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Which is the richest of them all? Comparing area-adjusted plant diversities of Mediterranean- and tropical-climate regions

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Abstract

Mediterranean- and tropical-climate regions harbour the richest regional-scale floras globally. Until recently, however, comparisons of their diversities have been hindered by a lack of comprehensive inventories of tropical floras. Using taxonomically verified floras, we analyse area-adjusted plant diversities of five Mediterranean- and 35 tropical-climate regions to determine which are the most species-rich regions on Earth. On average, the Neotropics and tropical Southeast Asia support the most diverse floras globally. However, the area-adjusted diversities of the richest floras in these tropical regions are matched by those of two Mediterranean-climate floras, namely the Cape (second richest) and Mediterranean Basin (sixth richest). Except for Madagascar and Burundi, the Afrotropical regions were substantially less diverse than other tropical floras and half of the Afrotropical floras were poorer than the least diverse Mediterranean-climate region, namely Central Chile. We evaluate the likely ecological and evolutionary drivers of these plant diversity patterns in terms of three hypotheses that are apposite for global scale comparisons, namely water-energy dynamics, biome stability, and ecological heterogeneity. Water-energy dynamics appear to have little influence in explaining these diversity patterns: nodes of high global plant diversity are associated with climates that support year-round plant production (tropical climates) and those where the growing season is constrained by a winter rainfall regime (Mediterranean-type climates). Moreover, while the Afrotropics have higher primary production than the Neotropics and Southeast Asian tropics, they have markedly lower plant diversity. Instead, these patterns appear to be consistent with the hypothesis that the synergy of historical biome stability (reducing extinction rates) and high ecological heterogeneity (promoting speciation rates) better explain global patterns of regional-scale plant diversity.

Highlights

- We conducted a species–area analysis of comprehensive regional floras of three tropical and the five Mediterranean-climate regions of the world.
- Among tropical regions, the highest diversities were recorded in the Neotropics and Southeast Asia, with the Afrotropics generally recording the lowest diversities.
- The floras of Mediterranean-climate regions showed high variation: the Cape region recorded the second highest diversity after a Neotropical Andean flora; the Mediterranean Basin and Southwestern Australian floras were comparably rich as many Neotropical and Southeast Asian floras; and California and Chile have floras richer than many Afrotropical regions.
- The fact that the most plant-rich parts of the globe are shared amongst tropical and temperate regions challenges the hypothesis that global patterns of diversity are best explained by water–energy dynamics. Historical processes underpinned by high biome stability and high ecological heterogeneity are likely to be more effective predictors of global plant diversity patterns.

Keywords: Afrotropics, biome stability, ecological heterogeneity, global diversity patterns, Mediterranean-climate regions, Neotropics, Southeast Asia, species–area relationship

Introduction

It has been known for at least a century that surface area is the best predictor of species numbers

at the regional scale (areas > 1 km²) (Rosenzweig 1995, Lomolino 2000, Whittaker and Triantis 2012, Matthews et al. 2021). By fitting data to a species–area

curve, or by using gridded cells of equal-area, and thereby controlling for the effect of surface area, it is possible to make meaningful comparisons of diversity among different biotas. While there are no constraints on computing the area of a region for species–area analysis, building a comprehensive and defensible inventory of species is a much greater challenge. Even though such floristic inventories of Mediterranean-climate regions have been available for some decades (e.g., Hopper and Gioia 2004, Manning and Goldblatt 2012, Rundel et al. 2016, Treurnicht et al. 2017), this generally remains a challenge for poorly known tropical floras (Raven et al. 2020). However, the recent spate of taxonomically verified inventories from Neotropical (Ulloa Ulloa et al. 2017) and Southeast-Asian regions (Zhu 2016, Middleton et al. 2019, Cámara-Leret et al. 2020), and the prior existence of such inventories for tropical Africa (Sosef et al. 2017), has created the opportunity to compare the plant diversities of Mediterranean-climate (MC) and tropical-climate (TC) regions – both contenders for supporting the richest regional-scale floras on Earth (Cowling et al. 1996, Mutke and Barthlott 2005, Kreft and Jetz 2007, Rundel et al. 2016, Brummitt et al. 2020).

