plant families and 3,010 genera, and included angiosperms, gymnosperms, bryophytes (in the broad sense, including liverworts), and pteridophytes.

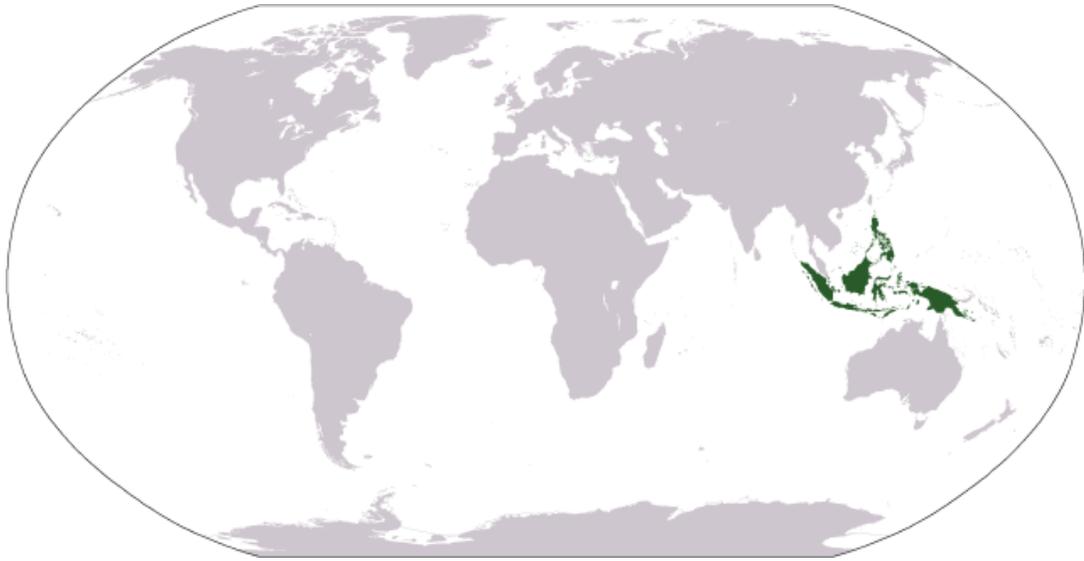


Figure 1.1. The Malay Archipelago, shown in green. Image from Wikipedia Creative Commons (2006).

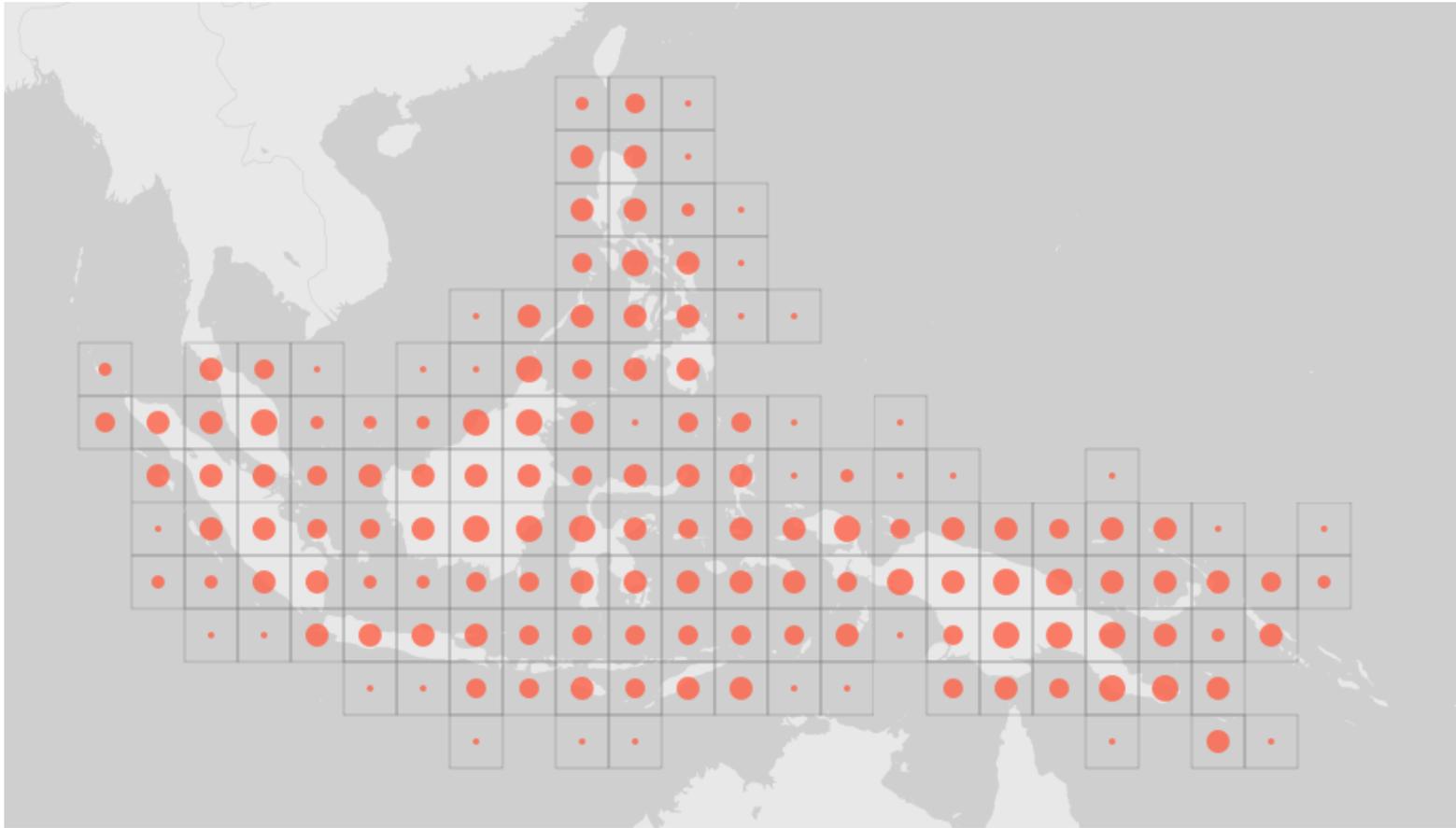


Figure 1.2. Distribution of herbarium records based on my query of the Global Biodiversity Information Faculty (GBIF). Image produced by GBIF using coordinates from the dataset with the size of circle (shown in red) proportional to the number of records within a given area (shown as a box), including records from small islands or with some rounding of coordinates based on uncertainty or intentional obscuring of location precision for protection of endangered species.

1.2.3 Elevation range-size of land plant families

Studies of Rapoport's rule use different methods to estimate range-size trends with elevation (Gaston et al. 1998, Ruggiero and Werenkraut 2007, McCain and Bracy Knight 2013). The most common method is the one established by Stevens (1989), where a species' range-size is calculated as the difference between the maximum and minimum elevation where a species has been recorded, and assumes that the species could occur at all points between those two elevations. Dividing the full elevation gradient into bins (*e.g.*, 100 m), the average range-size is calculated for all species present within an elevation bin, and the slope and intercept parameters describing the relationship between average range-size as a function of elevation bin are estimated with linear regression. The second approach, referred to as the mid-point method, is similar to the Stevens' method, but the mid-point method represents species occurrence only within a single bin, positioned at the half-way point of a species' range. Thus, while the mid-point method offers more statistical independence, there is a large loss of information about species' range limits, making richness curves harder to estimate. A third, less common approach is to use only the maximum elevation where a species has been observed, with the rationale being that this is the location most influenced by abiotic stressors or physiological constraints that limit where a species can occur (*e.g.*, the boundary point for freezing events). Here, I analyzed data using all three methods, and since the results were consistent, I will only present results based on Stevens' method.

To examine how species richness and average range-size of each family in my data set changes with elevation, I subdivided the full elevation gradient represented by all

records into 100 m bins to be consistent with methods used by Stevens (1989). Although the full dataset included records at elevations up to 4800 m (Puncak Jaya summit), very limited information was available on flora from the highest mountains, which dramatically increased uncertainty at these elevations. I therefore used 4500 m as the upper elevation threshold for all analyses. Using the data set described above, I did the following analyses for the species in each family. I calculated the total number of species present in each bin based on elevation range, using the method described above, as a metric of richness. Next, I calculated the mean elevation range-size for species present in each elevation bin, with variance calculated as differences in range-size across species occurring within the same bin. I then quantified the strength of Rapoport's rule using ordinary least squares linear regression to estimate the slope of the relationship between average range-size and elevation bin.

My criterion for families to be included in analyses was that they needed to contain ≥ 100 species, including only species with a minimum of two herbarium records with information on the elevation from where plants were collected. Although Podocarpaceae included only 69 species with elevation data available, I included this family as the sole representative of gymnosperms. In total, I selected 54 plant families, comprised of 15,822 species representing the majority of the overall land plant richness for the study region based on the richness of the dataset (21,012 species with two or more observations).

Some previous studies on Rapoport's rule excluded species considered to be extreme range-size outliers or conducted analyses by on a quantile basis, because

especially large-ranged species can have a disproportionate impact on calculation of range-size trends using methods by Stevens, especially in areas with lower richness (McCain and Bracy Knight 2013). To address concerns that outlier species with especially large range-sizes could skew results, and to reduce the impact of possibly erroneous entries where feet was used rather than meters, I excluded species outside of the upper 97.5 and lower 2.5 percentiles of the distribution of range-sizes observed for each family. In order to ensure that estimates of mean range-size in a bin were not strongly influenced by outliers, while maintaining narrow enough bins to capture smaller-scale variation in range-size and richness patterns, I required that all elevation bins must have thirty or more species present to be included in statistical analyses. The minimum of thirty species as a cutoff was based on my general assessment of the data and observation of consistency of results when using different richness sizes. The combination of the previously mentioned criterion reduced variation caused by low sample size and trimmed the lower and uppermost tails of the distribution curves for each family.

For each plant family, I compiled information from the literature on their biogeographic history and geographic distribution (Table 1.1). Whenever possible, I added information on node age of the family (millions of years) or biogeographic origin, latitudinal extent, and predominant habitat association for the majority of the species within each group (Table 1.1). I utilized classifications by Hawkins et al. (2011) for predominant growth forms (herbaceous, arborescent, and mixed/other) of angiosperm families and applied similar methods to categorize non-angiosperm families with respect to growth form.

1.2.4 Examination of ecological, biogeographic, and taxonomic correlates of the strength of Rapoport's rule

For each plant family, I estimated the elevation where species richness peaked using polynomial regression, as implemented in the "poly" and "predict" functions in the R statistical package ("stat" package v3.4.3) (Supplemental 4.1). Next, I examined the breadth of each families' elevation distribution, calculated as the maximum minus minimum elevation where any species in the family occurred. I also examined the correlation between family-level elevation breadth (meters) and latitudinal breadth (degrees), using latitudinal data from a supplemental table by Hawkins et al. (2011). Latitude values potentially extended to areas beyond the Southeast Asia region, however an additional re-query of elevation values for each family was beyond the scope of this paper (*e.g.* Orchidaceae alone has over 28,000 species distributed across the globe).

To compare distribution patterns of families with different growth forms (Table 1.1), I performed three Student's *t*-tests using 1) elevation for where richness peaks, 2) elevation breadth for family distribution curves, and 3) the strength of Rapoport's rule (slope), as different response variables, using data reported in Table 1.2. For these analyses, the unit of replication was family, with a total of 16 families categorized as arborescent and 20 described as herbaceous. Families described as having either mixed or other growth forms ($n = 17$) were excluded. To test for patterns across plant families, I used linear regression to determine if the strength of Rapoport's rule (slope) depended upon where species richness peaked along an elevation gradient. I also performed comparable analysis using the elevation breadth of distribution for each family as a predictor. For both of these analyses, each point represents a plant family ($n = 54$).

Table 1.1a. General patterns of distribution and age of major angiosperm families.

Family	Primary Habitat	Centers of Diversity	Ma.	Lat. Range (Degrees)	Growth Form	Reference
Acanthaceae	Tropical forests	Pantropical	42.63	79.941	Mixed/Other	1
Anacardiaceae	Tropical forests	Americas, Africa, Asia, southern Europe	42.88	68.387	Arborescent	1
Annonaceae	Tropical forests	Pantropical	78.89	42.594	Arborescent	1
Apocynaceae	Tropical forests	Americas, Africa, Australia, Europe, Asia	67.05	110.495	Mixed/Other	1
Araceae	Tropical forests	Americas, Africa, Australia, Europe, Asia	122.3	115.302	Herbaceous	1
Araliaceae	Cloud forests	Pantropical, temperate	69.44	73.862	Mixed/Other	1
Arecaceae	Tropical forests	Americas, Eurasia, Pacific	106.9	66.972	Arborescent	1
Asteraceae	Cosmopolitan	Pantropical	42.31	132.163	Mixed/Other	1
Begoniaceae	Cloud forests	Global	48.1	47.686	Herbaceous	1
Clusiaceae	Tropical forests	Pantropical	58.92	85.509	Arborescent	1
Cyperaceae	Wetlands	SE Asia, South America	44	131.486	Herbaceous	1
Dipterocarpaceae	Tropical forests	SE Asia	67.47	19.384	Arborescent	1,2
Elaeocarpaceae	Tropical forests	Pantropical	53.15	26.982	Arborescent	1
Ericaceae	Tropical montane, healthlands, or temperate	Global	76.81	131.509	Arborescent	1,3
Euphorbiaceae	Tropical forests	Global	57.38	122.052	Mixed/Other	1
Fabaceae	Tropical forests	Pantropical	63.8	131.344	Mixed/Other	1
Fagaceae	Tropical mountains, Cloud forests	temperate areas	63.81	55.403	Arborescent	1
Gesneriaceae	Cloud forests	Pantropical	57.11	40.244	Herbaceous	1

Lamiaceae	Tropical forests	Global	39.73	127.702	Mixed/Other	1
Lauraceae	Cloud forests	Pantropical	99.81	60.169	Arborescent	1
Loranthaceae	Tropical forests	Pantropical	114.5	61.207	Mixed/Other	1
Malvaceae	Tropical forests	Pantropical	65.83	119.809	Mixed/Other	1
Melastomataceae	Cloud forests	Pantropical	66.48	51.524	Mixed/Other	1
Meliaceae	Tropical forests	Pantropical, China, Australia	49.35	61.414	Mixed/Other	1
Moraceae	Tropical forests	Pantropical	25.23	98.762	Mixed/Other	1
Myristicaceae	Tropical forests	Pantropical	101.5	36.041	Arborescent	1
Myrtaceae	Tropical forests	SE Asia, South America, Australia	80.91	64.941	Arborescent	1
Orchidaceae	Cloud forests	Global	96.49	118.75	Herbaceous	1
Pandanaceae	Tropical forests	Pantropical	67.17	13.077	Arborescent	1
Phyllanthaceae	Tropical forests Grasslands, all habitat types	Pantropical, southern temperate	73.49	88.501	Mixed/Other	1
Poaceae		Global	40.95	131.518	Herbaceous	1
Primulaceae	Cloud forests	Global	36.69	101.043	Herbaceous	1
Rosaceae	Tropical montane or temperate	Northern Hemisphere	72.98	126.897	Mixed/Other	1
Rubiaceae	Tropical forests	Pantropical	76.5	128.779	Arborescent	1
Rutaceae	Tropical forests	Pantropical	53.37	98.994	Mixed/Other	1
Sapindaceae	Tropical forests	Global	58.75	88.47	Mixed/Other	1
Sapotaceae	Tropical forests	Global	93.14	47.251	Arborescent	1
Urticaceae	Cloud forests	Global	25.23	125.917	Mixed/Other	1
Zingiberaceae	Tropical forests	Pantropical	66.49	41.815	Herbaceous	1

Table 1.1b. Non-angiosperms (bryophytes, gymnosperms, pteridophytes).

Family	Primary Habitat	Centers of Diversity	Ma	Lat. Range (Degrees)	Growth Form	Reference
Lejeuneaceae	Cosmopolitan	Global	449		Herbaceous	4
Sematophyllaceae	Cosmopolitan	Global			Herbaceous	
Podocarpaceae	Tropical montane or temperate	Pantropical, southern temperate	94		Arborescent	5
Aspleniaceae	Cloud forests	Global	94.52		Herbaceous	4
Athyriaceae	Cloud forests	Global			Arborescent	
Cyatheaceae	Cloud forests	Pantropical, Australia	159		Herbaceous	4
Dryopteridaceae	Cosmopolitan	Global			Herbaceous	
Hymenophyllaceae	Cloud forests	Global	280		Herbaceous	4
Polypodiaceae	Tropical montane or temperate	Global			Herbaceous	
Pteridaceae	Cloud forests	Global			Herbaceous	
Selaginellaceae	Cloud forests	Global			Herbaceous	
Tectariaceae	Cloud forests	Global			Herbaceous	
Thelypteridaceae	Cloud forests	Global			Herbaceous	

References: 1) Hawkins et al. 2011, 2) Ashton 1988, 3) Schwery et al. 2015, 4) Schneider et al. 2004, 5) Biffin et al. 2011.

1.3 Results

1.3.1 Distribution of species richness by taxonomic group

When grouping families into four major taxonomic categories, angiosperms, gymnosperms, bryophytes, and pteridophytes, only angiosperms had a richness peak at lower elevations (close to sea-level). Gymnosperms, bryophytes, and pteridophytes had richness peaks from 1000 - 1500 m (Fig 1.3), which is where lower montane forests transition to cloud forests. For individual plant families, species richness peaks were distributed at different points across elevation gradient. For instance, Orchidaceae, the family with by far the highest species richness (2,353 species within our dataset), peaked at ~1200 m. In contrast, for the family with the next highest richness, Rubiaceae (909 species), the number of species peaked closest to sea-level. Breadths of species richness curves also differed between families. Some families, such as Dipterocarpaceae and Anacardiaceae, were limited in elevation breadth, generally restricted to areas that are warmer, temperature stable, or coastal habitats, whereas others, such as Asteraceae and Poaceae were much more cosmopolitan with broad distributions that spanned from sea-level to the highest mountain summits (Table 1.2).

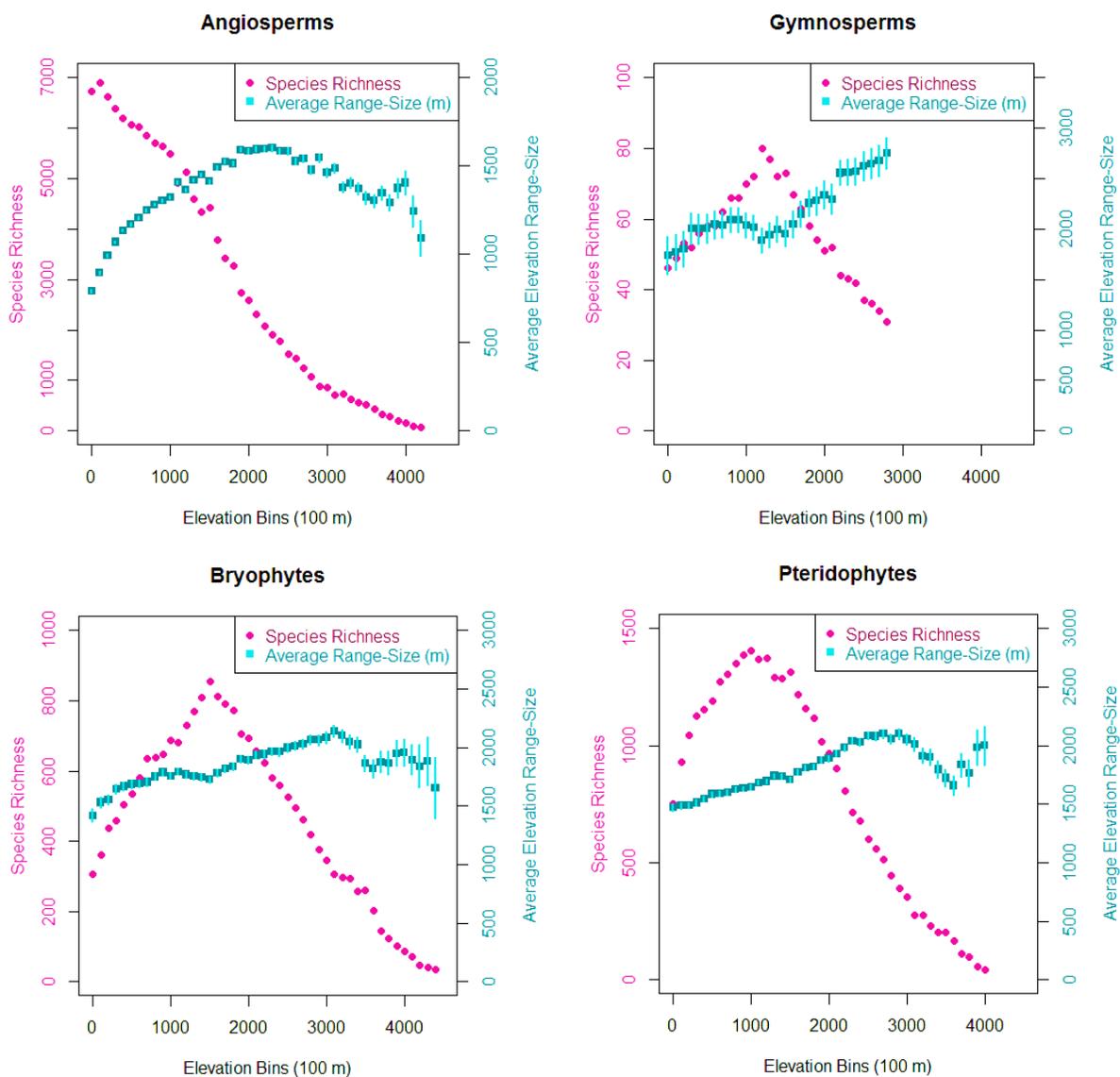


Figure 1.3. Plots of species richness and range-size against elevation for four major taxonomic groups. All plots show the same x axis for elevation, but y axes are scaled based on each dataset. Standard error bars represent the variation in the elevation ranges of the species present within that elevation bin.

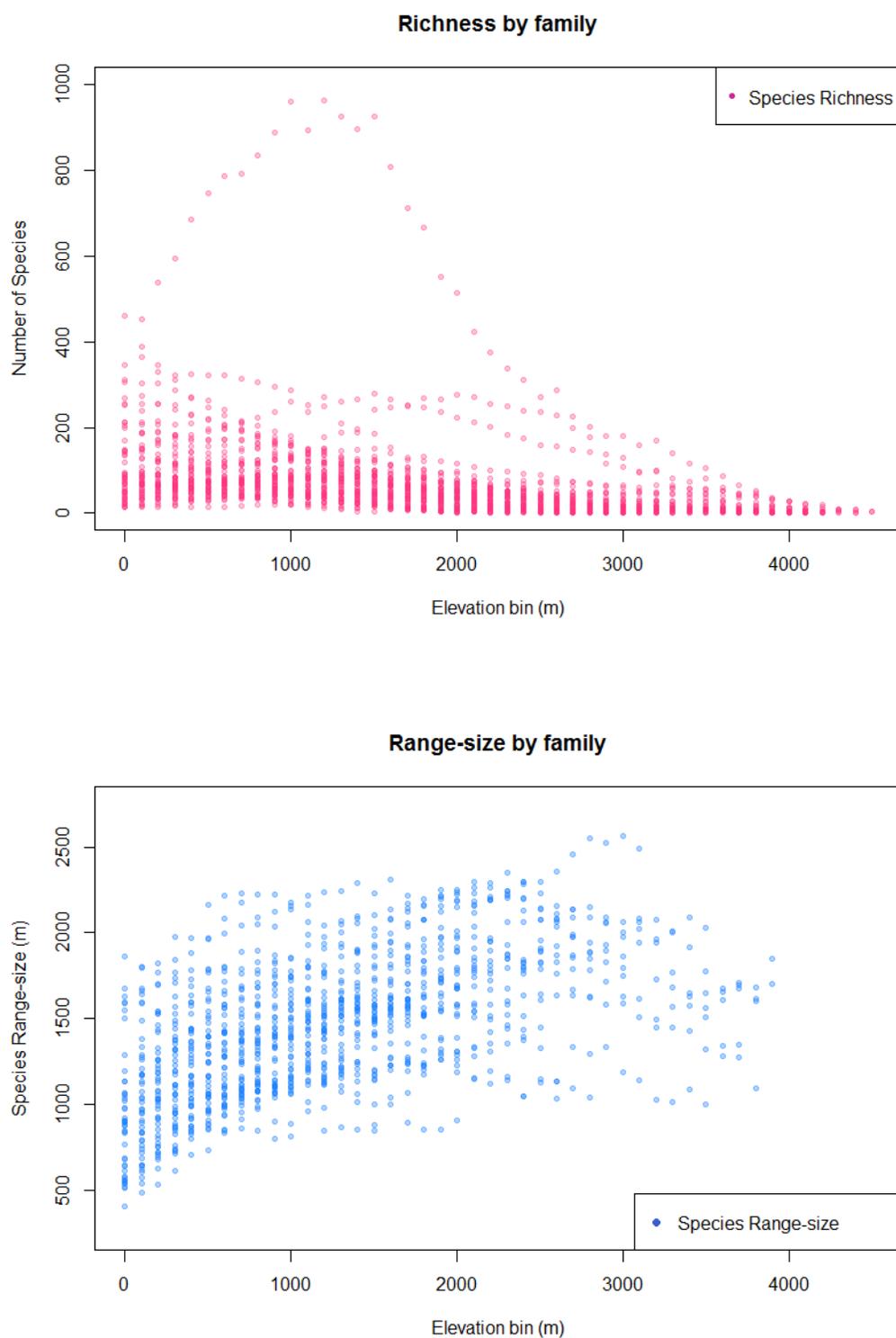


Figure 1.4. Plots of species richness (top) and average range-size (bottom) within each 100 m elevation bin, for 54 plant families. Each set of semi-transparent points represents data for a plant family, recalculated for each elevation bin.

1.3.2 The strength of Rapoport's rule, replicated by family

There was general support for Rapoport's rule when grouping all species together, and by taxonomic subgroups (Fig. 1.3, 1.4). When using the entire dataset of more than 20,000 species and without taxonomic distinction, there was a significant, albeit weak, relationship between range-size and elevation ($R^2=0.13$, slope = 0.07, $df = 43$, F -statistic 7.8, $P = 0.008$). In contrast, family-level analyses revealed substantial variation, with the strength of Rapoport's rule (slope of the relationship between range-size and elevation) spanning from - 0.27 (Rosaceae) to 0.72 (Dipterocarpaceae). Overall, slopes were positive across all families (Fig. 1.5), with an average of 0.26. For 4 out of the 54 families examined (Ericaceae, Podocarpaceae, Lejeuneaceae, and Thelypteridaceae) the slope did not differ significantly from zero (Table 1.1, Supplemental Figures 4.2).

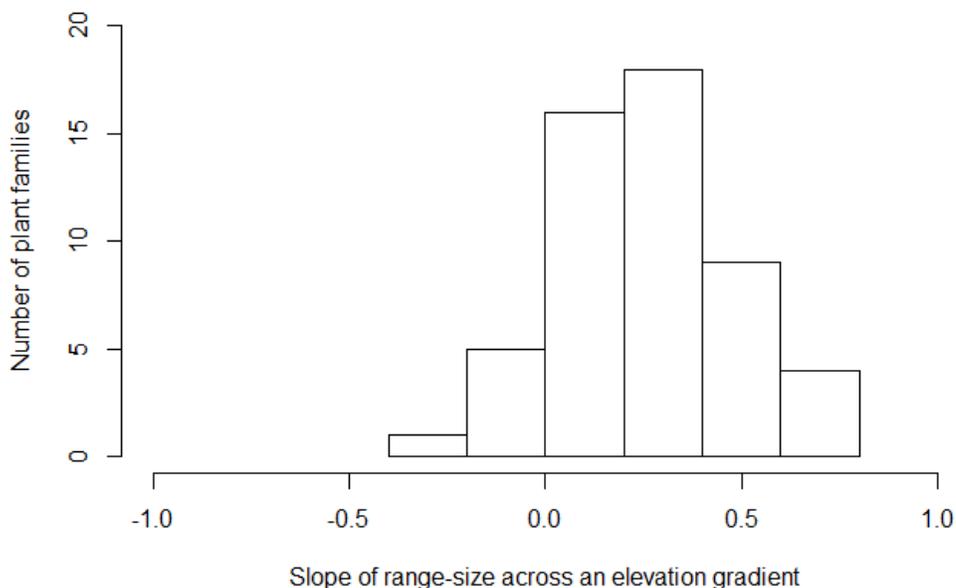


Figure 1.5. Histogram of the slope the relationship between average elevation range-size and elevation for 54 land plant families, used as a metric to represent the strength of Rapoport's rule.

Table 1.2. Summary of results by family for 54 species-rich plant families, presented by taxonomic group. "No. Species" is the richness from the dataset, including only species with two or more observations; "Richness Peak" is the elevation where richness is predicted to peak; the remaining four columns are results from testing Rapoport's rule, using average range-size as a function of elevation bin for each family, with "Slope" was calculated using Ordinary Least Squares (OLS) and is used as a metric of the strength of Rapoport's rule, with the *P* value as indication of whether the slope is significantly different from zero, with "NS" indicating non-significant.

	No. Species	Richness Peak (m)	Intercept (m)	Slope	Adj. R^2	df	<i>P</i> value
ANGIOSPERMS	15922	60					
Eudicots							
Acanthaceae	103	0	878	0.24	0.46	11	0.006
Anacardiaceae	98	23	640	0.63	0.98	7	< 0.001
Apocynaceae	284	12	931	0.28	0.83	19	< 0.001
Araliaceae	149	963	1197	0.27	0.86	24	< 0.001
Asteraceae	239	1300	2139	-0.10	0.16	37	0.007
Begoniaceae	141	919	774	0.18	0.67	14	< 0.001
Clusiaceae	127	0	578	0.56	0.98	8	< 0.001
Dipterocarpaceae	246	0	403	0.72	0.99	7	< 0.001
Elaeocarpaceae	212	246	1318	0.15	0.62	24	< 0.001
Ericaceae	593	1978	1674	-0.02	0.02	36	NS
Euphorbiaceae	445	41	1049	0.29	0.75	22	< 0.001
Fabaceae	601	0	740	0.52	0.94	17	< 0.001
Fagaceae	104	1026	1238	0.17	0.53	16	< 0.001
Gesneriaceae	435	920	716	0.11	0.46	19	< 0.001
Lamiaceae	219	58	909	0.47	0.95	16	< 0.001
Loranthaceae	98	219	1423	0.26	0.84	19	< 0.001
Malvaceae	246	0	577	0.70	0.96	11	< 0.001
Melastomataceae	220	934	983	0.14	0.70	20	< 0.001
Meliaceae	132	108	1048	0.36	0.94	15	< 0.001
Moraceae	299	182	1078	0.45	0.97	20	< 0.001
Myrtaceae	381	0	1173	0.34	0.84	26	< 0.001
Phyllanthaceae	375	108	993	0.34	0.89	19	< 0.001
Rosaceae	116	3201	2350	-0.27	0.83	18	< 0.001
Rubiaceae	909	22	953	0.10	0.33	27	0.001
Rutaceae	184	162	1211	0.12	0.26	23	0.006
Sapindaceae	205	0	965	0.40	0.93	16	< 0.001
Sapotaceae	132	0	600	0.61	0.93	9	< 0.001
Urticaceae	169	1075	1248	0.13	0.57	24	< 0.001

	No. Species	Richness Peak (m)	Intercept (m)	Slope	Adj. R ²	df	P value		
ANGIOSPERMS							<i>continued</i>		
Magnoliids									
Annonaceae	313	80	571	0.57	0.94	12	< 0.001		
Lauraceae	370	97	846	0.26	0.80	17	< 0.001		
Myristicaceae	225	53	578	0.54	0.93	12	< 0.001		
Primulaceae	221	1119	1241	0.24	0.89	26	< 0.001		
ANGIOSPERMS									
Monocots									
Araceae	177	94	636	0.52	0.95	12	< 0.001		
Arecaceae	421	83	719	0.45	0.98	16	< 0.001		
Cyperaceae	216	0	1351	0.24	0.68	29	< 0.001		
Orchidaceae	2353	1197	1097	0.04	0.11	34	0.025		
Pandanaceae	168	0	862	0.22	0.30	14	0.016		
Poaceae	486	0	1715	0.08	0.08	38	0.040		
Zingiberaceae	405	154	900	0.20	0.90	19	< 0.001		
GYMNOSPERMS									
Podocarpaceae	115	1255	67	1381	2160	- 0.02	0.05	15	NS
BRYOPHYTES									
Dicranaceae	1744	1543	110	1913	2259	- 0.05	0.21	28	0.007
Lejeuneaceae	140	144	1611	0.02	-0.02	21	NS		
Sematophyllaceae	113	1296	1311	0.21	0.80	19	< 0.001		
PTERIDOPHYTES									
Aspleniaceae	2703	1054	130	925	1675	0.19	0.72	23	< 0.001
Athyriaceae	140	1120	1306	0.12	0.53	20	< 0.001		
Cyatheaceae	179	1244	1482	0.15	0.73	27	< 0.001		
Dryopteridaceae	202	1285	1341	0.18	0.87	28	< 0.001		
Hymenophyllaceae	199	1084	1613	0.29	0.95	30	< 0.001		
Polypodiaceae	549	1383	1736	0.06	0.22	37	0.001		
Pteridaceae	200	806	1448	0.33	0.97	24	< 0.001		
Selaginellaceae	97	286	1036	0.37	0.97	14	< 0.001		
Tectariaceae	127	180	847	0.36	0.88	11	< 0.001		
Thelypteridaceae	332	974	1238	-0.03	0.04	25	NS		

1.3.3. Ecological, biogeographic, and taxonomic correlates of the strength of Rapoport's rule

Families with mostly arborescent growth forms had peaks in richness at lower elevations, and a more narrow elevation distribution, compared to families with mostly herbaceous growth forms (richness: $t = -2.40$, $P = 0.02$, arborescent richness peak at 382 m, herbaceous richness peak at 861 m, Fig. 1.6a; elevation breadth: $t = -2.70$, $P = 0.01$, average arborescent breadth = 1762.5 m, herbaceous breadth = 2490, Fig. 1.6b).

Rapoport's rule was stronger among families with mostly arborescent growth forms compared to herbaceous families with a slightly positive slope (slope: $t = 2.167$, $P = 0.04$, mean arborescent slope = 0.33, mean herbaceous slope = 0.19, Fig. 1.6c). In addition, for Angiosperms there was a positive relationship between latitudinal and elevational range-size ($cor = 0.52$, $df = 37$, $P < 0.001$; Fig. 1.7).

