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Could the environment limit dispersal between Sunda and Sahul?

Liam A. Trethowan 🄳

Herbarium, Royal Botanic Gardens, Kew, Richmond, London, UK

Correspondence
Liam A. Trethowan, Herbarium, Royal Botanic Gardens, Kew, Richmond, London TW93AE, UK.
Email: l.trethowan@kew.org

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Summary

Dispersal limitation is cited as the driver of biogeography in archipelagic southeast Asia. Could environmental filtering play an equally important role? From west to east across the archipelago there are three bioregions: Sunda, Wallacea and Sahul. Historic spatial separation of Sunda and Sahul is thought to limit species exchange. Here, I hypothesise that the Wallacean environment may be too stressful for many lineages originating from Sunda and Sahul — limiting dispersal between these two regions. I highlight that Wallacea has: (a) proportionally less lowland habitat; (b) more phytotoxic, heavy metal-rich ultramafic soils; (c) sea currents flowing toward drought-prone seasonal areas; and (d) forests that may be shorter with a different biotic environment. Preliminary results show that genera previously identified as originating from Sunda (using fossil and phylogenetic data) are shorter in stature (an indicator of stress tolerance), are more likely to be found in the smaller lowland areas and seasonal habitat of Wallacea and occupy islands further east. Shorter genera originating from Sahul are more likely to occupy ultramafic-rich areas of Wallacea and to be found further west. Incorporating species strategies, such as stress tolerance, into future work should clarify environmental filtering's influence upon southeast Asian biogeography.

KEYWORDS
dispersal limitation, Grime's CSR theory, Janzen's seasonality hypothesis, southeast Asia, Wallacea

1 | INTRODUCTION

Biogeographic patterns are underpinned by which species from the regional source pool are found in local communities (Zobel, 2016). Species have to overcome the spatial distance required to reach the community (dispersal limitation) and cope with the environmental variables found there (environmental filtering). In southeast Asia, there is a western source pool (Sunda), an eastern source pool (Sahul) and a region in between known as Wallacea (Figure 1a, b). Sunda, part of the Asian continental plate, and Sahul, the Australian, were historically more distant until they collided c. 26 million years ago, causing the uplift of Wallacea (Hall, 2017). The communities of Wallacea then assembled via dispersal from the two adjacent source pools (Pärtel & Zobel, 1999). Wallacean uplift also increased dispersal between Sunda and Sahul (Sniderman & Jordan, 2011; Crayn et al., 2015). Dispersal is referred to herein as both movement of a propagule between areas and establishment in the novel area. Evidence suggests current distributions of species may be a result of dispersal being limited by the past spatial separation of the two source pools (Schuster, 1972). However, Wallacea's environment is potentially more stressful than that in Sunda and Sahul. This is important because successful dispersal between Sunda and Sahul is

less likely to occur if the intervening land area is unsuitable for the lineages dispersing across it (Giarla et al., 2018). Environmental filtering could therefore be limiting which type of species successfully disperse across the archipelago.

Sunda and Sahul are currently similar in size. However, at the time of Asian and Australian plate collision most of New Guinea was yet to form (Baldwin et al., 2012) and the wet tropical regions of Australia had substantially contracted (Hill et al., 1999). Therefore, the source pool area of Sahul was far smaller than that of Sunda at the time of Wallacean island uplift. The legacy of this should not be forgotten when thinking about the environmental variables presented later.