Our purpose here is to present the diversity patterns associated with TC and MC regions to inform the debate on where are the most plant-rich parts of the globe (Lamont et al. 1977, Gentry 1992, Cowling et al. 1996, Latimer et al. 2005, Mutke and Barthlott 2005, Kreft and Jetz 2007, Eiserhardt et al. 2017, Ulloa Ulloa et al. 2017, Brummitt et al. 2020, Raven et al. 2020). We also discuss the likely ecological and evolutionary drivers of these plant diversity patterns. Three hypotheses are apposite for global-scale comparisons; these are water–energy dynamics, biome stability, and ecological heterogeneity (Latham and Ricklefs 1993, Rosenzweig 1995, Francis and Currie 2003, Ricklefs 2006, Kreft and Jetz 2007, Mittelbach et al. 2007, Cowling et al. 2015).

Water–energy dynamics (O’Brien 1993, O’Brien 1998, O’Brien 2006) has long been invoked to explain the gradient of declining plant diversity from low to high latitudes (e.g., Francis and Currie 2003, Hawkins et al. 2003, Mutke and Barthlott 2005); the high richness of TC regions is attributed to the optimization there of available energy – “not too much, not too little” (O’Brien 1993) – and maximization of available moisture. It is argued the year-round, high productivity of these TC regions is linked to greater ecological opportunity for speciation than in the less productive ecosystems at higher latitudes (Francis and Currie 2003, Hawkins et al. 2003, O’Brien 2006).

Others have invoked explanations underpinned by historical events, notably the age-and-area or biome-stability hypothesis. This hypothesis predicts highest diversity in regions where, because of muted climate change, biome distributions have remained relatively stable over most of the Cenozoic (Latham and Ricklefs 1993, Ricklefs 2006, Forest et al. 2007). Biome stability promotes the accumulation of species by reducing extinction rates and maintaining speciation rates (Ricklefs 2006, Cowling et al. 2017, Colville et al. 2020). While most TC regions have high biome stability

(Latham and Ricklefs 1993, Jansson and Dynesius 2002, Mittelbach et al. 2007), this is also the case for several extratropical areas, notably the Cape and Southwestern Australian MCs (Hopper 2009, Cowling et al. 2015).

Finally, there is wide consensus that regions of high ecological heterogeneity, measured for example, as topographic, climatic or edaphic complexity, would support more plant species than physiographically more uniform regions (Whittaker 1972, Rosenzweig 1995). High ecological heterogeneity provides increased ecological opportunity for speciation and reduces extinction rates by providing refugia for shrinking populations (Rosenzweig 1995, Fine 2015, Colville et al. 2020). Both water–energy and biome stability interact positively with ecological heterogeneity in models for regional plant species diversity (Field et al. 2005, Colville et al. 2020).

Our focus is on the outcomes of diversification, namely contemporary plant species richness in TC and MC regions, and not in the mechanisms (e.g., trait evolution) and associated traits that produced this diversity. These mechanisms will vary from region to region, not unexpected given that the floras in the different MC and TC regions have different phylogenetic structures. Here, we evaluate these diversity outcomes in terms of physiographic drivers of ecological opportunity for diversification, namely stability, productivity and heterogeneity. While trait-based relationships are important for understanding the evolution of diversity within regions or among phylogenetically related regions [e.g., Rundel et al. (2016, 2018) for MCs and Fine and Baraloto (2016), Onstein et al. (2017) and Wang et al. (2022) for TCs], we suggest that they are less useful for seeking explanations of global diversity patterns.

Materials and Methods

Species–area data for MC and TC regions (Data S1) were collated from taxonomically reliable flora inventories. The TC regions included the Neotropics, Afrotropics and tropical Southeast Asia. Our dataset comprised a total of 40 regions (Figure 1a). We included in our dataset continental tropical islands (e.g., Borneo and Madagascar) that are too large to register an island effect (Kreft et al. 2008). Mediterranean-climate regions ($n = 5$) included floras of the Cape (Manning and Goldblatt 2012), California, Chile, the Mediterranean Basin and Southwestern Australia (Rundel et al. 2016). Data for the Afrotropics ($n = 19$) were gathered from Sosef et al. (2017) and included species numbers for Benin, Burundi, Cameroon, Central African Republic, Côte d’Ivoire, Democratic Republic of the Congo, Equatorial Guinea, Ethiopia, Gabon, Ghana, Kenya, Liberia, Malawi, Mozambique, Nigeria, Rwanda and Tanzania. The size of Madagascar’s Afrotropical island flora was taken from Cámara-Leret et al. (2020). For the Neotropics ($n = 8$), we extracted data from Ulloa-Ulloa et al. (2017), including species numbers for the following regions: Bolivia, Brazil, Central America (comprising Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua and Panama), Colombia, Ecuador, the Guianas (comprising French Guiana, Guyana and