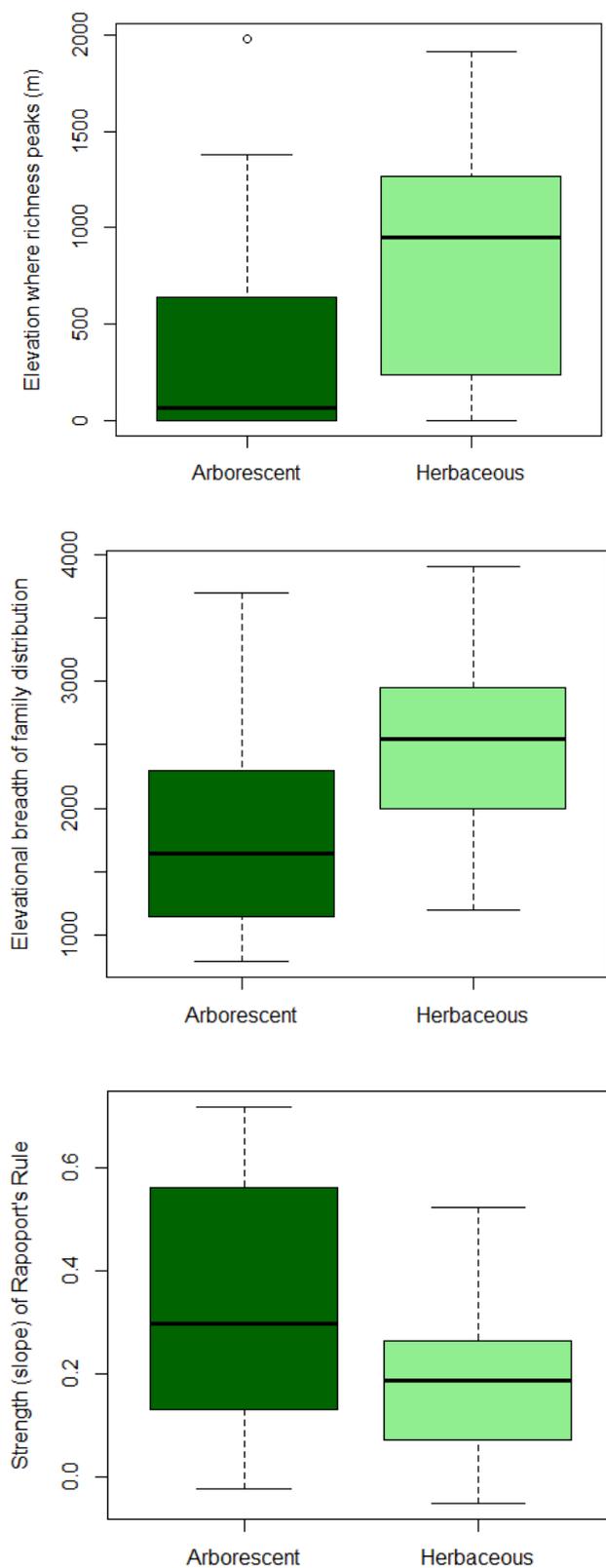


Figure 1.6. Comparisons of species distribution patterns based on growth form, calculated by plant family. All analyses were significant. The top figure illustrates differences in the elevation where arborescent, as compared to herbaceous, families have peaks in richness. Middle figure illustrates differences based on the elevational breadth (sum of 100 m bins where at least thirty species occur concurrently). Bottom figure illustrates the difference in the strength of Rapoport's rule, being the slope of the relationship between range-size and elevation bin, replicated by family.

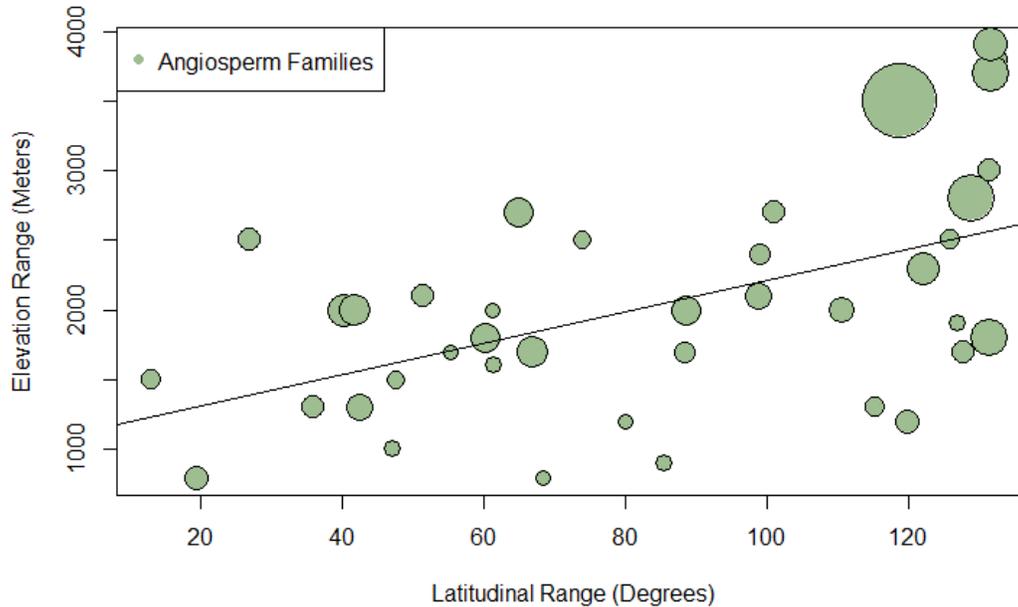


Figure 1.7. Relationship between latitudinal range-size and elevational range-size for different families of angiosperms. Latitudinal values estimated by Hawkins et al. 2011. Point size is scaled with the number of species within each family.

The strength of Rapoport's rule changed with the elevation where richness peaked for each family (Adjusted $R^2 = 0.49$, F -statistic 51.02, $df = 51$, P -value < 0.001 ; Fig. 1.8), but did not depend on the number of species within each family (Adjusted $R^2 = 0.01$, F -statistic 1.25, $df = 51$, P -value = 0.27). When richness peaked at lower elevations within wet tropical forests from 0 - 500 m, support for Rapoport's rule was highest, with an average slope of 0.40 and declined with increasing elevation (Fig. 1.8). However, within lower elevation areas there was also considerable variation across families. For example, for families with peaks in richness nearest sea-level, the observed minimum slope was for Poaceae with 0.08 whereas Dipterocarpaceae had a maximum slope of 0.72. Other families with peaks at lower elevations included Euphorbiaceae, Fabaceae, Pandanaceae, Myristicaceae, and Myrtaceae.

A second major grouping of families had richness peaks in mid-elevation areas near 1250 m (spanning approximately from 800 to 1500 m), generally corresponding with the transition to montane cloud forests (Fig. 1.8) in habitat noted for oak, ferns, conifers, and epiphytes. Mid-elevation areas had moderate to low support for Rapoport's rule, with an average slope of 0.14. Examples of mid-elevation families includes Cyatheaceae, Orchidaceae, Fagaceae, Podocarpaceae, Polypodiaceae, and Sematophyllaceae. Plants with richness peaks near or above 1900 m tended to have no support for Rapoport's rule and a slope that was either not significantly different from zero (e.g., Dicranaceae with a slope of - 0.05; Ericaceae with a slope of -0.02) or negative (e.g., Rosaceae with a slope of - 0.27) (Table 1.2, Supplemental Figures 4.2).

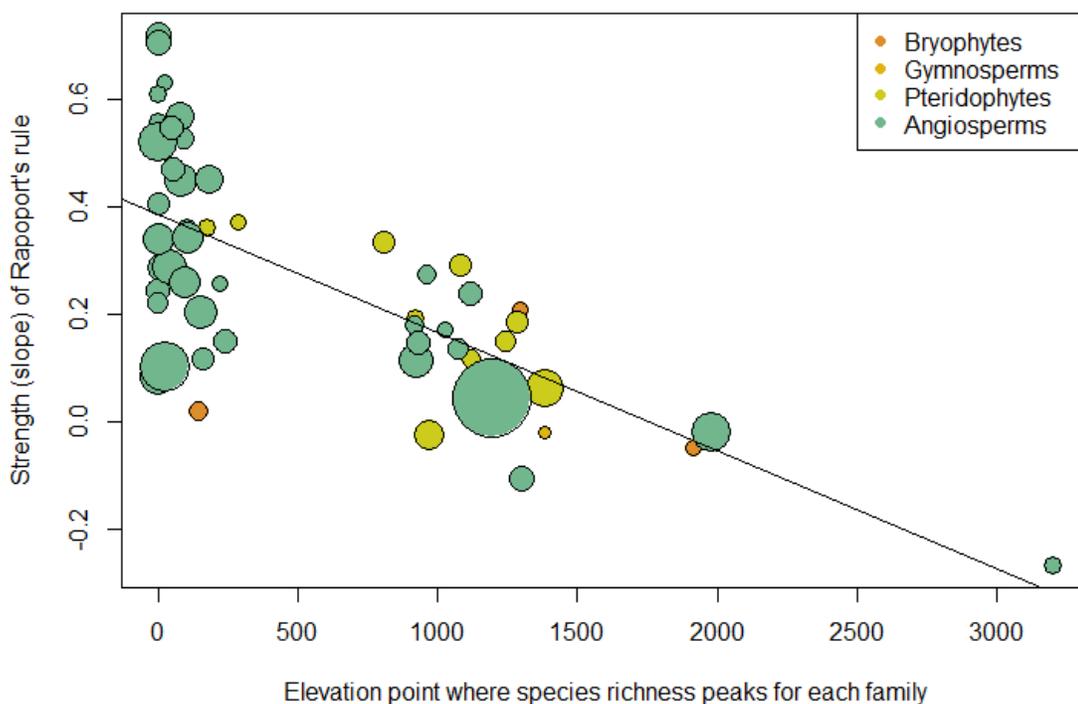


Figure 1.8. Across plant families ($n = 54$), the strength of Rapoport's rule declined with the elevation where species richness was highest. The y axis values are based on slopes from linear regression models, replicated by plant families where species range-size is a function of elevation (results shown in Table 1). Point size is scaled with species richness of the family.

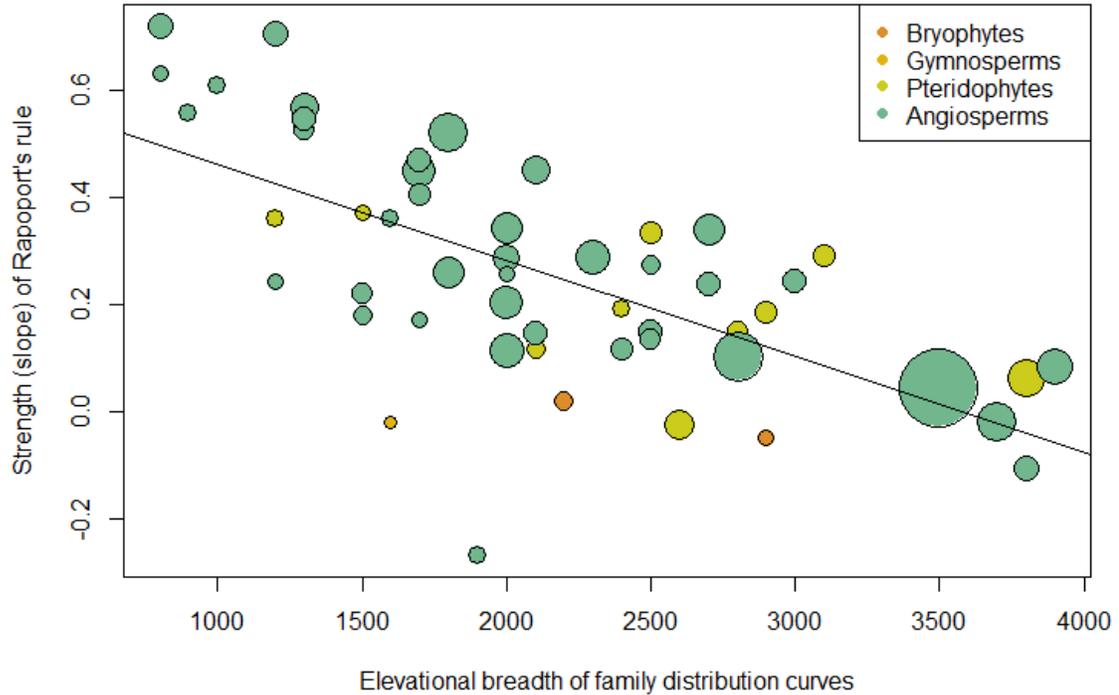


Figure 1.9. Across plant families ($n = 54$) analysis on the strength of Rapoport's rule as a function of the breadth of species distribution curves at the family-level. The family elevation breadth is defined as the summation of consecutive 100 m elevation bins with thirty or more species, as used in the linear regression models summarized in Table 1.1. As the elevation breadth for each family increased, the support for Rapoport's rule decreased. Point size is scaled with the species richness of the family.

The elevation breadth of each family also correlated strongly with the strength of Rapoport's rule (Adjusted $R^2 = 0.43$, F -statistic 39.87, $df=51$, $P < 0.001$; Fig. 1.9).

Overall, families with very narrow distribution breadth had the steepest positive slopes, whereas families with broad distribution breadth had minimal support for Rapoport's rule. For instance, both Anacardiaceae and Poaceae had a peak in richness near sea-level (Table 1.2) but differed in that Anacardiaceae had very narrow elevation breadth of ~800 m and slope of 0.63, whereas Poaceae was more cosmopolitan with a broad elevation breadth of ~3900 m and a slope of 0.08. For families with extremely large elevation breadths, such as Asteraceae (~3800 m), the shallow negative slope (- 0.10) may be attributed to non-linear range-size trends (convex hump, with tapering of average species range-size when approaching of elevation minimum and maximum). However, this was not always the case, because some families, such as Ericaceae, with an elevation distribution of ~3700 m, had a flatter slope that was not statistically different from zero.

1.4 Discussion

By comparing patterns across taxonomic groups and families, this study offers new insights on Rapoport's rule in relation to elevational distributions and natural history of Southeast Asian flora. Specifically, the increase in average range-size along an elevation gradient is contingent upon a scenario where either richness peaks nearest sea-level, or when a plant family is restricted to a very narrow portion of the elevation gradient, especially for arborescent growth forms. In contrast, families with peaks in richness at higher elevations, that had very broad geographic distributions, or had an herbaceous growth form, showed minimal variation in range-size. My results suggest that the

strength of Rapoport's rule depends on taxonomic affiliation and ecological history reflecting unique characteristics of each plant family in relation to the landscape.

1.4.1 Role of ecological, biogeographic, and taxonomic variation in determining the strength of Rapoport's rule

Studies that consider biogeographic origin of plant species along elevational gradients have found strong support for Rapoport's rule for groups categorized as tropical, and minimal support for those considered to be more temperate in origin (Feng et al. 2016). This is counter to observations of latitudinal trends, where in general there is more support for Rapoport's rule for species from biomes closer to polar regions than equatorial regions (Ruggiero and Werenkraut 2007). This contradiction could be attributed to the differences in approach and scale of analyses. There was overall weak support for Rapoport's rule when all species were analyzed together, some families exhibited substantial variation in their support for Rapoport's rule, with some strongly supporting it, and others showing no support at all. These differences may be related to the biogeographic histories of these families.

The majority of plant families included in this study can be broadly described as having points of origin within the tropics or having unresolved origins and cosmopolitan distribution worldwide. However, some especially species rich clades nested within tropical families have temperate or more mountainous association (Hawkins et al. 2011, Schwery et al. 2015), which may explain why higher elevation flora in particular had less support for Rapoport's rule. For instance, the genus *Rhododendron*, which represents

approximately half of the Ericaceae species for the region (255 species included in the dataset), displayed consistent range-sizes across the elevation gradient with species occupying diverse habitat types spanning from near sea-level to mountain summits. *Rhododendron* may be a good example of how tolerance of abiotic stressors enables broad distributions, and even though the results are counter to expectations under Rapoport's rule, the pattern produced is still consistent with of the underlying explanation that sensitivity to climatic variability is what drives range-size variation.

At the opposite end of the spectrum, Dipterocarpaceae with a positive slope of 0.72 and the strongest support for Rapoport's rule, are a prime example of flora with high degrees of habitat specialization within the context of minimal climatic variability (Palmiotto et al. 2004, Russo et al. 2007b, 2008). In other words, Dipterocarps are model taxa for "why mountain passes are higher in the tropics" (Janzen 1967). The spatial distributions of Dipterocarpaceae indicate that the majority of species have very narrow latitudinal range-sizes (strictly tropical) and elevation maximums (Ashton 1988, Hawkins et al. 2011).

Differences among growth forms in the elevation where richness peaks have previously been noted (Whittaker et al. 1973, Grau et al. 2007), but whether growth forms varied in their support of Rapoport's rule has not been well investigated (Lee et al. 2013). In general, liverworts and bryophytes do not show support for Rapoport's rule (Grau et al. 2007) whereas angiosperms, specifically woody trees, displayed mixed results depending on the study (Weiser et al. 2007). From a physiological perspective, trees are more limited in where they can grow than smaller stature growth forms which can occur in with greater abiotic stressors, such as sub-alpine zones (Körner 1998).

Herbaceous species also may have larger range-sizes overall because of differences in other attributes, such as smaller seeds dispersed by wind or more of an opportunistic life history strategy (Morin and Chuine 2006).

1.4.2 Conclusion

Overall, this study reinforces the need to examine variation in the strength of support for Rapoport's rule among plant families with respect to ecological, biogeographic, or evolutionary factors.



Fougères arborescentes. *Les merveilles de la végétation*. 1866.

CHAPTER 2

Soil specialization and vegetation zones define elevation range-sizes for Mt. Kinabalu regional flora

2.1 Introduction

Some of the most striking macroecological trends observed at large scales include global patterns in species diversity. Along latitudinal gradients, it is often observed that species richness is higher in tropical regions, and declines towards the poles (Currie and Paquin 1987, Wright 1992, Hawkins et al. 2003, Nogués-bravo and Araújo 2006). Another macroecological trend is Rapoport's rule, which describes the increase in average species range-size (extent) along environmental gradients, such as range-size increasing with latitude, elevation, or water depth (Stevens 1989, 1992, 1996).

One explanation for Rapoport's rule is that it is a response to asymmetry in the environmental conditions, including climate and light regime, that species are subjected to along geographical gradients (Stevens 1992). For instance, species at the northern or southern-most portions of a global-scale latitudinal gradient may experience pronounced seasonality, whereas species in equatorial areas experience more constant amounts of light and greater temperature stability over a year, especially at lower elevations. Similarly, along an elevation gradient, species at the summit of a mountain are subject to

greater diurnal and seasonal environmental variation than species at lower elevations (Janzen 1967, Stevens 1992, Sanders 2002).

Support for Rapoport's rule has been found across many taxonomic and functional groups, including mammals, birds, insects, bacteria, and trees (Stevens 1989, 1992, Morin and Lechowicz 2013). Applied to water depth, where greater depth is associated with species with larger range-sizes, Rapoport's rule has mixed support among marine species (Stevens 1996, Tomašových et al. 2015) in part due to differences in response to thermal gradients and potentially methods of dispersal. Some studies show lack of support for Rapoport's rule (Bhattarai and Vetaas 2006, McCain and Bracy Knight 2013, Tomašových et al. 2015), or dramatic variation in the strength of Rapoport's rule, which is often quantified as the slope of the relationship between range-size and the gradient of interest. For instance, a comprehensive study of 160 datasets examining Rapoport's rule for montane vertebrates found conflicting support depending on the taxonomic group examined (McCain and Bracy Knight 2013). Other studies specifically targeting habitats with the greatest temperature stability found trends counter to Rapoport's rule (Tomašových et al. 2015).

Discrepancies in support for Rapoport's rule can also emerge if range-size is not determined by a single environmental variable for all taxa. Although temperature is linearly related to elevation, other environmental factors affecting species ecological niches also vary along these gradients. For example, species may respond differently to environmental stressors based on life history strategy or evolutionary history (Janzen 1967, Grubb 1977). If a combination of environmental factors that vary in contrasting ways across gradients determines the distributions of species in a given taxon, then taxa

may vary in their support for Rapoport's rule, especially at the regional scale. Other ecological mechanisms also may influence species' range-size distribution trends, such as the size of the organism; mechanisms of dispersal, colonization, or establishment into new habitat types; response to competitive pressure or stochastic events; or the rate of niche expansion or specialization (Whittaker et al. 1973, May 1974, Vazquez and Givnish 1998, Morin and Chuine 2006).

Geometric constraints, in which maximum potential for range-sizes must conform to the spatial limits of a given area, can result in truncation of possible ranges that can exist (Colwell and Hurtt 1994, Šizling et al. 2009). Hard boundaries, where occurrence beyond a certain point is impossible (*e.g.*, areas below sea level or above a mountain summit), would thus create smaller range-sizes for species adjacent to these boundaries as compared to species without geometric constraints which are positioned towards the center of a gradient. If hard boundaries exist at both ends of a gradient, then a convex shaped trend in average range-sizes would be thus be produced. However, if only a single hard boundary exists within an area examined, such as a transect from sea-level to mid-elevation areas, then a positive slope, based on the increase in average range-size with elevation, would be produced and appear to support Rapoport's rule.

Outlier species with especially large range-sizes can complicate analyses of Rapoport's rule, with calculations of average range-size disproportionately skewed by these outlier species in areas with lower richness (McCain and Bracy Knight 2013). Differences in sampling intensity along a gradient (Brehm et al. 2007) also can obscure metrics of richness and range-size. Despite these obstacles complicating research on Rapoport's rule, investigating the effects of ecological and geometric mechanisms that

underlie patterns in species' range-sizes can help us understand how diversity is structured globally and on elevation gradients.

Mountains near the equator are especially suitable for examining range-size trends because of their dramatic climatic gradients, reduced seasonality, and lack of widespread glaciation. Equatorial mountains with summits at 4000 m and above can be subject to freezing events, a scenario that is quite distinct relative to the surrounding conditions within tropical forests at lower elevations (Hope 1976, Kitayama 1992). Tropical regions of the globe also have a higher species richness that allows for more comprehensive examination across broader taxonomic groups and larger sample sizes.

Along elevation gradients, especially for mountains in the tropics, it has long been recognized that there are distinct vegetation zones that often correspond with changes in resource availability (Whittaker 1960, Holdridge et al. 1971, Stevens and Fox 1991, Kitayama 1992). The elevation of cloud cover strongly affects moisture and sunlight and the form that precipitation takes (*e.g.* rain showers as compared to constant mist), which strongly affects the vegetation (Kitayama 1992). Lower elevation forests tend to have periodic rainfall, mid elevation forests have frequent fog immersion, and the highest elevation shrublands can alternate between mist and even drought in areas above the cloud layer (Kitayama 1992). The treeline is another distinct vegetation transition, and it may represent a boundary that affects species elevation ranges, since a key adaptation (*e.g.* freezing tolerance) is needed for species to occur in the area above this threshold (Stevens and Fox 1991, Körner 1998, Rehm and Feeley 2015). These ecotones would constitute ecological boundaries where significant habitat filtering and range truncation could occur (Stevens and Fox 1991).

Vegetation zones also can reflect the geological history of an area. Differences in weathering of the underlying substrate, along with variation in the parent material, can strongly influence soil conditions (Kitayama et al. 1998, Russo et al. 2008). Edaphic conditions also can be associated with distinct communities of species, with some of the most stressful or extreme low nutrient soil types limiting the species present to only those with specialized adaptations to those environments (Whittaker 1954, Harrison 1997, Proctor 2003, Russo et al. 2008). Flora that specialize in the most extreme edaphic conditions also may display distribution patterns or life history strategies that contrast with that of flora influenced more by climate based gradients (Harrison 1997, Fernandez-Going et al. 2012).

I examined the joint effects of ecological and geometric factors on the relationship between range-size with elevation in a tropical southeast Asian flora. I used data on elevation distributions and edaphic specialization for 3,060 vascular plant species from 193 families from the mountainous Mt. Kinabalu region of northern Borneo. Mountains in this region reach up to 4095 m above sea-level with distinct vegetation zones distributed across an elevation gradient (Kitayama 1992). In addition, there is dramatic edaphic variability ranging from infertile and stressful ultramafic (serpentine) soils to more fertile alluvial soils, to which many plant species are specialized (Kitayama et al. 1998, van der Ent et al. 2014). Therefore, this region offers an ideal system in which to examine how variation in different environmental factors, and potential ecological strategies of species, affects macroecological patterns of range-size on an elevation gradient. Specifically, I assessed differences in the elevation where species richness peaks based on soil specializations of these Bornean plant species, and whether variation

in the strength of Rapoport's rule was structured by distinct vegetation zones and their boundaries. If range-size was determined primarily by temperature, and if all organisms responded in a comparable manner, then I predicted that the relationship between elevation range-size and elevation would be defined by a single positive slope that corresponds with the linear decline in temperature with elevation. However, if multiple environmental factors interact to create boundaries between habitat types, then I predicted that some species would display non-linear relationships or negative slopes that depend on position along the elevation gradient and the soil type to which a species is affiliated.

2.2 Methods

2.2.1 Study site

I focused on the vascular flora of the Sabah region of northern Borneo (Malaysia), with the center of interest being Mt. Kinabalu, the tallest mountain in Southeast Asia (4095 m), located at approximately 6° 05' N, 116° 35' E, but with the region also including Mt. Tomboyukon and the Crocker Range. The study area includes a variety of habitat types, from tropical wet forest to cloud forests and upper montane scrublands (Kitayama 1992, Grytnes and Beaman 2006). The area above the treeline is mostly granite with extremely shallow soils, extreme sun and wind exposure, and occasional freezing events. This region of Borneo has been the center of intensive botanical surveys and ecological research for more than a century and a half with approximately 5000 plant taxa described, many of which are endemic (Parris et al. 1992, Wood et al. 1993, Beaman and Beaman 1998, Beaman et al. 2001, Beaman and Anderson 2004, Grytnes and Beaman 2006).

Sabah includes some of the world's most expansive patches of ultramafic (serpentine) soil, estimated to cover 3200 km², or 4.6% of the total landmass (van der Ent et al. 2014), distributed across many elevations. Over 1500 different plant species in the region have been identified as either being specific to, or tolerant of, ultramafic soil types (van der Ent et al. 2014). Examples of species restricted to ultramafic soils include *Nepenthes rajah* (Nepenthaceae), *Rinorea bengalensis* (Violaceae), and *Phyllanthus balgooyi* (Phyllanthaceae), with the latter two having well-known physiological means to hyperaccumulate heavy metals at levels usually toxic to most other plants (Proctor 2003, van der Ent et al. 2014). Other species commonly associated with ultramafic soil include *Rhododendron ericoides* (Ericaceae) and many species of podocarps, ferns, and orchids (Argent 2006, Kitayama et al. 2011, van der Ent et al. 2014). Vegetation growing on ultramafic soil is also distinct in stature, generally exhibiting stunted growth compared to vegetation on adjacent non-ultramafic soil and forming shrublands. Ultramafic soil is associated with reduced water retention, high deposits of heavy metals, and nutrients that are either limited, or in such excess, that they require specialized physiological adaptations (Kruckeberg 2002, Proctor 2003, van der Ent et al. 2014).

2.2.2 Herbarium database

I utilized a database on plant species occurrence for this region that I compiled from multiple sources, with an emphasis on the flora of Mt. Kinabalu. First, I used an extensive preexisting herbarium database from Sabah Parks, with descriptions of collection localities, observations of habitat, the general composition of neighboring vegetation, and soil type. This database has been used as the foundation for a series of

comprehensive botanical monographs encompassing trees, forbs, grasses, orchids, and ferns (Parris et al. 1992, Wood et al. 1993, Beaman and Beaman 1998, Beaman et al. 2001, Beaman and Anderson 2004, van der Ent et al. 2014), as well as for a study on the distribution of species richness for the Mt. Kinabalu area (Grytnes and Beaman 2006). Second, I drew information from the literature and historic surveys on ultramafic plants of Sabah, including newly discovered species (van der Ent et al. 2014). Lastly, I queried Global Biodiversity Information Faculty (GBIF) records using a species list from the combined database, adding 12,397 new records for 1,799 species. The additional records helped to better represent species that extend into lower elevation areas outside of the Mt. Kinabalu park boundaries, which is the location with the most intensive botanical sampling.

I integrated various datasets and took several steps to ensure quality of the data, such as excluding (1) duplicated records based on a combination of unique identifiers, (2) records with incomplete scientific names, (3) any record not identified to the species level and (4) any record without elevation data. The portion of the Mt. Kinabalu herbarium database that I used included only elevation values (coordinates were excluded to protect the exact location of threatened or endangered species). Additional information from published monographs and GBIF records either did not include coordinates from which to extract elevation data from or were excluded due to questions about the quality and spatial resolution of the data being too coarse to represent the highest elevation areas. Standardization of the data included converting all records to meters. If an elevation of a single record was estimated as a range rather than a point, I used the midpoint of the values shown. Individual records flagged as extreme outliers relative to the elevation

where that species is normally observed were manually checked and compared to the relevant Mt. Kinabalu botanical monograph entry. After cleaning the combined datasets, I extracted the minimum and maximum elevation for each species. I then calculated elevation range-size (extent) as maximum minus minimum elevation. Lastly, the combined dataset was further parsed down to exclude species with an elevation range-size of zero or fewer than two observations.

Based on botanical monograph descriptions, I categorized each species in the dataset according to its edaphic association, defining three categories: 1) ultramafic specialists, 2) ultramafic tolerant species, and 3) species with no association with ultramafic soil (Table 2.1). I defined ultramafic specialists as species that predominately or exclusively occur on ultramafic soils, as indicated by descriptions in species records and literature, such as "ultramafic obligate association," "ultramafic indicator species," "ultramafic preferential," or "ultramafic endemic," as well as "especially," "mostly," or "often" on ultramafic soil. I also used location of where a plant was sampled, specifically sites known to be exclusively ultramafic (*e.g.* Mt. Tomboyukon), to infer soil association. Species also be could categorized as ultramafic specialists if they were recorded as occasionally occurring on different, yet still extremely stressful, habitat types (*e.g.* granite outcrops or former mining sites). Ultramafic tolerant species were defined as those that only occasionally, but not predominantly, occur on ultramafic soil as indicated by descriptions such as "facultative association," or as "sometimes," "probably," or "possibly" occurring on ultramafic soil. Many of these species are also described as opportunistic or ruderal, occurring in areas with a history of site disturbance. Non-ultramafic species were defined as all other species either without a particular

association, or repelled by, ultramafic soil. Distinction between the three categories was refined by cross-validation with published botanical monographs and published literature if I was uncertain about the classification of any species (Kitayama et al. 1998, Argent 2006, van der Ent et al. 2014).

My final dataset encompassed 3,060 species, representing 879 genera and 193 families, consisting of 34,148 records in total with an average of 11 records per species (range: 2-126 records per species). Soil association categories included 1,895 (62%) non-ultramafic species, 641 (21%) ultramafic tolerant species, and 524 (17%) ultramafic specialists (Table 2.1). Venn diagrams of the taxonomic distribution of plant species suggests that all three soil association categories are generally evenly represented (Figure 2.1). For instance, 79 plant families had species within each of the soil classification categories, relative to a smaller proportion of families restricted to a single soil classification (non-ultramafic 49, ultramafic tolerant 8, ultramafic specialists 11 families).

Table 2.1. Summary of number and percent of the 3,060 species in the final data set that are in each soil association category, along with the number of plant families that those species represent.

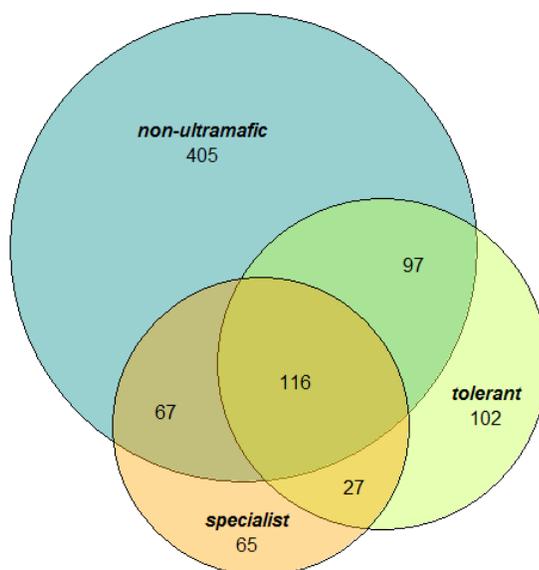
Category	Number of Species	Number of Plant Families
Ultramafic Specialist	524 (17%)	107
Ultramafic Tolerant	641 (21%)	121
Non-Ultramafic	1895 (62%)	169

2.2.3 Evaluating variation in species richness and Rapoport's rule

To examine variation in species richness and average range-size with elevation, I used a commonly used approach, referred to as "Steven's method" (Stevens 1992). The merits of this approach are described in Chapter 1, Section 1.2.3. For this study I partitioned the elevation gradient (0 - 4095 m) into 100 m bins. Based on its minimum and maximum

elevation, each species was categorized as either present or absent from each bin, with the assumption that occurrence is possible in any bin encompassed by its elevation range. I calculated the elevation range-size (elevation maximum minus minimum) for each species. For each bin, I calculated species richness and the mean elevation range-size by averaging across all species present. I also identified the elevation where species richness peaked, using methods described in Chapter 1, Section 1.2.4.

Venn Diagram of plant genera



Venn Diagram of plant families

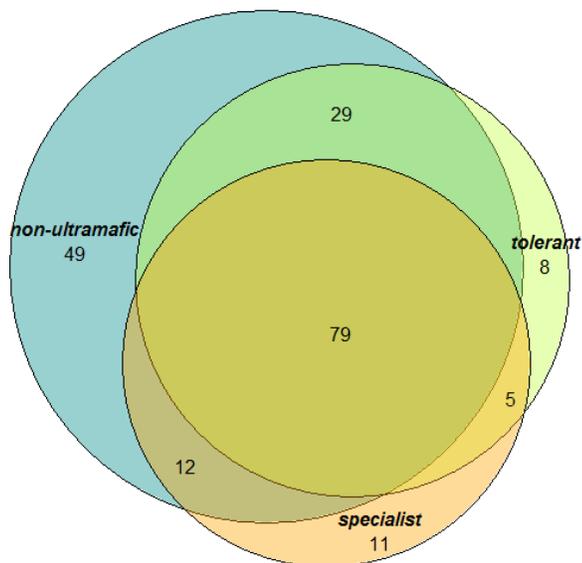


Figure 2.1. Venn diagrams showing the taxonomic distribution of soil association categories (non-ultramafic, ultramafic tolerant, and ultramafic specialist species). The center of the diagram refers to the number of families or genera with species represented in each of the three soil categories, whereas outer most numbers are indicative of taxonomic groups where all species are restricted to a single category.

