RESEARCH ARTICLE

Environmental stress influences Malesian Lamiaceae distributions

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Abstract

Dual effects of spatial distance and environment shape archipelagic floras. In Malesia, there are multiple environmental stressors associated with increasing uplands, drought, and metal-rich ultramafic soils. Here, we examine the contrasting impacts of multifactorial environmental stress and spatial distance upon Lamiaceae species distributions. We used a phylogenetic generalized mixed effects model of species occurrence across Malesia's taxonomic database working group areas from Peninsular Malaysia to New Guinea. Predictor variables were environmental stress, spatial distance between areas and two trait principal component axes responsible for increasing fruit and leaf size and a negative correlation between flower size and plant height. We found that Lamiaceae species with smaller fruits and leaves are more likely to tolerate environmental stress and become widely distributed across megadiverse Malesian islands. How global species distribution and diversification are shaped by multifactorial environmental stress requires further examination.

KEYWORDS
biogeography, dispersal, macroecology, Malesia, mints, stress tolerance, Wallacea

TAXONOMY CLASSIFICATION
Biogeography

1 | INTRODUCTION

The relative influence of either dispersal distances or the environment upon the occurrence of species in communities across large scales is unclear (Bemmels et al., 2018; Carvajal-Endara et al., 2017; Dexter et al., 2017; Ibanez et al., 2018). The geographic or spatial distance between sites consistently shapes the composition of communities (Wallace, 1869). In general, the shorter the dispersal distance between communities the more species they share (Condit et al., 2002; Nekola and White, 1999). Similar environments are also more likely to share species (Weigelt et al., 2015; Whittaker, 1960). However, in archipelagos, examples of species distributions shaped more by the environment than spatial distance between islands are less frequent (König et al., 2021; Carvajal-Endara et al., 2017; Giarla et al., 2018; Ng et al., 2017). A global analysis of oceanic islands found that altitude can significantly shape which plants are present (König et al., 2021). In the Galapagos, climate was found to be the main driver of island floras (Carvajal-Endara et al., 2017). Malesia, the phytogeographical region stretching from Peninsular Malaysia to New Guinea, offers another opportunity to compare the effects of dispersal distances and the environment upon archipelagic species distributions. The region houses more diversity per unit area than any other tropical region but has little coverage in studies of island plant biogeography (Raven et al., 2020; Trethowan, 2021).

Here, we examine whether multifactorial environmental stress influences Malesian plant distributions. A recent definition states that stressors are "any deviation in the value of an external environmental ... variable from the range of values that is favorable for ... an entity" (Love and Wagner, 2022). Here our "entity" is plants, and the "deviation" in question are differences from a seasonal wet tropical lowlands either with altitude, drought, or metal-rich ultramafic soils. The "favorable" lowland wet tropics enable plant communities to achieve both high biomass and their greatest levels of productivity (Cleveland et al., 2011; Shenkin et al., 2019). Crucially, this simple definition can be applied to large-scale studies. This differs from the definition used in fine-scale studies of populations that focuses upon differences from optimum conditions in stressful environments (Love and Wagner, 2022; MacLean et al., 2013), an approach that is less tractable across large scales and many taxa (McGill, 2019). The three stressors focused upon here all have documented examples of how they damage plant function (Zandalinas et al., 2021). First, drought causes hydraulic failure, carbon starvation, and increased pathogen attack and herbivory (Anderegg et al., 2015; Anderegg et al., 2012; Choat et al., 2018; Fensham et al., 2009; McDowell et al., 2008; Powers et al., 2020). Second, ultramafic soils with toxic high metal content damage enzymes, DNA, and cell membranes (Küpper and Andresen, 2016; Singh et al., 2013). Ultramafic soils also have low P, K, and Ca – all key nutrients for plant growth (Proctor, 2003). Likewise, altitude poses difficulties through reductions in temperature and soil fertility (Asner et al., 2014; Grubb, 1977). In Malesia, we can compare the effects of these stressors and dispersal distances between islands upon species distributions (Brambach et al., 2020; Joyce et al., 2020b; Kooyman et al., 2019; Trethowan, 2021).

Traits should influence how plants overcome dispersal distances and environmental stress (Crayn et al., 2015; Grime, 1977; Ottaviani et al., 2020; Schrader et al., 2021; van Steenis, 1962; Yap et al., 2018). There has been evidence from island systems that traits may vary consistently dependent upon the traits of close relatives on the mainland. Known as the "island rule"; traits of insular species with large relatives on the mainland show lower trait values, whereas species with small mainland relatives show increases (Biddick et al., 2019). These changes depend upon the trait in question but also upon the environmental conditions of islands (Biddick et al., 2019; García-Verdugo et al., 2019). By focusing upon the environmental drivers of species traits, we can hypothesize how traits influence both inter-island dispersal and toleration of environmental stress. Leaf size and height in tropical ecosystems generally declines when species are better adapted toward stressful environments (Fajardo et al., 2019; Wright et al., 2017). Smaller leaves are less at risk of extreme water loss via transpiration (Wright et al., 2017) and shorter species have smaller conduit size that reduces chance of embolism-linked death (Olson et al., 2018). Fruit size likely follows a similar pattern whereby low-productivity high-stress environments limit the production of large, high-energy cost fruit (McConkey et al., 2022; Moles et al., 2007). Smaller fruit, however, could also promote dispersal because they can be consumed by both small and large frugivores meaning dispersal is possible via a greater number

of agents (Chen and Moles, 2015; Green et al., 2022). Smaller flowers may be advantageous for drought stress tolerance because they lose less water via transpiration (Galen, 1999). Alternatively, because small flowers are more likely to be resource cheap and short-lived than larger flowers, they could promote dispersal by enabling fast reproduction in newly occupied habitat (Roddy et al., 2021). Small flowers can also be high cost and therefore long-lived, attracting a greater range of pollinators, increasing the chance of successful pollination in a new area (Roddy et al., 2021). Some traits, therefore, could support both the tolerance of environmental stress and long-distance dispersal. To address this, we compare how these traits improve the chances of overcoming either stress or the distances between islands. The results will help determine how these traits shape plant distributions at large scales.

The Lamiaceae (mint family) is ideal for studying the drivers of species distributions in Malesia: there are 281 native species, widely distributed across the region and found in almost all vegetation types; plants vary from weedy pioneers to species restricted to mature forest. The family also has substantial variation in stature from herbs to large trees. Crucially, recent floristic work by Bramley et al. (2019) enables accurate species identification, ensuring species distributions and trait data are reliable. Using a dataset built from the description data in Bramley et al. (2019), we examine how traits, dispersal distances, and environmental stress interact to shape Lamiaceae species distribution in Malesia.

2 | MATERIALS AND METHODS

2.1 | Study area

Malesia (10° S - 19° N, 94° E - 151° E) is the region spanning the countries of Malaysia, the Philippines, Indonesia, Timor Leste, and Papua New Guinea. Other than mainland Peninsular Malaysia, the region consists of islands separated by seas. Climate varies from the wet tropics to drought-prone seasonally dry tropics. Altitude shapes habitats from mangroves at sea level to alpine mountain peaks. The region is also home to the tropics' largest area of ultramafic soil/rock which outcrops across most islands (Galey et al., 2017; Garnica-Díaz et al., 2022).