2 | HYPOTHESES

This essay outlines how Wallacea may be unsuitable for the dispersal of species lacking stress tolerance traits. The next four sections each focus upon a different aspect of the Wallacean environment: (a) less lowland is available for dispersing lowland lineages; (b) greater frequency of ultramafic soils may limit lineages unable to tolerate high heavy-metal concentrations; (c) sea-dispersed wet tropical lineages may be limited by prevailing sea currents that flow toward the few islands that have a major dry season; (d) understorey species may be limited by different microenvironments caused by a possibly more stunted canopy.
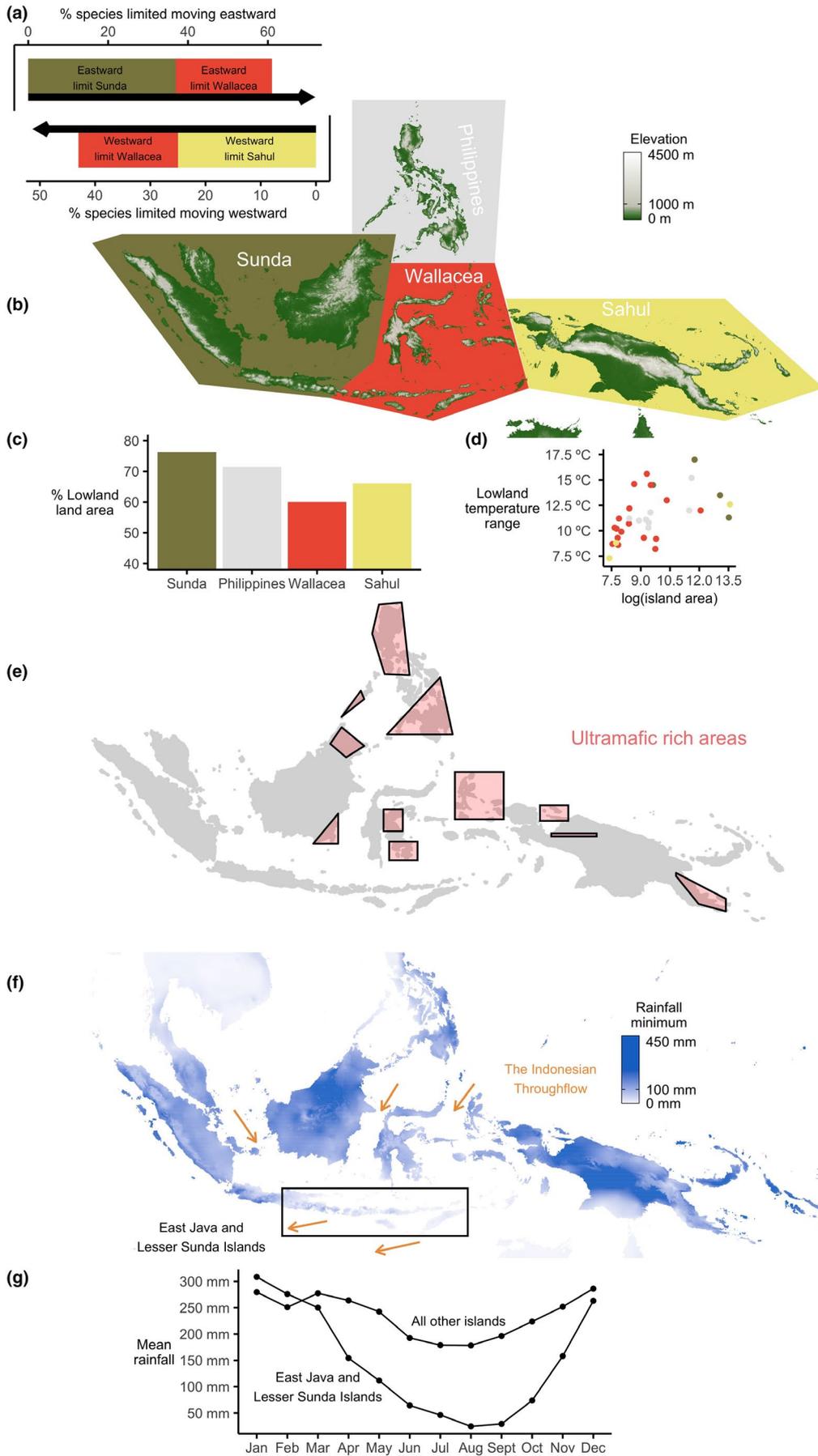
I suggest that incorporating species' ecological strategies will be useful for future work (Grime, 1977; Westoby, 1998). I propose that stress tolerance should promote dispersal between Sunda and Sahul due to the stressful nature of the Wallacean environment. As a preliminary test of this hypothesis, I examine whether a decrease in plant height increases the chance of a genus being distributed across southeast Asia and whether this interacts with the stressful environmental variables found across the region (detailed methods and code in Appendices S1 and S2). I use plant height as a measure of stress tolerance as it decreases in response to stress imposed by soils, seasonality, and elevation (Fernandez-Going et al., 2013; Girardin et al., 2014; Givnish et al., 2014) and increases in more productive conditions where species are better adapted for competition (Grime, 1977).