Rapoport's rule states that there should be a positive relationship between species range-size and elevation (Stevens 1992). To test for this relationship in a way that is comparable to previous studies, I first used linear regression without any distinction between habitat types (elevation as the only predictor) as a simple metric for comparison to findings from literature. Then, for the primary focus of this study, I used three models of varying complexity, replicated by the three soil association categories, for a total of nine analyses. In the simplest model (model 1), I used linear regression across the full elevation range, repeated for each of the three soil association categories. For models 2 and 3, I tested the importance of vegetation zone boundaries using break-point analyses and piece-wise regression, also repeated by soil association category. The first of the forced break-point analyses (model 2) was informed by the primary vegetation zone boundaries described in literature (Kitayama 1992), observed at approximately 1200 m and 2800 m, followed by model selection to identify the most supported elevation of each breakpoint within 300 m +/- from these points. These breakpoints are associated with the transition from tropical wet forest (< 1200 m) to cloud forest (1200 – 2800 m), and the upper montane which extends to the subalpine zone and mountain summit (> 2800 m) without distinction as to whether the upper boundaries of species occurrence ended at the treeline (~3800 m) or mountain summit (4095 m). The average breakpoint for lower elevation areas was 1500 (based on the three soil categories), and the upper elevation average was 2700; these two values were then used as the breakpoints for all model 2 analyses. For this reason, I refer to model 2 as a fixed break point analysis, which is beneficial in that it allows for comparison of trends along the same portions of the elevation gradient. In contrast, the model 3 analyses use a non-forced break-point

analysis approach, in which there is no predetermined number or position of breakpoints, and the breakpoints are instead fit to the data using the R package *strucchange* (Zeileis et al. 2001). The non-forced analysis would capture any substantial changes in range-size trends that may not be represented in the other models, based either on biological mechanisms or geometric artifacts. The minimum segment size for non-forced breakpoints was set to be six or more consecutive elevation bins. I then used Akaike's Information Criterion (AIC) for model selection, replicated for each soil association category. If two models had similar AIC values, then I chose the simpler model.

2.2.4 Null models testing the effects of soil association on elevation range-size patterns

I developed null models to differentiate the role of soil association on patterns of species richness, elevation range-size (extent) and the slopes of range-size change across an elevation gradient (strength of Rapoport's rule). First, I randomized soil association categories across species, keeping each species' elevation minimum and maximum constant and maintaining the observed number of species in each soil association group. For each soil association category, I used 1000 randomizations to construct null distributions of average elevation range-size and species richness in each elevation bin and used the 2.5% and 97.5% percentiles as the parameters to construct 95% confidence intervals for each bin. Observed average range-size and species richness was then compared to the 95% confidence interval for each bin as a metric of significance. I also examined differences in the strength of Rapoport's rule, expressed as the slope (using ordinary least squares) of average elevation range-size as a function of elevation bin, for

the top model selected for each soil association category as compared to the null distribution slope values. If a piecewise model was selected as best, then I used the same procedure, but for each segment of the elevation gradient.

2.3 Results

2.3.1 Peaks in species richness

When grouping all plant species together, I found a hump-shaped peak in species richness at approximately 1200 m, with a total of 1,811 out of 3,060 species (59%) occurring at this point in the gradient (Figure 2.2). The average range-size for species overlapping, or within, the 1200 m elevation bin was $1181 \text{ m} \pm \text{SE } 597 \text{ m}$. When I examined richness by subsets based on soil association categories (Figure 2.3), I found that both non-ultramafic and ultramafic tolerant species displayed a peak in richness at 1200 m (1,065 species, 56%; 414 species, 65%). In contrast, ultramafic species richness peaked higher in elevation at 1500 m with 360 species, or 69% of that data subset.

The observed species richness for ultramafic species was greater than the null model prediction for majority of the mid to high elevation areas ($> 1,100 \text{ m}$) (Fig. 2.3). Ultramafic tolerant species had higher richness than expected predominately within lower elevation areas ($< 1,200 \text{ m}$) and scattered along other portions of the gradient. In contrast, non-ultramafic species had lower richness across the majority of the elevation gradient as compared to expectations based on the null model, despite having an overall greater number of species within this soil category.

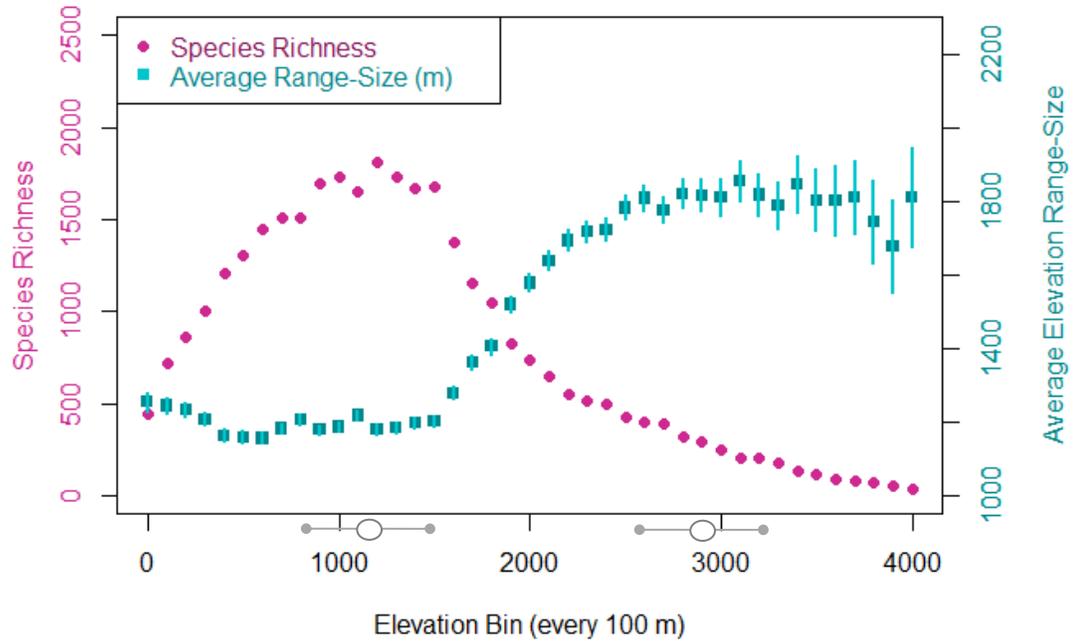


Figure 2.2. Variation in the richness (left ordinate) and elevation range-size in meters (right ordinate) of 3,060 Bornean plant species with elevation. Points show mean range-size within each elevation bin, and error bars are \pm one standard error. The circles in grey represent the areas described in literature as vegetation transition zones.

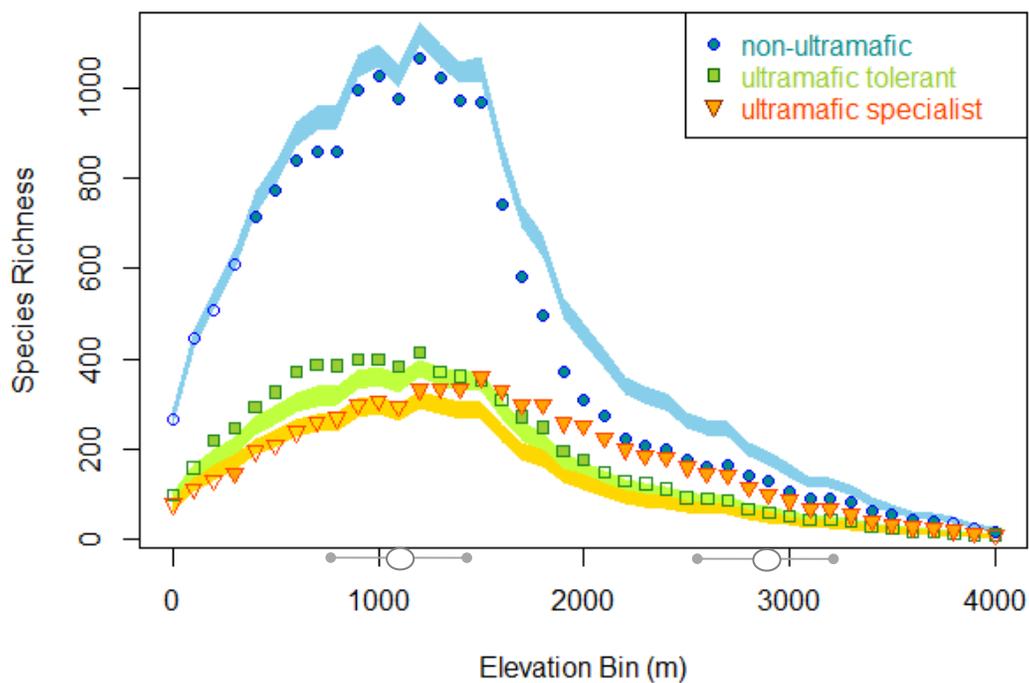


Figure 2.3. Variation in species richness versus elevation for Bornean plant species in three soil association categories. Confidence intervals based on a null model are shown as ribbons, and observed richness values are shown in points for each bin, with values significantly different from the null prediction shown with solid points, and values not different from the null prediction shown with hollow points. The circles in grey represent the areas described in literature as vegetation transition zones.

2.3.2 Variation in elevation range-size patterns

When grouping together all 3,060 species, the average species range-size increased with elevation ($F = 177.6$, $df = 39$, adjusted $R^2 = 0.82$, $P < 0.001$), thus lending general support for Rapoport's rule (Figure 2.2). However, the pattern itself would be best described as non-linear. Moreover, the shape of the range-size-elevation relationship varied among species with different soil associations, possibly reflecting differing responses to environmental factors along this elevation gradient (Table 2.2; Figure 2.4).

For ultramafic specialists, model 3, using piece-wise regression with non-forced break points at 1400 m and 3300 m, was the most supported model (Table 2.2 & 2.3). For ultramafic tolerant species, the most supported model was also based on piece-wise regression, but with non-forced break points at positioned at 600 m, 1800 m, and 3400 m (Table 2.2 & 2.4). For non-ultramafic species, the most supported model was the piece-wise regression with forced break-points (model 2) at 1500 m and 2700 m, being the elevations of vegetation transition zones observed in literature (Table 2.2& 2.5).

Species with different soil associations showed varying levels of support for Rapoport's rule, which also depended upon the section of the elevation gradient examined (Figure 2.4, Tables 2.3, 2.4, and 2.5). In particular, for all three soil association groups the middle elevation areas exhibited the strongest support (expressed as the steepest positive slopes) for Rapoport's rule. In contrast, at the lowest and highest elevations, there was little to no support for Rapoport's rule. Overall, ultramafic specialists and tolerant species had range-size trends that were more similar, with gradual changes in range-size at break-point locations, whereas non-ultramafic species had distinct in changes in slope at vegetation zone boundaries.

Table 2.2 Model selection using Akaike Information Criterion (AIC) comparing three different types of models for each soil association category. The first model is based on linear regression, the second model is using piece-wise regression with forced break points based on natural history observations, the third model is also based on piece-wise regression, but non-forced breakpoints that reflect points of dramatic change in the data trends. Deltas with the lowest value indicate the top model selected.

Ultramafic Specialists Models	AIC	K	Deltas
1. Linear Model	494.4	3	82.1
2. Piece-wise, forced break points (1500, 2700)	435.8	9	23.4
3. Piece-wise, non-forced break points (1400 m, 3300 m)	412.3	9	0
Ultramafic Tolerant Models	AIC	K	Deltas
1. Linear Model	514.8	3	102
2. Piece-wise, forced break points (1500,2700)	471	9	58.2
3. Piece-wise, non-forced break points (600 m, 1800 m, 3400 m)	412.8	11	0
Non-Ultramafic Models	AIC	K	Deltas
1. Linear Model	538.6	3	96.4
2. Piece-wise, forced break points (1500, 2700)	442.2	9	0
3. Piece-wise, non-forced break points (1400 m, 2000 m, 2600 m, 3200 m)	451.2	13	9

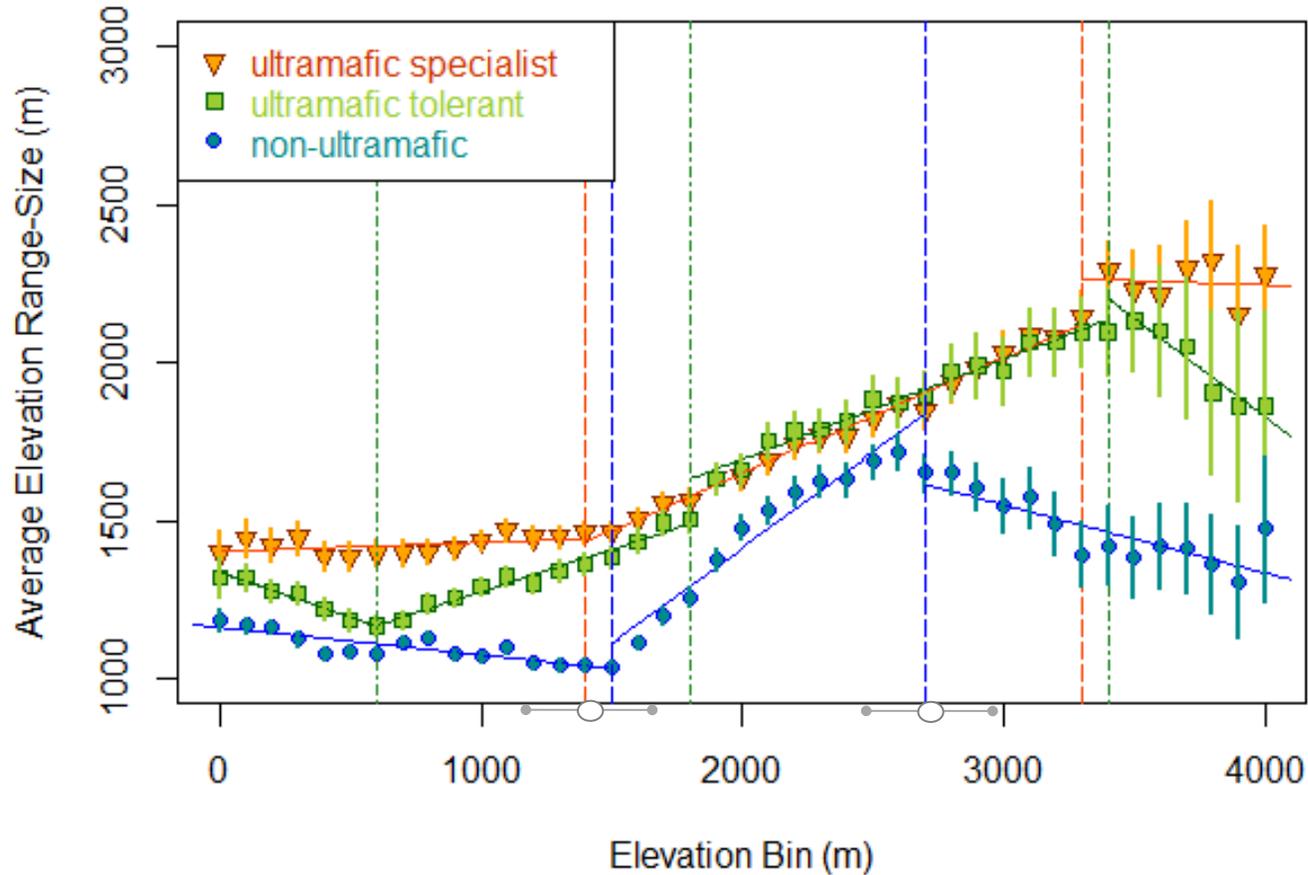


Figure 2.4. Variation in the elevation range-size for Bornean plant species in three soil association categories with elevation. Lines are predictions from the best-fit piece-wise regression models for each soil association category (refer to Table 2.2 for model comparisons), and points are the observed mean elevation range in each elevation bin. Elevation break-points for the best model for each soil category are shown as dashed vertical lines, with colors corresponding to soil association category. The circles in grey represent the areas described in literature as vegetation transition zones, with grey bars representing a 300 m +/--buffer added for breakpoint analyses.

Table 2.3. Summary statistics for the most supported model selected for **ultramafic specialists**, which used piece-wise regression with non-forced break-points at 1400 and 3300 m. This model had $df = 33$, $Adj. R^2 = 0.99$, F -statistics = 547.4, and $P < 0.001$.

	Intercept (m)	Std. Error	<i>t</i> value	<i>P</i> value
Intercept low elevation (< 1400 m)	1404	16.8	83.7	< 0.001
Intercept mid elevation (1400 - 3300 m)	921	36.2	25.5	< 0.001
Intercept high elevation (> 3300 m)	2356	231.5	10.2	< 0.001
	Slope	Std. Error	<i>t</i> value	<i>P</i> value
Slope low elevation (< 1400 m)	0.03	0.02	1.3	NS
Slope mid elevation (1400 - 3300 m)	0.36	0.02	24.3	< 0.001
Slope high elevation (> 3300 m)	-0.03	0.06	-0.4	NS

Table 2.4. Best model selected for **ultramafic tolerant species**, piece-wise regression with non-forced break-points at 600, 1800, and 3400 m. This model had $df = 31$, $Adj. R^2 = 0.99$, F -statistics = 808.8, and $P < 0.001$.

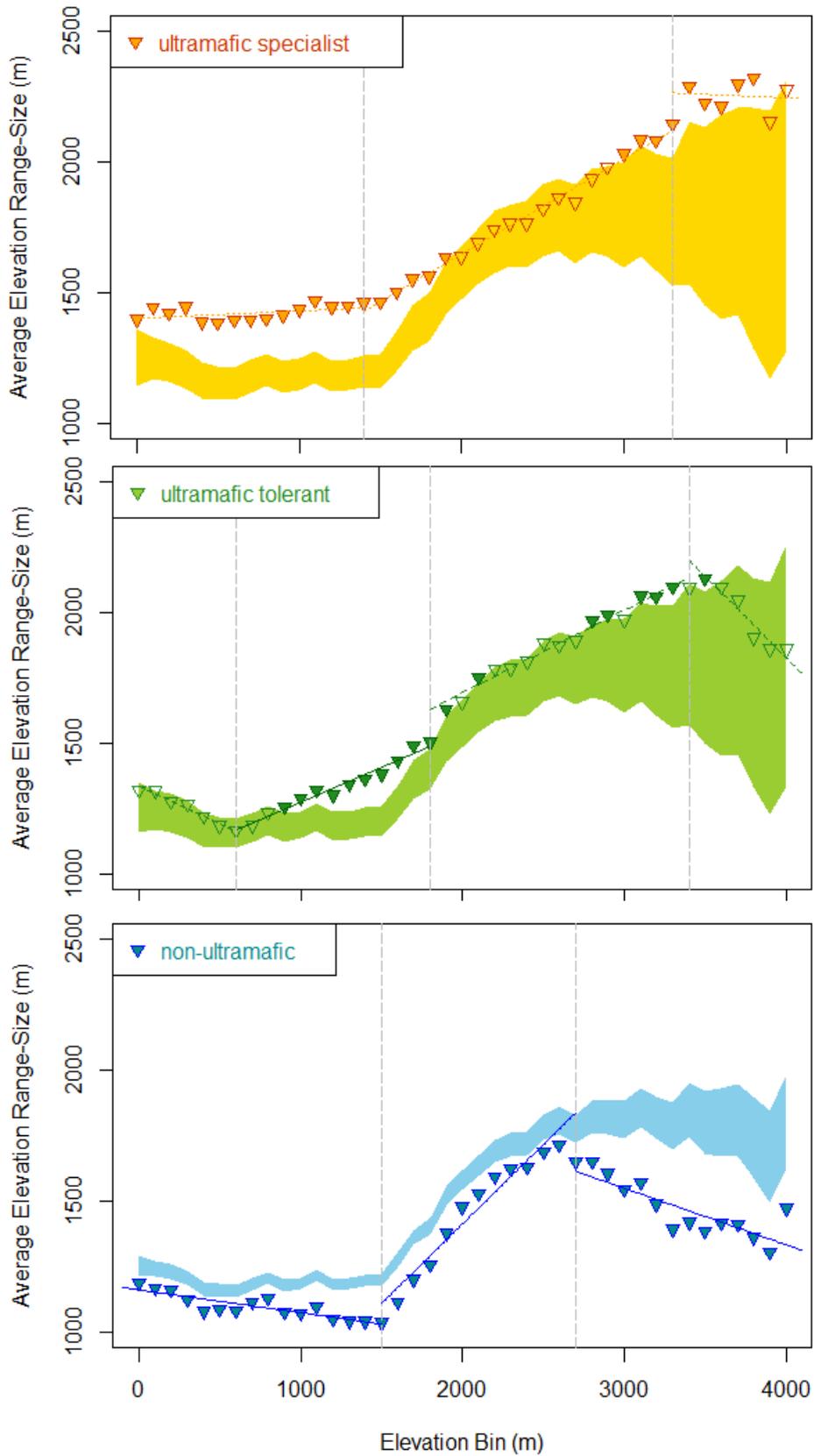
	Intercept (m)	Std. Error	<i>t</i> value	<i>P</i> value
Intercept low elevation (< 600 m)	1338	17.6	76.0	< 0.001
Intercept low-mid elevation (600 - 1800 m)	1008	25.9	39.1	< 0.001
Intercept mid elevation (1800 - 3400 m)	1064	35.7	29.8	< 0.001
Intercept high elevation (> 3400 m)	4326	216.1	20.0	< 0.001
	Slope	Std. Error	<i>t</i> value	<i>P</i> value
Slope low elevation (< 600 m)	-0.29	0.06	-5.1	< 0.001
Slope low-mid elevation (600 - 1800 m)	0.27	0.02	13.2	< 0.001
Slope mid elevation (1800 - 3400 m)	0.32	0.01	23.2	< 0.001
Slope high elevation (> 3400 m)	-0.62	0.06	-10.8	< 0.001

Table 2.5. Best model selected for **non-ultramafic species**, piece-wise regression with forced break-points at 1500 and 2700 m. This model had $df = 33$, $Adj. R^2 = 0.96$, F -statistics = 122.9, and $P < 0.001$.

	Intercept (m)	Std. Error	<i>t</i> value	<i>P</i> value
Intercept low elevation (< 1500 m)	1163	23.4	49.695	< 0.001
Intercept mid elevation (1500 - 2700 m)	200	96.4	2.075	0.0459
Intercept high elevation (> 2700 m)	2198	120.7	18.218	< 0.001
	Slope	Std. Error	<i>t</i> value	<i>P</i> value
Slope low elevation (< 1500 m)	-0.09	0.03	-3.1	0.004
Slope mid elevation (1500 - 2700 m)	0.61	0.05	13.4	< 0.001
Slope high elevation (> 2700 m)	-0.22	0.04	-6.2	< 0.001

Null models demonstrated differences in elevation range-sizes by soil association (Figures 2.5a-c). Ultramafic specialist species (2.5a) had larger than expected range-sizes within lower, and some higher elevation areas, and no significant difference in slope by elevation gradient segment as compared to the null model. Ultramafic tolerant species (2.5b) had mixed results, except within the elevation segment spanning 600 - 1800 m, where range-size was larger than expected and slope differed from the null model. Non-ultramafic species (2.5c) had significantly smaller range-sizes, and slopes that were steeper than the null model that tended to have more gradual changes in range-size. Overall, species that specialize in, or are tolerant of, ultramafic soil had range-size patterns that were more similar to each other, whereas non-ultramafic species were distinct.

Figure 2.5a-c (figure on following page). Variation in elevation range-size with elevation for Bornean plant species in three soil association categories as compared to null models. Break-points shown as vertical grey dashed lines based on the top model selected for each soil association category. Significant differences in slopes for each elevation segment shown as a solid line, non-significant as a lighter toned dotted line.



2.4 Discussion

This study generally supports Rapoport's rule for a diverse array of plant taxa and growth forms along elevational gradients in the Mt. Kinabalu region of Sabah, Borneo. However, these results also demonstrate that patterns in elevation range-size depend on the location of elevational vegetation zone boundaries and the soil associations of the species considered. Rather than using a standard linear regression model to quantify the strength of Rapoport's rule, piece-wise regressions with breakpoints informed by natural history observation of habitat types along the elevation gradient of Mt. Kinabalu (Kitayama 1992) offers a better means to evaluate elevation range-size patterns. In addition, elevation range-size patterns also depended on the soil association of plant species.

2.4.1 Peaks in species richness

The humped-shaped peak in species richness for non-ultramafic and ultramafic tolerant species at 1200 m is consistent with observations from the region (Grytnes and Beaman 2006), and other mountainous studies for different locations or taxonomic groups (Terborgh 1977, Rahbek 2004). Along the elevation gradient of Mt. Kinabalu in particular, this location (1200 m) is described as the transition zone between tropical lowland forest and lower montane forest (Kitayama 1992), and the area potentially support species in both habitat types thus leading to higher richness within a very small span of distance.

Where ultramafic flora peaked in richness (1,500 m) is distinct as compared to other soil categories and notable because it is the point in elevation where tree species

richness begins to decline, and is the elevation where the richness of other short-statured plants such as ferns and orchids has been observed to be higher (Grytnes and Beaman 2006). The richness peak for ultramafic species relatively higher in elevation than the two other soil categories might also reflect the interplay between larger range-sizes which in turn would change the location where richness peaks. A different interpretation is that 1,500 is the point along the elevation gradient where ultramafic species are at less of a competitive disadvantage as compared to non-ultramafic flora.

2.4.2 Differences in Average Range-Size

The question emerges as to why average range-sizes differs by soil association along the elevation gradient. One possibility is that specialization in stressful habitat types, such as ultramafic soil, also enables plants to also tolerate a wider range of other types of stressors, such as climatic conditions (Grime 1977, Fernandez-Going et al. 2012). Under this scenario it is possible for ultramafic species to have a very broad elevational range-size (fundamental niche), while simultaneously being restricted to small patches of ultramafic soil due to competitive exclusion from adjacent higher resource areas (realized niche), as noted with other stress-tolerant flora (Vetaas 2002).

Non-ultramafic species had relatively higher species richness within any given elevation bin compared to the other two soil classification groups, and thus non-ultramafic species may be subject to more complex relationships with other species within the same area due to the higher number of possible combinations of interaction types that can occur. Greater competitive pressure could lead to a negative relationship

between range-size and species richness within a group, provided competition selects for either spatially narrower habitat niches or greater ecological distinction between species that are co-occurring (Hutchinson 1959, Levin 1970, MacArthur 1972, Whittaker et al. 1973, Stevens 1992, Morin and Chuine 2006). Species with smaller range-sizes are also more likely to occur within a single vegetation zone, rather than bridging across multiple zones, and thus may be more sensitive to changes in habitat conditions relative to broadly distributed species (Morin and Chuine 2006, Slatyer et al. 2013). In contrast, species that are tolerant of ultramafic soil, but do not specialize in it, displayed little difference in range-size across elevation than null model expectations. One interpretation is that ultramafic tolerant species occupy an intermediate position relative to the two other soil categories and may have more of an opportunistic, or ruderal, life history strategy (Grime 1977) with more resilience to changes in their environment.

The most supported model for non-ultramafic flora closely matched points in elevation noted as being the boundaries between vegetation zones (Kitayama 1992). For non-ultramafic flora, the slopes for each segment of the partitioned elevation gradient also differed from the null model, with a dramatic increase in slope from lower to higher elevation areas. One explanation is that the area nearest 1200 m marks a point where community composition shifts from being shaped predominately by biotic interactions to instead being shaped by abiotic stressors, thus restricting occurrence for some species while simultaneously enabling range expansion for species that can tolerate an increase in climatic stressors.

For both ultramafic tolerant and ultramafic specialists, the change in range-size was minimal at low elevations, potentially because within this area range-size is determined by non-climate based factors such as dispersal distance (Morin and Chuine 2006). The location of break points also differed between ultramafic associated and non-ultramafic flora. It is uncertain if break-point locations are due to biological factors, such as different responses to climate compared to non-ultramafic flora, or distortions of range-size trends due to lower species richness at the lower and upper most portions of the elevation gradient.

Interestingly, the non-forced analysis for all soil groups found a breakpoint transition at approximately 3300 m, an area described as the start of the sub-alpine zone (Kitayama 1992). At this point in elevation there is an abrupt change from low canopy forests and shrublands to a granite plateau with minimal pockets of soil that is only present in rock cracks and depressions. Plants above this elevation are extremely stunted in size, generally including ferns, grasses, mosses, orchids. One of the few woody species near the summit of Mt. Kinabalu is *Rhododendron ericoides*, a species restricted to ultramafic soil at lower elevations (Argent 2006, Grytnes and Beaman 2006). Above 3300 m, I found that there was also much greater variance in range-sizes, partially confounded due to the smaller number of species present within this area and by the hard boundary of the mountain summit. Such high uncertainty in the direction of range-size trends means that it is harder to assess the applicability of Rapoport's rule for mountainous flora compared to plants in lower elevation areas.

In the future, it would be recommended to expand upon research on ecological mechanisms that define patterns of species richness and range-sizes via a comparative analysis across multiple tropical mountains with distinct vegetation zones and habitats that are subject to freezing events (*e.g.* Mt. Kilimanjaro, Mt. Wilhelm, or the Andes). However, one limitation with comparing Mt. Kinabalu to other mountains is that there are few other tropical locations on Earth with ultramafic soil present across a vast elevation range, which would constrain examination of the role stressful edaphic conditions in determining elevation range-size patterns. An alternate approach may be to investigate range-size trends in other regions noted as hotspots of ultramafic or serpentine species diversity, such as the Siskiyou mountains of Oregon and California (Whittaker 1960, Whittaker et al. 1973, Harrison 1997). A latitudinal study of habitat types described as having "extremely stressful" abiotic conditions (Prance 1996, Porembski and Barthlott 2000, Kruckeberg 2002, López-Angulo et al. 2018) might also offer novel insights on range-size trends relative to flora on adjacent habitat with higher resource availability.

2.4.3 Conclusion

Distinct plant communities, whether defined by vegetation zones or edaphic association, are important to incorporate into analyses that encompass broad environmental gradients and to test ecological theories such as Rapoport's rule. Species that specialize in especially stressful habitat types are in the minority when considering species richness, but they can provide intriguing insights, and challenge our assumptions, for many longstanding ecological rules regarding patterns of species richness or range-size trends.



Rhododendron malayanum. Curtis's botanical magazine. 1873.

CHAPTER 3

Playing by a different set of rules: how

Rhododendron species maintain a stress-tolerant
ecological strategy along tropical elevation gradients

3.1 Introduction

Functional traits are measurable structural and ecophysiological characteristics of organisms that reflect the strategies that species use to persist in their environments (Reich et al. 1999, Wright et al. 2004, Givnish 2008, Swenson et al. 2011b). Functional traits can be used as a common currency to compare plant taxonomic groups, species, or individuals. Fundamental life history tradeoffs can be inferred based on functional trait covariation, such as described by the leaf economic spectrum (LES), and can be used to describe the speed of return for how nutrients are invested in leaves, spanning from slow to fast (Reich et al. 1999, Wright et al. 2004). Important leaf functional traits include concentrations of key nutrients (*e.g.*, nitrogen) that are essential for plant growth, reproduction, and maintenance of physical structures (von Liebig 1840, Reich et al. 1997). Some functional traits are standardized metrics integrate aspects of structure and morphology, such as specific leaf area (SLA), which is the ratio of fresh lamina area to dry mass. For example, high SLA values are often correlated with fast individual growth

rate and leaves with relatively few defenses, compared to low SLA values that are indicative of slow growth and highly defended leaves, indicating a trade-off in function (Coley et al. 1985, Reich et al. 1999, Santiago and Wright 2007).

Plants can display differing levels plasticity depending on the functional trait examined. Some functional trait values may dramatically change in response to environmental factors, such as temperature, nutrient and light availability, or ultraviolet radiation, whereas other traits can be conserved with little to no variation across different ecological contexts. Some functional traits, such as high concentrations of secondary compounds or tough leathery leaves that are hard to puncture, are associated with defenses against herbivory or pathogens (Coley et al. 1985, Ackerly et al. 2002, Kraft et al. 2007). While many commonly used functional traits are complex phenotypes that integrate multiple functions, they nonetheless offer a consistent approach to compare species that are vastly different in size, growth form, or geographic location (Wright et al. 2004).

Factors that are most influential in shaping plant functional trait variation can change along environmental gradients because what is optimal for survival depends on location and ecological context (Givnish 2008, Cornwell and Ackerly 2009, Swenson et al. 2011b, Pearse and Hipp 2012, Wisz et al. 2013, Klanderud et al. 2015, López-Angulo et al. 2018). In areas of higher resource availability, biotic competition may be the strongest factor for determining both which species occur within those areas, as well as the degree of trait dissimilarity relative to neighboring plants (Tilman 1982, 1994, Schemske et al. 2009). For example, in lower elevation tropical forests, functional trait

diversity is often more variable than expected by chance (Swenson et al. 2011b), indicating that functional dissimilarity may be important in community assembly. In contrast, sites with higher abiotic stressors, such as high elevation areas or habitats with extreme resource limitation, tend to have plant communities that display a more conserved range of traits due to habitat filtering (Grubb 1977, Hulshof et al. 2013), with exclusion of species that do not have traits that allow them to either tolerate or avoid stressful conditions such as freezing events, fluctuations in temperature, or irregular moisture availability.

Most broad-scale and community-level studies on functional trait variation across environmental gradients tend to aggregate species from many taxonomic groups (Reich et al. 1997, 1999, Niklas et al. 2007, Swenson et al. 2011b), but examining ecological variation among species of a single genus can reveal aspects of trait variation that are not discernible when many species from different taxa are grouped (Thuiller et al. 2004, Pearse and Hipp 2012). A complication with sampling distantly related species is that the sample pool would tend to encompass a wide range of possible ecological strategies and it can be harder to disentangle environmental from taxonomic mechanisms for why these strategies may differ along a gradient. An alternate approach is to instead focus on asking "how can a single genus maintain a relatively constant ecological strategy across a wide environmental gradient?" In order to investigate variation in functional traits of species with a relatively consistent ecological strategy and how it relates to different habitat types, I used a single genus approach with tropical species from *Rhododendron* (Ericaceae).

Rhododendron species have a relatively prescribed ecological strategy of stress tolerance (Vetaas 2002, Niinemets et al. 2003, Tulyananda and Nilsen 2017). However, *Rhododendrons* are widely distributed across many biomes and habitat types, occurring in extremes of soil fertility and elevation (Vetaas 2002, Argent 2006, Goetsch et al. 2011), raising questions of how functional trait variation mediates *Rhododendron* ecological strategies and species distributions. The genus *Rhododendron* is one of the most species-rich on Earth, with over 1,000 species (Frodin 2004). Many *Rhododendron* species are associated with shallow or nutrient poor soils supporting low plant biomass and tend to be competitively excluded from more fertile soils or resource rich areas (Vetaas 2002). Within tropical regions of South-East Asia, *Rhododendron* species occur from sea-level to mountain summits, including upper elevation meadows above the tree-line, ultramafic (serpentine) soil, areas of recent disturbance or landslides, forest edges, former mining sites, riparian zones, and even above the forest canopy growing as epiphytes (Stevens 1985, Argent 2006).