2.2 | Malesian Lamiaceae traits

The dataset (Table S1) consists of 222 species in 38 genera. These are all the native species with recorded maximum height, leaf length, leaf width, fruit size, calyx length, and corolla length in Flora Malesiana (Bramley et al., 2019). The 59 native species not analyzed lacked one or more of these recorded measurements. Midpoint leaf length and width (maximum plus minimum values divided by two) are used here alongside maximum values for other traits, because maximum values were often the only measurement recorded in the description. Log-transformed and scaled (z-scores)

species traits were reduced to two principal component (PC) axes via singular value decomposition. The two axes were responsible for 73% variation in traits amongst 222 Lamiaceae species in Malesia (Figure S1). Principal component loadings showed that the first axis corresponds to increasing leaf length (PC axis loading = 0.51), width (PC axis loading = 0.5), and fruit size (PC axis loading = 0.45) and the second a negative correlation between flower size (Calyx length PC axis loading = 0.57, Corolla length PC axis loading = 0.59) and species height (PC axis loading = −0.51) (Figure S2). For simplicity, herein we refer to the two axes as (1) leaf and fruit size and (2) flower size vs height.

2.3 | Environmental stress

Environmental stress was a single PC axis responsible for covariation in increasing ultramafic soil area (PC axis loading = 0.52) and decreasing minimum monthly rainfall (PC axis loading = −0.44) and lowland area (PC axis loading = −0.73) (Figure 1a) in Malesia's nine taxonomic database working group (tdwg) areas: Peninsular Malaysia, Sumatra, Borneo, Philippines, Java, Sulawesi, the Lesser Sundas, Moluccas, and New Guinea (Brummitt, 2001). This axis represented 53% variation in the environmental variables (Figure S3).

Lowland area was the percentage area below 400m. A 400m cutoff was chosen because at these altitudes there are noticeable shifts in plant traits and in certain locations in Malesia, montane flora is observed (Holthuis and Lam, 1942; Trethowan, 2021; Umaña and Swenson, 2019). Ultramafic soil area was estimated as the percentage covering tdwg areas from the map presented in Galey et al. (2017). There is currently not an ultramafic soil layer available. Minimum monthly rainfall values were taken from WorldClim, these were values recorded from 1970–2000 (Exposito-Alonso, 2017) (Table S2). All these variables were scaled prior to the PC analysis. The environmental stress values peak at the archipelago's center, in Sulawesi, Moluccas, Lesser Sundas, and the Philippines, where there is least lowland, most ultramafic soils, and the strongest dry season (Figure 1b).

2.4 | Environmental stress and Malesian Lamiaceae distributions

To test the effect of environmental stress upon species occurrence, we built the following phylogenetic generalized mixed effects model (Li et al., 2020):

$$Y_i \sim \text{Bernoulli}(p_i)$$

$$\text{logit}(p_i) = \alpha + \beta\gamma + \delta\gamma + \beta\theta + \delta\theta + a_{spp[i]} + b_{spp[i]}$$

$$a \sim \text{Gaussian}(0, \sigma_a^2 I_n)$$

$$b \sim \text{Gaussian}(0, \sigma_b^2 \Sigma_{spp})$$

Greek letters above refer to fixed effects and latin to mixed effects (Gelman and Hill, 2006; Li et al., 2017). Here, Y_i represents the observations i of presence/absence n across Malesia's nine tdwg areas m according to Bramley et al. (2019). The logit-transformed probability of species presence p_i was modeled as a function of leaf and fruit size β and flower size vs height δ and their interaction with environmental stress γ and a spatial eigenvector θ. The spatial eigenvector θ was the first selected Moran's eigenvector of spatial distance between tdwg centroids (Dray et al., 2012; Griffith, 1996) (Figure 1b). This involved calculation of a Gabriel neighbor graph between tdwg centroids and subsequent unweighted orthogonalization of the resulting distance matrix (Dray et al., 2012). The intercept α estimates species average presence in tdwg areas.

We included two random effects for species identity: one without $a_{spp[i]}$ and one with $b_{spp[i]}$ the covariance in species effects decided by phylogenetic distance between them $\sigma_b^2 \Sigma_{spp}$ (Ives, 2018; Li and Ives, 2017). $spp[i]$ connects observations to species. Σ_{spp} represents the $n \times n$ phylogenetic distance matrix that assumed a Brownian motion model of evolution and was calculated from a phylogeny built for all species in the dataset (Li et al., 2020). The species random effect without phylogenetic covariance was drawn from a Gaussian distribution with mean 0 and variance σ^2. Phylogenetic data were derived from the latest Lamiaceae backbone (Zhao et al., 2021). Genera missing from the backbone were manually placed, using *phytools* (Revell, 2012), based upon more finescale phylogenetic studies (Li et al., 2016; Steane et al., 2004). Species not in the backbone phylogeny were randomly imputed alongside congeners to produce a bifurcating tree using *pez* (Pearse et al., 2015). This is not expected to affect overall variability in phylogenetic distances between species used in the random effect $b_{spp[i]}$ (Li et al., 2019).

To account for more species-rich areas sharing more species simply because of sample size, we took 25 randomly sampled communities the size of the least species-rich area and repeated the model for each of these (Cardoso et al., 2009; Nash, 1950; Stier et al., 2016). The averaged effects and Wald test p values from these models were used to identify significant effects of predictor variables upon species occurrence.

To further explore model behavior, we extracted predicted occurrences of species. This allowed us to examine species-predicted occurrence across the phylogeny, tdwg areas, and the environmental stress gradient.

All analyses were carried out in R version 4.0.2.

3 | RESULTS

Phylogenetic generalized mixed effects models of species presence-absence across tdwg areas showed that increasing fruit and leaf size had a negative effect upon species occurrence across Malesia (mean effect score = −0.17 and mean Wald test p from 25 model iterations < 0.05) (Figure 1c) and that increasing leaf and fruit size decreased the chance that species occurred in areas of high environmental stress (mean effect score = −0.13 and mean Wald test
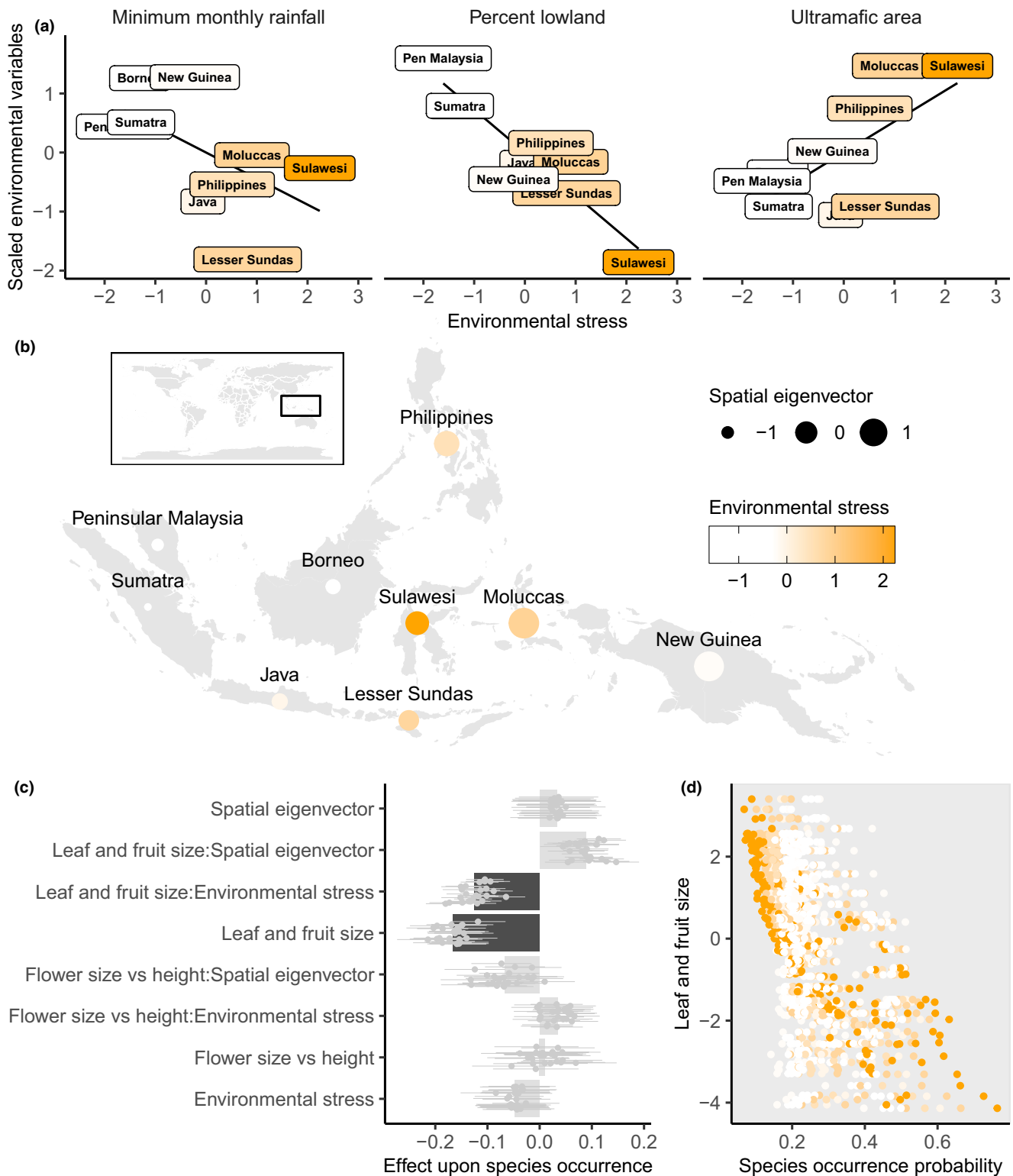
FIGURE 1 (a) The contributions of ultramafic soils, minimum monthly rainfall, and lowland area to environmental stress – which is a principal component axis that accounts for 53% variation in these variables. (b) Spatial eigenvector scores and environmental stress across taxonomic database working group (tdwg) areas of Malesia and their global position (inset map). (c) Drivers of Lamiaceae species occurrence across Malesia according to phylogenetic generalized mixed effects models. We ran 25 separate models each with a randomly selected number of species equal to the tdwg area of least species richness – each point represents effect score and standard error from each model. Gray and black bars are the mean effect. Bar colors correspond to mean $p < .05$ (black) and mean $p > .05$ (gray). (d) Predicted occurrences of species with varying leaf and fruit size across the environmental stress gradient of Malesian tdwg areas.