3 | LESS LOWLAND HABITAT AVAILABLE IN WALLACEA

Proportionally more of Wallacea's landmass is made up of small islands compared to Sunda and Sahul. In general, the switch from lowland to montane vegetation occurs at lower elevations on smaller islands (Irl et al., 2016). Small Wallacean islands therefore have less "lowland" habitat available despite having many areas at identical lowland elevations to Sunda and Sahul. Additionally, Wallacea has proportionally less area of lowland elevation available compared to the adjacent bioregions (Figure 1c). Could many of the lowland lineages that have not dispersed successfully between Sunda and Sahul have been limited by a lack of suitable lowland habitat in Wallacea?

Smaller islands have montane forests at lower elevations because maritime temperatures stabilise the temperatures of their lowlands (Figure 1d; Pouteau et al., 2018). Greater climatic stability means little flux to cooler temperatures. Species are then less exposed to the lower temperatures they need to tolerate at higher elevation and are therefore more likely to be restricted to lower elevations (Janzen, 1967). The smaller the island, the greater the stabilising effect of maritime temperature upon lowlands (Figure 1d) and the greater the decrease in temperature variability that species are exposed to and can tolerate — resulting in species with reduced elevational ranges (Janzen, 1967). The effect is such that the change from lowland to montane vegetation on small southeast Asian islands can be found at elevations less than 400 m (Proctor, 2003). So, while lowland habitat on Sunda and Sahul may reach 1,000 m (Paijmans, 1976; Kitayama, 1992), the majority of lowland habitat on the smaller islands of Wallacea should be found at much lower elevations. As a result, far less lowland habitat is available for lowland lineages dispersing from Sunda and Sahul into Wallacea. Although many lowland lineages are found in both Sunda and Sahul (Hartley, 1986) there are still many that have failed to disperse eastward or westward across Wallacea (Baker & Couvreur, 2012; Culmsee & Leuschner, 2013). These lineages are all candidates for limitation caused by the lack of lowland habitat availability on the smaller Wallacean islands.

FIGURE 1 (a) The percentage of plant species limited by the east or west boundaries of southeast Asia's bioregions according to Flora Malesiana (van Welzen et al., 2011). (b) Elevation across the islands of southeast Asia. (c) Percentage of lowlands across the three bioregions and the Philippines. Elevation data from the Shuttle Radar Topography Mission. The lowland cut-off point used in (c) is 400 m because environmental shifts shape plant traits at these elevations (Umaña & Swenson, 2019a; Umaña & Swenson, 2019b) and in the most remote mountains of the archipelago, montane flora can be found at these elevations (Holthuis & Lam, 1942; Trethowan personal observation). In the larger islands that dominate Sunda and Sahul lowland flora is found at higher elevations (MacKinnon et al., 1996; Utteridge & Edwards, 2009; Marshall & Beehler, 2012); therefore, the pattern of less lowland in Wallacea should be even greater than seen in (c). (d) The relationship between lowland temperature range and log island area in southeast Asia. Temperature range is the difference between maximum and minimum monthly temperature from Worldclim. (e) Ultramafic soils across southeast Asia. Adapted from Galey et al. (2017). Currently available soil distribution data sets do not differentiate areas of mafic and ultramafic soils; therefore, simple polygons are used to reflect the Galey et al. (2017) map (edited for Sulawesi from field observations). The greater proportion of Wallacea with ultramafic areas compared to Sunda and Sahul is observable visually. Small areas of ultramafic soils, e.g. those present in Sumatra and the Lesser Sunda Islands, are not shown. (f) Sea currents flow toward seasonal East Java and Lesser Sunda Islands. (g) Mean rainfall per month in East Java and the Lesser Sunda Islands and on all other islands in Wallacea, Sunda and Sahul (i.e. excluding the Philippines). Rainfall data from WorldClim

(a) % species limited moving eastward

Eastward limit Sunda | Eastward limit Wallacea

Westward limit Wallacea | Westward limit Sahul

% species limited moving westward

(b)

Elevation
4500 m
1000 m
0 m

Philippines

Sunda

Wallacea

Sahul

(c)

% Lowland land area

Sunda | Philippines | Wallacea | Sahul

(d)

Lowland temperature range

log(island area)

(e)

Ultramafic rich areas

(f)

Rainfall minimum
450 mm
100 mm
0 mm

The Indonesian Throughflow

East Java and Lesser Sunda Islands

(g)