Using data on leaf functional traits of 169 tropical and subtropical *Rhododendron* species spanning a wide elevation gradient in Southeast Asia, I addressed the following research questions. First, where do *Rhododendron* species occur within the LES? Second, does the position of *Rhododendron* species position along the LES support the assumption that this genus has a stress-tolerant ecological strategy and follows the expected functional trait correlations that define the LES? Third, how do *Rhododendron* functional traits change along environmental gradients and how does this variation compare to other plants? Fourth, do *Rhododendron* species with epiphytic growth forms

or that specialize in especially infertile soil types occupy a distinct and narrower trait space than more generalist *Rhododendron* species?

I predicted that *Rhododendron* species would have a more stress-tolerant ecological strategy as compared to other plants, which would manifest as lower SLA, lower foliar nutrient concentration, and smaller, thicker, tougher or more succulent leaves, compared to other vascular plant species (Figure 3.1). I also predicted that *Rhododendron* functional trait variation would be limited relative to other vascular plant species, expressed as low yet consistent levels of functional diversity, regardless of location along an elevation gradient (Figure 3.1). In addition, I predicted that *Rhododendron* species specializing in extremely stressful habitat types, such as being epiphytic or associated with ultramafic soil, would have lower SLA, lower nutrients, smaller, thicker, tougher or more succulent leaves compared to species of the same genus with more generalist habitat associations. Underlying this prediction is the idea that if an ecological strategy is unique, and that strategy is reflected by the suite of functional traits and associated life history trade-offs that a group of species has, then the trend in how those traits change along an environmental gradient will also be distinct relative to other species.

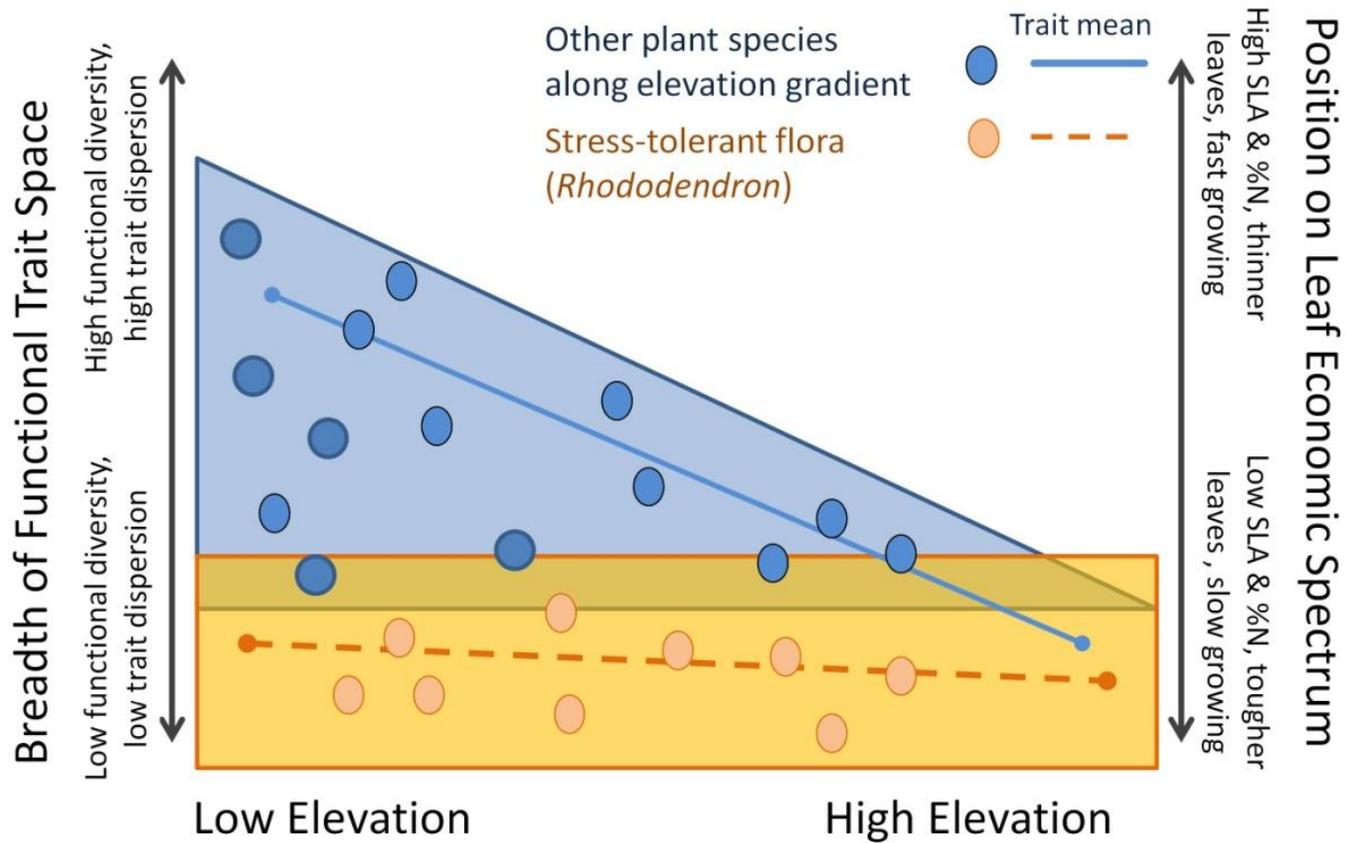


Figure 3.1. Conceptual model of *Rhododendron* functional trait variation along an elevation gradient, contrasted with those of other plant species potentially occurring along the gradient. If the ecological strategy is similar among species in the genus (stress tolerance), then I predict that mean values of traits will be similar, with low trait dispersion among species along this gradient.

3.2 Methods

3.2.1 *Rhododendron* species

I selected 169 species from the genus *Rhododendron* (Ericaceae), section *Schistanthe* (commonly referred to as Vireya) as the model taxonomic group, utilizing tropical and subtropical species from South-East Asia (Table 3.1, Figure 3.2). All *Rhododendron* species sampled for functional traits were grown in greenhouses as part of long-term living plant collections, managed by the Royal Botanical Garden in Edinburgh (UK), Rhododendron Species Foundation in Federal Way, Washington (USA), or Bovees Rare Plant Nursery in Portland, Oregon (USA). The majority of *Rhododendron* species sampled originated from wild-collected cuttings from individuals of known provenance. Non-wild collected plants were obtained from seed or cutting exchanges with other arboreta or private collectors, also with known provenance. I excluded ornamental cultivars and horticultural hybrids. For each individual, I recorded accession codes and details on collection history based on the information available (Supplemental Table 4.3). Whenever possible, I sampled multiple individuals from each species (Table 3.1), including distinct subspecies or varieties originating from different geographic areas, to better represent the range of traits for each species.

Greenhouse conditions for all sites included controlled temperature settings above freezing, air circulation, pest or disease management as needed, and a regular watering regime designed for optimal growth. I did not use gardens as a random effect for analyses because plants came from one of three locations (too few levels for the random effect to be estimated well; at least five levels would have been needed). Plants were grown in

pots with epiphyte medium (mix of bark, clay pellets or vermiculite with minimal soil or nutrient additions). The average age of plants was 29 years since the date of establishment within a greenhouse.

Plant functional traits can vary plastically in response to the environment, and so one benefit of using plants grown in a controlled, common greenhouse setting is that differences in leaf traits can be attributed more to the genetic distinctions between species, but without confounding location-specific environmental factors which can cause variation in trait values. In addition, use of living plant collections makes investigation of macroscale questions about model taxa that are distributed across vast geographic areas logistically more feasible relative to the inherent difficulty of sampling plants from multiple countries. However, functional trait data collected *in-situ* is a more direct reflection of the habitat for which a species is adapted, therefore I tried to review *Rhododendron* literature for any record of field collected traits as point of comparison to data collected for plants grown within a greenhouse whenever possible.

Table 3.1. Summary of the number of individuals sampled for major tropical *Rhododendron* clades (nomenclature and taxonomy based on Argent 2016).

Clade	Species	Average number of individuals sampled
<i>Albovireya</i>	6	1.50
<i>Discovireya</i>	13	1.69
<i>Hadranthe</i>	16	1.81
<i>Malayovireya</i>	10	1.70
<i>Pseudovireya</i>	10	2.20
<i>Schistanthe</i>	110	1.94
<i>Siphonovireya</i>	4	1.25
Grand Total	169	1.88



Figure 3.2. Map of *Rhododendron* distribution across the Malay Archipelago and Papua New Guinea. Each color represents a different species using coordinate information provided by the Global Biodiversity Information Faculty (GBIF) database.

3.2.2 *Rhododendron* functional traits

To quantify plant functional traits (Table 3.2) for each *Rhododendron* species, I sampled an average of five healthy, mature leaves from different branches or shoots from each individual, with preference for leaves with maximum light exposure. Immediately after sampling, leaves were wrapped in moist paper towels within a sealable plastic bag and stored in a cool, dark location. Fresh leaf traits were measured within a few hours after collection. First, I cut the petiole from the lamina, and each was individually weighed to the nearest 0.01 g. Lamina area (cm²) was calculated from scanned images (Canon CanoScan LiDE 220) of laminas using the image analysis software Image J ver. 1.51 (Abramoff et al. 2004). Highly rugose or curled leaves were cut into sections so that they could be pressed flat on the scanner in order to more accurately estimate lamina area. Leaf thickness (mm) was measured at two points of the lamina intercostal tissue, one on each side of the mid-vein halfway between base and the tip of the lamina avoiding secondary veins, with a Digi-Micrometer (AccuRemote), and an absolute Digimatic Indicator ID-C series 543 (Mitutoya) for smaller leaves. Leaf toughness was measured at the same two points using a penetrometer (Chatillon by Amtek) using a constant tip size, which estimates the force (g) needed to puncture the leaf surface when held in a plexiglass frame to ensure that the same penetrometer angle was used for every measurement. For small leaves (< 3 cm width), lamina toughness was not measurable given the penetrometer tip size relative to lamina area and vein density. Dry lamina and petiole weights were measured using an Ohaus Explorer Pro (0.001 g accuracy) after material was dried at approximately 40° Celsius for a minimum of 36 hours. Dry lamina material (excluding the midvein) was ground into a fine powder using a ball grinder

(Retsch MM400) and then a subsample of approximately 3.5 mg was packed in tins for analysis at the Ecosystems Analysis Lab at the University of Nebraska - Lincoln, USA. Total carbon and total nitrogen were estimated via dry combustion GC analysis (Analytical Elemental Combustion System 4010 by Costech). Total phosphorous was calculated using colorimetry on acid-reduced, ashed samples (Quick Chem 8500 series 2 by Lachat). Lamina carbon and nitrogen were calculated as a percentage of dry mass, being g of nutrient/g of dry leaf matter. Ratios of the two nutrients, C:N ratio, were calculated as % carbon/ % nitrogen. Specific leaf area (SLA) was calculated as cm^2 lamina area / g lamina dry mass. Leaf dry matter content (LDMC) was g of lamina dry mass / lamina wet mass / mg, but note that leaves were not fully hydrated, but were kept moist and weighed as close as possible to the time when sampled from the plant. Lamina tissue density was calculated as g of lamina dry mass / (cm^2 lamina area * cm lamina thickness). Lamina succulence was calculated as (wet mass g - dry mass g) / lamina area (cm^2). Nitrogen mass per leaf area (N_{area}) was calculated from foliar N concentration and the inverse of SLA converted to m^2 . Species-level averages of functional traits were calculated by first averaging leaf-level values across leaves within an individual, and then averaging across individuals for each species.

Table 3.2. Functional traits of *Rhododendron* species included in this study

Functional Trait	Abbreviation	Definition (units)
Lamina area	LA	Lamina area (cm ²)
Specific leaf area	SLA	lamina area (cm ²) / lamina dry mass (g)
Leaf dry matter content	LDMC	lamina dry mass (g) / lamina wet mass (mg)
Lamina thickness	Thickness	(mm)
Lamina density	Density	SLA * lamina thickness (cm)
Lamina surface area	SA	Lamina area (cm ²) * Thickness (cm)
Toughness	Toughness	grams of force (g) used to puncture leaf with a 3.25 mm diameter pin
Succulence	Succulence	(Lamina wet mass (g) - lamina dry mass (g) / lamina area (cm ²)
Percent nitrogen content	% N	nitrogen (mg) / leaf dry mass (mg)
Percent carbon content	% C	carbon (mg) / leaf dry mass (gm)
Carbon: nitrogen ratio	C:N	% carbon / % nitrogen
Nitrogen per unit lamina area	N _{area}	(1/SLA) * 10 *nitrogen (mg)

3.2.3 *Rhododendron* distribution, growth form, and soil associations

Information on the elevational distribution of *Rhododendron* species was obtained primarily from botanical monographs (Argent 2006, Gibbs et al. 2011), supplemented with records from the Global Biodiversity Information Faculty (GBIF), if elevation range for a species was not listed in a published monograph. Elevation values used in statistical analyses were based on the mid-point between the minimum and maximum elevation for where each species occurs. A map of *Rhododendron* species for this study is shown in Figure 3.2.

I obtained information on primary growth form and soil association for each species from habitat descriptions and keyword searches of botanical monographs and

herbarium records (Table 3.3). Each *Rhododendron* species was then categorized as either mostly terrestrial, or with the ability to grow as an epiphyte, grouping together species that ranged from strictly epiphytic to opportunistic. I also categorized whether each species occurs on ultramafic soil, grouping together species that ranged from ultramafic tolerant to ultramafic endemic or specialist species. In general, epiphytic species are associated with lower elevation habitats and tend to have longer tailed seeds (Argent 2006), a characteristic that may help with either wind dispersal or anchoring to branches. Ultramafic associated species are distributed across the elevation gradient in a way that mirrors the soil distribution which spans from sea-level to ~3,500 m. My full *Rhododendron* dataset included means for 12 foliar traits, growth form, elevation midpoint, and soil association for 169 species (Supplemental Table 4.4 & 4.5).

3.2.4 Statistical analyses

I conducted a series of analyses to evaluate my conceptual model (Figure 3.1). First, I evaluated whether *Rhododendron* species conform to the expected LES patterns of trait covariation using a Pearson's correlation matrix of all pairwise *Rhododendron* functional trait combinations. Second, I compared functional trait covariation of *Rhododendron* species to other vascular plants using a broad selection of species from data publicly available from the Global Plant Trait Network (Gloptnet) database (Wright et al. 2004). The Gloptnet database includes plant species from biomes, growth forms, and locations around the globe with additional information on data sources. I plotted the relationship between lamina % nitrogen and SLA for *Rhododendron* species against the Gloptnet data

(accessed on 3/28/2018), which consisted of 1,959 species with information available on the two traits of interest. All trait data were averaged at the species-level, and \log_{10} transformed prior to analyses for comparison to the primary literature associated with the leaf economic spectrum (Wright et al. 2004). I tested whether the slope and intercept of the relationship between the two traits for *Rhododendron* species differed from the species in the Glopnet dataset using standardized major axis regression (SMA) with the R package "smatr" (Warton et al. 2012). I predicted that *Rhododendron* species would exhibit trait covariation (similar slope) comparable to other plants, but that the *Rhododendron* data points would be positioned more towards the slower end of the LES relative to other species.

Third, I quantified *Rhododendron* functional trait variation with elevation using ordinary least squares (OLS) linear regression using elevation as the predictor variable. Elevation values were based on the mid-point of each species' elevation range derived from herbarium data (described in section 3.2.2) and therefore should be considered a trait of a species. To compare differences in trait variation with elevation between *Rhododendron* and other woody plant species in the same region, I performed a pan-tropical meta-analysis for two of the most commonly cited functional traits in literature, SLA and % N, for which data were available for species from a wide array of taxonomic groups. Keywords used in meta-analysis literature search included descriptions of different tropical forest types, such as "lowland rainforest" and "montane cloud forest", with emphasis on regions with higher moisture availability (Supplemental 4.6). Data tables on functional traits from each study were obtained either from supplemental

information, or manually copied from the text or interpolated from plots using the program ImageJ. Elevation was based either on information available in each dataset or inferred from the coordinates or description of study sites. Data from a Southeast Asian lowland tropical forest was also included (S.E. Russo, unpublished data for Lambir forest plot in Borneo). I collected growth form information when available and restricted the data used in analyses to mature leaves from adult tree species, thus excluding ferns, lianas, and herbaceous species, as well some woody understory plants. For all plants included in the meta-analysis, I calculated functional trait, and elevation where sampled, averages at the species level.

Fourth, I tested whether *Rhododendron* species display narrower trait variation with elevation, using various functional diversity metrics (functional richness - FRic, functional dispersal - FDis, functional divergence - FDiv, functional evenness - FEve) which are based on convex hull estimates of the multivariate trait space, calculated with the FD package for R (Laliberté and Legendre 2010, Laliberté et al. 2014). The FD package is designed to also reduce the number of principal coordinate analysis (PCoA) axes used depending on the loading characteristics of the variables selected. I subdivided the elevation gradient into nine evenly spaced bins 500 m in size, from 0 to 4500 m asl, and classified each species as being either present or absent from each bin based on their elevation mid-point (meaning each species could only occur within one bin). Functional diversity metrics were then calculated based on the pool of species present in each bin. Ordinary least squares (OLS) linear regression was used to evaluate the relationships between functional diversity metrics with elevation for *Rhododendron* species, with the

analysis performed across bins which allows for comparison of assemblages of species at different intervals along a gradient rather than a single metric that encompasses the entire gradient.

Lastly, I addressed how *Rhododendron* leaf traits differ by growth form (epiphytic versus terrestrial) and edaphic association (species associated with ultramafic soil versus non-ultramafic soil) using a series of Student's t-tests for each trait. I also did analogous tests in a multivariate context using permutational analysis of variance (adonis function) to test for differences in the centroid of the functional trait space and a multivariate version of Levine's test for homogeneity of variances (betadisper function), performed using the "vegan" package for R (Oksanen et al. 2018). Because ultramafic species represented a minority of the total *Rhododendron* richness, I performed an additional analysis in which I accounted for differences in sample size using randomization. I calculated functional diversity metrics for the non-ultramafic species by randomly sampling from the full non-ultramafic data set a number of species equal to the number of ultramafic species. This procedure was repeated 999 times, and the diversity metrics calculated for each iteration produced an expected distribution of metrics for non-ultramafic species given the same sample size as for the ultramafic species, with significance based on the rank of observed values for ultramafic species in the randomized distribution. For multivariate analyses all traits were used except for leaf toughness because of missing values.

3.3 Results

3.3.1 Trait correlation matrix

Covariation between several traits was statistically significant, including SLA, C:N ratio, and succulence (Table 3.3). Most correlations matched expectations based on known functional trait trade-offs, such as the negative relationship between SLA and LDMC ($r = -0.40$, $P < 0.001$) and the positive relationship between SLA and % N ($r = 0.54$, $P < 0.001$). Leaf succulence provided a different perspective on leaf characteristics by having a positive relationship with thicker leaves ($r = 0.82$, $P < 0.001$) yet a negative relationship with lamina density ($r = -0.17$, $P = 0.029$), likely because succulent leaves are thicker and contain more water. In general, leaves with low SLA were smaller, thicker, and tougher and had greater density with reduced nitrogen concentration.

3.3.2 *Rhododendron* traits on the world wide leaf economic spectrum (LES)

Compared to the trait variation represented in the Glopnet dataset, *Rhododendron* species were clustered towards the lower end of the LES, indicating a stress-tolerant ecological strategy (Figure 3.3). Between the *Rhododendron* and the Glopnet datasets, there was no significant difference in the slope of the relationship between SLA and % N ($P = 0.12$), meaning that there is a consistent functional trait trade-off across all plant groups, including *Rhododendron*. However, there was a difference in the intercept ($P < 0.001$), with *Rhododendron* species having higher SLA for a given % nitrogen as compared to other plants, which can also be thought of as having a lower % nitrogen for a given SLA and indicative of greater resource use efficiency.

	Lamina Area	SLA	LDMC	Toughness	Thickness	Lamina Density	Succulence	% Carbon	% Nitrogen	C:N Ratio	N _{area}
Lamina Area		-0.32		0.27	0.20		0.42			0.19	<i>0.19</i>
SLA	-0.32		-0.40	-0.26	-0.71	-0.28	-0.67	-0.25	0.54	-0.56	-0.57
LDMC		-0.40				0.61	-0.33	0.31	-0.36	0.39	
Toughness	0.27	-0.26			0.39					<i>0.20</i>	
Thickness	0.20	-0.71		0.39		-0.38	0.82		-0.35	0.39	0.47
Lamina Density		-0.28	0.61		-0.38		<i>-0.17</i>	<i>0.18</i>	-0.28	0.28	
Succulence	0.42	-0.67	-0.33	0.29	0.82	<i>-0.17</i>			-0.32	0.34	0.45
% Carbon		-0.25	0.31			<i>0.18</i>				0.21	0.28
% Nitrogen		0.54	-0.36		-0.35	-0.28	-0.32			-0.93	0.50
C:N Ratio	<i>0.19</i>	-0.56	0.39	<i>0.20</i>	0.39	0.28	0.34	0.21	-0.93		-0.28
N _{area}	<i>0.19</i>	-0.57			0.47		0.45	0.28	0.50	-0.28	

Table 3.3. Correlation coefficients (r) between leaf functional traits for 169 *Rhododendron* species. Text in bold represents significance levels of < 0.001, non-bold < 0.01, italic < 0.05; blank means non-significant correlations.

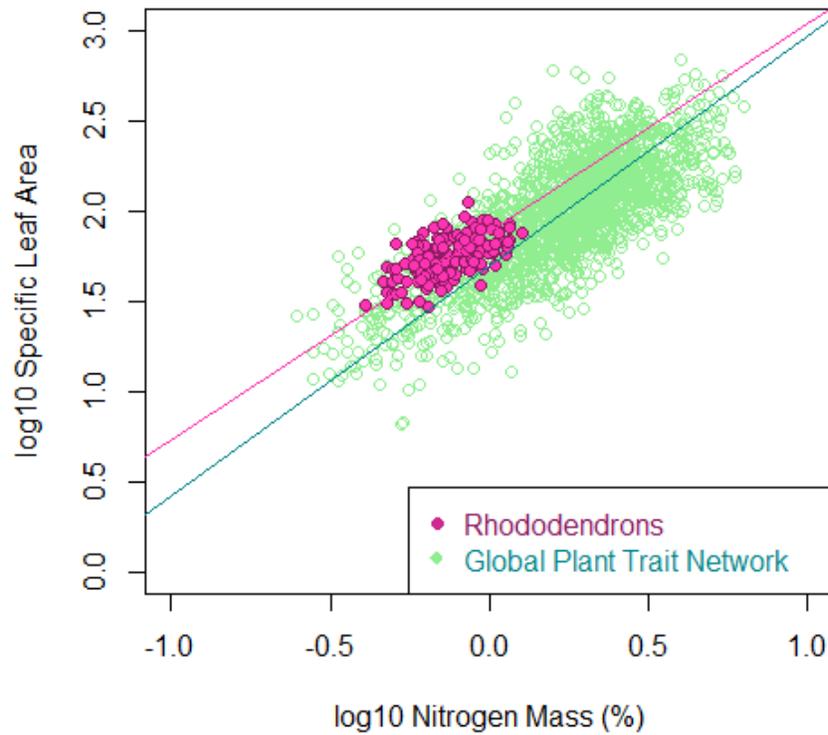


Figure 3.3. Variation in specific leaf area (cm^2/g) and foliar nitrogen (% of lamina weight g) of 169 *Rhododendron* species (maroon) on the leaf economic spectrum compared with 1,958 vascular plant species (teal) from the global plant trait network (Gloptnet) database.

3.3.3. *Rhododendron* traits along elevation gradients, with comparison to other woody tropical plant species

For *Rhododendron* species, only four out of the eleven traits tested showed significant variation in mean values with elevation (Table 3.4; Figure 3.4). Lamina area (cm²) declined with elevation ($P = 0.013$), ranging from a maximum of 135.5 cm² at lower elevations (*R. intranervatum*), to 0.04 cm² at higher elevations (*R. ericoides*). The three other significant traits all corresponded with leaf chemical composition: % C, % N, and N_{area} which increased with elevation ($P < 0.001$, 0.011, 0.003, respectively), whereas C:N remained constant with elevation. Other *Rhododendron* traits with no significant variation with elevation included SLA, LDMC, toughness, thickness, and lamina density. In contrast, meta-analysis species showed a strong negative relationship for % N and SLA with elevation (Fig. 3.5a, $n = 366$, $P < 0.001$; Figure 3.5b, $n = 506$, $P < 0.001$).

Table 3.4. Summary table of linear regression statistics for tests of functional trait variation with elevation for *Rhododendron* species. NS stands for non-significant.

Functional Trait	<i>F</i> -statistic	<i>df</i>	Adj. <i>R</i> ²	<i>P</i> -value
Lamina Area	6.38	167	0.03	0.013
Specific Leaf Area	0.09	167	-0.01	NS
Leaf Dry Matter Content	0.01	167	-0.01	NS
Toughness	1.18	135	0.01	NS
Thickness	1.07	167	0.00	NS
Lamina Density	3.31	167	0.14	NS
Succulence	0.00	167	-0.01	NS
% C	20.31	167	0.10	< 0.001
% N	6.56	167	0.32	0.011
C:N Ratio	2.32	167	0.01	NS
N _{area}	9.249	167	0.05	0.003

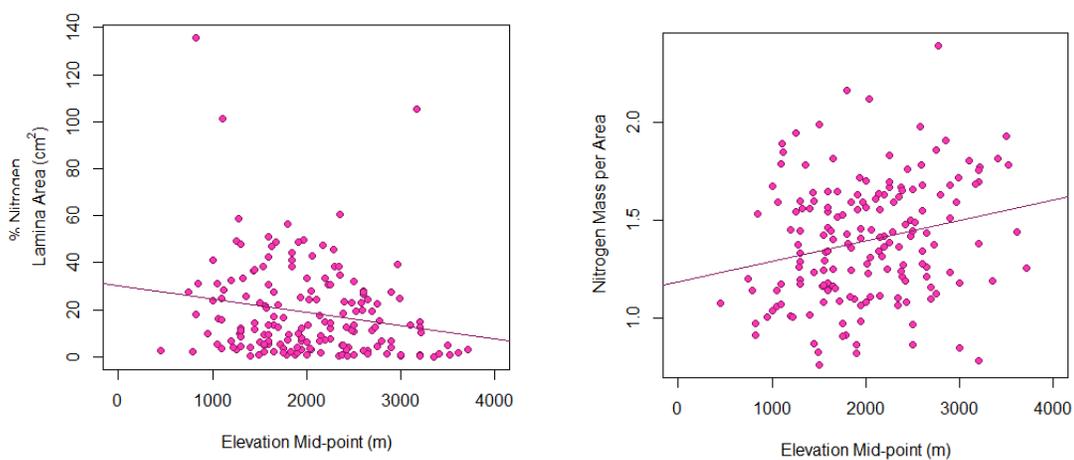


Figure 3.4. Significant relationships for variation in functional with elevation for *Rhododendron* species. Each point represents the average for a species. Summary of statistical results shown in Table 3.4.

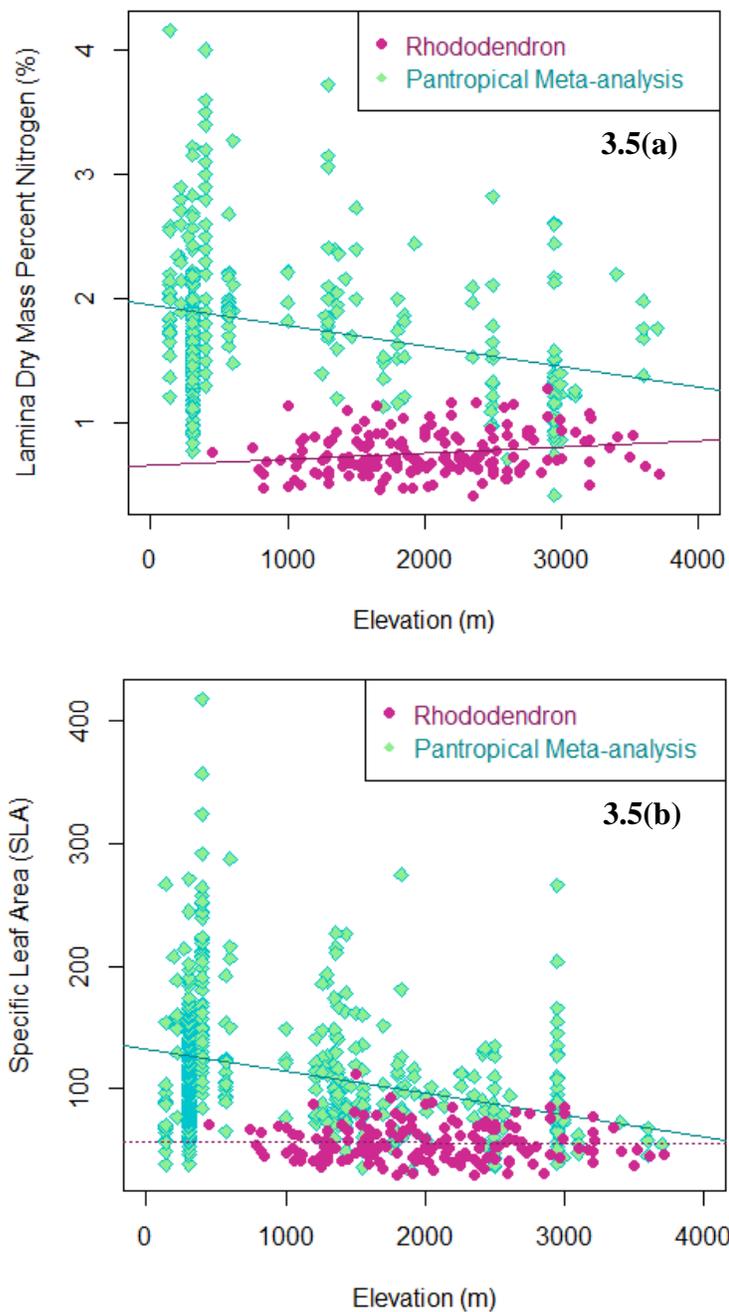


Figure 3.5 Variation in functional traits for *Rhododendron* species compared to other tropical woody species with elevation: (a), % N (percent nitrogen) and (b), SLA (cm²/g). Solid line indicates significant relationship; dashed line indicates non-significant.

3.3.4 *Rhododendron* functional diversity

The functional diversity and species richness within an elevation bin were positively correlated for *Rhododendron* species ($r = 0.87$, $df = 5$, $t = 3.9109$, $P = 0.01$), and both of these metrics peaked in the bin spanning from 1500 - 1999 m. However, most metrics of functional diversity in an elevation bin did not correlate significantly with elevation (richness, $df = 6$, $P = 0.924$; functional diversity, $df = 5$, $P = 0.599$; functional divergence, $df = 5$, $P = 0.069$; functional evenness, $df = 5$, $P = 0.335$), except for functional dispersion ($df = 5$, $P = 0.039$) which declined slightly with elevation (Table 3.5).

Table 3.5. *Rhododendron* functional diversity metrics by elevation bin. NA refers to non-applicable based on the sample size minimum for the metric.

Elevation Bin (m)	Species Richness	Functional Diversity	Functional Dispersion	Functional Divergence	Functional Evenness
0	1	NA	NA	NA	NA
500	6	11.10	3.31	0.75	0.83
1000	32	75.33	2.98	0.77	0.89
1500	47	114.09	2.90	0.74	0.86
2000	41	58.18	2.62	0.73	0.88
2500	27	99.43	2.80	0.75	0.86
3000	11	29.31	2.94	0.82	0.85
3500	4	0.85	2.40	0.85	0.78

3.3.5. Differences in trait-space based on growth form or edaphic association

Functional traits of epiphytic ($n = 93$) and terrestrial ($n = 76$) *Rhododendron* species did not differ significantly for individual traits, or for multivariate analyses comparing trait space centroid or dispersion ($P = 0.51$, $P = 0.49$; Fig. 3.6a & b). Comparing ultramafic and non-ultramafic species, three traits showed significant differences: ultramafic species had lower SLA ($P = 0.019$; mean non-ultramafic = 57.19, ultramafic = 50.03) and % N ($P = 0.011$, mean non-ultramafic = 0.77, ultramafic = 0.70), and greater succulence ($P = 0.011$, mean non-ultramafic = 0.029, ultramafic = 0.033). In multivariate analyses, however, there were no differences in leaf trait values ($P = 0.20$; Fig. 3.6c) or dispersion ($P = 0.89$, Fig. 3.6) between species associated with ultramafic soil ($n = 25$) versus non-ultramafic species ($n = 144$). For analyses of functional diversity metrics using randomization, the results were also non-significant, but were more informative in that ultramafic species were consistently in the lower ~15% of the randomized distribution of functional diversity metrics.