$p < .05$) (Figure 1c). All other predictor variables had considerably lower effect scores none of which were significant (maximum mean effect score = 0.088 all mean $p > .05$, Figure 1c). This indicates that species with smaller fruit and leaves are more likely to occur in areas of high environmental stress in Malesia.

Environmental stress effects upon predicted occurrence vary across the phylogeny. The general pattern being species from clades with greater diversity in the tropics tend to have lower predicted occurrence in high-stress environments, except for the genera *Vitex* and *Premna* (Figure 2). Species belonging to clades/genera most diverse in temperate and subtropical regions (e.g., *Leucas* and *Salvia*) have consistently high predicted occurrence in stressful environments (Figure 2).

4 | DISCUSSION

Species occurrence across island communities is often driven by the spatial distance between them (Ibanez et al., 2018; MacArthur and Wilson, 1963). We have shown here that a gradient of environmental stress that represents variation in drought, altitude, and ultramafic soils influence distributions of Lamiaceae species in Malesia (Hulshof and Spasojevic, 2020; Sheldon et al., 2018), whereas previously, plant growth and survival in experimental settings have been shown to be negatively affected by multifactorial stress (Zandalinas et al., 2021), our results show its importance for the distribution of species at large scales. Previous study has shown that low-temperature stress of temperate regions and high altitude irrespective of latitude drive similarities in plant communities (Segovia et al., 2020). Similar convergence because of additional stressors may occur (Rillig et al., 2019; Zandalinas et al., 2021). For instance, in the Neotropics, stressors include altitude in the Andes, nutrient deficiency of white sands, and drought/fire in the seasonal biome – similarities in how they shape biogeography could be sought (Fine et al., 2014; Pérez-Escobar et al., 2017; Segovia et al., 2020; Simon et al., 2009).

Our study focuses upon the Lamiaceae; other plant family distributions may or may not follow the pattern we have observed. Firstly, Lamiaceae species have relatively small drupaceous or schizocarpic fruits, families that have larger and different fruit types such as drupes and berries could be more closely linked to frugivore distributions across islands (Crayn et al., 2015; McConkey et al., 2022; McFadden et al., 2022; Yap et al., 2018). Wind-dispersed seeds may also facilitate patterns different to our observations; noticeably, wind-dispersed Asteraceae have been shown to be less speciose than expected on islands except when insular diversification has occurred (König et al., 2021). Asteraceae are not particularly species rich in Malesia (Mandel et al., 2019), which suggests that again their dispersal mechanism is not linked to greater insular diversity. Asteraceae versus Lamiaceae also highlights differences in floral morphology. Asteraceae and other families that are more diverse in Malesia, such as the Myrtaceae (Joyce et al., 2020a), have open flowers that differ from the typically tubular, closed flowers of Lamiaceae species. An

open flower may enable a wider range of pollinators compared to closed flowers, which could be advantageous in multiple environments with varying pollinator communities (Herrera, 2020).

There has been little clarity as to what factors determine the ability of plant species to colonize new islands and then diversify in Malesia (Shee et al., 2020). We have shown here that environmental stress influences species occurrence: could the ability to tolerate stress also enable access to unoccupied islands and novel conditions – driving diversification (Gavrilets and Losos, 2009; Pillon et al., 2014)? In this study, we demonstrate that a reduction in leaf and fruit size increased the chance that Lamiaceae species were able to cope with environmental stress, allowing them to establish across Malesia's islands. Similarly, non-Lamiaceae clades may have strategies that allow species to occupy islands across the archipelago. For instance, many clades (e.g., Palms, Cercidoideae, and *Caesalpinia*) that are diverse and widely distributed in Malesia have strategies to cope with stress such as reduced height and stature, often becoming more shrubby or lianescent, compared to species of the same clade outside Malesia (Couvreur et al., 2015; Gagnon et al., 2019; Sinou et al., 2020; Trethowan, 2021; Westoby, 1998). A switch to lianescence could have a positive effect upon dispersal because it increases the opportunity to access tree fall gaps and occupy lower canopied forests where lianas become most abundant (Dalling et al., 2012). By gathering trait data from museum specimens to allow sampling of a high percentage of a clade's species, it should be possible to identify whether traits linked to ecological strategies, such as stress tolerance, encourage dispersal events that precede lineage diversification on islands (Cacho and Strauss, 2014; Esquerré et al., 2020; Heberling and Isaac, 2017). The growing understanding of evolutionary relationships for clades that are speciose in Malesia make examination of this achievable (Atkins et al., 2019; Bellot et al., 2020; Kuhnhäuser et al., 2021; Murphy et al., 2020).

In this study, we have analyzed species rather than lineages, and therefore, we are not able to identify insular speciation events that may influence the patterns we observe. For instance, altitude, drought, and ultramafic soils have been implicated as drivers of insular speciation (Garot et al., 2019; Pillon et al., 2014; Steinbauer et al., 2016). To address this, we need greater sampling of Malesian Lamiaceae species in published phylogenies. However, our results do allow us to survey model predictions of species occurrence across the phylogeny and observe how different clades are affected by tdwg areas with varying environmental stress. What is striking about these results is that the genera *Clerodendrum* and *Teijsmanniodendron*, that have diversified mostly in the tropics, have low predicted occurrence in high-stress environments, whereas genera that are most diverse in temperate or subtropical regions (*Leucas*, *Salvia*, etc) have consistently high predicted occurrence in stressful environments. This could help inform where we expect to find diversification within islands. For instance, *Vitex*, a speciose tropical genus has high predicted occurrence in stressful environments which could be linked to insular diversification.