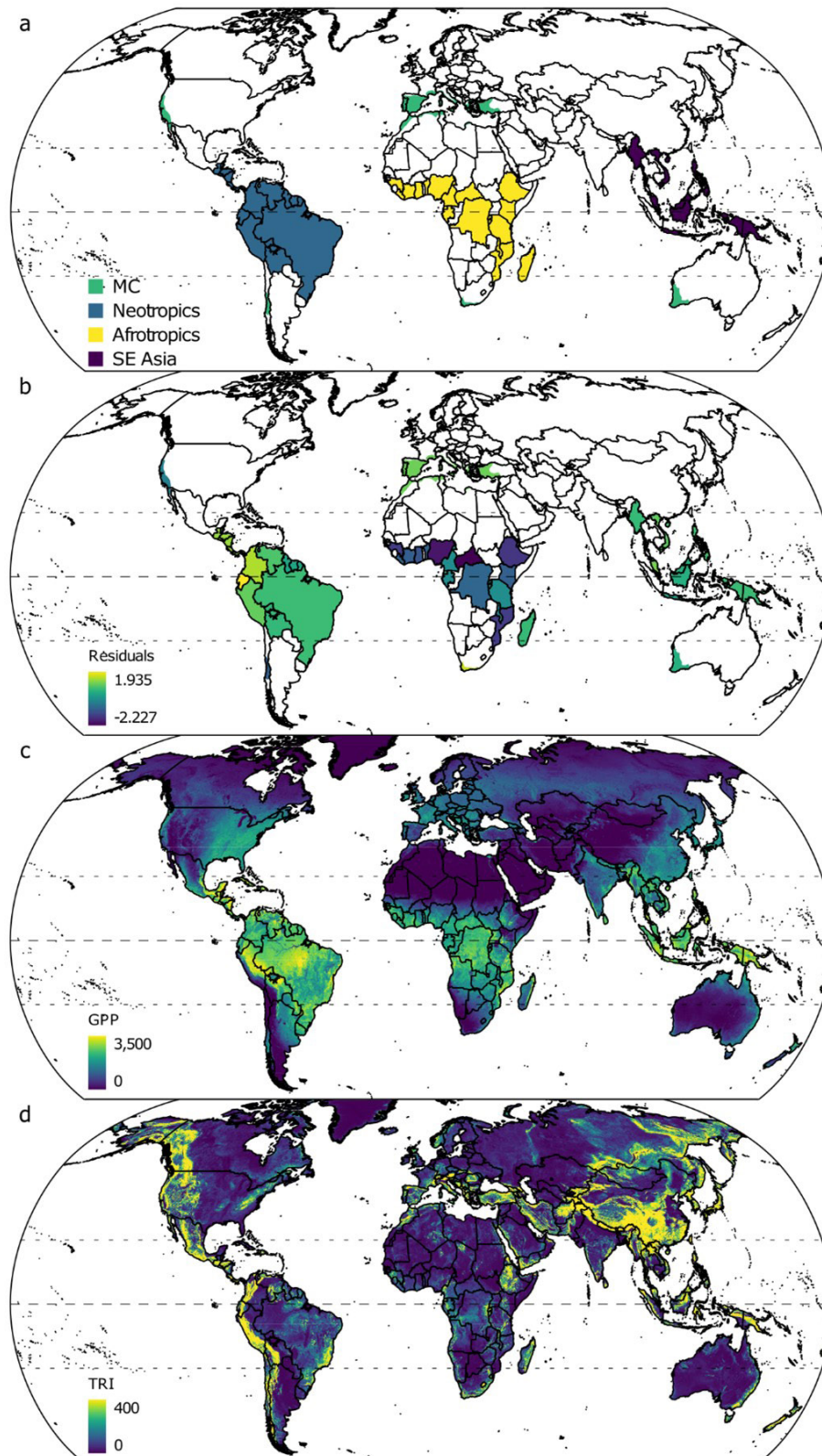


Figure 1. The distribution of Mediterranean- and tropical-climate regions and their relative plant diversities in relation to ecological drivers of global plant diversity. (a) Distribution of 40 floras considered in this study, including those of Mediterranean-climate, Neotropical, Afrotropical and Southeast-Asian regions. (b) Studentized residuals of the global species–area regression model for the 40 floras. (c) Mean annual gross primary production (GPP; $\text{g C m}^{-2} \text{yr}^{-1}$) (Zhang et al. 2017) as a proxy for water–energy dynamics. (d) Mean terrain ruggedness index (TRI) (Amatulli et al. 2018) as a proxy for ecological heterogeneity.