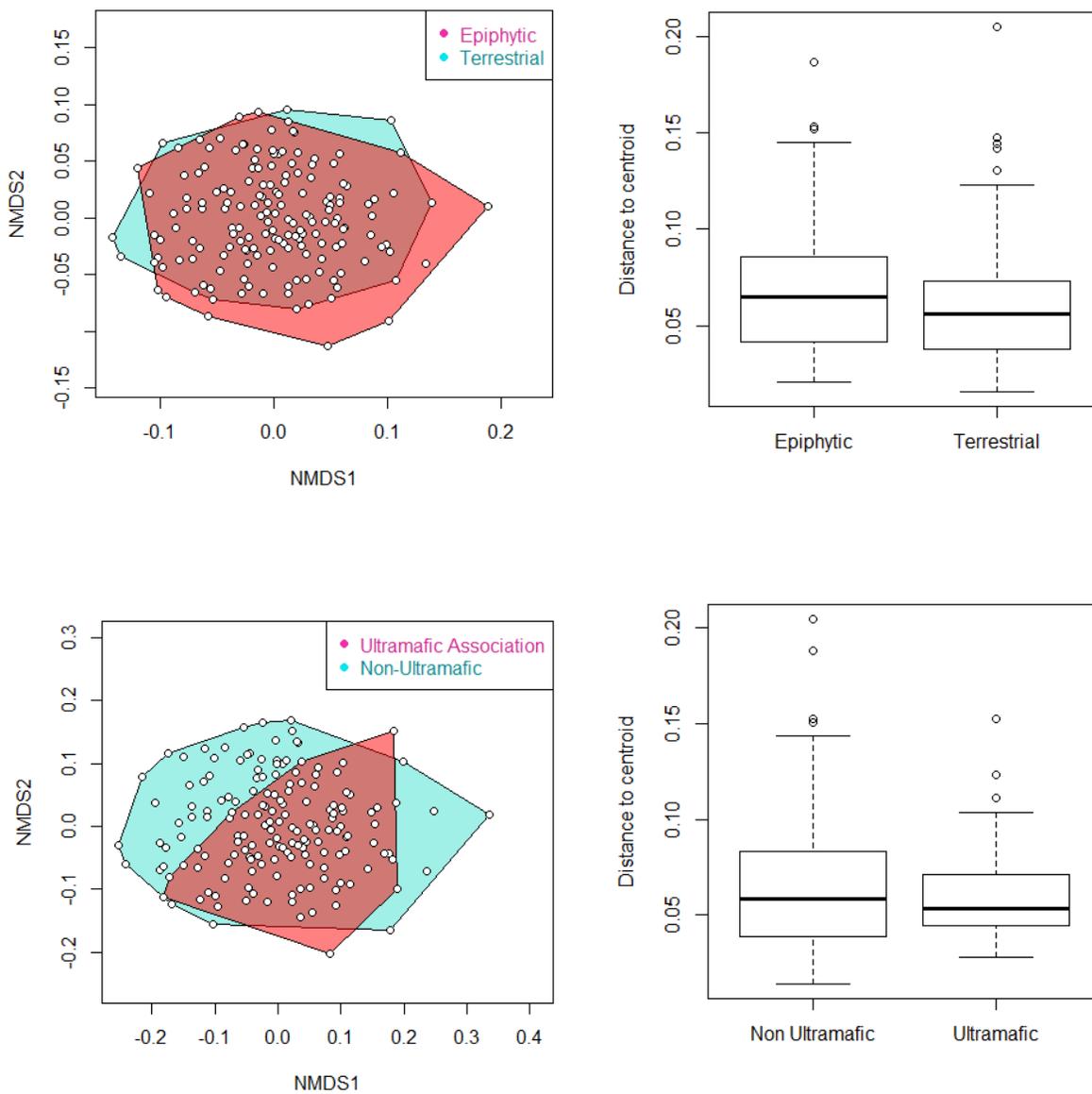


Figure 3.6. Multivariate variation in *Rhododendron* leaf traits between growth forms (epiphytic versus terrestrial) and edaphic association (ultramafic soil association and non-ultramafic).

3.4 Discussion

One mechanism by which communities are structured is via competitive exclusion (Gause 1932), in which a species that is a sufficiently poor competitor in a given habitat it will eventually be excluded (Hardin 1960, Levin 1970). Based on this rationale, slow growing plant species, such as those with a stress-tolerant ecological strategy, should not occur within high resource habitats (Grime 1977), a pattern that is often found within tropical forest communities (Fine et al. 2004, Russo et al. 2005). Along an elevation gradient, species with a stress-tolerant ecological strategy are predicted to be more likely to be competitively excluded within lower elevation areas as compared to higher elevation areas, except for within patches of habitat that are resource limited (*e.g.* white sands habitat, inselbergs) which can act as refugia for species with adaptations suitable for those stressors (Prance 1996, Frasier et al. 2008).

In the instance of *Rhododendron*, species of the genus are often forced into more extreme habitats, such as treeline shrublands at high elevations where they are commonly observed as a dominant feature of the montane vegetation community (Körner 2003, Argent 2006, Wang et al. 2012). For example, a prior study on four *Rhododendron* species of the Himalayas found that the upper boundaries of their distributions were defined by abiotic conditions, whereas the lower elevation boundaries were defined by competitive exclusion, based on the findings that same species were capable of growing at warmer conditions within horticultural gardens where competition was controlled for (Vetaas 2002). However, a conundrum with making generalities about the *Rhododendron* genus is that some species demonstrate extremely high competitive ability, to the point where they are listed as invasive (*e.g.* *R. ponticum*) and a threat to biodiversity (Niinemets et al. 2003, Hulme et al. 2009). In some temperate regions, *Rhododendron*

species (*e.g. R. maximum*) can form impenetrable thickets that exclude other plants from co-occurring and can dramatically influence patterns of forest succession (Phillips and Murdy 1985, Baker and Van Lear 1998). Whether *Rhododendron* species are competitively excluded, or have either a negative or more neutral relationship with co-occurring species, may depend on trade-offs relative to the ecological context and habitat examined. At both extremes of the competitive ability gradient, one generality about *Rhododendron* does emerge - that majority of species within the genus have a suite of functional traits associated with a stress-tolerant ecological strategy.

Stress-tolerant traits may act as a dual mechanism for both survival within low nutrient environments as well as mitigation or avoidance of competitive pressures. For instance, *Rhododendron* leaves are highly resistant to herbivory based on a combination of physical toughness and chemical deterrents (Doss et al. 1986); attributes which may also indirectly inhibit the growth or survival of neighboring plants via allelopathy, slow decomposition rate of leaves, or simply overshadowing seedlings with dense understory growth (Nilsen et al. 1999, Wurzburger and Hendrick 2007). In addition, *Rhododendron* often demonstrate higher nutrient use efficiency relative to other plants, which can be very advantageous when combined with increased nutrient acquisition aided by symbioses with ericoid mycorrhizal fungi (Jansa and Vosátka 2000, Niinemets et al. 2003, Wurzburger and Hendrick 2007).

3.4.1 Trait correlations and ecological strategy

Within this study, *Rhododendron* trait values and their position on the LES confirms that the majority of *Rhododendron* species have a relatively stress-tolerant ecological strategy (Grime 1977, Chapin et al. 1993). The correlation matrix of *Rhododendron* traits (Table

3.3) illustrates that these species follow expected functional trait trade-offs, especially the relationship between SLA and % N with a slope that is parallel to one derived from a worldwide sampling of plants (Fig. 3.3). The intercept from the SLA and % N relationship for *Rhododendron* species suggests that at a given SLA, *Rhododendron* species have a lower %N than other vascular plant species, consistent with a slower growth, more efficient resource use strategy.

When compared to slow-growing woody trees and shrubs with needle-like leaves, I found that tropical *Rhododendron* occupies trait-space that was especially similar to other plant species associated with nutrient-depleted soils. For instance, *Rhododendron* SLA values ($\bar{x} = 56.13$ $sd = 14.56$, range = 29.75 - 112.20) were similar to ones observed within the Glopnet database for *Abies alba* (Silver Fir), *Metrosideros polymorpha* (O'hia), and *Vaccinium vitis-idaea* (Lingonberry). Similarly, *Rhododendron* % N values ($\bar{x} = 0.76$, $sd = 0.17$, range = 0.41 - 1.27) were comparable to species of *Hakea*, *Protea*, and *Leucadendron* associated with Fynbos or heathland ecosystems.

I found limited information on *Rhododendron* trait values collected *in-situ* from field sites to compare with greenhouse grown plants given that most published studies on *Rhododendron* have a temperate, rather than tropical, emphasis. However, there are some accounts of the *Rhododendron* of Mt. Wilhelm in New Guinea (*R. aurigeranum*, *R. culminicolum*, and *R. macgregoriacae*) by Körner (1998). The lamina area (cm²) for these species sampled in the wild was 23, 20, 19 in size, as compared to the same species (33, 15, 22 cm² in size) that I sampled in greenhouses. Similarly, I estimated SLA values as shown in a figure within the Körner (1998) paper using the program ImageJ, and found that these three species had SLA values of 38.0, 37.9, and 31.9 for plants in the wild, as

compared to my sample (55.5, 40.5, and 79.0) from greenhouses. I also found a single record of % N for *R. superbum*, also from Papua New Guinea, by Edwards and Grubb (1977) with a value of 0.44% for field sampled plants, compared to an average of 0.69% for plants grown in greenhouses. It is hard to draw any firm conclusions from these functional trait comparisons due to limited sample size, but my general impression is that values for SLA and %N are most likely lower for *Rhododendron* species in the wild.

3.4.2 Functional trait trends along elevation gradients

While reduced trait variation is expected among closely related congeneric species, it is unusual to have such reduced trait variation between species from opposite ends of a nearly 4000 m elevation gradient. These results are directly counter to expectations from larger review of literature on functional traits along environmental gradients (Cornwell and Ackerly 2009, Moles et al. 2014). From sea-level to mountain summits, *Rhododendron* species appear to have a remarkably consistent, and rather conserved, trait space (e.g. SLA) relative to other tropical woody species examined in my meta-analysis (Fig. 3.5). Similarly, there was no change in functional diversity and minimal decline in functional trait dispersion for assemblages of *Rhododendron* species along the elevation gradient (Table 3.5). The small amount of trait-space variation observed for *Rhododendron* species is possibly a reflection of differences in microhabitat preferences or genetic drift as a neutral explanation for why some variation occurs between species.

The decrease in lamina area with elevation was the single trait that matched physiological expectations broadly observed across plant families (Grubb 1977, Milla and Reich 2011), with leaf size being nearly an order of magnitude larger for *Rhododendron* species associated with lower elevations as compared to those at higher elevations. A

unique characteristic for a subset of tropical *Rhododendron* is that some species, such as *R. ericoides* or *R. stenophyllum*, have leaves that bear close resemblance to conifer needles, rather than the broader elliptical leaves associated with temperate species. Metrics such as shape and rugosity were not quantified in this study, but would be worth further investigation especially because tropical species of *Rhododendron* display a greater diversity of these traits within the tropics relative to temperate *Rhododendron* species, however the reason for this is unknown (Argent 2006). The increase in foliar N with elevation may at first appear counter intuitive, as it directly contradicts the negative trend found with other woody species from the tropical meta-analysis (Fig. 3.5a). However, this result makes sense if factors other than nutrient availability limit leaf size and number of leaves at higher elevations, and thus lead to surplus of that nutrient relative to plants from lower elevations, which presumably grow faster in those more productive environments.

Other studies that place emphasis on Ericaceae functional traits trends along gradients may help offer additional insights on unifying themes for how this lineage responds to environmental stressors. One study that sampled tropical species from the genus *Rhododendron*, *Vaccinium*, and *Gaultheria* along an elevation gradient found no relationship between SLA and elevation when sampling across species, (Körner 1998), even though there was a slight decline in SLA when randomly sampling a small number ($n = 15$) of *Rhododendron* leaves (other metrics, such as leaf size, thickness, size and density of stomata showed no significant change). On an even broader latitudinal gradient, another study found minimal distinction between leaf traits of tropical versus temperate *Rhododendron* species (Nilsen 2003). However, *Rhododendron* specific

studies with examination of more micro-scale differences in internal leaf anatomy, generally associated with leaf-water relations such as thickness of cell walls or idioblast cell density, did find differences in *Rhododendron* species along environmental gradients and growth form (Körner 1998, Nilsen 2003, Tulyananda and Nilsen 2017), suggesting that *Rhododendron* species do respond to their environment in some phenotypic dimensions even if their overall ecological strategy remains largely unchanged.

3.4.3 Fluidity in growth form and habitat association

For tropical *Rhododendron*, species occur both across and within habitat types positioned at many different points along an elevation gradient. Within lower elevation habitats, *Rhododendron* species ability to maintain a stress-tolerant ecological strategy was most likely facilitated by either competition avoidance, such as via colonization of recently disturbed habitats, or from opportunistic expansion into novel habitat types that would also be described as stressful (*e.g.* limited nutrient availability). The ability to plastically adjust growth form from terrestrial to epiphytic may have been a means to access areas of the canopy with higher light availability that they would have otherwise been competitively excluded from due to slow growth or limits on maximum height. Within *Rhododendron* leaves, idioblast cells are also thought to have facilitated in the expansion of *Rhododendron* into epiphytic growth forms via improved water use efficiency (Tulyananda and Nilsen 2017). However, since the epiphytic habit is associated with severe reductions in soil resource availability, presumably adaptations to tolerate extreme edaphic stress would also allow *Rhododendron* species to become epiphytic, and thus

escape the competition that they would have otherwise experienced if growing terrestrially in fertile soils.

The lack of difference between the overall trait-space of *Rhododendron* species associated with ultramafic, as compared to non-ultramafic, soil was surprising but reaffirms that the majority of *Rhododendron* have a suite of traits applicable across even the most stressful conditions and may facilitate opportunistic colonization of novel habitat types. Multiple *Rhododendron* species, including those regarded as ultramafic specialists, have been observed within areas associated with post-industrial mining for gold or copper in soil conditions described as extremely toxic and nutrient limited (Argent 2006, van der Ent et al. 2014). Post-mining sites also represent an especially novel habitat type when considering the landscape from an evolutionary time scale. Symbiotic association of *Rhododendron* with mycorrhizal fungi may facilitate both epiphytic growth forms, as well as colonization of former mining sites, in a manner similar to orchids (Rasmussen 1995, Otero et al. 2002, Shefferson et al. 2008).

3.4.4 Steady stress, novel niche hypothesis

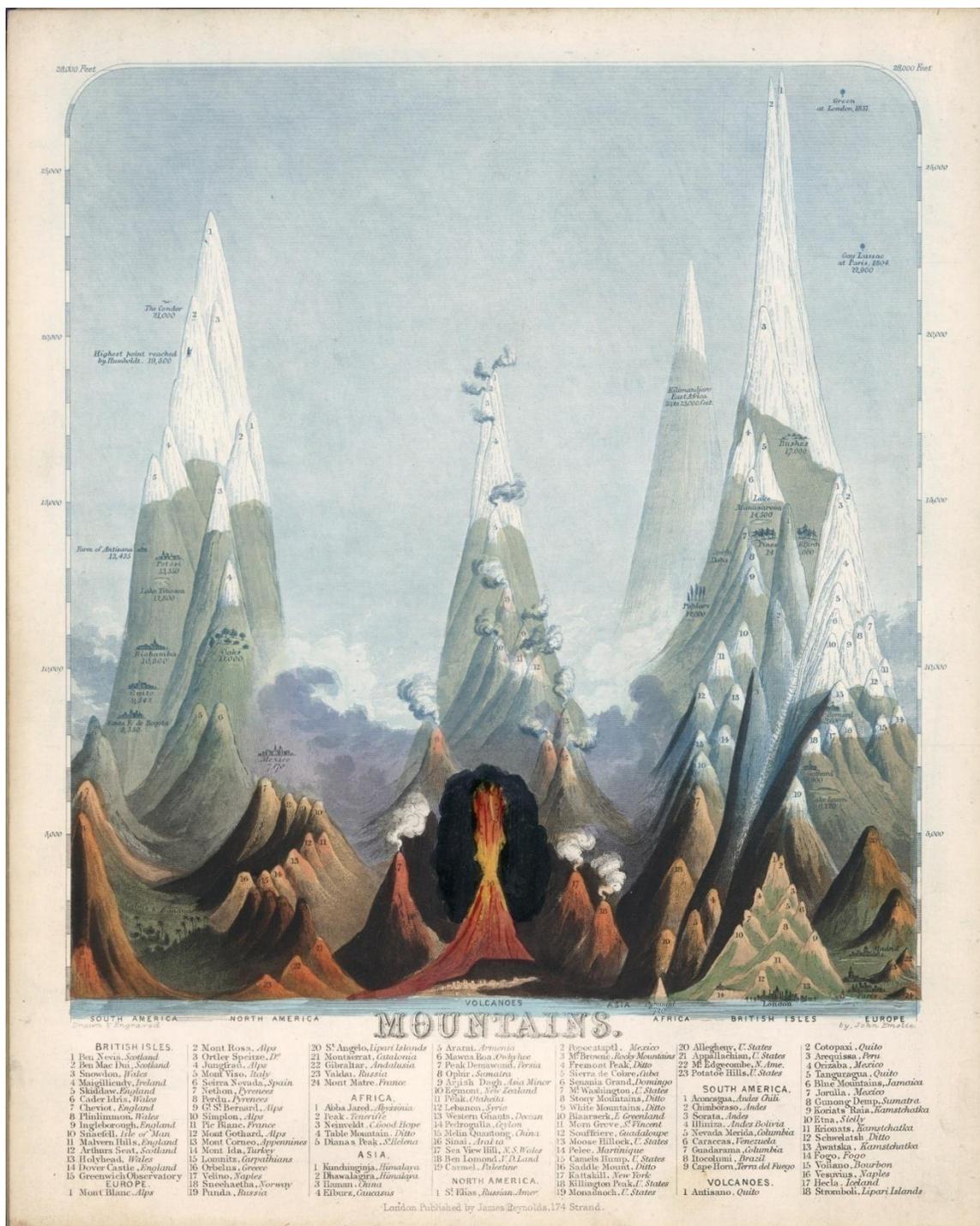
I propose the "steady stress, novel niche" hypothesis as a means to describe why tropical *Rhododendron* species are able to maintain an ecological strategy across a broad elevation gradient. If a species has a general suite of functional traits that enables tolerance of multiple abiotic stressors, and if it is able to avoid competition by being either very flexible or opportunistic in its habitat association, then the primary filtering constraints on where a species can occur along an environmental gradient will be minimized and thus the trait space can remain relatively unchanged. However, a caveat of

the "stead stress, novel niche" hypothesis is that it may be directionally dependent upon the ancestral habitat or region from where a taxonomic group originates, applicable when the taxa is coming from a relatively resource-limited area, but not applicable if coming from a relatively resource-rich area. For instance, if the point of origin was within lower elevation habitats, then expansion into higher elevations would require a shift in ecological strategy and associated functional traits in accordance with greater exposure to abiotic stressors. In contrast, if the point of origin was within higher elevations, then expansion into lower elevations could be met with two possible responses: either a change in strategy to match increasing competitive pressures, or no-change but contingent upon establishment into novel habitats without competitive exclusion.

In the instance of *Rhododendron*, the ancestral center of distribution for the genus is considered to be near the temperate foothills of the Himalayas, with diversification eastwards through the subtropical Yunnan Province (China) to Taiwan and Japan (Goetsch et al. 2011), followed by rapid speciation in tropical regions of the Malay Archipelago and Northern Australia (Craven et al. 2011, Goetsch et al. 2011, Webb and Ree 2012). Within the tropics, *Rhododendron* most likely colonized mountainous habitats first (Schwery et al. 2015), and given their temperate origins (Brown et al. 2006, Goetsch et al. 2011), I speculate that the majority of species would have already been adapted to abiotic stressors and tolerance of a wide suite of growing conditions originally attributed to origins in areas with seasonality and freezing events. While biogeographic history and overall stress-tolerance of *Rhododendron* offers a scenario that would fit the "novel niche, stable stress" hypothesis, I would recommend further testing by examining functional trait variation of other stress-tolerant plant taxa along similar gradients.

3.4.5 Conclusion

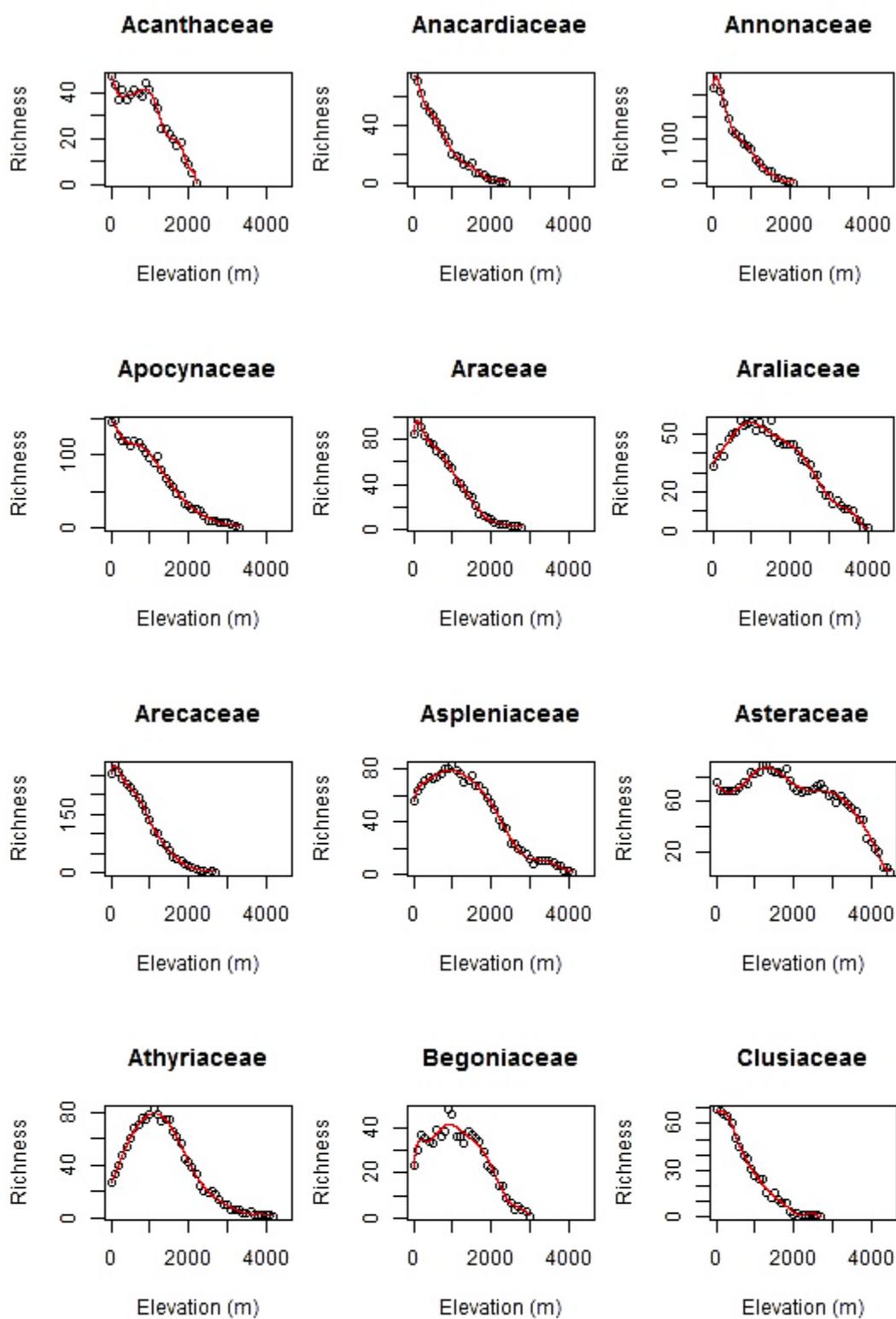
Results of this study reinforce the concept that an ecological strategy can remain relatively constant across a broad geographic gradient provided there are other functional adaptations that covary along the gradient that ameliorate competition. Based on their functional trait variation, I found that *Rhododendron* species occupy the slow end of the slow-fast continuum described by the LES. Yet, *Rhododendron* species are not restricted to high elevation habitats, owing to a variation in a key trait, growth form. Being epiphytic allows them to colonize lower elevation habitats, from which they would otherwise be competitively excluded, owing to their conservative trait variation. In addition, functional traits associated with general stress-tolerance enables *Rhododendron* species the flexibility to opportunistically occur across a wide range of habitat types along a tropical elevation gradient.

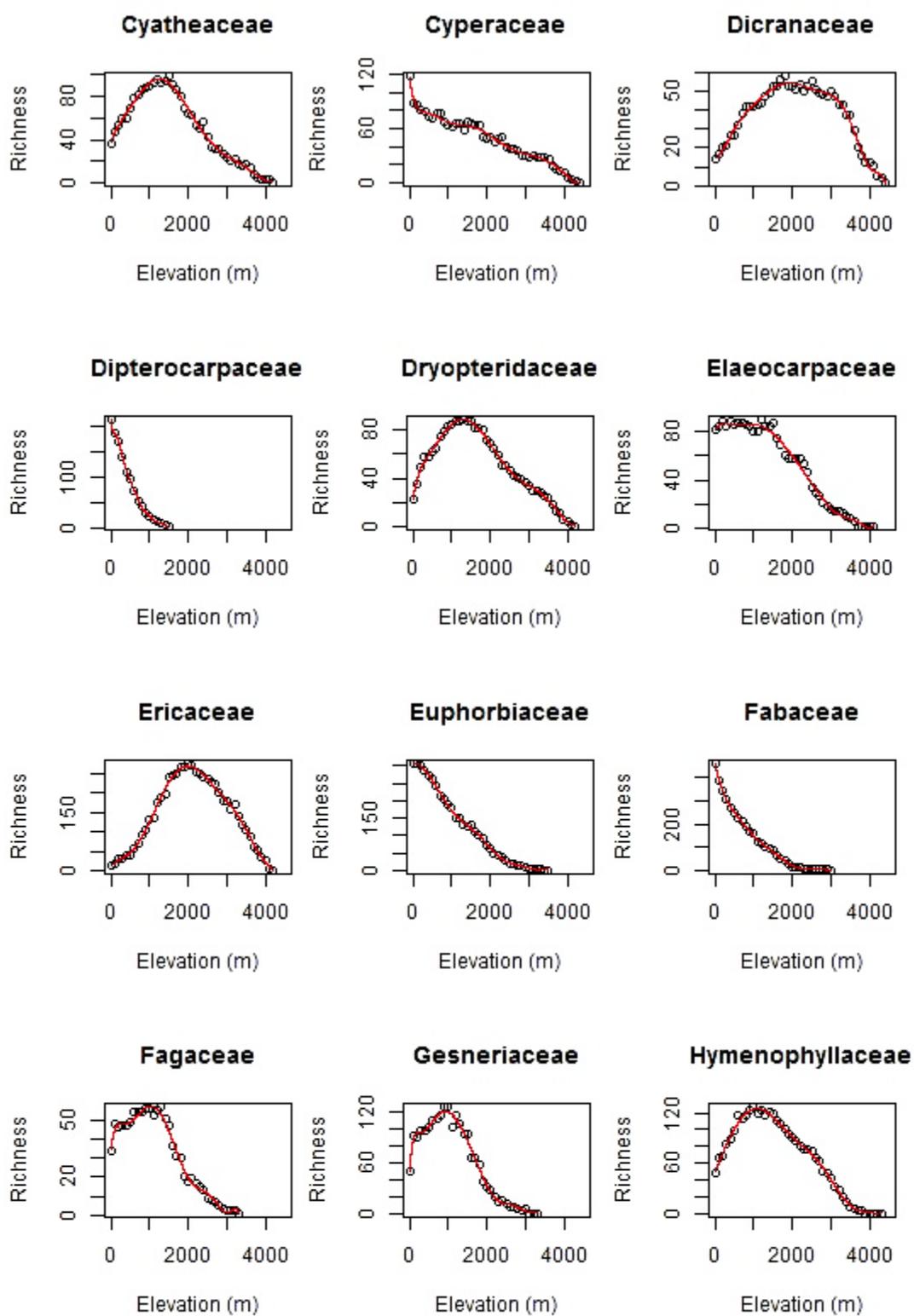


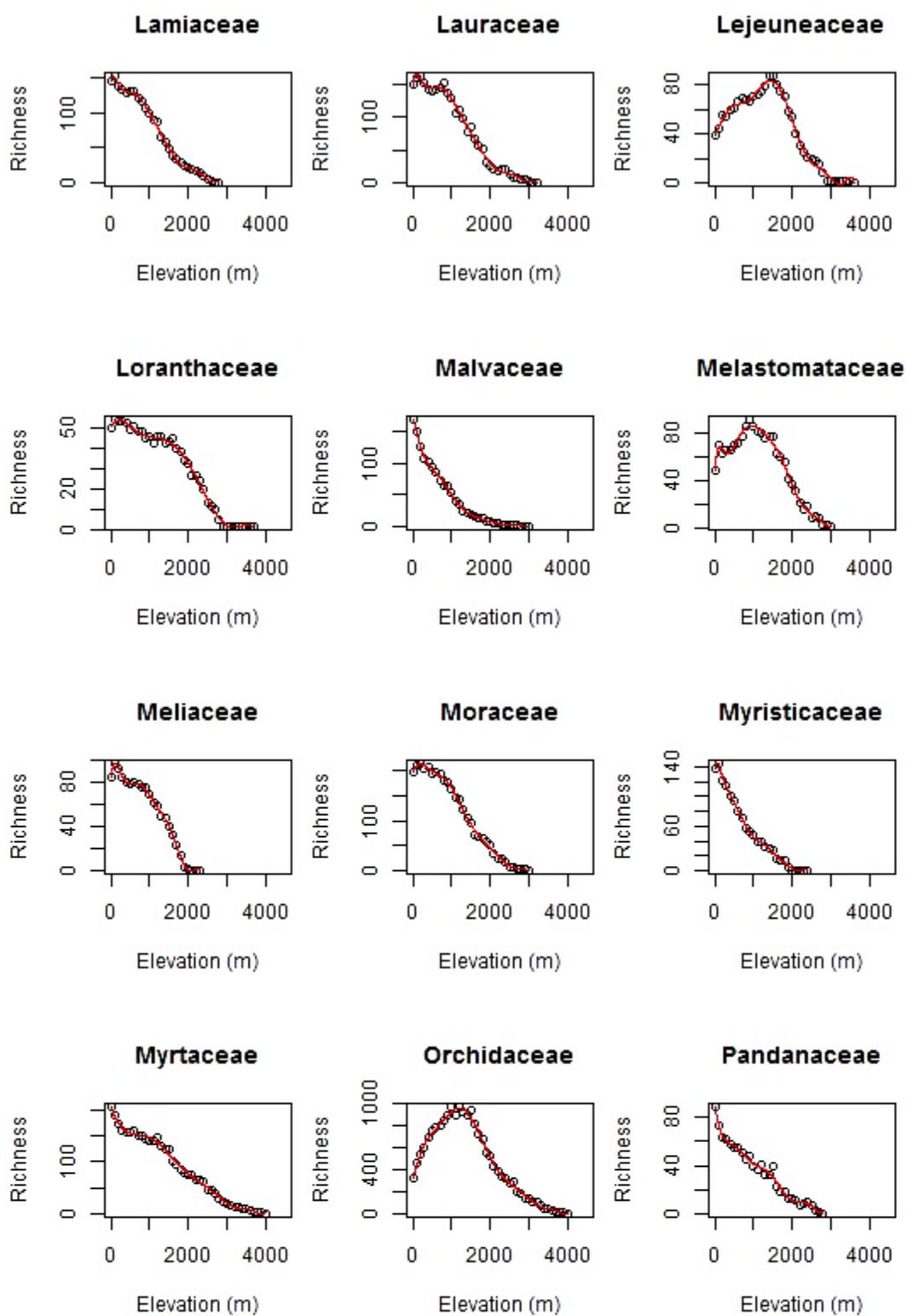
Mountains. Geological Diagrams. 1851.