Multifactorial environmental stress may help explain diversification more generally. For diversification to occur species must
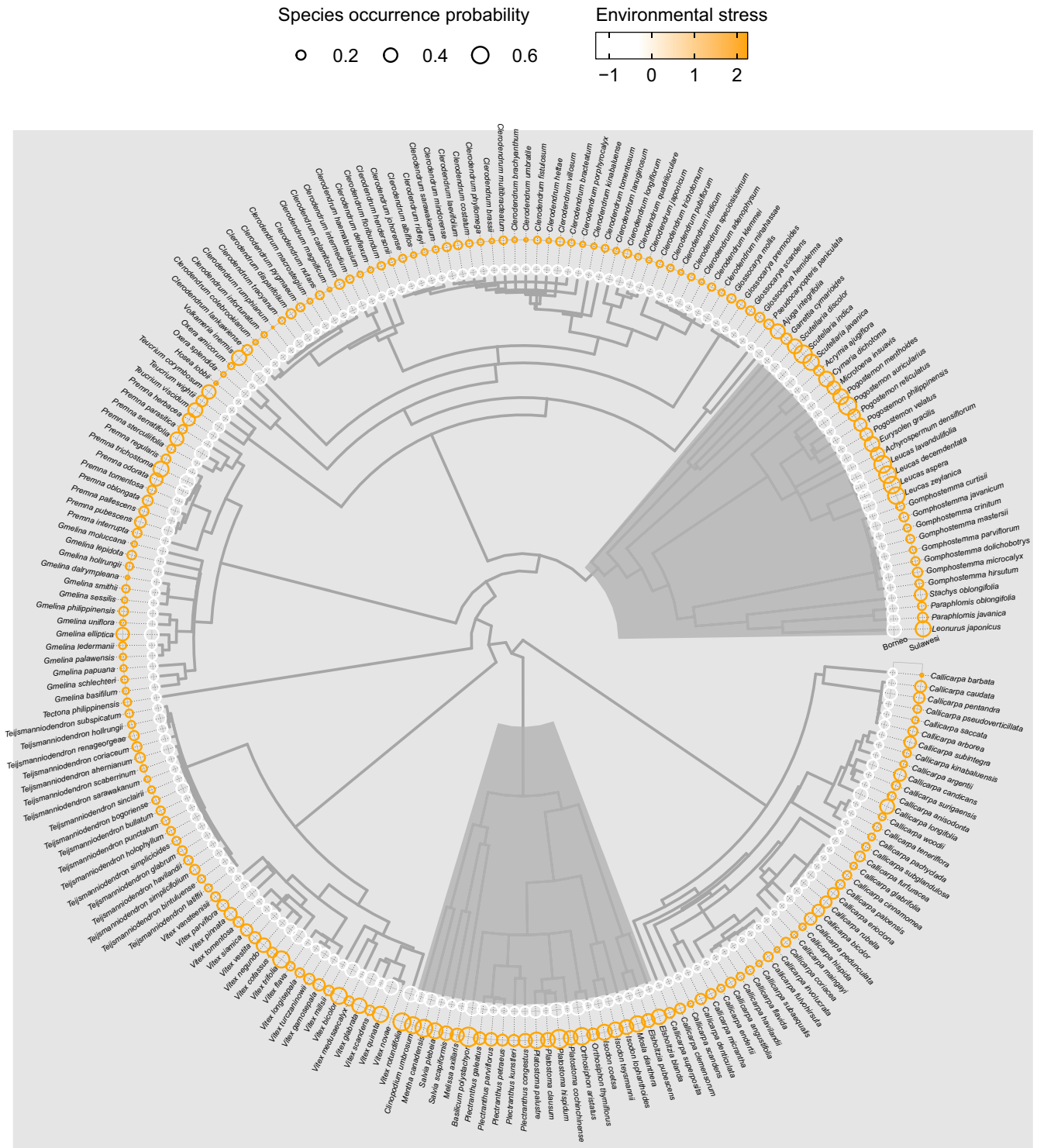
FIGURE 2 Phylogenetic context of species occurrence probabilities in Borneo and Sulawesi. Two of nine taxonomic working group regions selected to highlight large environmental stress differences between spatially adjacent islands. This also means the probabilities are better visualized than if all data from nine areas were plotted. Species occurrence probabilities are their mean value resulting from the 25 model iterations. Lineages highlighted in dark gray are most diverse in temperate and subtropical regions.

become differentiated. Benign environments without sharp stress gradients lack a potential axis of differentiation (Bouchenak-Khelladi et al., 2015; Gavrilets and Losos, 2009; Hart and Marshall, 2013). Stress gradients could underpin why mountain ranges with high percentages of ultramafic soils are some of the

most diverse regions on earth (Rahbek et al., 2019). There are many examples of diversification across single variable stress gradients. For instance, *Diospyros*, *Codia*, and *Geissosis* diversify across the ultramafic non-ultramafic soil mosaic of New Caledonia (Paun et al., 2016; Pillon et al., 2014, 2009). Likewise, diversification

of the Burseraceae subfamily Protieae is linked to occupation of Neotropical low-nutrient white sands and flooded forests (Fine et al., 2014). In Malesia, the Lamiaceae genus *Callicarpa* has a center of diversity in the Philippines, islands that have many stressful ultramafic soils, a defined dry season, and many mountains. Philippine montane gradients have been shown to drive mammal diversification (e.g., Heaney et al., 2018). For *Callicarpa*, multifactorial stress, including altitudinal, drought, and soil stress, could be tied to their diversification. Combining variables such as these to identify general environmental stress-driven diversification would be a tractable approach for studies at local or global scales. This would complement fine-scale studies showing how stressors can increase population phenotypic plasticity (Levis et al., 2020). Experimental studies also highlight how the effects of stressors are not always consistent between populations or species (Love and Wagner, 2022). Similarly, extratropical clades could experience stress in the warm wet tropics. Therefore, a stress gradient in reverse to that presented in this study could drive diversification of clades with extratropical origins (Baldwin and Wagner, 2010).

This study has not explored human-caused stressors. Deforestation, non-natural fires, and domestic livestock-driven herbivory are all stressors that require examination (Donlan et al., 2002; Gaveau et al., 2021; Nolan et al., 2021; Voigt et al., 2021). Incorporation of these factors alongside climate change predictions will be crucial when modeling future scenarios for the Malesian flora. How species traits affect toleration of anthropogenic stressors, like we have shown for environmental stressors, may prove useful for predicting change on megadiverse islands.

5 | CONCLUSIONS

Overall, we have identified the importance of environmental stress over large scales. By simplifying Malesia to a gradient of environmental stress, the abiotic influence upon Lamiaceae distributions was clear. Questions remain about how the formation of stressors in relation to rapid island uplift in Malesia has contributed to the diversification of species over time. Comparison of the effects of island and environmental stress formation in diversification rate analyses would address this. Environmental stress could offer an elegant and simple explanation for the distribution and diversity of species.

AUTHOR CONTRIBUTIONS

Liam A. Trethowan: Conceptualization (lead); data curation (equal); formal analysis (lead); writing – original draft (lead); writing – review and editing (equal). **Camilla Arvidsson:** Data curation (equal); writing – review and editing (equal). **Gemma L. C. Bramley:** Conceptualization (equal); data curation (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Rmarkdown document to build the article and all data, including the phylogenetic tree, is available here: https://figshare.com/projects/Malesian_Mints/149389.