Suriname), Peru and Venezuela. For TCs from Southeast Asia ($n = 8$), we included floras of Borneo and New Guinea (Cámara-Leret et al. 2020), Java (Backer and Bakhuizen van den Brink, Jr. 1963), the Philippines (Pelser et al. 2011), Hainan and Vietnam (Zhu 2016), Myanmar (Yang et al. 2020), and Peninsular Malaysia (Middleton et al. 2019).

The relationship between surface area and species diversity at the regional scale ($> 1 \text{ km}^2$) is non-linear and best formalised as a power function:

$$S = cA^z$$

where S represents the species number, A the surface area, c the intercept and z the slope (Arrhenius 1921, Gould 1979, Rosenzweig 1995). To compare the diversities of various regions, we fitted our species–area data to a double-logarithmic (using \log_{10}) regression model – an effective and widely used approximation of the power curve (Rosenzweig 1995) – thus allowing us to control for the effect of area on species numbers and to make meaningful comparisons of diversity between regions. Following Rosenzweig (1995), we used this regression analysis to estimate the c - and z -values for the global dataset (i.e., combining in one analysis the MC, Afrotropical, Neotropical and Southeast Asian data). To assess the

relative diversities of individual MC and TC regions, we analysed the studentized residuals of the global species–area regression model, in conjunction with model prediction intervals (80% and 90%), to identify those with higher- and lower-than-predicted diversities. All analyses were conducted using R 4.1.0 statistical software (R Core Team 2021), with additional use of the ‘tidyverse’ (Wickham et al. 2019) and ‘patchwork’ (Pedersen 2020) R packages for data wrangling and visualization.

Results

Analysis of the residuals of the global species–area regression model (Fig. 2; Table 1) showed significant variation in area-adjusted diversity between regions (ANOVA: $F_{3,36} = 14.540$; $P = 2.310e^{-7}$). Floras of Neotropical and Southeast-Asian TCs were generally richer than predicted, while diversity varied substantially among MCs, with some being richer than predicted, and others being poorer (Figure 1b). Afrotropical TCs were generally poorer in species than predicted, with the lower diversity in this region compared with all others supported by statistical evidence (Tukey post-hoc test: $P \leq 0.022$; Figure S1). We found no statistical support for the group average