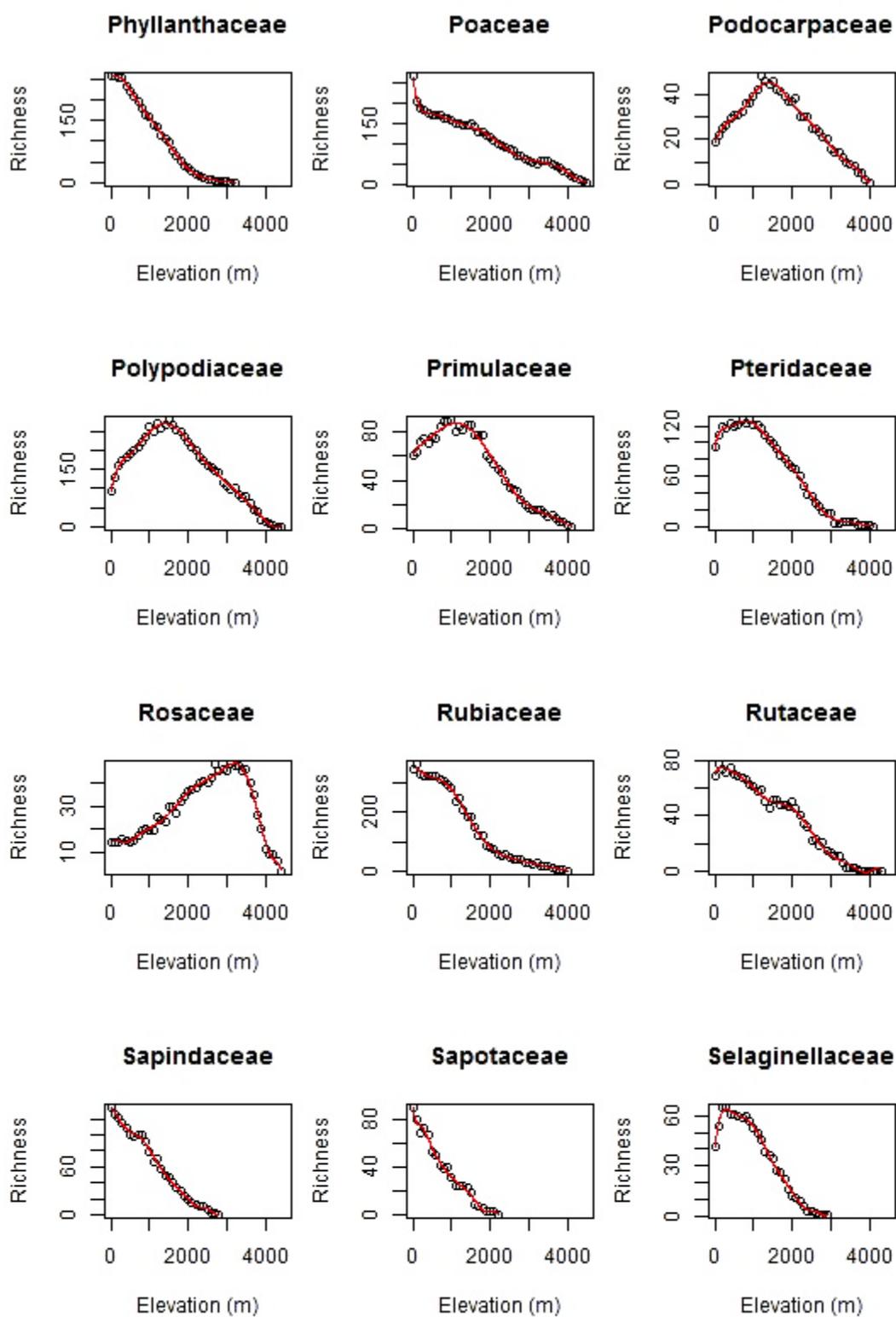
CHAPTER 4 - SUPPLEMENTAL SECTION

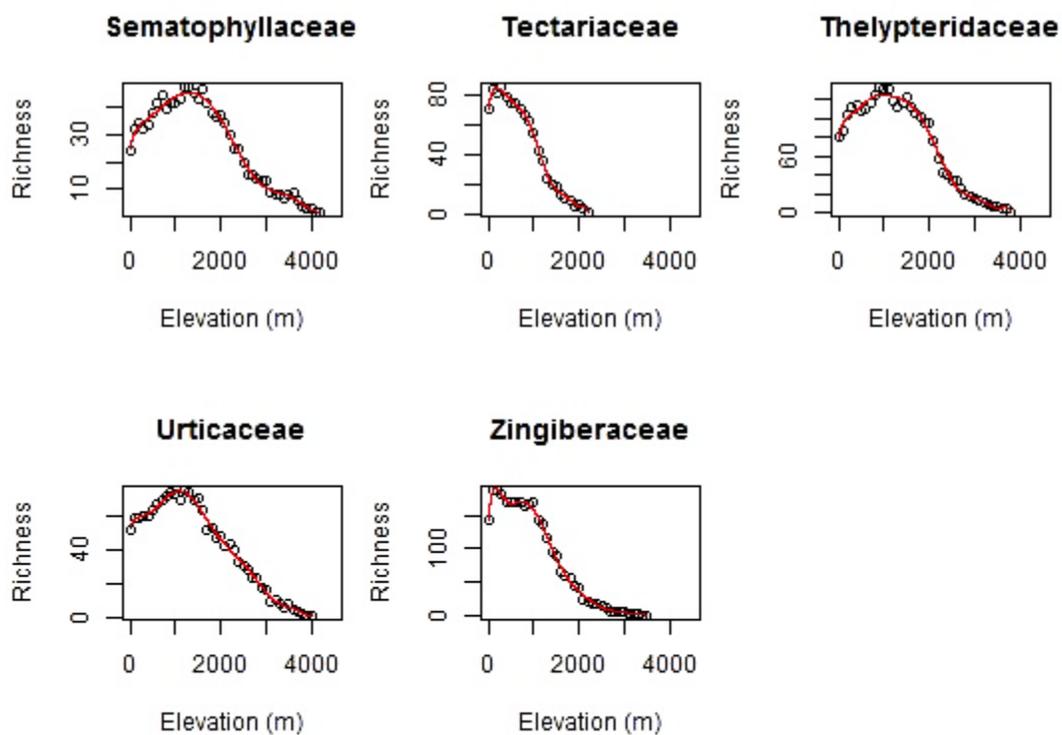
- 4.1. Species richness plots for each plant family; polynomial regression used to predict the elevation where richness peaks.
- 4.2. Richness and range-size plots for each family, including correlation coefficient (slope) for the relationship between range-size and elevation used in cross family analyses.
- 4.3. Accession list of all *Rhododendron* individuals sampled, with garden reference ID and notes on if wild collected.
- 4.4. *Rhododendron* leaf functional trait data, averaged by species.
- 4.5. *Rhododendron* taxonomy, growth form, and soil association
- 4.6. Bibliography for meta-analysis of tropical woody plant traits.
- 4.7. Herbarium list for institutions that provided species occurrence records

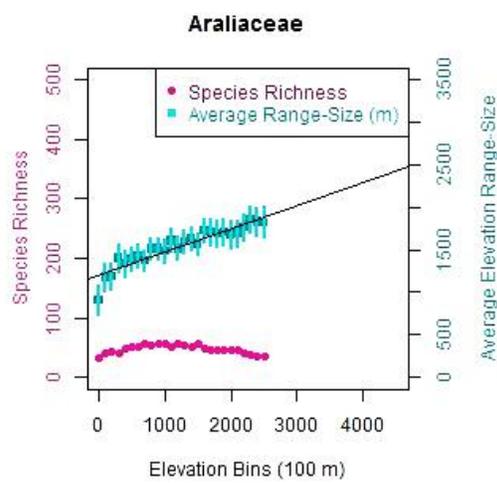
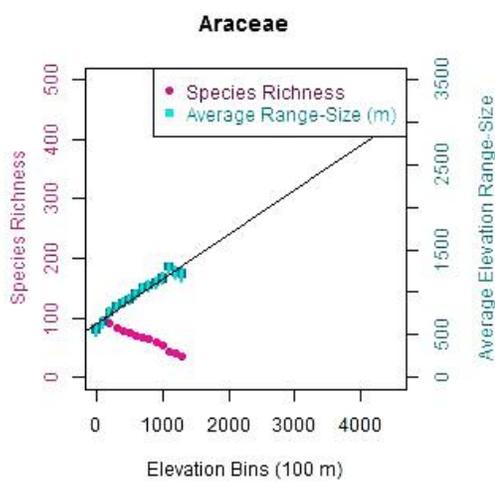
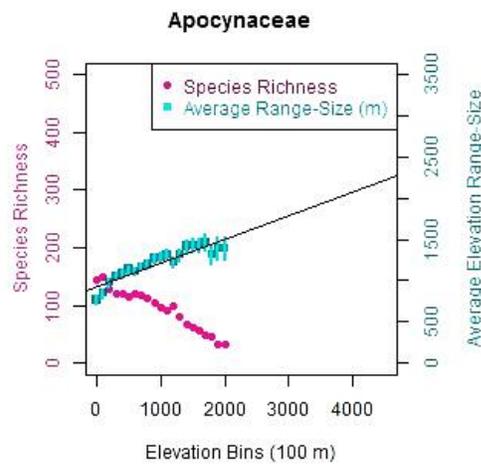
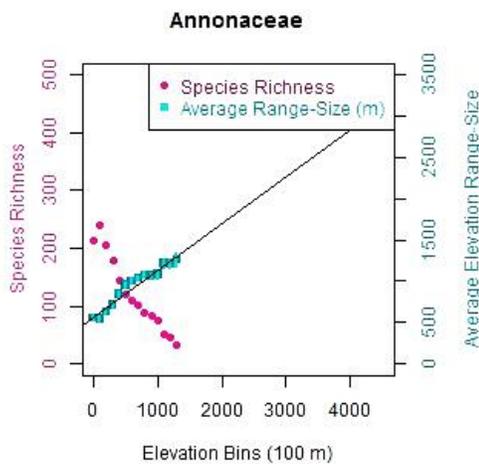
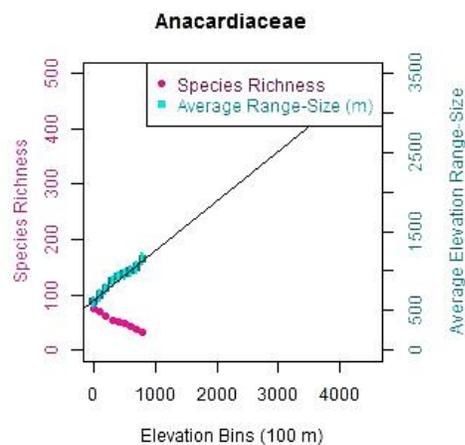
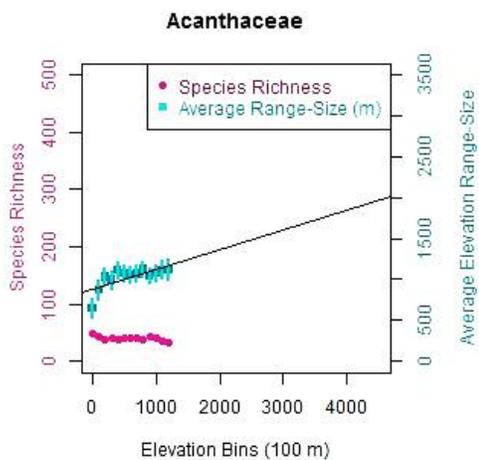


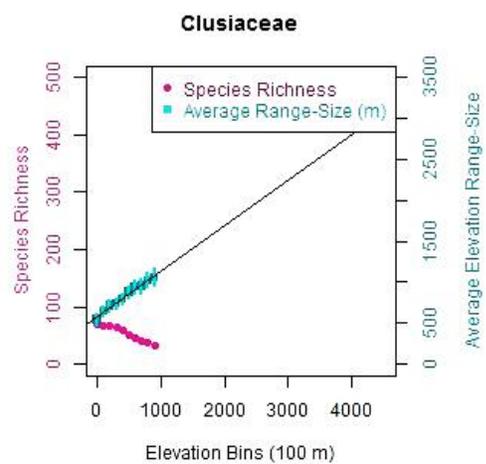
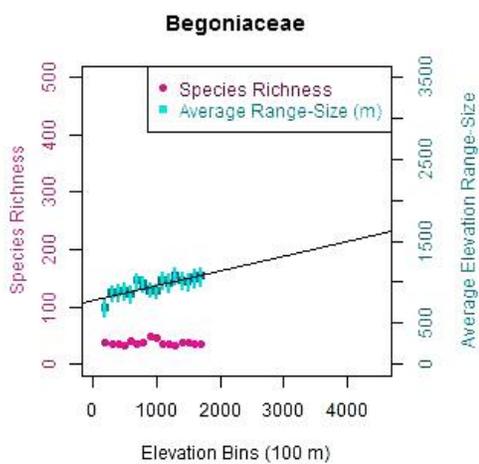
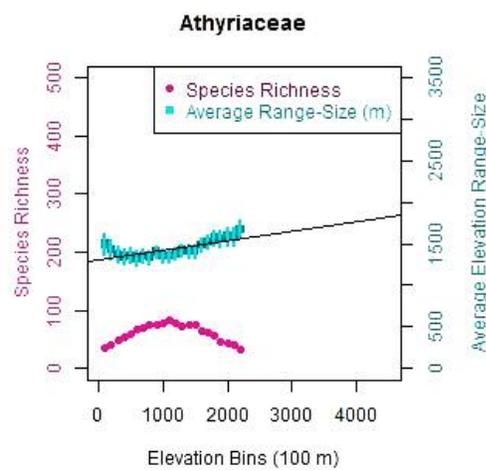
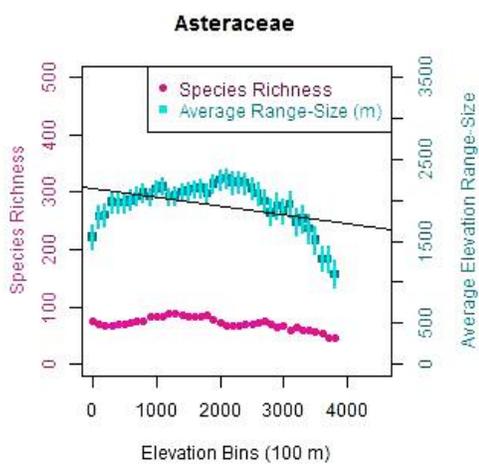
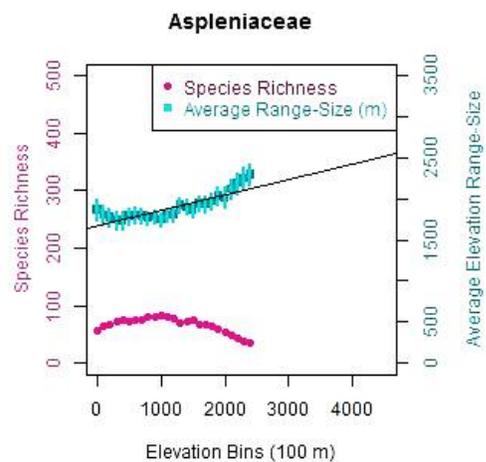
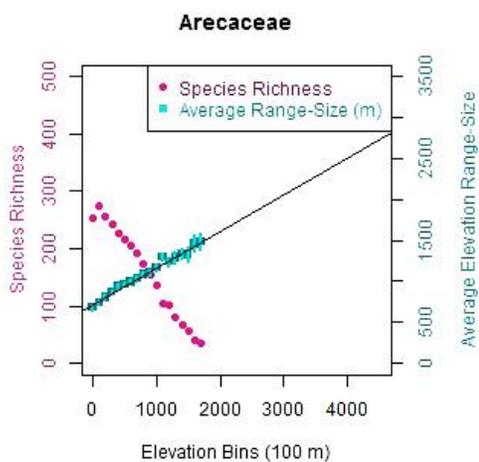


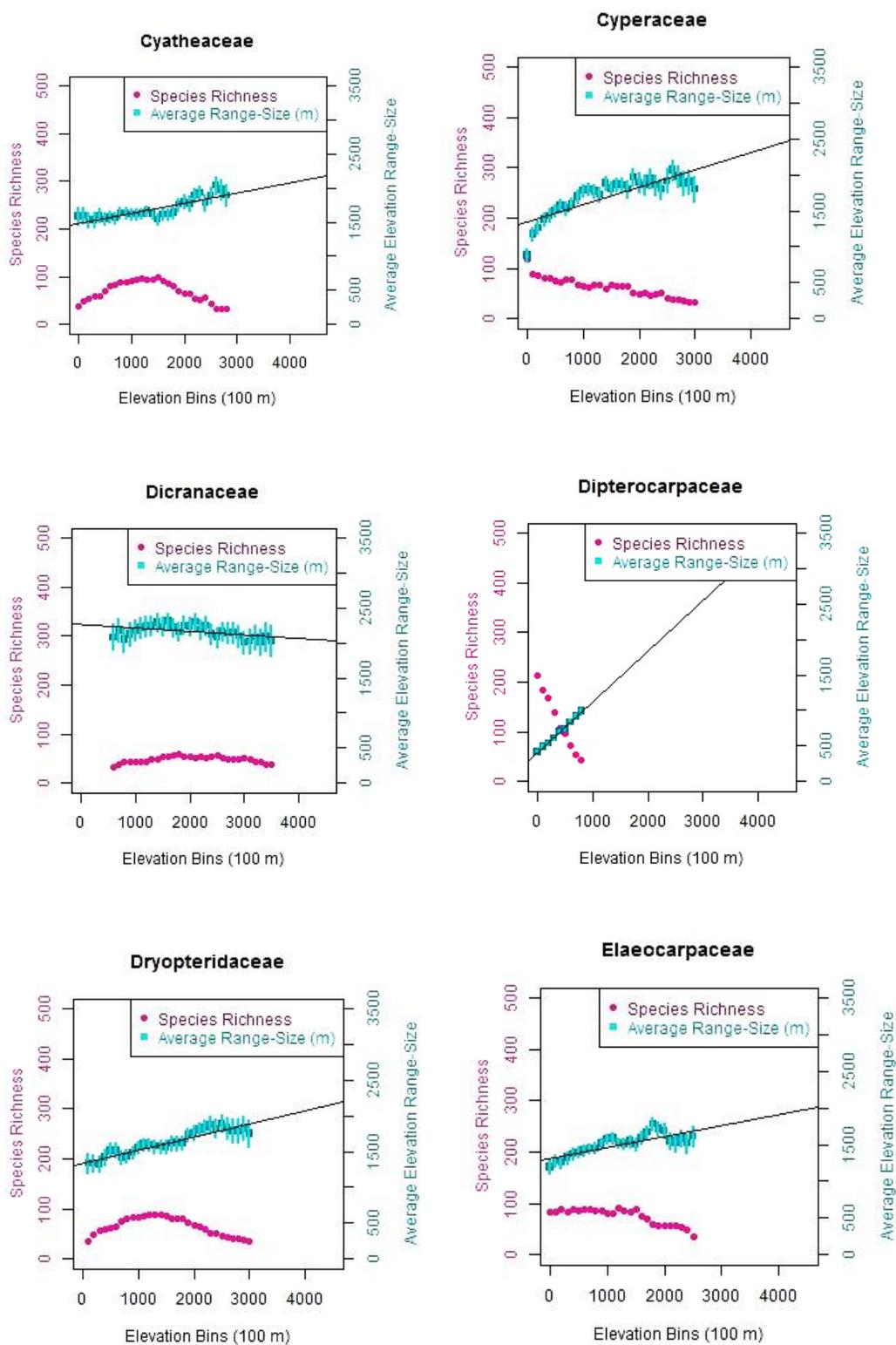


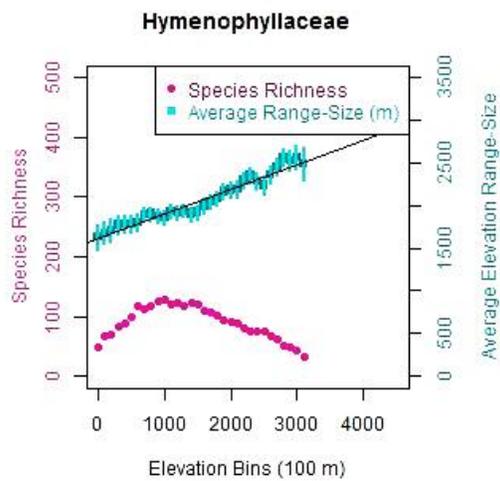
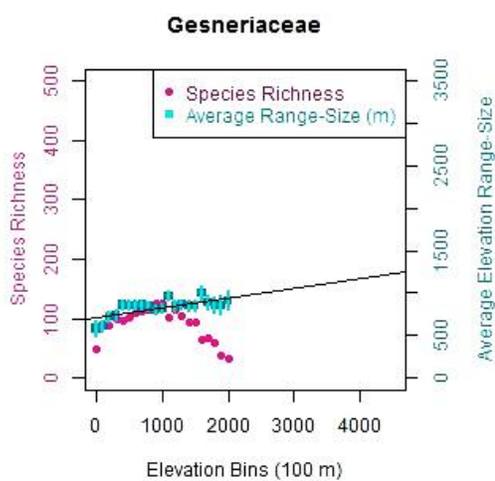
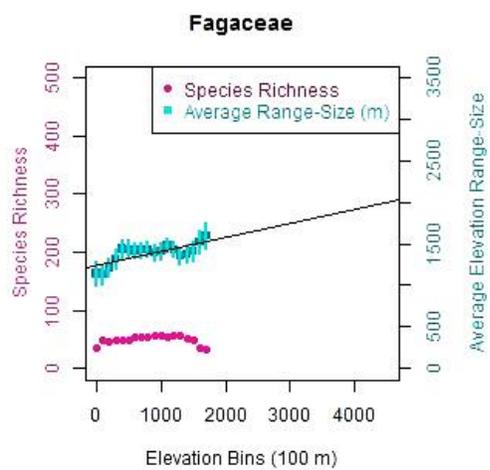
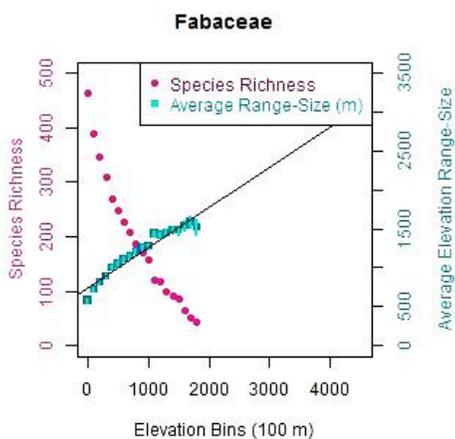
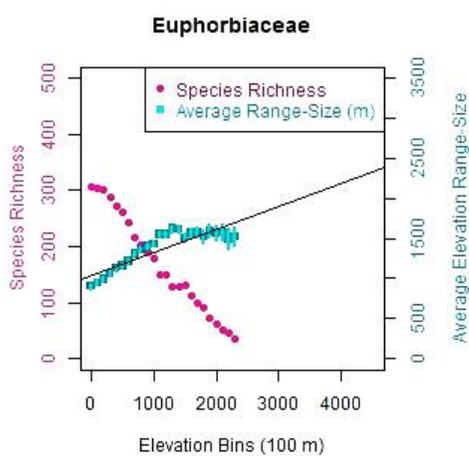
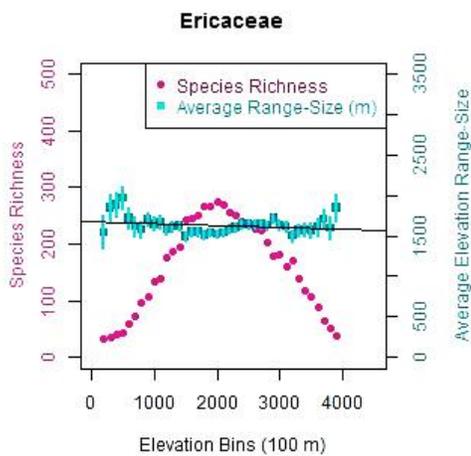


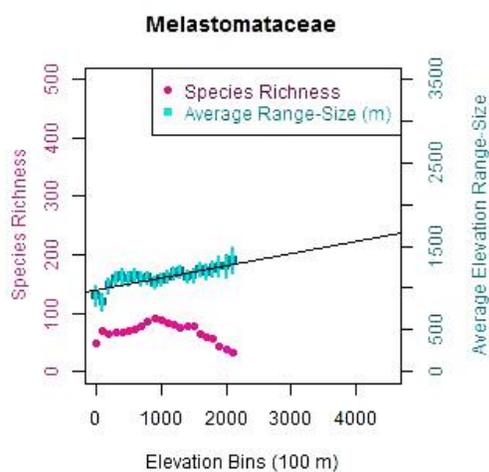
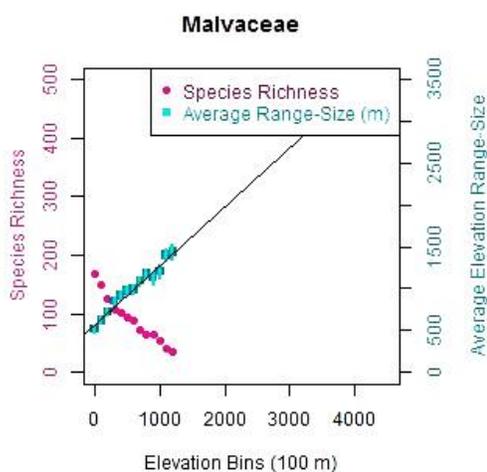
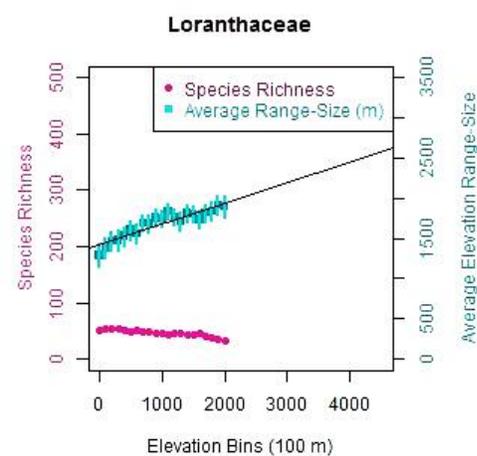
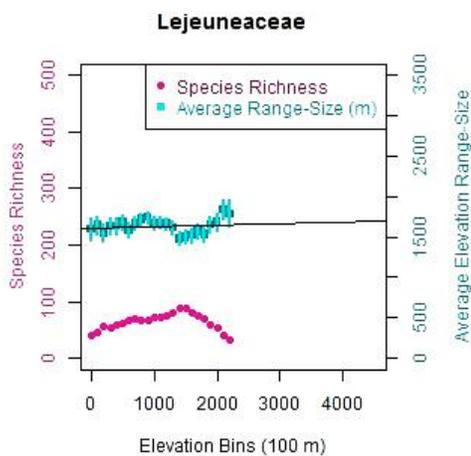
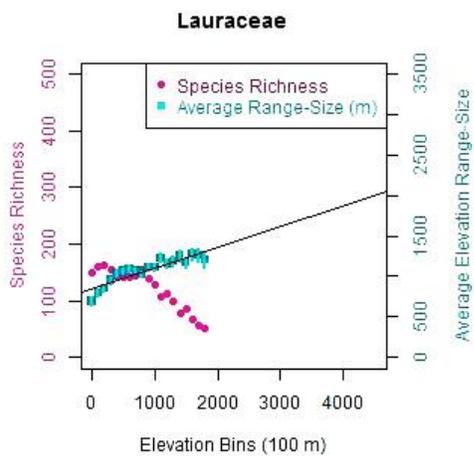
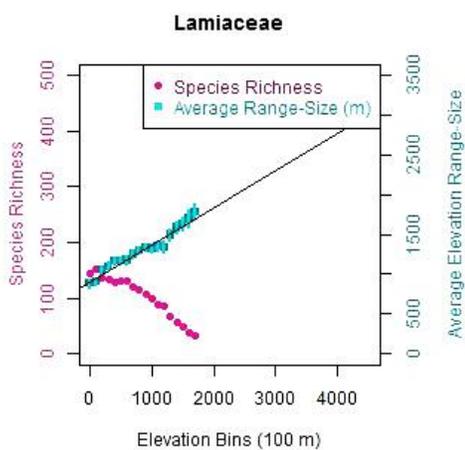


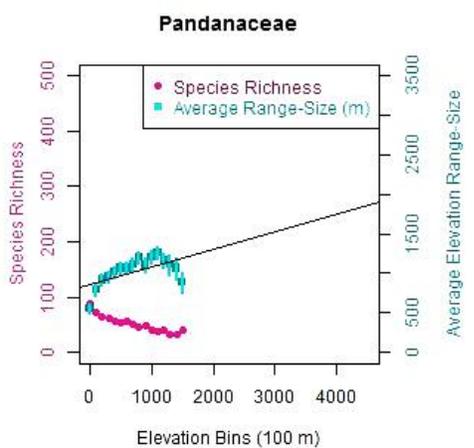
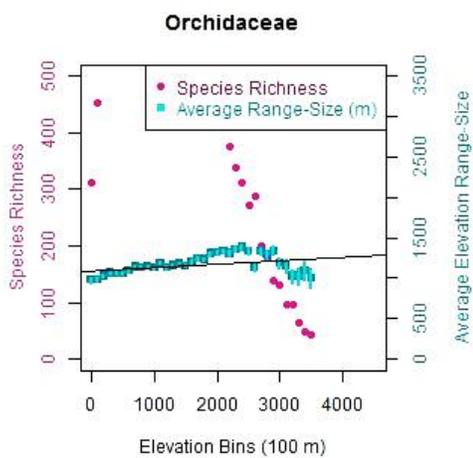
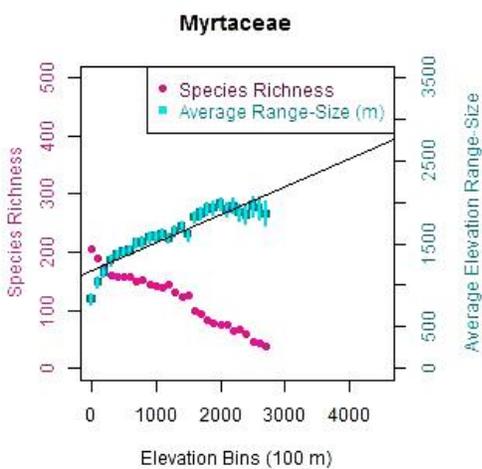
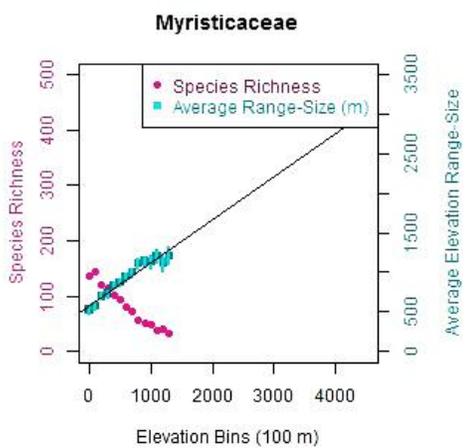
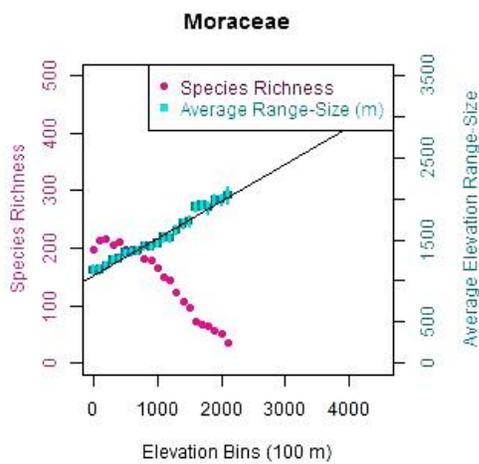
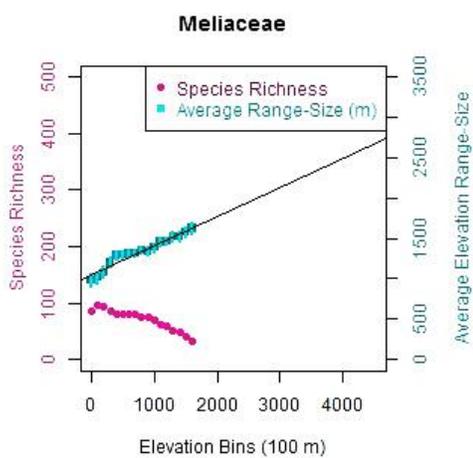


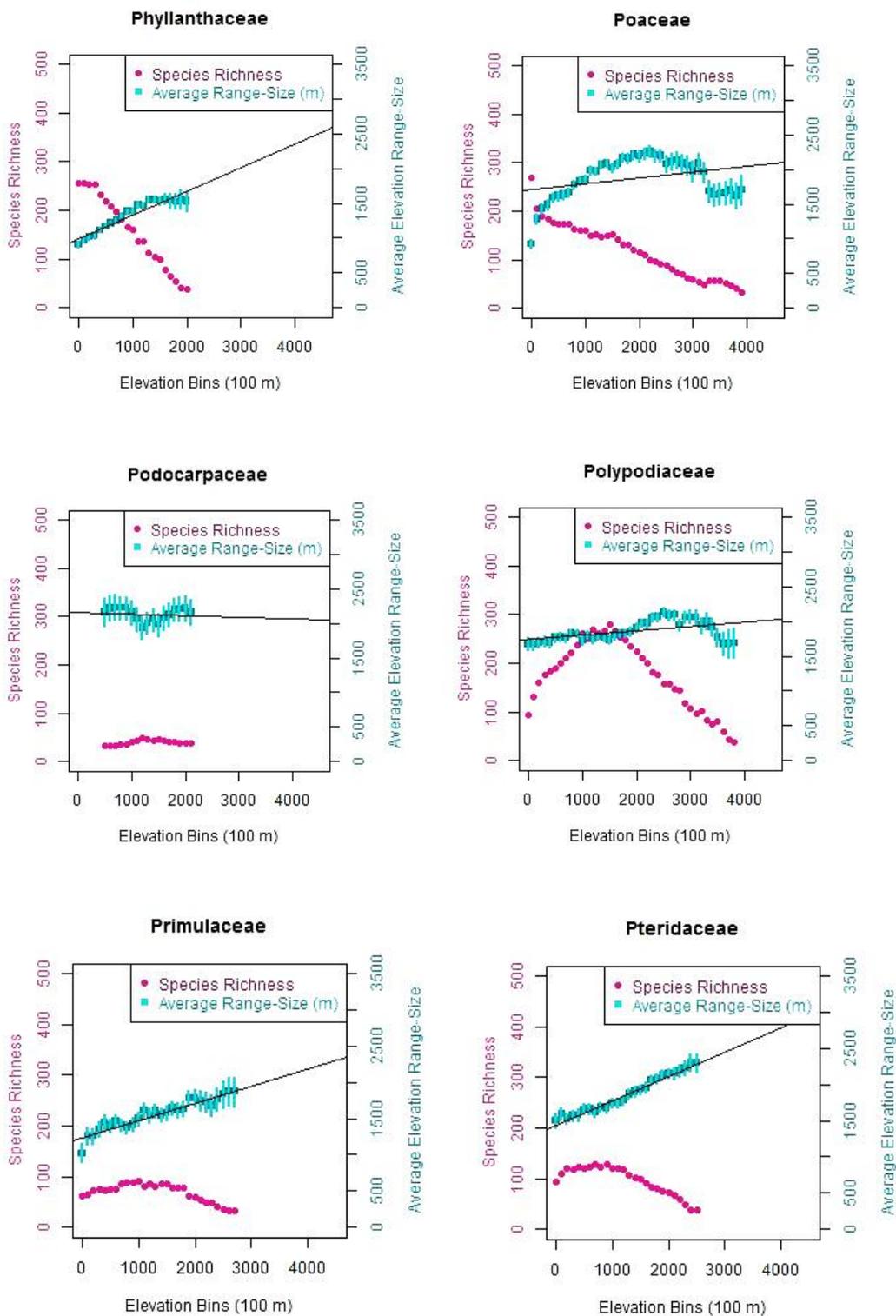


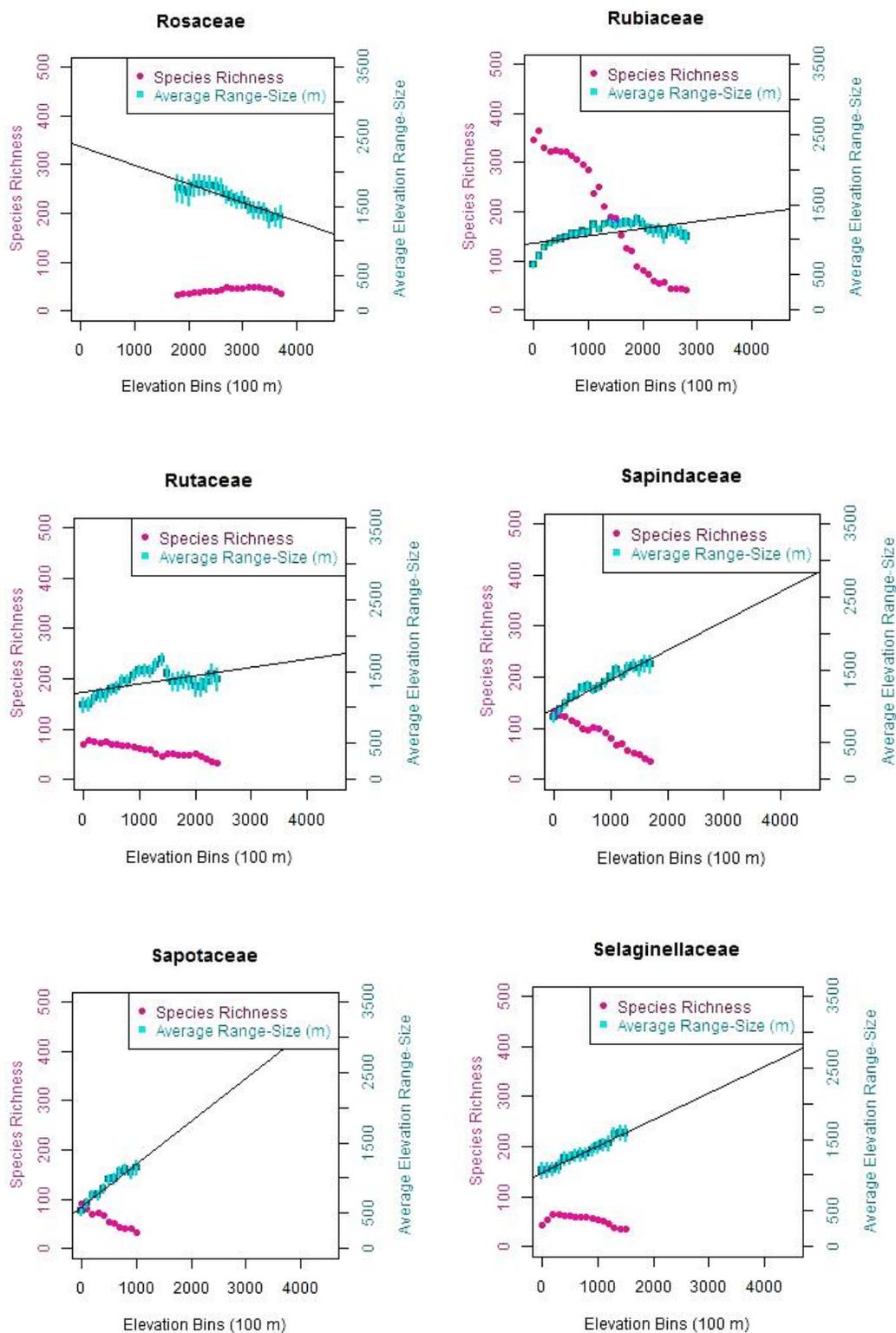


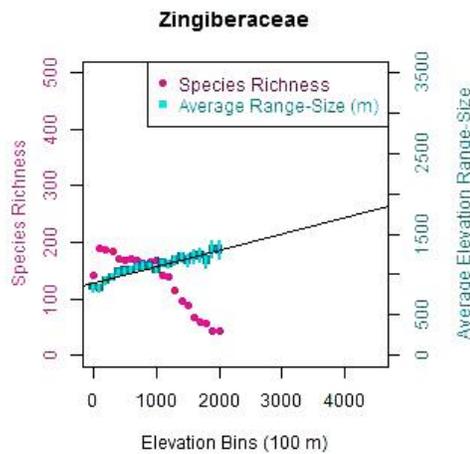
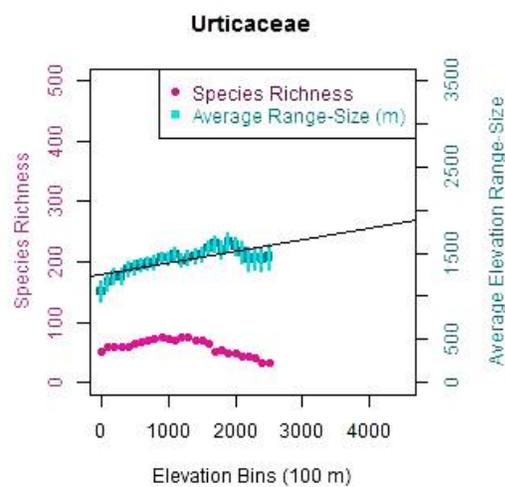
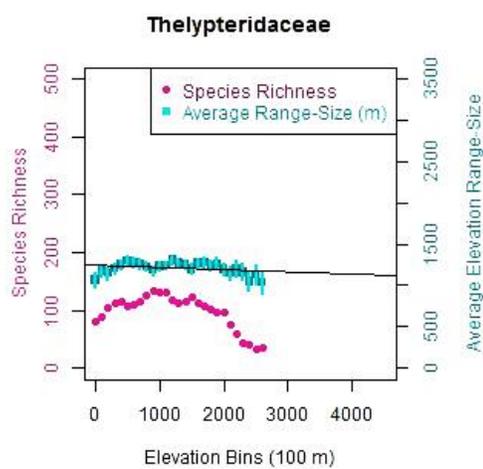
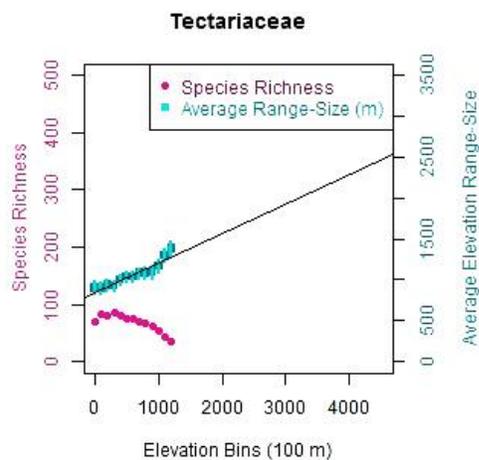
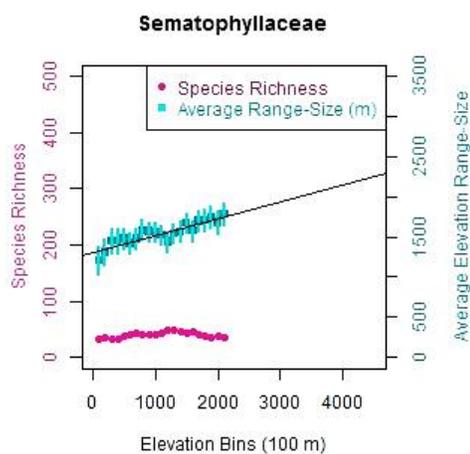