Mean rainfall

All other islands

East Java and Lesser Sunda Islands

Jan Feb Mar Apr May Jun Jul Aug Sept Oct Nov Dec

4 | ULTRAMAFIC SOILS ARE MORE PREVALENT IN WALLACEA

The impact of soil variability upon southeast Asian biogeography is largely unknown (Ashton, 2014). Southeast Asia has the tropics' largest areas of ultramafic soils (van der Ent, Baker, van Balgooy, et al., 2013). There are far greater areas of ultramafic soils in Wallacea compared to Sunda and Sahul (Figure 1e; Galey et al., 2017). For plants, these soils are influential because of their detrimentally high heavy-metal content (Proctor, 2003). Cell membranes, enzymes and DNA are all damaged by heavy metals (Proctor, 2003). To cope with ultramafic soils, plants often exclude soil metal or less frequently tolerate increased internal metal content (van der Ent, Baker, Reeves, et al., 2013). Limitation of species that lack coping strategies subsequently dictates the composition of ultramafic plant communities (Pillon et al., 2010). In southeast Asia, this results in an increase in Sahul lineages in ultramafic communities (Brambach et al., 2020). Lineages most successful in the non-ultramafic soils widespread in Sunda and Sahul should be limited by the ultramafic soils of Wallacea.

5 | RAINFALL SEASONALITY AND SEA CURRENTS

The clearest climatic difference in the southeast Asian Archipelago is between the seasonal tropical area of East Java and the Lesser Sunda Islands and the rest of the islands that are predominantly wet tropical (van Steenis, 1979). This is most obviously demarcated by rainfall, where islands from East Java to Timor have lower minimum rainfall values that persist for a number of months (Figure 1f, g). Restriction of plant lineages to either the seasonal or wet tropics is common (Crisp et al., 2009), although there are lineages that are able to cross a seasonality gradient. However, even within these clades dispersal tends to be into seasonal areas from the wet tropics and not the reverse (Pennington & Lavin, 2016). This suggests seasonal areas of Wallacea could limit dispersal for lineages unable to tolerate the conditions and, equally, limit tolerant lineages that are unable to disperse back into the predominantly wet tropical areas of Sunda and Sahul.

The relatively small landmass of the seasonal islands in the south may limit their influence. However, the direction of sea currents in the archipelago makes their importance more likely. The Indonesian throughflow current is primarily responsible for water movement in the archipelago. Water flows from the Pacific to the Indian Ocean, predominantly North to South (Hu et al., 2015) (Figure 1f). This increases the chance that water-dispersed propagules will be transported toward Wallacea's seasonal islands (Wu et al., 2018), meaning propagules of wet tropical species that enter Wallacea are less likely to be transported to appropriate wet tropical areas of Sunda and Sahul where establishment success is more likely. Therefore, seasonality gradients (Dalsgaard et al., 2014) and directional limits to sea dispersal in Wallacea (Wu et al., 2018) may restrict the movement of lineages between Sunda and Sahul.

6 | SHORT FORESTS OF WALLACEA

There is some evidence that Wallacea's forest canopy tends to be shorter than that in Sunda and Sahul (Venter et al., 2017; Scheffer et al., 2018; Trethowan et al. unpublished data for Sulawesi and Sumbawa). Some studies do not support this, however (Simard et al., 2011; Tao et al., 2016). If confirmed by more field-based observations, the shorter canopy in Wallacea should have consequences for plant distributions. Changing canopy height causes parallel shifts in environmental conditions experienced by species within the understorey (Blonder et al., 2018). The change in the understorey environment causes differences in the relationship between plant and invertebrate communities (Spicer et al., 2017) and alters plant–plant competitive dynamics (Blaser et al., 2013). One result of this is that tall trees seem to create environmental conditions that perpetuate the success of other tall trees (Banin et al., 2012). In the tallest forests juveniles tend to be canopy species, whereas shorter forests contain more understorey species (Banin et al., 2012; Brambach et al., 2017). If environmental variables do not support the initial formation of tall forest, then taxa that rise up the competitive hierarchy only when tall will likely struggle to establish in Wallacea. Could this be the case for dipterocarps — the tropics' tallest trees, which dominate on Borneo but not in Wallacea or islands further east (Brearley et al., 2016)? I suggest that Wallacea's shorter forest environment may limit dispersal of lineages that are most successful when in taller forest environments.