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REFERENCES

Anderegg, W. R. L., Berry, J. A., Smith, D. D., Sperry, J. S., Anderegg, L. D. L., & Field, C. B. (2012). The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *PNAS*, *109*, 233–237. https://doi.org/10.1073/pnas.1107891109

Anderegg, W. R. L., Hicke, J. A., Fisher, R. A., Allen, C. D., Aukema, J., Bentz, B., Hood, S., Lichstein, J. W., Macalady, A. K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J. D., Stephenson, N. L., Tague, C., & Zeppel, M. (2015). Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist*, *208*, 674–683. https://doi.org/10.1111/nph.13477

Asner, G. P., Martin, R. E., Tupayachi, R., Anderson, C. B., Sinca, F., Carranza-Jiménez, L., & Martinez, P. (2014). Amazonian functional diversity from forest canopy chemical assembly. *PNAS*, *111*, 201401181. https://doi.org/10.1073/pnas.1401181111

Atkins, H. J., Bramley, G. L. C., Johnson, M. A., Kartonegoro, A., Nishii, K., Kokubugata, G., Moeller, M., & Hughes, M. (2019). A molecular phylogeny of Southeast Asian *Cyrtandra* (Gesneriaceae) supports an emerging paradigm for Malesian plant biogeography. *Frontiers of Biogeography*, *12*, e44814. https://doi.org/10.21425/F5FBG44184

Baldwin, B. G., & Wagner, W. L. (2010). Hawaiian angiosperm radiations of North American origin. *Annals of Botany*, *105*, 849–879. https://doi.org/10.1093/aob/mcq052

Bellot, S., Bayton, R. P., Couvreur, T. L. P., Dodsworth, S., Eiserhardt, W. L., Guignard, M. S., Pritchard, H. W., Roberts, L., Toorop, P. E., & Baker, W. J. (2020). On the origin of giant seeds: The macroevolution of the double coconut (*Lodoicea maldivica*) and its relatives (Borasseae, Arecaceae). *New Phytologist*, *228*, 1134–1148. https://doi.org/10.1111/nph.16750

Bemmels, J. B., Wright, S. J., Garwood, N. C., Queenborough, S. A., Valencia, R., & Dick, C. W. (2018). Filter-dispersal assembly of lowland neotropical rainforests across the Andes. *Ecography*, *41*, 1–13. https://doi.org/10.1111/ecog.03473

Biddick, M., Hendriks, A., & Burns, K. C. (2019). Plants obey (and disobey) the Island rule. *PNAS*, *116*, 17632–17634. https://doi.org/10.1073/pnas.1907424116

Bouchenak-Khelladi, Y., Onstein, R. E., Xing, Y., Schwery, O., & Linder, H. P. (2015). On the complexity of triggering evolutionary radiations. *New Phytologist*, *207*, 313–326. https://doi.org/10.1111/nph.13331

Brambach, F., Leuschner, C., Tjoa, A., & Culmsee, H. (2020). Predominant colonization of Malesian mountains by Australian tree lineages. *Journal of Biogeography*, *47*, 355–370. https://doi.org/10.1111/jbi.13747

Bramley, G., Bongcheewin, B., Davies, N., de Kok, R. P. J., Mabberley, D. J., Suddee, S., Walsingham, L., & Wearn, J. S. (2019). Lamiaceae. Flora Malesiana-Series 1. *Spermatophyta*, *23*, 1–424.

Brummitt, R.K. (2001). World geographical scheme for recording plant distributions [WWW Document]. Retrieved from http://www.tdwg.org/standards/109

Cacho, N. I., & Strauss, S. Y. (2014). Occupation of bare habitats, an evolutionary precursor to soil specialization in plants. *PNAS*, *111*, 15132–15137. https://doi.org/10.1073/pnas.1409242111

Cardoso, P., Borges, P. A., & Veech, J. A. (2009). Testing the performance of beta diversity measures based on incidence data: The robustness to undersampling. *Diversity and Distributions*, 15, 1081–1090. https://doi.org/10.1111/j.1472-4642.2009.00607.x

Carvajal-Endara, S., Hendry, A. P., Emery, N. C., & Davies, T. J. (2017). Habitat filtering not dispersal limitation shapes oceanic Island floras: Species assembly of the Galápagos archipelago. *Ecology Letters*, 20, 495–504. https://doi.org/10.1111/ele.12753

Chen, S.-C., & Moles, A. T. (2015). A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. *Global Ecology and Biogeography*, 24, 1269–1280. https://doi.org/10.1111/geb.12346

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, 558, 531–539. https://doi.org/10.1038/s41586-018-0240-x

Cleveland, C. C., Townsend, A. R., Taylor, P., Alvarez-Clare, S., Bustamante, M. M. C., Chuyong, G., Dobrowski, S. Z., Grierson, P., Harms, K. E., Houlton, B. Z., Marklein, A., Parton, W., Porder, S., Reed, S. C., Sierra, C. A., Silver, W. L., Tanner, E. V. J., & Wieder, W. R. (2011). Relationships among net primary productivity, nutrients and climate in tropical rain forest: A pan-tropical analysis. *Ecology Letters*, 14, 939–947. https://doi.org/10.1111/j.1461-0248.2011.01658.x

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Núñez, P., Aguilar, S., Valencia, R., & Villa, G. (2002). Beta-diversity in tropical forest trees. *Science*, 295, 666–669. https://doi.org/10.1126/science.1066854

Couvreur, T. L., Kissling, W. D., Condamine, F. L., Svenning, J.-C., Rowe, N. P., & Baker, W. J. (2015). Global diversification of a tropical plant growth form: Environmental correlates and historical contingencies in climbing palms. *Frontiers in Genetics*, 5, 452. https://doi.org/10.3389/fgene.2014.00452

Crayn, D. M., Costion, C., & Harrington, M. G. (2015). The Sahul–Sunda floristic exchange: Dated molecular phylogenies document Cenozoic intercontinental dispersal dynamics. *Journal of Biogeography*, 42, 11–24. https://doi.org/10.1111/jbi.12405

Dalling, J. W., Schnitzer, S. A., Baldeck, C., Harms, K. E., John, R., Mangan, S. A., Lobo, E., Yavitt, J. B., & Hubbell, S. P. (2012). Resource-based habitat associations in a neotropical liana community. *Journal of Ecology*, 100, 1174–1182. https://doi.org/10.1111/j.1365-2745.2012.01989.x

Dexter, K. G., Lavin, M., Torke, B. M., Twyford, A. D., Kursar, T. A., Coley, P. D., Drake, C., Hollands, R., & Pennington, R. T. (2017). Dispersal assembly of rain forest tree communities across the Amazon basin. *PNAS*, 114, 2645–2650. https://doi.org/10.1073/pnas.1613655114

Donlan, C. J., Tershy, B. R., & Croll, D. A. (2002). Islands and introduced herbivores: Conservation action as ecosystem experimentation. *Journal of Applied Ecology*, 39, 235–246. https://doi.org/10.1046/j.1365-2664.2002.00710.x

Dray, S., Pélissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P. R., Bellier, E., Bivand, R., Blanchet, F. G., Cáceres, M. D., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., & Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, 82, 257–275. https://doi.org/10.1890/11-1183.1

Esquerré, D., Donnellan, S., Brennan, I. G., Lemmon, A. R., Moriarty Lemmon, E., Zaher, H., Grazziotin, F. G., & Keogh, J. S. (2020). Phylogenomics, biogeography, and morphometrics reveal rapid phenotypic evolution in pythons after crossing Wallace's line. *Systematic Biology*, 69, 1039–1051. https://doi.org/10.1093/sysbio/syaa024

Exposito-Alonso, M. (2017). Rbioclim: Improved getData function from the raster r package to interact with past, present and future climate data from worldclim.org.