Supplemental 4.3: Accession list of *Rhododendron* species sampled. Species and subspecies names based on nomenclature used by Argent 2016. "Code" refers to the unique species identifier used within this study. "Indiv" refers to the individual sampled for each species. Abbreviations for botanical gardens are as follows: Bovees Rare Plant Nursery (B); Rhododendron Species Foundation (RSF); Royal Botanical Gardens in Edinburgh (RBE). Accession code/number is the unique plant identifier used by the botanical garden from where an individual was sampled; if an individual was propagated using a plant from another garden then the original base plant accession number was used. Year refers to the date when a plant first entered a botanical garden live plant collection. "Wild" refers to whether the plant sampled originated from a seed, cutting, or seedling collected from the species native habitat range; if blank then the individual plant origin or cultivation history is unknown. Species in grey were sampled, but not included in analyses at this point in time.

Species	Subspecies	Indiv	Garden	Accession	Year	Wild
<i>abietifolium</i>		1	RBE	19801268	1980	Yes
<i>acrophilum</i>		1	RSF	2002/018	2002	
<i>acrophilum</i>		2	RBE	19922785	1992	Yes
<i>acuminatum</i>		1	RBE	19952743	1995	Yes
<i>aequabile</i>		1	B	V100	1989	
<i>aequabile</i>		2	RBE	19750002	1975	Yes
<i>aerophilum</i>		1	B	V710	n/a	
<i>alborugosum</i>		1	B	V717	n/a	Yes
<i>alborugosum</i>		2	RBE	19962371	1996	Yes
<i>album</i>		1	B	V711	n/a	
<i>alticola</i>		1	RBE	19710182	1971	
<i>anagalliflorum</i>		1	RBE	19821953	1982	
<i>apiense</i>		1	RBE	19781745	1978	Yes
<i>apoanum</i>		1	RBE	19922812	1992	Yes
<i>apoanum</i>		2	RBE	19922797	1992	Yes
<i>arenicolum</i>		1	RBE	20000587	2000	Yes
<i>armitii</i>		1	RSF	1987/037	1987	
<i>armitii</i>		2	RBE	19682068	1968	Yes
<i>asperulum</i>		1	RSF	2013/011	2013	
<i>atropurpureum</i>		1	RSF	1997/112	1997	
<i>aurigeranum</i>		1	B	V138	1987	Yes
<i>aurigeranum</i>		2	RBE	19832077	1983	Yes
<i>aurigeranum</i>		3	RBE	19902940	1990	Yes
<i>baconii</i>		1	RBE	19952766	1995	Yes
<i>baenitzianum</i>		1	RBE	19973613	1997	
<i>baenitzianum</i>		2	RBE	19901315	1990	
<i>bagobonum</i>		1	RBE	19821504	1982	Yes

<i>bagobonum</i>		2	RGBE	20000530	2000	Yes
<i>beyerinckianum</i>		1	B	V587	n/a	
<i>beyerinckianum</i>		2	RGBE	19882537	1988	Yes
<i>blackii</i>		1	RSF	n/a	n/a	
<i>blackii</i>		2	RGBE	19832074	1983	Yes
<i>borneense</i>	<i>villosum</i>	1	RGBE	19821510	1982	Yes
<i>brassii</i>		1	RGBE	19930917	1993	Yes
<i>brassii</i>		2	RGBE	19941411	1994	Yes
<i>burttii</i>		1	RSF	1987/039	1987	
<i>burttii</i>		2	RGBE	19821527	1982	Yes
<i>buxifolium</i>		1	RGBE	19962012	1996	
<i>caliginis</i>		1	RGBE	19943024	1994	
<i>caliginis</i>		2	RGBE	19882535	1988	Yes
<i>camtschaticum</i>		1	RSF	1973/054	1973	
<i>carringtoniae</i>		1	RSF	1987/040	1987	
<i>carringtoniae</i>		2	RGBE	19741502	1974	Yes
<i>celebicum</i>		1	B	V670	n/a	
<i>christi</i>		1	B	n/a	1970	
<i>christi</i>		2	RGBE	19861600	1986	Yes
<i>christi</i>		3	RGBE	19861623	1986	Yes
<i>christinae</i>		1	RGBE	19731628	1973	Yes
<i>ciliatum</i>		1	RGBE	19941445	1994	Yes
<i>ciliilobum</i>		1	RGBE	20050529	2005	Yes
<i>cinchoniflorum</i>		1	RGBE	20001929	2000	Yes
<i>citrinum</i>		1	RGBE	19842322	1984	Yes
<i>coelorum</i>		1	RGBE	20001920	2000	Yes
<i>commonae</i>		1	B	V242	n/a	Yes
<i>commonae</i>		2	RGBE	19832059	1983	Yes
<i>crassifolium</i>		1	RSF	1987/041	1987	
<i>crassifolium</i>		2	RGBE	19820920	1982	Yes
<i>crenulatum</i>		1	RGBE	20020501	2002	Yes
<i>cruttwellii</i>		2	RSF	n/a	n/a	
<i>cruttwellii</i>		3	RSF	1983/054	1983	
<i>culminicola</i>	<i>culminicola</i>	1	RGBE	19682558	1968	Yes
<i>culminicola</i>		2	RGBE	19902944	1990	Yes
<i>cuneifolium</i>		1	RGBE	20061661	2006	Yes
<i>cuneifolium</i>		2	RGBE	19952781	1995	Yes
<i>curviflorum</i>		1	RGBE	19930957	1993	Yes
<i>curviflorum</i>		2	RGBE	19930981	1993	Yes
<i>densifolium</i>		1	RSF	1985/022	1985	
<i>densifolium</i>		2	RGBE	20051611	2005	Yes

<i>dielsianum</i>		1	RSF	1985/023	1985	
<i>dielsianum</i>	<i>dielsianum</i>	2	RGBE	19861695	1986	Yes
<i>durionifolium</i>	<i>sabahense</i>	1	B	V427	n/a	
<i>durionifolium</i>	<i>sabahense</i>	2	RGBE	19821498	1982	Yes
<i>edanoi</i>	<i>pneumonanthum</i>	1	RGBE	19930606	1993	Yes
<i>edanoi</i>	<i>pneumonanthum</i>	2	RGBE	19902933	1990	Yes
<i>edgeworthii</i>		1	RSF	2002/198	2002	
<i>emarginatum</i>		1	B	V433	n/a	Yes
<i>emarginatum</i>		2	RGBE	19951613	1995	Yes
<i>ericoides</i>		1	RGBE	19871806	1987	Yes
<i>ericoides</i>		2	RGBE	20031331	2003	
<i>excelens</i>		2	RSF	1994/380	1994	
<i>excellens</i>		1	RSF	1999/050	1999	
<i>exuberans</i>		1	RGBE	19841213	1984	Yes
<i>fallacinum</i>		1	B	V912	n/a	
<i>fallacinum</i>		2	RGBE	19781728	1978	Yes
<i>flavoviride</i>		1	RGBE	19930925	1993	Yes
<i>fleuryi</i>		1	RSF	1996/040	1996	
<i>gardenia</i>		1	RGBE	19650265	1965	Yes
<i>gardenia</i>		2	RGBE	19761327	1976	Yes
<i>gaultheriifolium</i>		1	RGBE	19941405	1994	Yes
<i>genestierianum</i>		1	RSF	2005/040	2005	
<i>genestierianum</i>		2	RSF	1998/372	1998	
<i>glabriflorum</i>		1	RGBE	20061687	2006	Yes
<i>goodenoughii</i>		1	B	V389	n/a	Yes
<i>goodenoughii</i>		2	RGBE	19772400	1977	Yes
<i>goreri</i>		1	RSF	2005/249	2002	
<i>gracilentum</i>		1	B	V715	1978	Yes
<i>gracilentum</i>		2	RSF	1978/103	1978	
<i>gracilentum</i>		3	RGBE	19680266	1968	Yes
<i>gracilentum</i>		4	RGBE	19722842	1972	Yes
<i>habbema</i>		1	RGBE	20001994	2000	Yes
<i>hancockii</i>		1	RSF	1998/710	1998	
<i>hellwigii</i>		1	RGBE	19861639	1986	Yes
<i>hellwigii</i>		2	RGBE	19861598	1986	Yes
<i>herzogii</i>		1	B	V434	1987	Yes
<i>herzogii</i>		2	RGBE	19614126	1961	Yes
<i>himantodes</i>		1	B	V729	n/a	
<i>himantodes</i>		2	RSF	2003/342	2003	
<i>himantodes</i>		3	RGBE	19781723	1978	Yes
<i>hyacinthosmum</i>		1	RSF	1983/064	1983	

<i>hyacinthosmum</i>		2	RGBE	19951954	1995	Yes
<i>impositum</i>		1	B	V669	n/a	
<i>inconspicuum</i>		1	RGBE	19930810	1993	Yes
<i>inconspicuum</i>		2	RGBE	19750105	1975	Yes
<i>inconspicuum</i>		3	RGBE	19614237	1961	Yes
<i>insculptum</i>		1	B	n/a	n/a	
<i>intranervatum</i>		1	RGBE	19622876	1962	Yes
<i>inundatum</i>		1	B	V908	n/a	
<i>jasminiflorum</i>		1	RSF	1978/102	1978	
<i>jasminiflorum</i>	<i>obligifolium</i>	2	B	V610	n/a	
<i>jasminiflorum</i>	<i>punctatum</i>	3	B	V580	n/a	
<i>jasminiflorum</i>		4	RGBE	19820742	1982	Yes
<i>javanicum</i>		1	B	Vn/a	n/a	
<i>javanicum</i>	<i>palawanense</i>	2	RGBE	19922762	1992	Yes
<i>javanicum</i>	<i>schadenbergii</i>	3	RGBE	19922744	1992	Yes
<i>javanicum</i>	<i>javanicum</i>	4	RGBE	19680840	1968	
<i>javanicum</i>	<i>brookianum</i>	5	RGBE	19852168	1985	Yes
<i>javanicum</i>	<i>brookianum</i>	6	RGBE	19841173	1984	Yes
<i>javanicum</i>	<i>cladotrichum</i>	7	RGBE	19952758	1995	Yes
<i>javanicum</i>	<i>cockburnii</i>	8	RGBE	20061648	2006	Yes
<i>javanicum</i>	<i>gracile</i>	9	RGBE	19851907	1985	Yes
<i>javanicum</i>	<i>moultonii</i>	10	RGBE	n/a	1991	
<i>javanicum</i>	<i>brookianum</i>	11	B	V724	n/a	
<i>kawakamii</i>		1	RSF	1999/290	1999	
<i>kawakamii</i>		2	RSF	1979/026	1979	
<i>kawakamii</i>		3	RGBE	19710098	1971	Yes
<i>kochii</i>		1	B	V325	1990	Yes
<i>kochii</i>		2	RGBE	19972500	1997	Yes
<i>konori</i>		1	B	V97	n/a	Yes
<i>konori</i>		2	B	V35	n/a	
<i>konori</i>		3	RSF	1999/283	1999	
<i>laetum</i>		1	B	V3	n/a	
<i>laetum</i>		2	B	V333	n/a	
<i>lagunculicarpum</i>		1	RGBE	20000730	2000	Yes
<i>lagunculicarpum</i>		2	RGBE	20000620	2000	Yes
<i>lambianum</i>		1	RGBE	19913764	1991	Yes
<i>lamrialianum</i>	<i>gunsalamianum</i>	1	RGBE	19952747	1995	Yes
<i>lanceolatum</i>		1	B	V318	n/a	Yes
<i>leptanthum</i>		1	RSF	1985/043	1985	
<i>leptanthum</i>		2	RGBE	19630476	1963	
<i>leptobrachion</i>		1	B	V666	n/a	Yes

<i>leptobrachion</i>	2	RGBE	19981656	1998	Yes
<i>leucogigas</i>	1	RSF	1978/093	1978	
<i>leucogigas</i>	2	RGBE	19682431	1968	
<i>leucogigas</i>	3	RGBE	20031335	2003	
<i>levinei</i>	1	RSF	n/a	n/a	
<i>leytense</i>	1	RGBE	19991947	1999	Yes
<i>lineare</i>	1	RGBE	19913767	1991	Yes
<i>lineare</i>	2	RGBE	19913771	1991	Yes
<i>loboense</i>	1	RGBE	19991941	1999	Yes
<i>lochiae</i>	1	RGBE	19961298	1996	Yes
<i>lochiae</i>	2	RGBE	19510365	1951	
<i>longiflorum</i>	1	RGBE	19801300	1988	Yes
<i>longiflorum</i>	2	RGBE	19801307	1980	Yes
<i>loranthiflorum</i>	1	RSF	1978/099	1978	
<i>lowii</i>	1	RSF	n/a	2000	
<i>lowii</i>	2	B	V577	1996	Yes
<i>lowii</i>	3	RGBE	19952344	1995	Yes
<i>lowii</i>	4	RGBE	19952800	1995	Yes
<i>luraluense</i>	1	B	V596	n/a	
<i>macgregoriae</i>	1	B	V604	n/a	
<i>macgregoriae</i>	2	RGBE	19602617	1960	Yes
<i>madulidii</i>	1	RGBE	19922766	1992	Yes
<i>madulidii</i>	2	RGBE	20071881	2007	Yes
<i>maius</i>	1	RSF	1989/006	1989	
<i>maius</i>	2	RGBE	19861647	1986	Yes
<i>malayanum</i>	1	B	V668	n/a	Yes
<i>malayanum</i>	2	B	V602	n/a	
<i>malayanum</i>	3	RSF	1997/592	1997	
<i>maxwellii</i>	1	B	V233	n/a	
<i>maxwellii</i>	2	RGBE	19801241	1980	Yes
<i>meijeri</i>	1	RGBE	19952774	1995	Yes
<i>meliphogidum</i>	1	RGBE	19880268	1988	Yes
<i>mendumiae</i>	1	RGBE	19981798	1998	Yes
<i>mendumiae</i>	2	RGBE	20031269	2003	Yes
<i>micranthum</i>	1	RSF	1976/125	1976	
<i>micromalayanum</i>	1	RGBE	19851926	1985	Yes
<i>mindanaense</i>	1	RGBE	19922757	1992	Yes
<i>mindanaense</i>	2	RGBE	19922821	1992	Yes
<i>minus</i>	1	RSF	1994/066	1994	
<i>monodii</i>	1	RGBE	20000553	2000	Yes
<i>monodii</i>	2	RGBE	20000558	2000	Yes

<i>multicolor</i>		1	B	V619	n/a	
<i>multicolor</i>		2	RGBE	19741756	1974	Yes
<i>multinervium</i>		1	RGBE	19762044	1976	
<i>nanophyton</i>		1	RGBE	20000560	2000	Yes
<i>nervulosum</i>		1	RGBE	19801157	1980	Yes
<i>niewenhuisii</i>		1	RGBE	19781725	1978	Yes
<i>niewenhuisii</i>		2	RGBE	20030137	2003	
<i>niveoflorum</i>		1	RGBE	19672550	1967	Yes
<i>orbiculatum</i>		1	RGBE	19982489	1998	Yes
<i>pauciflorum</i>		1	RGBE	19750119	1975	Yes
<i>perakense</i>		1	B	V613	1990	Yes
<i>phaeochitum</i>		1	RSF	1986/022	1986	
<i>pleianthum</i>		1	RGBE	19925007	1992	
<i>poilanei</i>		1	RGBE	20051570	2005	
<i>polyanthemum</i>		1	RSF	n/a	n/a	
<i>polyanthemum</i>		2	RGBE	19801295	1980	Yes
<i>praetervisum</i>		1	RSF	1988/049	n/a	
<i>prainianum</i>		1	RGBE	20001987	2000	Yes
<i>pubitubum</i>		1	B	V672	1996	
<i>pudorinum</i>		1	RSF	1997/053	1997	
<i>pulleanum</i>		1	RGBE	20002004	2000	Yes
<i>quadrasianum</i>		1	B	V671	1996	
<i>quadrasianum</i>	<i>malindangense</i>	2	RGBE	19922799	1992	Yes
<i>quadrasianum</i>	<i>marivelesense</i>	3	RGBE	19972467	1997	Yes
<i>quadrasianum</i>	<i>rosmarinifollum</i>	4	RGBE	19973089	1997	Yes
<i>quadrasianum</i>	<i>quadrasianum</i>	5	RGBE	19972544	1997	Yes
<i>quadrasianum</i>	<i>davauense</i>	6	RGBE	19972548	1997	Yes
<i>radians</i>		1	RSF	1997/063	1997	
<i>radians</i>		2	RGBE	20000501	2000	Yes
<i>rappardii</i>		1	RGBE	20090776	2009	Yes
<i>rappardii</i>		2	RGBE	20090832	2009	Yes
<i>rarilepidotum</i>		1	B	V595	n/a	
<i>rarilepidotum</i>		2	RGBE	19881445	1988	Yes
<i>rarum</i>		1	RSF	1985/001	1985	
<i>rarum</i>		2	RGBE	19861656	1986	Yes
<i>renschianum</i>		1	B	V903	n/a	
<i>renschianum</i>		2	RGBE	19942176	1994	Yes
<i>retivenium</i>		1	B	V603	1996	Yes
<i>retivenium</i>		2	RSF	n/a	n/a	
<i>retusum</i>		1	RSF	1979/027	1979	
<i>retusum</i>		2	RGBE	20141210	2014	

<i>reynosoi</i>	1	RGBE	20080279	2008	Yes
<i>rhaeochitium</i>	1	RSF	1999/311	1999	
<i>rhodoleucum</i>	1	B	V388	n/a	
<i>rhodoleucum</i>	2	RGBE	19682180	1968	Yes
<i>rhodopus</i>	1	B	V667	n/a	
<i>rhodopus</i>	2	B	V672	n/a	
<i>robinsonii</i>	1	RSF	1983/066	1983	
<i>roseiflorum</i>	1	RGBE	20001921	2000	Yes
<i>rosendahlii</i>	1	RGBE	20001923	2000	Yes
<i>rousei</i>	1	RBGR	19902339	1990	
<i>rousei</i>	2	RSF	2002/015	2002	
<i>rousei</i>	3	RGBE	19902326	1990	Yes
<i>rubellum</i>	1	RGBE	19761951	1976	Yes
<i>rubineiflorum</i>	1	RSF	n/a	n/a	
<i>rugosum</i>	1	B	V151	n/a	
<i>rugosum</i>	2	RGBE	19952828	1995	Yes
<i>rugosum</i>	3	RGBE	19952819	1995	Yes
<i>rugosum</i>	4	RGBE	19952745	1995	Yes
<i>rugosum</i>	5	RGBE	19841177	1984	Yes
<i>rugosum</i>	6	RGBE	19841174	1984	Yes
<i>rugosum</i>	7	RGBE	19820909	1982	Yes
<i>rugosum</i>	8	RGBE	19820907	1982	Yes
<i>rugosum</i>	9	RGBE	19801354	1980	Yes
<i>rugosum</i>	10	RGBE	19801263	1980	Yes
<i>rugosum</i>	11	RGBE	19801162	1980	Yes
<i>rugosum</i>	12	RGBE	19762730	1976	Yes
<i>rugosum</i>	13	RGBE	19762665	1976	Yes
<i>rugosum</i>	14	RGBE	19670823	1967	Yes
<i>rugosum</i>	15	RGBE	19710912	1971	Yes
<i>rushforthii</i>	1	B	V407	n/a	
<i>rushforthii</i>	2	RSF	1997/087	1997	
<i>rushforthii</i>	3	RGBE	19933195	1993	Yes
<i>ruttenii</i>	1	RBGR	19871803	1987	
<i>ruttenii</i>	2	RGBE	19880509	1988	Yes
<i>salicifolium</i>	1	B	n/a	n/a	
<i>salicifolium</i>	2	B	V615	n/a	
<i>salicifolium</i>	3	RGBE	19943015	1994	Yes
<i>santapau</i>	1	B	V309	n/a	Yes
<i>santapau</i>	2	RSF	1998/020	1998	
<i>santapau</i>	3	RGBE	19830536	1983	
<i>sarcodes</i>	1	B	V921	n/a	

<i>saxifragoides</i>		1	RGBE	19930920	1993	Yes
<i>sayeri</i>		1	RGBE	19671323	1967	Yes
<i>scabridibracteum</i>		1	B	V264	n/a	
<i>scortechinii</i>		1	RGBE	20041584	2004	Yes
<i>searleanum</i>		1	RGBE	19741176	1974	Yes
<i>seinghkuense</i>		1	RSF	n/a	n/a	
<i>seranicum</i>	<i>sparsihirtus</i>	1	RGBE	20001339	2000	Yes
<i>seranicum</i>		2	RGBE	20000648	2000	Yes
<i>sessilifolium</i>		1	B	V616	n/a	
<i>sojolense</i>		1	RGBE	20000498	2000	Yes
<i>sojolense</i>		2	RGBE	20080949	2008	Yes
<i>solitarium</i>		1	B	V606	n/a	
<i>solitarium</i>		2	RGBE	19681395	1968	Yes
<i>sororium</i>		1	B	V905	n/a	
<i>sororium</i>		2	RGBE	20021048	2002	
<i>stamineum</i>		1	RSF	1976/380	1976	
<i>stapfianum</i>		1	B	V614	n/a	
<i>stapfianum</i>		2	RGBE	19821522	1982	Yes
<i>stenophyllum</i>		1	RSF	1987/050	1987	
<i>stenophyllum</i>		2	B	V316	n/a	
<i>stenophyllum</i>		3	RSF	1985/046	1985	
<i>stenophyllum</i>	<i>angustifolium</i>	4	RGBE	19672546	1967	Yes
<i>stenophyllum</i>	<i>angustifolium</i>	5	RGBE	19792888	1979	Yes
<i>stenophyllum</i>	<i>angustifolium</i>	6	RGBE	19913768	1991	Yes
<i>stenophyllum</i>	<i>angustifolium</i>	7	RGBE	19952736	1995	Yes
<i>stenophyllum</i>	<i>stenophyllum</i>	8	RGBE	19801190	1980	Yes
<i>stevensianum</i>		1	B	V906	n/a	
<i>stevensianum</i>		2	RGBE	19943030	1994	
<i>suaveolens</i>		1	B	V273	n/a	
<i>suaveolens</i>		2	RGBE	19792885	1979	Yes
<i>sumatranum</i>		1	B	V572	n/a	
<i>sumatranum</i>		2	RGBE	20010303	2001	Yes
<i>superbum</i>		1	B	V382	n/a	Yes
<i>superbum</i>		2	B	V323	n/a	
<i>superbum</i>		3	RGBE	19930919	1993	Yes
<i>syringoideum</i>		1	RGBE	20031333	2003	
<i>taxifolium</i>		1	B	V675	n/a	
<i>taxifolium</i>		2	RSF	n/a	n/a	
<i>taxifolium</i>		3	RGBE	19922826	1992	Yes
<i>tomentosum</i>		1	RSF	n/a	n/a	
<i>trancongi</i>		1	RGBE	20022355	2002	Yes

<i>truncolum</i>		1	RGBE	20021044	2002	
<i>tuba</i>		1	B	V314	n/a	
<i>tuba</i>		2	RGBE	19830538	1983	
<i>tuhanensis</i>		1	RGBE	19952753	1995	Yes
<i>vaccinioides</i>		1	B	V723	n/a	
<i>vaccinioides</i>		2	RSF	n/a	n/a	
<i>vaccinoides</i>		3	RGBE	19872104	1987	Yes
<i>vanvuurenii</i>		1	B	V918	n/a	Yes
<i>vanvuurenii</i>		2	B	V665	n/a	
<i>verticillatum</i>		1	B	V5383	n/a	
<i>vidalii</i>	<i>vidalii</i>	1	RGBE	19972468	1997	Yes
<i>villosulum</i>		1	RGBE	19930812	1993	Yes
<i>vinicolor</i>		1	RGBE	19990504	1999	Yes
<i>viriosum</i>		1	RGBE	19951543	1995	Yes
<i>viriosum</i>		2	RGBE	19812937	1981	Yes
<i>vitis-idaea</i>		1	RGBE	19722383	1972	Yes
<i>walongense</i>		1	RSF	1998/003	1998	
<i>wentianum</i>		1	B	V916	n/a	
<i>williamsii</i>		1	B	V437	n/a	
<i>wrightianum</i>		1	B	V285	n/a	
<i>xanthopetalum</i>		1	RGBE	19991950	1991	Yes
<i>yongii</i>		1	B	V585	n/a	
<i>zoelleri</i>		1	B	V30	n/a	
<i>zoelleri</i>		2	RGBE	19550409	1955	Yes
<i>zollingeri</i>		1	RGBE	19982668	1998	
<i>zollingeri</i>		2	RGBE	20000343	2000	Yes

Supplemental Table 4.4. Leaf functional trait data for tropical *Rhododendron* species. Traits in grey not included in analyses.

Species	Individuals	Lamina area	SLA	LDMC	Toughness	Thickness	Density	Succulence	%C	%N	%P
<i>abietifolium</i>	1	1.37	48.75	401.04		0.38	0.57	0.04	49.63	0.89	0.27
<i>acrophilum</i>	2	5.31	52.46	495.45	101.50	0.44	0.49	0.02	46.98	0.57	0.12
<i>acuminatum</i>	1	19.73	30.79	498.21	90.00	0.46	0.70	0.03	53.61	0.55	0.20
<i>aequabile</i>	2	23.07	57.11	361.61	106.50	0.46	0.40	0.03	50.88	1.13	0.27
<i>alborugosum</i>	2	30.60	56.67	339.48	112.00	0.47	0.39	0.04	49.88	0.83	0.26
<i>album</i>	1	14.43	58.50	460.42	329.33	0.35	0.48	0.02	48.85	0.72	0.24
<i>alticola</i>	1	13.40	51.53	437.06	137.00	0.39	0.49	0.03	50.60	0.93	0.23
<i>anagalliflorum</i>	1	0.15	61.47	458.75		0.51	0.32	0.02	50.00	0.65	0.25
<i>apiense</i>	1	51.07	38.42	401.27	189.00	0.56	0.46	0.04	47.09	0.63	0.32
<i>apoanum</i>	2	7.02	47.28	436.57	118.50	0.49	0.44	0.03	51.04	0.73	0.28
<i>arenicolum</i>	1	6.49	53.25	399.35	134.00	0.49	0.39	0.03	52.08	0.87	0.42
<i>armitii</i>	2	23.06	66.89	365.15	89.50	0.42	0.39	0.03	48.98	0.95	0.41
<i>asperulum</i>	1	0.75	88.35	367.83		0.29	0.38	0.02	49.91	0.95	0.17
<i>atropurpureum</i>	1	3.18	46.82	364.37	248.33	0.63	0.33	0.04	50.71	0.59	0.40
<i>aurigeranum</i>	3	33.37	55.52	399.35	111.83	0.41	0.45	0.03	47.77	0.87	0.26
<i>baconii</i>	1	7.42	38.73	410.81	107.00	0.62	0.42	0.04	50.15	0.71	0.32
<i>baenitzianum</i>	2	101.04	41.19	380.48	130.00	0.59	0.42	0.04	49.95	0.78	0.18
<i>bagobonum</i>	2	0.92	80.71	321.79		0.35	0.38	0.03	45.94	0.67	0.20
<i>beyerinckianum</i>	2	11.21	57.34	402.46	113.00	0.47	0.42	0.03	50.29	0.63	0.25
<i>blackii</i>	2	27.41	46.13	422.13	252.00	0.53	0.43	0.03	52.79	0.70	0.14

<i>borneense</i>	1	0.61	80.50	377.00		0.52	0.24	0.02	49.33	0.73	0.25
<i>brassii</i>	2	10.17	58.41	382.21	193.00	0.48	0.37	0.03	50.85	1.04	0.18
<i>burttii</i>	2	2.15	53.33	388.95	352.00	0.58	0.33	0.03	48.51	0.57	0.34
<i>buxifolium</i>	1	4.64	37.97	465.37	131.00	0.54	0.48	0.03	51.16	0.73	0.29
<i>caliginis</i>	2	2.46	58.09	448.80		0.31	0.59	0.02	47.70	0.73	0.19
<i>carringtoniae</i>	2	18.48	52.20	376.18	178.00	0.49	0.41	0.03	50.27	0.63	0.27
<i>celebicum</i>	1	7.22	85.16	355.43	312.67	0.38	0.31	0.02	49.66	1.16	0.44
<i>christi</i>	3	24.30	55.78	412.09	242.11	0.48	0.38	0.03	49.88	0.90	0.23
<i>christinae</i>	1	16.07	41.11	467.25	98.00	0.50	0.48	0.03	46.41	0.65	0.29
<i>ciliilobum</i>	1	0.64	67.25	395.28		0.35	0.42	0.02	49.38	0.74	0.19
<i>cinchoniflorum</i>	1	23.50	56.97	416.75	130.00	0.41	0.43	0.02	52.49	0.73	0.19
<i>citrinum</i>	1	6.77	47.74	395.06	170.00	0.55	0.40	0.03	48.44	0.67	0.20
<i>coelorum</i>	1	0.80	65.27	370.00		0.38	0.40	0.03	49.83	0.51	0.23
<i>commonae</i>	2	6.78	85.10	321.94	124.50	0.42	0.29	0.03	49.47	1.05	0.31
<i>crassifolium</i>	2	49.59	42.25	362.28	332.00	0.60	0.41	0.04	47.33	0.67	0.21
<i>cruttwellii</i>	2	30.55	71.76	361.40	160.50	0.43	0.32	0.02	47.63	0.89	0.16
<i>culminicola</i>	2	14.58	40.47	409.38	101.00	0.60	0.43	0.04	51.49	0.69	0.17
<i>cuneifolium</i>	2	1.85	75.78	447.97		0.30	0.51	0.02	47.40	0.62	0.21
<i>curviflorum</i>	2	38.20	45.15	411.06	136.00	0.52	0.43	0.03	49.76	0.72	0.27
<i>densifolium</i>	2	0.41	70.54	526.67		0.33	0.44	0.02	48.28	0.72	0.29
<i>dielsianum</i>	2	5.26	60.16	372.59	68.00	0.42	0.39	0.03	48.73	0.69	0.08
<i>durionfolium</i>	2	42.43	48.89	490.81	107.50	0.38	0.57	0.02	50.82	0.58	0.24
<i>edanoi</i>	2	11.87	44.37	399.27	75.50	0.53	0.43	0.03	49.66	0.65	0.26
<i>emarginatum</i>	3	3.11	52.20	441.25	104.00	0.47	0.41	0.02	47.76	0.68	0.18
<i>ericoides</i>	2	0.04	67.98	407.08		0.34	0.44	0.02	49.23	0.81	0.16
<i>exuberans</i>	1	13.59	50.54	367.77	171.00	0.61	0.32	0.03	46.01	0.71	0.22
<i>fallacinum</i>	2	48.88	44.08	490.90	148.00	0.42	0.58	0.02	53.52	0.72	0.30