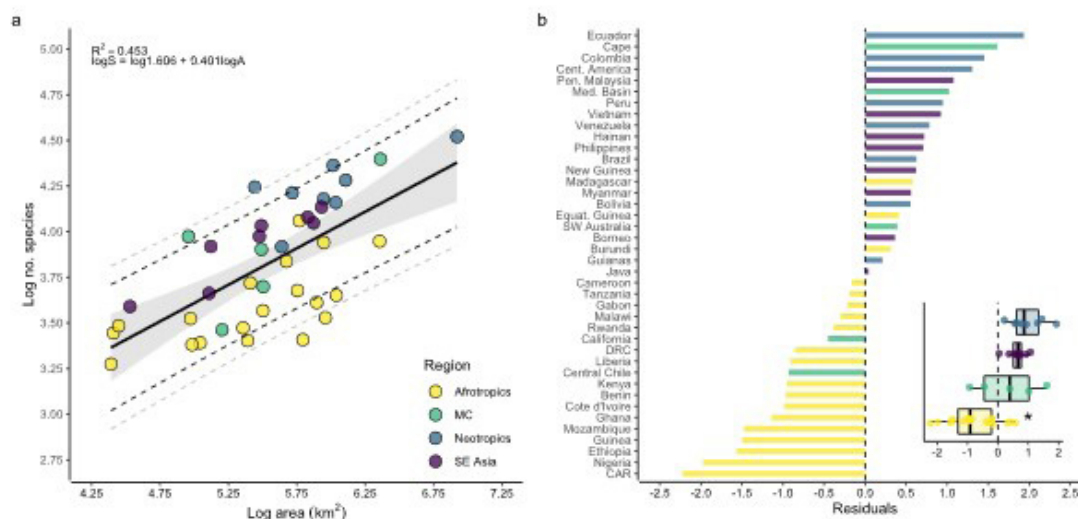


Figure 2 Comparative diversity of 40 floras of tropical- (Afrotropics, Neotropics, Southeast Asia) and Mediterranean-climate regions. (a) Global species–area curve for the floras. Data are \log_{10} -transformed. The grey ribbon indicates the 95% confidence interval for the curve; the (inner) black dashed line indicates the 80% prediction interval of the species–area regression model; and the (outer) grey dashed line indicates the 90% prediction interval of the model. Text in the upper-left provides the multiple- R^2 value and equation for the model, where S = number of species and A = area (km^2). Additional results for model fit are provided in Table 1. (b) Ranked studentized residuals of the species–area regression model for the 40 floras. Box-and-whisker inset shows variation of residuals within each region. Indicated are the median value (horizontal bar), the twenty-fifth and seventy-fifth percentiles (lower and upper bounds of box, respectively), and the range of values that are within $1.5 \times \text{IQR}$ (interquartile range) of the twenty-fifth and seventy-fifth percentiles (upper and lower bounds of “whiskers”). Jitter plots of residual values are superimposed on box-and-whisker plots. Note the comparatively low residuals of the Afrotropical region after area has been controlled for (*, Tukey post-hoc test: $P < 0.022$). Abbreviated names for sites: Cent. America, Central America; Pen. Malaysia, Peninsular Malaysia; Med. Basin, Mediterranean Basin; Equat. Guinea, Equatorial Guinea; SW Australia, Southwestern Australia; DRC, Democratic Republic of the Congo; CAR, Central African Republic.

Table 1 Results of linear regression analysis of the species–area relationship for all Mediterranean and tropical-climate floras.

	Estimate	SE	t	P
Intercept ($\log_{10} c$)	1.606	0.398	4.031	0.000258
\log_{10} area (z)	0.401	0.071	5.605	1.983e ⁻⁶
	R ²	Adjusted R ²	Residual SE (df)	P
Model summary	0.453	0.438	0.249 (38)	1.983e ⁻⁶

SE, standard error; df, degrees of freedom.

diversities of MCs, Neotropical and Southeast-Asian TCs being different (Tukey post-hoc test: $P > 0.399$; Figure S1).

The most significant positive outlier was the Neotropical flora of Ecuador – the only flora whose richness fell above the upper 90% prediction interval (PI) of the global species–area model – followed by the Mediterranean-climate Cape and Neotropical Colombia (both above upper 80% PI) (Fig. 2; Table S1). Central America also showed high diversity among Neotropical TCs. Among Southeast Asian TCs, Peninsular Malaysia and Vietnam had highest diversity, while the Mediterranean Basin MC had comparably high diversity. All significant negative outliers were floras of the Afrotropics: substantially lower-than-predicted diversity was found in Mozambique, Guinea and Ethiopia (all below lower 80% PI), while Nigeria and the Central African Republic (both below lower 90% PI) had markedly depauperate floras after accounting for the effect of area. Madagascar was the only Afrotropical TC with a markedly higher species richness than predicted by the global species–area model, with diversity comparable to that of some Neotropical (Bolivia, Brazil) and Southeast Asian (Myanmar, New Guinea) TCs. The Southwestern-Australian MC was as rich as the richest mainland Afrotropical TCs and its diversity was comparable to some Southeast Asian and Neotropical TCs, although these tended to be the poorer areas among the latter two tropical regions. The Californian and Chilean MCs had lower-than-predicted diversity, and markedly so for Chile, which was nonetheless richer than nine Afrotropical TCs, including Kenya, Ghana and the Central African Republic.

Discussion

There has been a longstanding and ongoing debate around the global distribution of biodiversity and the relative importance of contemporary environmental factors and environmental history in shaping these broad spatial patterns (Latham and Ricklefs 1993, Gaston 2000, Hawkins et al. 2003, Qian and Ricklefs 2004, Ricklefs 2006, Mittelbach et al. 2007, Svenning et al. 2015, Schluter 2016). The latitudinal diversity gradient is one of the most striking and general biogeographical patterns globally (Hillebrand 2004), with diversity of most taxa increasing towards the equator and concentrated within the tropics. The amount of ambient available environmental energy has been proposed as an important driver underpinning this diversity gradient (Gaston 2000). For plants, the

best predictors of global-scale diversity are measures that account for both heat and water availability (e.g., evapotranspiration or net primary productivity). These water–energy dynamics play a dominant role in determining global plant diversity patterns (Francis and Currie 2003, Hawkins et al. 2003, O'Brien 2006); however, there are regions that do not conform to the predictions of the water–energy dynamics hypothesis, most notably the hyperdiverse, extratropical Cape MC (Kreft and Jetz 2007). Furthermore, it has been proposed that the relationship between global plant diversity and water–energy dynamics is largely correlative rather than causative (McGlone 1996): as the tropics have enjoyed constant climate and high biome stability throughout the Cenozoic compared to most mid- and high-latitude regions (Latham and Ricklefs 1993, Jansson and Dynesius 2002), the differential levels of climatic fluctuations and biome contractions/expansions in these regions would have influenced the global diversity patterns evident today (Mittelbach et al. 2007, Svenning et al. 2015). Important centres of plant diversity can thus only be explained to a certain extent by contemporary water–energy dynamics without considering the historical contingencies of regional floras (Qian and Ricklefs 2004, Mutke and Barthlott 2005, Kreft and Jetz 2007). In addition, ecological heterogeneity – by increasing ecological opportunity and providing ecological refugia (Rosenzweig 1995, Fine 2015) – acts as a positive multiplier of regional plant diversity in models that invoke both water–energy dynamics (Field et al., 2005; Kreft and Jetz, 2007) and biome stability (Colville et al. 2020, Hagen et al., 2021).