Fajardo, A., McIntire, E. J. B., & Olson, M. E. (2019). When short stature is an asset in trees. *Trends in Ecology and Evolution*, 34, 193–199. https://doi.org/10.1016/j.tree.2018.10.011

Fensham, R. J., Fairfax, R. J., & Ward, D. P. (2009). Drought-induced tree death in savanna. *Global Change Biology*, 15, 380–387. https://doi.org/10.1111/j.1365-2486.2008.01718.x

Fine, P. V. A., Zapata, F., & Daly, D. C. (2014). Investigating processes of neotropical rain forest tree diversification by examining the evolution and historical biogeography of the Protieae (Burseraceae). *Evolution*, 68, 1988–2004. https://doi.org/10.1111/evo.12414

Gagnon, E., Ringelberg, J. J., Bruneau, A., Lewis, G. P., & Hughes, C. E. (2019). Global succulent biome phylogenetic conservatism across the pantropical *Caesalpinia* group (Leguminosae). *New Phytologist*, 222, 1994–2008. https://doi.org/10.1111/nph.15633

Galen, C. (1999). Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. *Bioscience*, 49, 631–640. https://doi.org/10.2307/1313439

Galey, M. L., van der Ent, A., Iqbal, M. C. M., & Rajakaruna, N. (2017). Ultramafic geoecology of South and Southeast Asia. *Botanical Studies*, 58, 18. https://doi.org/10.1186/s40529-017-0167-9

García-Verdugo, C., Caujapé-Castells, J., Mairal, M., & Monroy, P. (2019). How repeatable is microevolution on islands? Patterns of dispersal and colonization-related plant traits in a phylogeographical context. *Annals of Botany*, 123, 557–568. https://doi.org/10.1093/aob/mcy191

Garnica-Díaz, C., Berazaín Iturralde, R., Cabrera, B., Calderón-Morales, E., Felipe, F. L., García, R., Hechavarría, J. L. G., Guimarães, A. F., Medina, E., Paul, A. L. D., Rajakaruna, N., Restrepo, C., Siebert, S. J., van den Berg, E., van der Ent, A., Velasquez, G., & Hulshof, C. M. (2022). Global plant ecology of tropical ultramafic ecosystems. *The Botanical Review*. https://doi.org/10.1007/s12229-022-09278-2

Garot, E., Joët, T., Combes, M.-C., & Lashermes, P. (2019). Genetic diversity and population divergences of an indigenous tree (*Coffea mauritiana*) in Reunion Island: Role of climatic and geographical factors. *Heredity*, 122, 833–847. https://doi.org/10.1038/s41437-018-0168-9

Gaveau, D. L. A., Santos, L., Locatelli, B., Salim, M. A., Husnayaen, H., Meijaard, E., Heatubun, C., & Sheil, D. (2021). Forest loss in Indonesian New Guinea (2001–2019): Trends, drivers and outlook. *Biological Conservation*, 261, 109225. https://doi.org/10.1016/j.biocon.2021.109225

Gavrilets, S., & Losos, J. B. (2009). Adaptive radiation: Contrasting theory with data. *Science*, 323, 732–737. https://doi.org/10.1126/science.1157966

Gelman, A., & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press.

Giarla, T. C., Maher, S. P., Achmadi, A. S., Moore, M. K., Swanson, M. T., Rowe, K. C., & Esselstyn, J. A. (2018). Isolation by marine barriers and climate explain areas of endemism in an Island rodent. *Journal of Biogeography*, 45, 2053–2066. https://doi.org/10.1111/jbi.13392

Green, A. J., Baltzinger, C., & Lovas-Kiss, Á. (2022). Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. *Oikos*, 2022, e08327. https://doi.org/10.1111/oik.08327

Griffith, D. A. (1996). Spatial autocorrelation and eigenfunctions of the geographic weights matrix accompanying geo-referenced data. *The Canadian Geographer*, 40, 351–367. https://doi.org/10.1111/j.1541-0064.1996.tb00462.x

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111, 1169–1194. https://doi.org/10.1086/283244

Grubb, P. J. (1977). Control of forest growth and distribution on wet tropical mountains: With special reference to mineral nutrition. *Annual Review of Ecology and Systematics*, 8, 83–107. https://doi.org/10.1146/annurev.es.08.110177.000503

Hart, S. P., & Marshall, D. J. (2013). Environmental stress, facilitation, competition, and coexistence. *Ecology*, 94, 2719–2731. https://doi.org/10.1890/12-0804.1

Heaney, L. R., Kyriazis, C. C., Balete, D. S., Steppan, S. J., & Rickart, E. A. (2018). How small an Island? Speciation by endemic mammals (*Apomys*, Muridae) on an oceanic Philippine Island. *Journal of Biogeography*, 45, 1675–1687. https://doi.org/10.1111/jbi.13352

Heberling, J. M., & Isaac, B. L. (2017). Herbarium specimens as exaptations: New uses for old collections. *American Journal of Botany*, 104, 963–965. https://doi.org/10.3732/ajb.1700125

Herrera, C. M. (2020). Flower traits, habitat, and phylogeny as predictors of pollinator service: A plant community perspective. *Ecological Monographs*, 90, e01402. https://doi.org/10.1002/ecm.1402

Holthuis, L. B., & Lam, H. J. (1942). A first contribution to our knowledge of the flora of the Talaud islands and Morotai. *Blumea*, 5, 94.

Hulshof, C. M., & Spasojevic, M. J. (2020). The edaphic control of plant diversity. *Global Ecology and Biogeography*, 29, 1634–1650. https://doi.org/10.1111/geb.13151

Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Culmsee, H., Cordell, S., Florens, F. V., Franklin, J., Giardina, C. P., & Gillespie, T. W. (2018). Regional forcing explains local species diversity and turnover on tropical islands. *Global Ecology and Biogeography*, 27, 474–486. https://doi.org/10.1111/geb.12712

Ives, A. R. (2018). *Mixed and phylogenetic models: A conceptual introduction to correlated data*. Leanpub.

Joyce, E. M., Thiele, K. R., Slik, F. J. W., & Crayn, D. M. (2020a). Checklist of the vascular flora of the Sunda-sahul convergence zone. *Biodiversity Data Journal*, 8, e51094. https://doi.org/10.3897/BDJ.8.e51094

Joyce, E. M., Thiele, K. R., Slik, J. W., & Crayn, D. M. (2020b). Plants will cross the lines: Climate and available land mass are the major determinants of phytogeographical patterns in the Sunda–Sahul convergence zone. *Biological Journal of the Linnean Society*, 132, 374–387. https://doi.org/10.1093/biolinnean/blaa194

König, C., Weigelt, P., Taylor, A., Stein, A., Dawson, W., Essl, F., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Chatelain, C., Wieringa, J. J., Krestov, P., & Kreft, H. (2021). Source pools and disharmony of the world's Island floras. *Ecography*, 44, 44–55. https://doi.org/10.1111/ecog.05174

Kooyman, R. M., Morley, R. J., Crayn, D. M., Joyce, E. M., Rossetto, M., Slik, J. F., Strijk, J. S., Su, T., Yap, J.-Y. S., & Wilf, P. (2019). Origins and assembly of Malesian rainforests. *Annual Review of Ecology, Evolution, and Systematics*, 50, 119–143. https://doi.org/10.1146/annurev-ecolsys-110218-024737

Kuhnhäuser, B. G., Bellot, S., Couvreur, T. L. P., Dransfield, J., Henderson, A., Schley, R., Chomicki, G., Eiserhardt, W. L., Hiscock, S. J., & Baker, W. J. (2021). A robust phylogenomic framework for the calamoid palms. *Molecular Phylogenetics and Evolution*, 157, 107067. https://doi.org/10.1016/j.ympev.2020.107067

Küpper, H., & Andresen, E. (2016). Mechanisms of metal toxicity in plants. *Metallomics*, 8, 269–285. https://doi.org/10.1039/c5mt00244c

Levis, N. A., Fuller, C. G., & Pfennig, D. W. (2020). An experimental investigation of how intraspecific competition and phenotypic plasticity can promote the evolution of novel, complex phenotypes. *Biological Journal of the Linnean Society*, 131, 76–87. https://doi.org/10.1093/biolinnean/blaa095