7 | THE PHILIPPINES

Here Sunda is defined as Peninsular Malaysia, Sumatra, Java, and Borneo and Sahul as New Guinea plus surrounding islands (the islands in between being Wallacea) (Figure 1b). The Philippines are not included in this circumscription because: (a) floristically they lack similarity with Sunda (van Welzen et al., 2011); (b) they do not lie directly between Sunda and Sahul, so do not affect the most direct dispersal pathway between the two bioregions; and (c) the limitations outlined below should be less relevant to lineages that originate from the Philippines and disperse into Wallacea because these two regions have a relatively similar environment (van Steenis, 1979).

8 | BRINGING SPECIES STRATEGIES INTO SOUTHEAST ASIAN BIOGEOGRAPHY

The upcoming years will bring an increase in phylogenetic and trait data. Our ability to simplify these data and use it for coherent analyses will determine how much we learn about southeast Asian biogeography. Grime's CSR (Grime, 1977) could prove a useful starting point. The hypothesis simplifies the trait variation of plants into three strategies denoted by the letters C, S and R, referring respectively to competitive, stress-tolerant and ruderal strategies. Competitive species outcompete others in benign and little-disturbed environments, stress-tolerant species occupy

environments naturally detrimental to others, and ruderal species speedily occupy disturbed habitats. This classification allows a more mechanistic understanding of why or why not a dispersal event might happen.

Preliminary results show the importance of stress tolerance for dispersal in southeast Asia. I found that a decrease in minimum height (maximum height of the shortest species in the genus) increases the chance that a genus will be distributed across the archipelago (Figure S1). Additionally, stressful environmental variables most prevalent in Wallacea and spatial limitation significantly interact with minimum height to shape the genus distributions observed. Results differed for genera that originated from Sunda (that disperse east) or Sahul (that disperse west; see Brambach et al., 2020 for details of how genus origin was assigned). Models of genera originating from Sunda showed significant interactions between minimum height and lowland (<400 m) area and seasonality (all likelihood ratio tests [LRTs] $p < 0.05$) but little ultramafic soil influence (LRT $p > 0.05$). Conversely, ultramafic soils were the only environmental variable that interacted with minimum height to shape the distribution of genera originating from Sahul (LRT $p < 0.05$). For all genera (irrespective of origin), longitude (i.e. spatial limitation) interacts with minimum height to shape their distribution (LRTs $p < 0.05$). In summary, when faced with a stressful environment, reduction of height appears to increase the likelihood a genus will be able to disperse across southeast Asia.

More trait data are certainly needed for tractable tests of the importance of environmental filters in southeast Asia. Leaf traits have previously been defined by the CSR three-way trade-off (Pierce et al., 2017). Where competitive species have high leaf area, stress-tolerant species have high leaf dry matter content and ruderal species have high specific leaf area. Now an Indonesian forest plot network has been established (Brearley et al., 2019), a survey of leaf traits at sites would be a logical first aim. Equally, this essay made use of Flora Malesiana and taxonomic revisions (and therefore herbarium specimens), which store a wealth of trait data awaiting analysis.

Floral traits may also prove useful predictors of southeast Asian plant distributions (E-Vojtkó et al., 2020). For instance, self-compatibility enhances the likelihood of island colonisation (Grossenbacher et al., 2017) and fruit type may explain coupled distributions of flora and fauna (Delmas et al., 2020). Generally, the traits of species restricted to Sunda and Sahul should differ from species that both disperse into and across the more stressful Wallacean islands (de Bello et al., 2012).

9 | FUTURE STUDY

Analyses are needed at finer phylogenetic scales, that allow intrageneric/intraspecific variance, mean and median trait values to be examined (Hulshof & Swenson, 2010). Collected trait data will be key to understanding how lineages have responded to island uplift and past environmental flux (Sukumaran & Knowles,

2018). Over time, the influence of the stressful environmental variables emphasised above should pulse with their prominence across the archipelago. For instance, increased seasonality in the late Pleistocene (Hamilton et al., 2019) could have left a signature of draught tolerance in the islands' forests. Testing predictions that integrate past environmental change (Calatayud et al., 2019) and embrace relevant theory, such as Grime's CSR, should offer further evidence of how the environment shapes southeast Asian biogeography.

ORCID

Liam A. Trethowan https://orcid.org/0000-0002-0326-9828

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Statistical analysis

Appendix S2. Code to run analysis and produce figure S1

Appendix S3. Summary of phylogenetic generalised mixed effects model outputs

Appendix S4. Reference list for trait data

Appendix S5. Code to produce figure of the southeast Asian environment