Our results showed that, on average, the Neotropical and Southeast Asian TCs harbour the richest known area-adjusted floras globally and are considerably richer than those from the continental Afrotropics, thus confirming the findings of several previous studies (Richards 1973, Gentry 1992, Kreft and Jetz 2007, Parmentier et al. 2007, Couvreur 2015, Silva de Miranda et al. 2022). However, the diversity of the richest TCs is rivalled by that of some MCs, namely the Mediterranean Basin and especially the Cape – plant diversity of the latter MC is second only to that of Neotropical Ecuador. Similarly, the MC of Southwestern Australia, while being of moderate diversity compared to most Neotropical and Southeast Asian TCs, is richer than most Afrotropical TCs. Even the poorest MC flora – that of Central Chile – is richer than half of the Afrotropical floras, including rainforest regions in central and west Africa.

Here we discuss these diversity patterns in terms of the three hypotheses mentioned above, namely water–energy dynamics, biome stability and ecological heterogeneity. We acknowledge that our comments are not underpinned by a rigorous analysis of proxy explanatory variables for these models (but see Figure 1c, d). Furthermore, as stated in the Introduction, we do not discuss mechanisms of speciation (e.g., pollination processes, adaptation to soil chemical and moisture regimes, adaptation to disturbance regimes) that may operate within different MC and TC regions. Our focus is on the outcomes of speciation, irrespective of the mechanisms associated with these processes.

Water–energy dynamics

The water–energy dynamics hypothesis posits ecological opportunity, and hence species diversity, is maximized in environments with optimum energy and maximum moisture regimes (O'Brien 2006). Thus, this hypothesis predicts consistently higher diversity in TCs than MCs (Figure 1c). In MCs, with winter-rain and summer-drought regimes, plants must adapt to water stress under high-energy conditions (Esler et al. 2018) – very different from the energy and moisture regimes experienced in the perennially wet tropics (Lüttge 1997). This should constrain ecological opportunity for speciation in MCs relative to TCs, leading to lower diversities (Francis and Currie 2003, Hawkins et al. 2003, O'Brien 2006). However, we found that the Cape and Mediterranean Basin MCs are as rich as the most diverse TCs, and that even the poorest MC (Central Chile) is richer than half the Afrotropical TCs. Contrary to the predictions of the water–energy dynamics hypothesis, Hagen et al. (2021) found that median and maximum productivity (estimated by potential evapotranspiration in 110- × 100-km grid cells) was highest in the Afrotropics, which is the most species-poor TC region. Thus, the results of our study, together with those of Hagen et al. (2021), suggest that favourable water–energy dynamics do not consistently manifest high levels of regional plant diversity and that global diversity patterns are likely contingent on additional eco-evolutionary factors.

Biome stability

The biome stability hypothesis predicts that regions subject to muted climate change, especially during the Plio-Pleistocene when global climates fluctuated wildly (Jansson and Dynesius 2002), would support more species than regions where climate change was more marked, owing to limited biome shifts and associated low extinction rates and the maintenance of speciation rates (Latham and Ricklefs 1993, Ricklefs 2006, Mittelbach et al. 2007, Cowling et al. 2017, Colville et al. 2020). Support for this hypothesis comes from both MCs and TCs evaluated in our study. Thus, patterns of plant diversity among MC regions are well predicted by biome stability (Cowling et al. 2015, Rundel et al. 2016), as are patterns within the hyperdiverse Cape MC (Cowling et al. 2017, Forest et al. 2018, Colville et al. 2020, Mazijk et al. 2021). Biome

stability might have likely also played an important role in establishing the relatively species-poor Afrotropics as the “odd man out” (Richards 1973) among TCs. The Afrotropics experienced greater historical aridification during cold eras compared to other TCs (Anhuf et al. 2006), with this trend dating as far back as the Eocene (Couvreur 2015, Hagen et al. 2021). The exception in the Afrotropics is the high relative diversity of the Madagascan flora: although its known climate record is geographically sparse and dates only to the late Pleistocene (Goodman and Jungers 2014) (though beyond the Last Glacial Maximum), this mostly mountainous island likely experienced relatively muted Cenozoic climate change, with evidence of climate refugia contributing to the island's remarkable diversity and endemism (Vences et al. 2009).