<i>flavoviride</i>	1	12.34	49.20	421.32	126.00	0.47	0.45	0.03	52.54	0.86	0.09
<i>gardenia</i>	2	40.91	35.16	418.64	186.25	0.63	0.46	0.04	52.67	0.48	0.34
<i>gaultheriifolium</i>	1	0.65	50.46	517.20		0.47	0.42	0.02	52.64	0.90	0.11
<i>glabriflorum</i>	1	31.18	51.27	406.85	238.33	0.51	0.38	0.03	53.12	0.54	0.18
<i>goodenoughii</i>	2	33.31	40.17	433.99	295.17	0.60	0.43	0.03	49.92	0.65	0.17
<i>gracilentum</i>	4	0.78	58.31	396.76		0.46	0.38	0.03	48.60	0.72	0.18
<i>habbema</i>	1	12.47	48.13	430.95	235.00	0.49	0.43	0.03	52.91	0.66	0.22
<i>hellwigii</i>	2	43.03	34.25	417.96	226.00	0.64	0.46	0.04	51.85	0.50	0.25
<i>herzogii</i>	2	13.33	50.69	386.46	166.50	0.49	0.41	0.03	50.32	0.65	0.28
<i>himantodes</i>	3	1.99	52.16	499.46		0.33	0.60	0.02	49.12	0.65	0.16
<i>hyacinthosmum</i>	2	25.01	41.77	474.70	231.50	0.56	0.44	0.03	53.14	0.72	0.25
<i>impositum</i>	1	19.11	52.02	385.68	95.00	0.47	0.42	0.03	46.64	0.60	0.40
<i>inconspicuum</i>	3	2.70	58.87	476.88	104.33	0.39	0.46	0.02	53.33	0.99	0.14
<i>insculptum</i>	1	3.00	63.72	360.44	103.00	0.45	0.35	0.03	45.38	0.68	0.37
<i>intranervatum</i>	1	135.54	49.12	303.01	235.00	0.47	0.44	0.05	44.95	0.48	0.24
<i>jasminiflorum</i>	4	9.39	48.65	363.39	200.25	0.60	0.36	0.04	48.64	0.69	0.35
<i>javanicum</i>	11	58.49	52.42	380.56	152.15	0.46	0.43	0.03	48.01	0.72	0.25
<i>kawakamii</i>	3	6.32	59.61	337.06	97.67	0.55	0.32	0.03	47.00	0.93	0.33
<i>kochii</i>	2	27.48	78.57	368.16	77.50	0.36	0.40	0.02	47.74	0.91	0.32
<i>konori</i>	3	47.12	46.54	410.29	221.56	0.53	0.42	0.03	48.31	0.67	0.20
<i>laetum</i>	2	27.85	89.58	341.91	83.50	0.33	0.34	0.02	48.25	0.99	0.25
<i>lagunculicarpum</i>	2	3.78	76.06	379.51	57.00	0.33	0.43	0.02	50.84	1.27	0.28
<i>lambianum</i>	1	23.14	48.18	391.83	157.00	0.56	0.37	0.03	48.24	0.96	0.37
<i>lamrialianum</i>	1	12.76	34.70	537.23	155.00	0.55	0.54	0.03	52.83	0.51	0.41
<i>lanceolatum</i>	1	11.90	66.53	419.00	61.00	0.31	0.48	0.02	47.87	0.86	0.25
<i>leptanthum</i>	2	9.43	60.23	370.90	364.00	0.54	0.31	0.03	48.11	0.83	0.21
<i>leptobrachion</i>	2	10.71	71.45	375.60	86.50	0.39	0.36	0.02	48.18	0.69	0.25

<i>leucogigas</i>	3	49.17	36.18	361.88	179.17	0.66	0.43	0.05	52.01	0.70	0.13
<i>leytense</i>	1	23.97	47.65	545.74	111.00	0.51	0.42	0.03	45.27	0.49	0.22
<i>lineare</i>	2	2.02	54.87	455.46		0.34	0.57	0.02	53.36	0.63	0.13
<i>loboense</i>	1	31.14	44.94	393.07	100.00	0.51	0.45	0.04	48.34	0.69	0.10
<i>lochiae</i>	2	25.46	51.83	374.35	120.00	0.55	0.36	0.03	48.85	0.92	0.22
<i>longiflorum</i>	2	27.58	66.69	387.12	94.50	0.37	0.42	0.02	51.74	0.80	0.13
<i>loranthiflorum</i>	1	9.94	58.53	363.76	104.00	0.49	0.35	0.03	50.32	0.74	0.20
<i>lowii</i>	4	105.46	50.95	326.53	158.58	0.46	0.45	0.04	46.50	0.86	0.29
<i>luraluense</i>	1	6.45	87.67	343.31	54.00	0.40	0.28	0.02	49.10	0.89	0.32
<i>macgregoriae</i>	3	21.64	78.98	366.11	101.44	0.35	0.38	0.02	48.77	1.02	0.17
<i>madulidii</i>	2	12.32	55.64	375.74	87.00	0.47	0.39	0.03	49.55	0.91	0.28
<i>maius</i>	2	24.66	59.76	370.23	82.50	0.40	0.43	0.03	51.17	1.02	0.16
<i>malayanum</i>	3	13.53	45.98	460.94	168.00	0.40	0.57	0.03	48.61	0.71	0.25
<i>maxwellii</i>	2	26.65	39.81	385.65	121.50	0.56	0.45	0.04	50.06	0.62	0.26
<i>meijeri</i>	1	4.16	44.38	343.07	220.00	0.63	0.36	0.04	52.61	0.78	0.39
<i>meliphogidum</i>	1	3.97	69.47	395.88		0.43	0.34	0.02	48.40	0.60	0.19
<i>mendumiae</i>	2	9.43	54.04	453.25	95.00	0.41	0.45	0.02	49.97	0.84	0.30
<i>micromalayanum</i>	1	3.83	41.83	531.34		0.44	0.53	0.02	52.93	0.65	0.18
<i>mindanaense</i>	2	24.25	80.80	306.51	62.50	0.40	0.32	0.03	49.54	1.16	0.15
<i>monodii</i>	2	0.93	67.80	448.55		0.32	0.51	0.02	48.40	0.59	0.18
<i>multicolor</i>	2	6.12	112.20	278.57	68.00	0.27	0.37	0.02	45.39	0.85	0.22
<i>multinervium</i>	1	48.70	40.47	427.11	137.00	0.53	0.46	0.03	47.63	0.47	0.13
<i>nanophyton</i>	1	0.22	77.90	431.54		0.48	0.27	0.02	51.05	1.07	0.23
<i>nervulosum</i>	1	10.97	45.37	362.53	243.00	0.65	0.34	0.04	46.49	0.68	0.22
<i>niewenhuisii</i>	2	2.71	71.62	448.80		0.18	0.84	0.02	48.30	0.77	0.20
<i>niveoflorum</i>	1	22.10	35.03	380.77	195.00	0.90	0.33	0.05	51.21	0.53	0.33
<i>orbiculatum</i>	1	10.55	45.85	340.96	104.00	0.72	0.30	0.04	47.47	0.61	0.21

<i>pauciflorum</i>	1	3.37	70.92	354.71	103.00	0.51	0.28	0.03	47.97	0.69	0.52
<i>perakense</i>	1	2.07	76.50	329.28	204.00	0.30	0.44	0.03	49.85	0.85	0.31
<i>phaeochitum</i>	1	38.42	62.57	396.82	468.00	0.42	0.38	0.02	51.61	0.69	0.11
<i>pleianthum</i>	1	39.25	44.50	402.85	244.00	0.52	0.44	0.03	51.53	0.71	0.16
<i>polyanthemum</i>	2	56.40	29.75	418.05	364.67	0.89	0.38	0.05	48.97	0.64	0.07
<i>praetervisum</i>	1	11.58	42.56	417.00	167.00	0.53	0.45	0.03	50.81	0.68	0.21
<i>prainianum</i>	1	3.49	47.31	441.91		0.34	0.63	0.03	46.97	0.85	0.23
<i>pudorinum</i>	1	4.52	80.67	292.56	119.00	0.43	0.29	0.03	50.51	0.91	0.18
<i>pulleanum</i>	1	0.26	73.45	445.00		0.34	0.40	0.02	50.16	0.79	0.36
<i>quadrasianum</i>	6	1.61	92.62	426.51		0.24	0.51	0.02	50.11	0.84	0.23
<i>radians</i>	3	20.90	59.83	386.08	184.89	0.45	0.40	0.03	47.95	0.80	0.30
<i>rappardii</i>	2	24.24	40.35	391.56	111.25	0.62	0.40	0.04	51.19	0.50	0.26
<i>rarilepidotum</i>	2	16.44	64.52	334.87	200.50	0.49	0.33	0.03	48.19	0.99	0.16
<i>rarum</i>	2	3.25	69.65	347.06	167.00	0.40	0.37	0.03	48.15	0.83	0.20
<i>renschianum</i>	2	8.12	63.86	381.86	72.50	0.46	0.38	0.03	49.26	0.63	0.08
<i>retivenium</i>	2	34.72	43.22	414.61	123.00	0.46	0.50	0.03	45.27	0.70	0.21
<i>retusum</i>	2	4.97	69.91	347.47	184.33	0.49	0.30	0.03	49.31	1.17	0.26
<i>reynosoi</i>	1	6.86	67.00	382.71	63.00	0.38	0.40	0.02	47.50	0.90	0.37
<i>rhodoleucum</i>	2	19.15	52.53	415.55	117.00	0.45	0.44	0.03	50.39	0.78	0.33
<i>rhodopus</i>	2	27.94	70.94	383.65	183.00	0.34	0.42	0.02	49.30	0.90	0.38
<i>robinsonii</i>	1	36.36	67.15	368.64	142.00	0.41	0.38	0.03	46.73	1.10	0.63
<i>roseiflorum</i>	1	12.22	45.37	418.35	99.00	0.53	0.43	0.03	49.89	0.76	0.38
<i>rosendahlii</i>	1	17.75	65.21	404.74	79.00	0.37	0.41	0.02	49.10	0.59	0.26
<i>rousei</i>	3	8.35	52.28	423.53	91.00	0.54	0.41	0.03	51.47	0.84	0.41
<i>rubellum</i>	1	15.35	39.24	482.62	200.00	0.52	0.48	0.03	53.98	0.94	0.24
<i>rubineiflorum</i>	1	0.37	80.08	335.71		0.41	0.31	0.03	47.08	0.94	0.15
<i>rugosum</i>	15	30.60	37.27	420.13	122.32	0.53	0.52	0.04	51.49	0.63	0.24

<i>rushforthii</i>	3	17.15	63.04	360.36	138.00	0.49	0.32	0.03	48.47	1.14	0.22
<i>ruttenii</i>	2	15.01	75.28	329.40	98.50	0.43	0.32	0.03	51.53	1.07	0.26
<i>salicifolium</i>	3	9.89	69.71	430.93	145.83	0.25	0.65	0.02	45.55	0.70	0.23
<i>santapaui</i>	3	2.82	45.63	334.81	119.17	0.71	0.31	0.04	45.33	0.70	0.25
<i>saxifragoides</i>	1	1.81	45.30	361.74		0.61	0.37	0.04	49.38	0.65	0.12
<i>sayeri</i>	1	17.54	43.85	436.66	97.00	0.48	0.49	0.03	52.70	0.72	0.32
<i>scabridibracteum</i>	1	47.45	51.75	369.78	242.00	0.50	0.39	0.03	49.45	0.68	0.34
<i>scortechinii</i>	1	7.17	47.43	376.31	147.00	0.55	0.38	0.03	52.46	0.68	0.42
<i>searleanum</i>	1	60.46	30.03	472.26	405.00	0.71	0.46	0.04	51.89	0.41	0.18
<i>seranicum</i>	2	47.84	43.07	404.38	193.75	0.50	0.47	0.03	48.56	0.51	0.10
<i>sessilifolium</i>	1	38.44	70.55	380.18	153.00	0.37	0.38	0.02	47.06	0.82	0.19
<i>sojolense</i>	2	31.93	43.33	434.07	89.75	0.45	0.52	0.03	49.51	0.63	0.13
<i>solitarium</i>	2	44.00	64.56	392.33	72.50	0.32	0.52	0.02	54.10	0.80	0.14
<i>sororium</i>	2	4.70	55.67	418.72	84.50	0.42	0.46	0.03	48.15	0.65	0.39
<i>stapfianum</i>	2	4.11	59.26	397.44	61.00	0.29	0.63	0.03	50.50	0.59	0.17
<i>stenophyllum</i>	8	1.62	59.75	391.66		0.55	0.32	0.03	46.05	0.84	0.20
<i>stevensianum</i>	2	8.78	54.14	400.77	103.00	0.47	0.41	0.03	48.39	0.60	0.27
<i>suaveolens</i>	2	36.92	65.84	314.07	111.00	0.51	0.32	0.03	50.43	0.57	0.11
<i>sumatranum</i>	2	14.17	62.50	373.82	244.00	0.42	0.39	0.03	51.38	0.87	0.19
<i>superbum</i>	3	45.78	47.63	425.82	153.72	0.50	0.42	0.03	50.28	0.69	0.31
<i>syringoideum</i>	1	27.57	41.08	421.77	199.00	0.60	0.41	0.03	50.29	0.55	0.31
<i>taxifolium</i>	3	1.09	68.70	477.53		0.31	0.52	0.02	50.25	0.83	0.28
<i>trancongi</i>	1	11.36	41.06	407.24	159.00	0.67	0.37	0.04	48.32	0.59	0.11
<i>truncolum</i>	1	9.74	30.77	382.97		0.84	0.39	0.06	47.84	0.48	0.17
<i>tuba</i>	2	22.39	50.64	415.98	152.50	0.45	0.45	0.03	50.56	0.94	0.40
<i>tuhanensis</i>	1	1.12	31.75	431.97		0.88	0.36	0.05	50.05	0.61	0.20
<i>vaccinioides</i>	3	0.67	84.93	419.02		0.37	0.36	0.02	49.61	0.72	0.21

<i>vanvuureonii</i>	2	15.72	61.45	399.28	92.00	0.41	0.40	0.02	48.17	0.72	0.16
<i>verticillatum</i>	1	24.74	47.26	444.42	119.00	0.44	0.48	0.03	50.03	0.51	0.11
<i>vidalii</i>	1	5.18	50.77	442.08	77.00	0.49	0.41	0.03	49.44	0.63	0.14
<i>villosulum</i>	1	13.50	53.08	394.86	82.00	0.51	0.37	0.03	49.63	0.88	0.27
<i>vinicolor</i>	1	4.21	49.83	523.95		0.46	0.52	0.03	49.72	0.58	0.16
<i>viriosum</i>	2	28.56	47.20	377.38	116.00	0.61	0.35	0.04	47.13	0.87	0.25
<i>vitis-idaea</i>	1	4.75	38.93	399.51		0.67	0.38	0.04	49.92	0.64	0.13
<i>wentianum</i>	1	5.47	62.87	406.70	79.00	0.40	0.39	0.02	49.14	0.72	0.13
<i>williamsii</i>	1	38.43	65.55	368.64	147.00	0.45	0.35	0.03	48.68	1.04	0.27
<i>wrightianum</i>	1	3.27	49.52	388.89	120.00	0.53	0.38	0.03	49.78	1.05	0.19
<i>xanthopetalum</i>	1	32.52	41.90	426.75	117.00	0.55	0.44	0.03	47.13	0.61	0.11
<i>yongii</i>	1	33.16	52.55	331.70	478.67	0.62	0.32	0.04	49.13	0.89	0.48
<i>zoelleri</i>	2	40.93	68.08	363.04	163.17	0.35	0.42	0.03	47.87	1.14	0.21
<i>zollingeri</i>	2	6.65	69.08	367.51	49.38	0.35	0.41	0.03	49.93	0.93	0.13

Supplemental Table 4.5. Notes on *Rhododendron* taxonomy (based on classification by Argent, 2006), growth form, and soil association

Section	Subsection	Species	Growth Form	Soil Association
Albovireya		<i>aequabile</i>	terrestrial	
Albovireya		<i>album</i>	epiphyte	
Albovireya		<i>arenicolum</i>	terrestrial	
Albovireya		<i>lagunculicarpum</i>	epiphyte	
Albovireya		<i>pudorinum</i>	terrestrial	
Albovireya		<i>zollingeri</i>	terrestrial	
Discovireya		<i>borneense</i>	terrestrial	ultramafic
Discovireya		<i>ciliilobum</i>	terrestrial	
Discovireya		<i>cuneifolium</i>	terrestrial	ultramafic
Discovireya		<i>ericoides</i>	terrestrial	
Discovireya		<i>gaultheriifolium</i>	terrestrial	
Discovireya		<i>meliphogidum</i>	terrestrial	
Discovireya		<i>monodii</i>	terrestrial	
Discovireya		<i>nanophyton</i>	terrestrial	
Discovireya		<i>perakense</i>	epiphyte	
Discovireya		<i>pulleanum</i>	epiphyte	
Discovireya		<i>quadrasianum</i>	epiphyte	
Discovireya		<i>retusum</i>	terrestrial	
Discovireya		<i>scortechinii</i>	epiphyte	
Hadranthe		<i>beyerinckianum</i>	epiphyte	
Hadranthe		<i>caliginis</i>	terrestrial	
Hadranthe		<i>dielsianum</i>	epiphyte	
Hadranthe		<i>gardenia</i>	epiphyte	
Hadranthe		<i>hellwigii</i>	epiphyte	
Hadranthe		<i>hyacinthosmum</i>	terrestrial	
Hadranthe		<i>konori</i>	terrestrial	
Hadranthe		<i>leptanthum</i>	epiphyte	
Hadranthe		<i>phaeochitum</i>	terrestrial	
Hadranthe		<i>prainianum</i>	epiphyte	
Hadranthe		<i>rappardii</i>	epiphyte	
Hadranthe		<i>rarum</i>	epiphyte	
Hadranthe		<i>rubellum</i>	terrestrial	
Hadranthe		<i>solitarium</i>	terrestrial	ultramafic
Hadranthe		<i>superbum</i>	epiphyte	
Hadranthe		<i>truncolum</i>	terrestrial	

Malayovireya		<i>acuminatum</i>	terrestrial	ultramafic
Malayovireya		<i>apoanum</i>	epiphyte	
Malayovireya		<i>durionfolium</i>	epiphyte	
Malayovireya		<i>fallacinum</i>	terrestrial	ultramafic
Malayovireya		<i>himantodes</i>	epiphyte	
Malayovireya		<i>lamrialianum</i>	epiphyte	
Malayovireya		<i>lineare</i>	epiphyte	
Malayovireya		<i>malayanum</i>	epiphyte	ultramafic
Malayovireya		<i>micromalayanum</i>	terrestrial	
Malayovireya		<i>vinicolor</i>	epiphyte	
Pseudovireya		<i>asperulum</i>	epiphyte	
Pseudovireya		<i>densifolium</i>	terrestrial	
Pseudovireya		<i>emarginatum</i>	terrestrial	
Pseudovireya		<i>insculptum</i>	epiphyte	
Pseudovireya		<i>kawakamii</i>	epiphyte	
Pseudovireya		<i>rushforthii</i>	epiphyte	
Pseudovireya		<i>santapau</i>	epiphyte	
Pseudovireya		<i>sororium</i>	epiphyte	
Pseudovireya		<i>trancongii</i>	epiphyte	
Pseudovireya		<i>vaccinioides</i>	epiphyte	
Schistanthe	Euvireya	<i>alticola</i>	terrestrial	
Schistanthe	Euvireya	<i>apiense</i>	terrestrial	
Schistanthe	Euvireya	<i>aurigeranum</i>	terrestrial	
Schistanthe	Euvireya	<i>baconii</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>baenitzianum</i>	terrestrial	
Schistanthe	Euvireya	<i>blackii</i>	epiphyte	
Schistanthe	Euvireya	<i>celebicum</i>	epiphyte	
Schistanthe	Euvireya	<i>christi</i>	terrestrial	
Schistanthe	Euvireya	<i>christinae</i>	terrestrial	
Schistanthe	Euvireya	<i>crassifolium</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>culminicola</i>	terrestrial	
Schistanthe	Euvireya	<i>curviflorum</i>	epiphyte	
Schistanthe	Euvireya	<i>exuberans</i>	epiphyte	
Schistanthe	Euvireya	<i>glabriflorum</i>	terrestrial	
Schistanthe	Euvireya	<i>impositum</i>	terrestrial	
Schistanthe	Euvireya	<i>intranervatum</i>	terrestrial	
Schistanthe	Euvireya	<i>javanicum</i>	terrestrial	ultramafic
Schistanthe	Euvireya	<i>kochii</i>	epiphyte	
Schistanthe	Euvireya	<i>laetum</i>	terrestrial	
Schistanthe	Euvireya	<i>lanceolatum</i>	epiphyte	
Schistanthe	Euvireya	<i>leptobrachion</i>	epiphyte	

Schistanthe	Euvireya	<i>leucogigas</i>	epiphyte	
Schistanthe	Euvireya	<i>leytense</i>	epiphyte	
Schistanthe	Euvireya	<i>loboense</i>	terrestrial	
Schistanthe	Euvireya	<i>lochiae</i>	epiphyte	
Schistanthe	Euvireya	<i>longiflorum</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>lowii</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>luraluense</i>	epiphyte	
Schistanthe	Euvireya	<i>macgregoriae</i>	terrestrial	
Schistanthe	Euvireya	<i>madulidii</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>maxwellii</i>	terrestrial	ultramafic
Schistanthe	Euvireya	<i>mendumiae</i>	terrestrial	
Schistanthe	Euvireya	<i>mindanaense</i>	terrestrial	
Schistanthe	Euvireya	<i>nervulosum</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>orbiculatum</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>polyanthemum</i>	epiphyte	
Schistanthe	Euvireya	<i>praetervisum</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>rarilepidotum</i>	epiphyte	
Schistanthe	Euvireya	<i>renschianum</i>	terrestrial	
Schistanthe	Euvireya	<i>retivenium</i>	terrestrial	ultramafic
Schistanthe	Euvireya	<i>reynosoi</i>	terrestrial	
Schistanthe	Euvireya	<i>rhodopus</i>	terrestrial	
Schistanthe	Euvireya	<i>robinsonii</i>	epiphyte	
Schistanthe	Euvireya	<i>rosendahlia</i>	epiphyte	
Schistanthe	Euvireya	<i>rugosum</i>	epiphyte	ultramafic
Schistanthe	Euvireya	<i>salicifolium</i>	terrestrial	
Schistanthe	Euvireya	<i>sayeri</i>	terrestrial	
Schistanthe	Euvireya	<i>scabridibracteum</i>	epiphyte	
Schistanthe	Euvireya	<i>seranicum</i>	terrestrial	
Schistanthe	Euvireya	<i>sessilifolium</i>	terrestrial	
Schistanthe	Euvireya	<i>sojolense</i>	epiphyte	
Schistanthe	Euvireya	<i>stenophyllum</i>	terrestrial	ultramafic
Schistanthe	Euvireya	<i>sumatranum</i>	terrestrial	
Schistanthe	Euvireya	<i>vanvuurenii</i>	terrestrial	
Schistanthe	Euvireya	<i>verticillatum</i>	epiphyte	
Schistanthe	Euvireya	<i>villosulum</i>	epiphyte	
Schistanthe	Euvireya	<i>wentianum</i>	epiphyte	
Schistanthe	Euvireya	<i>williamsii</i>	terrestrial	
Schistanthe	Euvireya	<i>xanthopetalum</i>	epiphyte	
Schistanthe	Euvireya	<i>yongii</i>	epiphyte	
Schistanthe	Euvireya	<i>zoelleri</i>	epiphyte	
Schistanthe	Linnaeopsis	<i>anagalliflorum</i>	epiphyte	

Schistanthe	Linnaeopsis	<i>coelorum</i>	terrestrial	
Schistanthe	Linnaeopsis	<i>gracilentum</i>	epiphyte	
Schistanthe	Linnaeopsis	<i>rubineiflorum</i>	epiphyte	
Schistanthe	Malesia	<i>abietifolium</i>	terrestrial	
Schistanthe	Malesia	<i>acrophilum</i>	epiphyte	
Schistanthe	Malesia	<i>atropurpureum</i>	terrestrial	
Schistanthe	Malesia	<i>bagobonum</i>	epiphyte	
Schistanthe	Malesia	<i>brassii</i>	epiphyte	
Schistanthe	Malesia	<i>burtii</i>	terrestrial	
Schistanthe	Malesia	<i>buxifolium</i>	terrestrial	
Schistanthe	Malesia	<i>citrinum</i>	terrestrial	
Schistanthe	Malesia	<i>commonae</i>	epiphyte	
Schistanthe	Malesia	<i>flavoviride</i>	terrestrial	
Schistanthe	Malesia	<i>inconspicuum</i>	epiphyte	
Schistanthe	Malesia	<i>meijeri</i>	epiphyte	ultramafic
Schistanthe	Malesia	<i>multicolor</i>	epiphyte	
Schistanthe	Malesia	<i>niewenhuisii</i>	epiphyte	
Schistanthe	Malesia	<i>pauciflorum</i>	epiphyte	
Schistanthe	Malesia	<i>rousei</i>	terrestrial	ultramafic
Schistanthe	Malesia	<i>stevensianum</i>	epiphyte	
Schistanthe	Malesia	<i>taxifolium</i>	epiphyte	
Schistanthe	Malesia	<i>tuhanensis</i>	terrestrial	ultramafic
Schistanthe	Malesia	<i>vidalii</i>	epiphyte	
Schistanthe	Malesia	<i>viriosum</i>	epiphyte	
Schistanthe	Malesia	<i>vitis-idaea</i>	epiphyte	
Schistanthe	Malesia	<i>wrightianum</i>	epiphyte	
Schistanthe	Saxifragoidea	<i>saxifragoides</i>	terrestrial	
Schistanthe	Solenovireya	<i>alborugosum</i>	terrestrial	
Schistanthe	Solenovireya	<i>armitii</i>	terrestrial	
Schistanthe	Solenovireya	<i>carringtoniae</i>	terrestrial	
Schistanthe	Solenovireya	<i>cruttwellii</i>	terrestrial	
Schistanthe	Solenovireya	<i>edanoi</i>	epiphyte	
Schistanthe	Solenovireya	<i>goodenoughii</i>	epiphyte	
Schistanthe	Solenovireya	<i>jasminiflorum</i>	epiphyte	
Schistanthe	Solenovireya	<i>lambianum</i>	epiphyte	
Schistanthe	Solenovireya	<i>loranthiflorum</i>	terrestrial	
Schistanthe	Solenovireya	<i>maius</i>	epiphyte	
Schistanthe	Solenovireya	<i>multinervium</i>	epiphyte	
Schistanthe	Solenovireya	<i>niveoflorum</i>	epiphyte	ultramafic
Schistanthe	Solenovireya	<i>pleianthum</i>	epiphyte	
Schistanthe	Solenovireya	<i>radians</i>	terrestrial	

Schistanthe	Solenovireya	<i>rhodoleucum</i>	terrestrial	
Schistanthe	Solenovireya	<i>roseiflorum</i>	terrestrial	
Schistanthe	Solenovireya	<i>ruttenii</i>	terrestrial	
Schistanthe	Solenovireya	<i>stapfianum</i>	epiphyte	ultramafic
Schistanthe	Solenovireya	<i>suaveolens</i>	epiphyte	ultramafic
Schistanthe	Solenovireya	<i>syringoideum</i>	epiphyte	
Schistanthe	Solenovireya	<i>tuba</i>	terrestrial	
Siphonovireya		<i>cinchoniflorum</i>	epiphyte	
Siphonovireya		<i>habbema</i>	terrestrial	
Siphonovireya		<i>herzogii</i>	epiphyte	
Siphonovireya		<i>searleanum</i>	terrestrial	

Supplemental 4.6. Meta-analysis bibliography of tropical woody plant traits.

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Supplemental 4.7. Herbarium list for records used throughout dissertation.

Global Biodiversity Information Faculty list of herbariums that provided records for Chapters 1,2,3. GBIF.org (20 December 2017) GBIF Occurrence Download
<https://doi.org/10.15468/dl.jgphp2>

Query information available at <https://www.gbif.org/occurrence/download/0000506-171219132708484#datasets>

A global database for the distributions of crop wild relatives
 Actualización de las bases de datos de colecciones, especies en peligro de extinción, colecta y propagación de germoplasma
 Algae (S)
 Algae herbarium, NTNU University Museum
 Allan Herbarium (CHR)
 Australia's Virtual Herbarium
 Base de datos para la xiloteca del Instituto de Biología de la UNAM
 Bernice P. Bishop Museum
 Bioersivity Collecting Mission Database
 Botanical Research Intitute of Texas
 Botany (UPS)
 Botany Division, Yale Peabody Museum
 BOTUw - Xiloteca "Profra. Dra. Maria Aparecida Mourão Brasil"
 Bridel Herbar
 Bryophyte herbarium, Göttingen (GOET)
 Bryophyte herbarium, NTNU University Museum
 Canadian Museum of Nature Herbarium
 CAS Botany (BOT)
 Catálogo electrónico de especímenes depositados en el Herbario de la Universidad de Texas en Austin, Fase IV
 CeDoc de Biodiversitat Vegetal: BCN-Phycophyta
 Colección de plantas vasculares del herbario de la Universitat de València (VAL).
 Computarización de la xiloteca Dr. Faustino Miranda del Instituto de Ecología, AC CONN
 CSIC-Real Jardín Botánico-Colección de Hepáticas (MA-Hepat)
 CSIC-Real Jardín Botánico-Colección de Hongos Histórica (MA-Funhist)
 CSIC-Real Jardín Botánico-Colección de Musgos (MA-Musci)
 CSIC-Real Jardín Botánico-Colección de Plantas Vasculares (MA)
 DAO Herbarium Type Specimens
 DAV UC Davis Center for Plant Diversity
 DBG Kathryn Kalmbach Herbarium
 Desmidiaceae Engels
 DNA and Tissue Bank of the Natural History Museum of Denmark
 DUKE Bryophyte Collection
 Estonian Museum of Natural History

EURISCO, The European Genetic Resources Search Catalogue
 Fairchild Tropical Botanic Garden Virtual Herbarium Darwin Core format
 Field Museum of Natural History (Botany) Bryophyte Collection
 Field Museum of Natural History (Botany) Pteridophyte Collection
 Field Museum of Natural History (Botany) Seed Plant Collection
 Flora of Japan Specimen Database
 Harvard University Herbaria
 Herbaria of the University and ETH Zürich
 Herbario de la Universidad de Sevilla
 Herbario de la Universidad de Sevilla, SEV-Historico
 Herbario de Plantas Vasculares de la Universidad de Salamanca: SALA
 Herbarium Berolinense
 Herbarium Erlangense
 Herbarium Hamburgense
 Herbarium of Namur
 Herbarium Senckenbergianum (FR)
 Herbarium Senckenbergianum (GLM) - Lichenes
 Herbarium specimens of Jardins botaniques and Conservatoire Botanique of Nancy (NCY)
 Herbarium Specimens of Museum of Nature and Human Activities, Hyogo Prefecture, Japan
 Herbarium specimens of Société des Sciences Naturelles et Mathématiques de Cherbourg (CHE)
 Herbarium specimens of Université de Montpellier 2, Institut de Botanique (MPU))
 Herbarium WRSL, Main Collection
 HUEFS - Herbario da Universidade Estadual de Feira de Santana
 Institut Botanic de Barcelona, BC
 Instituto de Botánica Darwinion
 International Barcode of Life project (iBOL)
 Invertebrates Collection of the Swedish Museum of Natural History
 La colección briológica del Herbario Nacional (MEXU). Actualización 2000
 Los musgos de México
 Lund Botanical Museum (LD)
 Marie-Victorin Herbarium (MT) - Bryophytes
 McGill University Herbarium Database
 MEXU/Colección de Briofitas
 Moscow University Herbarium (MW)
 Mosses (S)
 MPM Milwaukee Public Museum Herbarium
 Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). Cryptogamic National Collection (BAc)
 Natural History Museum (London) Collection Specimens
 Natural History Museum, Vienna - Herbarium W
 Naturalis Biodiversity Center (NL) - Botany
 Naturalis Biodiversity Center (NL) - Mollusca
 Naturalis Biodiversity Center (NL) - Museum collection digitized at storage unit level

New Zealand Virtual Herbarium
NMNH Extant Specimen Records
Phanerogamic Botanical Collections (S)
Plant specimens deposited in Osaka Museum of Natural History, Japan.
PlantBank Records
Propuesta para sistematizar la colección palinológica de polen reciente y fósil del IGLUNAM
R - Herbário do Museu Nacional
R. L. McGregor Herbarium Vascular Plants Collection
RB - Rio de Janeiro Botanical Garden Herbarium Collection
Registros biológicos del género Piper en el herbario HUA
Royal Botanic Garden Edinburgh Herbarium (E)
Royal Botanic Garden Edinburgh Living Plant Collections (E)
Royal Botanic Gardens, Kew - Herbarium Specimens
Sabah Parks
Sistemática del género Polianthes L (Agavaceae)
Staatliches Museum für Naturkunde Stuttgart, Herbarium
SysTax - Herbaria
SysTax - Zoological Collections
Tallinn Botanic Garden
The AAU Herbarium Database
The Bergius Herbarium
The cryptogamy collection (PC) at the Herbarium of the Muséum national d'Histoire Naturelle (MNHN - Paris)
The New York Botanical Garden Herbarium (NY)
The vascular plants collection (P) at the Herbarium of the Muséum national d'Histoire Naturelle (MNHN - Paris)
Tropicos Specimen Data
Type herbarium, Göttingen (GOET)
University of British Columbia Herbarium (UBC) - Algae Collection
University of British Columbia Herbarium (UBC) - Bryophytes Collection
University of British Columbia Herbarium (UBC) - Vascular Plant Collection
University of California Museum of Paleontology
University of Florida Herbarium (FLAS)
University of Ghana - Ghana Herbarium
University of Graz, Institute of Plant Sciences - Herbarium GZU
University of South Florida Herbarium (USF)
University of Vienna, Institute for Botany - Herbarium WU
UPCB - Herbário do Departamento de Botânica
UTEP Plants (Arctos)
UTEX Culture Collection of Algae at The University of Texas Living Algae Holdings
Vascular Plant Collection - University of Washington Herbarium (WTU)
Vascular Plant Herbarium, Oslo (O)

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Thank you for taking the time to read my dissertation.