Li, B., Cantino, P. D., Olmstead, R. G., Bramley, G. L., Xiang, C.-L., Ma, Z.-H., Tan, Y.-H., & Zhang, D.-X. (2016). A large-scale chloroplast phylogeny of the Lamiaceae sheds new light on its subfamilial classification. *Scientific Reports*, 6, 1–18. https://doi.org/10.1038/srep34343

Li, D., Dinnage, R., Nell, L. A., Helmus, M. R., & Ives, A. R. (2020). Phyr: An r package for phylogenetic species-distribution modelling in ecological communities. *Methods in Ecology and Evolution*, 11, 1455–1463. https://doi.org/10.1101/2020.02.17.952317

Li, D., & Ives, A. R. (2017). The statistical need to include phylogeny in trait-based analyses of community composition. *Methods in Ecology and Evolution*, 8, 1192–1199. https://doi.org/10.1111/2041-210X.12767

Li, D., Ives, A. R., & Waller, D. M. (2017). Can functional traits account for phylogenetic signal in community composition? *New Phytologist*, 214, 607–618. https://doi.org/10.1111/nph.14397

Li, D., Trotta, L., Marx, H. E., Allen, J. M., Sun, M., Soltis, D. E., Soltis, P. S., Guralnick, R. P., & Baiser, B. (2019). For common community phylogenetic analyses, go ahead and use synthesis phylogenies. *Ecology*, 100, e02788. https://doi.org/10.1002/ecy.2788

Love, A. C., & Wagner, G. P. (2022). Co-option of stress mechanisms in the origin of evolutionary novelties. *Evolution*, 76, 394–413. https://doi.org/10.1111/evo.14421

MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387. https://doi.org/10.2307/2407089

MacLean, R. C., Torres-Barceló, C., & Moxon, R. (2013). Evaluating evolutionary models of stress-induced mutagenesis in bacteria. *Nature Reviews Genetics*, 14, 221–227. https://doi.org/10.1038/nrg3415

Mandel, J. R., Dikow, R. B., Siniscalchi, C. M., Thapa, R., Watson, L. E., & Funk, V. A. (2019). A fully resolved backbone phylogeny reveals numerous dispersals and explosive diversifications throughout the history of Asteraceae. *PNAS*, 116, 14083–14088. https://doi.org/10.1073/pnas.1903871116

McConkey, K. R., Campos-Arceiz, A., Corlett, R. T., Sushma, H. S., Ong, L., & Brodie, J. F. (2022). Megafruit and megafauna diversity are positively associated, while megafruit traits are related to abiotic factors, in tropical Asia. *Global Ecology and Biogeography*, 31, 740–752. https://doi.org/10.1111/geb.13464

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

McFadden, I. R., Fritz, S. A., Zimmermann, N. E., Pellissier, L., Kissling, W. D., Tobias, J. A., Schleuning, M., & Graham, C. H. (2022). Global plant-frugivore trait matching is shaped by climate and biogeographic history. *Ecology Letters*, 25, 686–696. https://doi.org/10.1101/2021.12.17.473099

McGill, B. J. (2019). The what, how and why of doing macroecology. *Global Ecology and Biogeography*, 28, 6–17. https://doi.org/10.1111/geb.12855

Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T., & Westoby, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography*, 16, 109–116. https://doi.org/10.1111/j.1466-8238.2006.00259.x

Murphy, B., Forest, F., Barraclough, T., Rosindell, J., Bellot, S., Cowan, R., Golos, M., Jebb, M., & Cheek, M. (2020). A phylogenomic analysis of *Nepenthes* (Nepenthaceae). *Molecular Phylogenetics and Evolution*, 144, 106668. https://doi.org/10.1016/j.ympev.2019.106668

Nash, C. B. (1950). Associations between fish species in tributaries and shore waters of western lake erie. *Ecology*, 31, 561–566. https://doi.org/10.2307/1931575

Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, 26, 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x

Ng, N. S., Wilton, P. R., Prawiradilaga, D. M., Tay, Y. C., Indrawan, M., Garg, K. M., & Rheindt, F. E. (2017). The effects of pleistocene climate change on biotic differentiation in a montane songbird clade from Wallacea. *Molecular Phylogenetics and Evolution*, 114, 353–366. https://doi.org/10.1016/j.ympev.2017.05.007

Nolan, R. H., Collins, L., Leigh, A., Ooi, M. K. J., Curran, T. J., Fairman, T. A., Resco de Dios, V., & Bradstock, R. (2021). Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment*, 44, 3471–3489. https://doi.org/10.1111/pce.14176

Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., León-Gómez, C., Dawson, T., Martínez, J. J. C., Castorena, M., Echeverría, A., Espinosa, C. I., Fajardo, A., Gazol,

A., Isnard, S., Lima, R. S., Marcati, C. R., & Méndez-Alonzo, R. (2018). Plant height and hydraulic vulnerability to drought and cold. *PNAS*, *115*, 7551–7556. https://doi.org/10.1073/pnas.1721728115

Ottaviani, G., Keppel, G., Götzenberger, L., Harrison, S., Opedal, Ø. H., Conti, L., Liancourt, P., Klimešová, J., Silveira, F. A. O., Jiménez-Alfaro, B., Negoita, L., Doležal, J., Hájek, M., Ibanez, T., Méndez-Castro, F. E., & Chytrý, M. (2020). Linking plant functional ecology to Island biogeography. *Trends in Plant Science*, *25*, 329–339. https://doi.org/10.1016/j.tplants.2019.12.022

Paun, O., Turner, B., Trucchi, E., Munzinger, J., Chase, M. W., & Samuel, R. (2016). Processes driving the adaptive radiation of a tropical tree (*Diospyros*, Ebenaceae) in New Caledonia, a biodiversity hotspot. *Systematic Biology*, *65*, 212–227. https://doi.org/10.1093/sysbio/syv076

Pearse, W. D., Cadotte, M. W., Cavender-Bares, J., Ives, A. R., Tucker, C. M., Walker, S. C., & Helmus, M. R. (2015). Pez: Phylogenetics for the environmental sciences. *Bioinformatics*, *31*, 2888–2890. https://doi.org/10.1093/bioinformatics/btv277

Pérez-Escobar, O. A., Chomicki, G., Condamine, F. L., Karremans, A. P., Bogarín, D., Matzke, N. J., Silvestro, D., & Antonelli, A. (2017). Recent origin and rapid speciation of Neotropical orchids in the world's richest plant biodiversity hotspot. *New Phytologist*, *215*, 891–905. https://doi.org/10.1111/nph.14629

Pillon, Y., Hopkins, H. C., Rigault, F., Jaffré, T., & Stacy, E. A. (2014). Cryptic adaptive radiation in tropical forest trees in New Caledonia. *New Phytologist*, *202*, 521–530. https://doi.org/10.1111/nph.12677

Pillon, Y., Munzinger, J., Amir, H., Hopkins, H. C., & Chase, M. W. (2009). Reticulate evolution on a mosaic of soils: Diversification of the New Caledonian endemic genus *Codia* (Cunoniaceae). *Molecular Ecology*, *18*, 2263–2275. https://doi.org/10.1111/j.1365-294X.2009.04178.x

Powers, J. S., Vargas, G. G., Brodribb, T. J., Schwartz, N. B., Pérez-Aviles, D., Smith-Martin, C. M., Becknell, J. M., Aureli, F., Blanco, R., Calderón-Morales, E., Calvo-Alvarado, J. C., Calvo-Obando, A. J., Chavarría, M. M., Carvajal-Vanegas, D., Jiménez-Rodríguez, C. D., Chacon, E. M., Schaffner, C. M., Werden, L. K., Xu, X., & Medvigy, D. (2020). A catastrophic tropical drought kills hydraulically vulnerable tree species. *Global Change Biology*, *26*, 3122–3133. https://doi.org/10.1111/gcb.15037