Ecological heterogeneity

The ecological heterogeneity hypothesis predicts that regions with higher heterogeneity of climates, soils and topographies will have more ecological opportunities for speciation, and hence more species, than physiographically more uniform regions (Whittaker 1972, Rosenzweig 1995). Generally, there is a great deal of support for this hypothesis from both MCs (Bradshaw and Cowling 2014, Cowling et al. 2015, Rundel et al. 2016, Mazijk et al. 2021) and TCs (Kreft and Jetz 2007, Hagen et al. 2021). Thus, the lower diversity of the Afrotropics can be attributed in part to the virtual absence in this region of the large areas of high-rainfall–low-energy climate (mean annual rainfall > 3,300 mm, mean annual temperature < 13 °C) (Hagen et al. 2021) found in the two other TC regions (Kreft and Jetz 2007, Parmentier et al. 2007). The Afrotropics, therefore, lack the large areas of humid, high-elevation habitats and the opportunities these provide for speciation (Pérez-Escobar et al. 2017, Cámara-Leret et al. 2020). Further support for the ecological heterogeneity hypothesis is that the richest TCs – Ecuador, Colombia and Central America – are all topographically complex regions (Figure 1d; Veblen et al. 2007), where mountainous terrain would have provided opportunities for speciation and a buffering effect against historical climatic change and associated biome shifts (Muellner-Riehl et al. 2019), however muted these would have been (Scotese et al. 2021). In the context of Southeast Asia, the same pattern emerges, with topographically heterogeneous, mountainous regions like Malaysia and Vietnam (Gupta 2005) hosting the most diverse floras. Furthermore, the two richest MCs – the Cape and Mediterranean Basin – are also the most topographically heterogeneous among MCs (Woodward 2009, Bradshaw and Cowling 2014).

Conclusion

Our study is consistent with a growing number of studies demonstrating that muted Cenozoic climate change, in combination with high ecological heterogeneity, is associated with high concentrations of plant species within and among biomes, globally

(Cowling et al. 2015, Colville et al. 2020, Hagen et al. 2021, Suissa et al. 2021). These drivers act in synergy: in both MCs and TCs, global diversity gradients appear to be underpinned by biome stability, which reduces extinction rates, and ecological heterogeneity, which promotes speciation via ecological niche differentiation (Cowling et al. 2015, Colville et al. 2020, Hagen et al. 2021). However, the relative role of these two drivers – and their impacts on trait evolution – in producing the differential diversities of MCs and TCs is likely to be highly region-specific (Cowling et al. 2015, Lamont and He 2017, Hagen et al. 2021). While ecological heterogeneity is comparatively easily quantified, for example through proxies of topographic, climatic and edaphic complexity, measuring historical biome stability remains a challenge. Most studies that seek to quantify biome stability employ surrogate variables of climatic change and its modelled impact on biome distributions (Allen et al. 2020, e.g., Colville et al. 2020, Huntley et al. 2021). However, these methods fail to account for important ecological interactions between climatic regimes, disturbance regimes and edaphic factors, all of which have bearing on historical (and future) biome shifts. Studies that improve our understanding of biome stability, its influence on extinction and speciation, and the enumeration of these processes therefore present an important frontier for future biogeographical research.

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Author contributions

BAG and RMC contributed equally to all aspects of this work.

Data Accessibility

All data analysed in this study are available as supplementary material (Data S1).

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Data S1. Species–area data for 40 floras of Mediterranean- and tropical-climate regions analysed in this study.

Figure S1. Tukey HSD post-hoc test results for comparisons of residuals from species–area regression of Mediterranean–Climate (MC) and tropical-climate floras.

Table S1. Ranked studentized residuals of sites from linear regression on species–area data of Mediterranean- and tropical-climate floras.