Proctor, J. (2003). Vegetation and soil and plant chemistry on ultramafic rocks in the tropical far east. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*, 105–124. https://doi.org/10.1078/1433-8319-00045

Rahbek, C., Borregaard, M. K., Antonelli, A., Colwell, R. K., Holt, B. G., Nogues-Bravo, D., Rasmussen, C. M. Ø., Richardson, K., Rosing, M. T., Whittaker, R. J., & Fjeldså, J. (2019). Building mountain biodiversity: Geological and evolutionary processes. *Science*, *365*, 1114–1119. https://doi.org/10.1126/science.aax0151

Raven, P. H., Gereau, R. E., Phillipson, P. B., Chatelain, C., Jenkins, C. N., & Ulloa Ulloa, C. (2020). The distribution of biodiversity richness in the tropics. *Science Advances*, *6*, eabc6228. https://doi.org/10.1126/sciadv.abc6228

Revell, L. J. (2012). Phytools: An r package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Rillig, M. C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C. A., Buchert, S., Wulf, A., Iwasaki, A., Roy, J., & Yang, G. (2019). The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science*, *366*, 886–890. https://doi.org/10.1126/science.aay2832

Roddy, A. B., Martínez-Perez, C., Teixido, A. L., Cornelissen, T. G., Olson, M. E., Oliveira, R. S., & Silveira, F. A. (2021). Towards the flower economics spectrum. *New Phytologist*, *220*, 665–672. https://doi.org/10.1111/nph.16823

Schrader, J., Wright, I. J., Kreft, H., & Westoby, M. (2021). A roadmap to plant functional Island biogeography. *Biological Reviews*, *96*, 2851–2870. https://doi.org/10.1111/brv.12782

Segovia, R. A., Pennington, R. T., Baker, T. R., de Souza, F. C., Neves, D. M., Davis, C. C., Armesto, J. J., Olivera-Filho, A. T., & Dexter, K. G. (2020). Freezing and water availability structure the evolutionary diversity of trees across the Americas. *Science Advances*, *6*, eaaz5373. https://doi.org/10.1126/sciadv.aaz5373

Shee, Z. Q., Frodin, D. G., Cámara-Leret, R., & Pokorny, L. (2020). Reconstructing the complex evolutionary history of the Papuasian *Schefflera* radiation through herbariomics. *Frontiers in Plant Science*, *11*, 258. https://doi.org/10.3389/fpls.2020.00258

Sheldon, K. S., Huey, R. B., Kaspari, M., & Sanders, N. J. (2018). Fifty years of mountain passes: A perspective on Dan Janzen's classic article. *The American Naturalist*, *191*, 553–565. https://doi.org/10.1086/697046

Shenkin, A., Chandler, C., Boyd, D., Jackson, T., Jami, J. B., Disney, M., Majalap, N., Nilus, R., Foody, G., & Reynolds, G. (2019). The world's tallest tropical tree in three dimensions. *Frontiers in Forests and Global Change*, *2*, 32. https://doi.org/10.3389/ffgc.2019.00032

Simon, M. F., Grether, R., de Queiroz, L. P., Skema, C., Pennington, R. T., & Hughes, C. E. (2009). Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *PNAS*, *106*, 20359–20364. https://doi.org/10.1073/pnas.0903410106

Singh, H. P., Mahajan, P., Kaur, S., Batish, D. R., & Kohli, R. K. (2013). Chromium toxicity and tolerance in plants. *Environmental Chemistry Letters*, *11*, 229–254. https://doi.org/10.1007/s10311-013-0407-5

Sinou, C., Cardinal-McTeague, W., & Bruneau, A. (2020). Testing generic limits in Cercidoideae (Leguminosae): Insights from plastid and duplicated nuclear gene sequences. *Taxon*, *69*, 67–86. https://doi.org/10.1002/tax.12207

Steane, D. A., de Kok, R. P. J., & Olmstead, R. G. (2004). Phylogenetic relationships between clerodendrum (Lamiaceae) and other Ajugoid genera inferred from nuclear and chloroplast DNA sequence data. *Molecular Phylogenetics and Evolution*, *32*, 39–45. https://doi.org/10.1016/j.ympev.2003.11.011

Steinbauer, M. J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H. J. B., Borges, P. A. V., Cardoso, P., Chou, C.-H., De Sanctis, M., de Sequeira, M. M., Duarte, M. C., Elias, R. B., Fernández-Palacios, J. M., Gabriel, R., Gereau, R. E., Gillespie, R. G., Greimler, J., … Beierkuhnlein, C. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, *25*, 1097–1107. https://doi.org/10.1111/geb.12469

Stier, A. C., Bolker, B. M., & Osenberg, C. W. (2016). Using rarefaction to isolate the effects of patch size and sampling effort on beta diversity. *Ecosphere*, *7*, e01612. https://doi.org/10.1002/ecs2.1612

Trethowan, L. A. (2021). Could the environment limit dispersal between Sunda and Sahul? *Journal of Vegetation Science*, *32*, e12978. https://doi.org/10.1111/jvs.12978

Umaña, M. N., & Swenson, N. G. (2019). Intraspecific variation in traits and tree growth along an elevational gradient in a subtropical forest. *Oecologia*, *191*, 153–164. https://doi.org/10.1007/s00442-019-04453-6

van Steenis, C. (1962). The mountain flora of the Malaysian tropics. *Endeavor*, *21*, 183–193.

Voigt, M., Supriatna, J., Deere, N. J., Kastanya, A., Mitchell, S. L., Rosa, I. M. D., Santika, T., Siregar, R., Tasirin, J. S., Widyanto, A., Winarni, N. L., Zakaria, Z., Mumbunan, S., Davies, Z. G., & Struebig, M. J. (2021). Emerging threats from deforestation and forest fragmentation in the Wallacea centre of endemism. *Environmental Research Letters*, *16*, 94048. https://doi.org/10.1088/1748-9326/ac15cd

Wallace, A. R. (1869). *The Malay archipelago*. Macmillan; Co.

Weigelt, P., Daniel Kissling, W., Kisel, Y., Fritz, S. A., Karger, D. N., Kessler, M., Lehtonen, S., Svenning, J.-C., & Kreft, H. (2015). Global patterns

and drivers of phylogenetic structure in Island floras. *Scientific Reports*, *5*, 12213. https://doi.org/10.1038/srep12213

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227. https://doi.org/10.1023/A:1004327224729

Whittaker, R. H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecological Monographs*, *30*, 279–338. https://doi.org/10.2307/1943563

Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, Ü., Reich, P. B., Sack, L., Villar, R., Wang, H., & Wilf, P. (2017). Global climatic drivers of leaf size. *Science*, *357*, 917–921. https://doi.org/10.1126/science.aal4760

Yap, J.-Y. S., Rossetto, M., Costion, C., Crayn, D., Kooyman, R. M., Richardson, J., & Henry, R. (2018). Filters of floristic exchange: How traits and climate shape the rain forest invasion of Sahul from Sunda. *Journal of Biogeography*, *45*, 838–847. https://doi.org/10.1111/jbi.13143

Zandalinas, S. I., Sengupta, S., Fritschi, F. B., Azad, R. K., Nechushtai, R., & Mittler, R. (2021). The impact of multifactorial stress combination on plant growth and survival. *New Phytologist*, *230*, 1034–1048. https://doi.org/10.1111/nph.17232

Zhao, F., Chen, Y.-P., Salmaki, Y., Drew, B. T., Wilson, T. C., Scheen, A.-C., Celep, F., Bräuchler, C., Bendiksby, M., Wang, Q., Min, D.-Z., Peng, H., Olmstead, R. G., Li, B., & Xiang, C.-L. (2021). An updated tribal classification of Lamiaceae based on plastome phylogenomics. *BMC Biology*, *19*, 2. https://doi.org/10.1186/s12915-020-00931-z

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.