References

- Allen, J.R.M., Forrest, M., Hickler, T., Singarayer, J.S., Valdes, P.J. & Huntley, B. (2020) Global vegetation patterns of the past 140,000 years. *Journal of Biogeography*, 47, 2073–2090. <https://doi.org/10.1111/jbi.13930>
- Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J. & Jetz, W. (2018) A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, 5, 180040. <https://doi.org/10.1038/sdata.2018.40>
- Anhuf, D., Ledru, M.-P., Behling, H., et al. (2006) Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 239, 510–527. <https://doi.org/10.1016/j.palaeo.2006.01.017>
- Arrhenius, O. (1921) Species and area. *Journal of Ecology*, 9, 95. <https://doi.org/10.2307/2255763>
- Backer, C.A. & Bakhuizen van den Brink, Jr., R.C. (1963) *Flora of Java*. Walters and Noordhoff, Groningen.
- Bradshaw, P.L. & Cowling, R.M. (2014) Landscapes, rock types and climate of the Greater Cape Floristic Region. In: *Fynbos: ecology, evolution, and conservation of a megadiverse region*. (ed. by N. Allsopp, J.F. Colville, and G.A. Verboom), pp. 26–46, Oxford University Press, Oxford.
- Brummitt, N., Araújo, A.C. & Harris, T. (2020) Areas of plant diversity—what do we know? *Plants, People, Planet*, 3, 33–44. <https://doi.org/10.1002/ppp3.10110>
- Cámara-Leret, R., Frodin, D.G., Adema, F., et al. (2020) New Guinea has the world's richest island flora. *Nature*, 584, 579–583. <https://doi.org/10.1038/s41586-020-2549-5>
- Colville, J.F., Beale, C.M., Forest, F., Altwegg, R., Huntley, B. & Cowling, R.M. (2020) Plant richness, turnover, and evolutionary diversity track gradients of stability and ecological opportunity in a megadiversity center. *Proceedings of the National Academy of Sciences USA*, 117, 20027–20037. <https://doi.org/10.1073/pnas.1915646117>

- Couvreur, T.L.P. (2015) Odd man out: why are there fewer plant species in African rain forests? *Plant Systematics and Evolution*, 301, 1299–1313. <https://doi.org/10.1007/s00606-014-1180-z>
- Cowling, R.M., Bradshaw, P.L., Colville, J.F. & Forest, F. (2017) Levyns' Law: explaining the evolution of a remarkable longitudinal gradient in Cape plant diversity. *Transactions of the Royal Society of South Africa*, 72, 184–201. <https://doi.org/10.1080/0035919X.2016.1274277>
- Cowling, R.M., Potts, A.J., Bradshaw, P.L., et al. (2015) Variation in plant diversity in mediterranean-climate ecosystems: the role of climatic and topographical stability. *Journal of Biogeography*, 42, 552–564. <https://doi.org/10.1111/jbi.12429>
- Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K. & Arianoutsou, M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, 11, 1996. [https://doi.org/10.1016/0169-5347\(96\)10044-6](https://doi.org/10.1016/0169-5347(96)10044-6)
- Eiserhardt, W.L., Couvreur, T.L.P. & Baker, W.J. (2017) Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome. *New Phytologist*, 214, 1408–1422. <https://doi.org/10.1111/nph.14516>
- Esler, K.J., Jacobsen, A.L. & Pratt, R.B. (2018) *The Biology of Mediterranean-Type Ecosystems*. Oxford University Press, Oxford. <https://doi.org/10.1093/oso/9780198739135.001.0001>
- Field, R., O'Brien, E.M. & Whittaker, R.J. (2005) Global models for predicting woody plant richness from climate: development and evaluation. *Ecology*, 86, 2263–2277. <https://doi.org/10.1890/04-1910>
- Fine, P.V.A. (2015) Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics*, 46, 369–392. <https://doi.org/10.1146/annurev-ecolsys-112414-054102>
- Fine, P.V.A. & Baraloto, C. (2016) Habitat endemism in white-sand forests: insights into the mechanisms of lineage diversification and community assembly of the Neotropical flora. *Biotropica*, 48, 24–33. <https://doi.org/10.1111/btp.12301>
- Forest, F., Colville, J.F. & Cowling, R.M. (2018) Evolutionary diversity patterns in the Cape Flora of South Africa. In: *Phylogenetic Diversity*. (ed. by R. Scherson and D. Faith), pp. 167–187, Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-93145-6_9
- Forest, F., Nänni, I., Chase, M.W., Crane, P.R. & Hawkins, J.A. (2007) Diversification of a large genus in a continental biodiversity hotspot: temporal and spatial origin of *Muraltia* (Polygalaceae) in the Cape of South Africa. *Molecular Phylogenetics and Evolution*, 43, 60–74. <https://doi.org/10.1016/j.ympev.2006.08.017>
- Francis, A.P. & Currie, D.J. (2003) A globally consistent richness-climate relationship for angiosperms. *The American Naturalist*, 161, 523–536. <https://doi.org/10.1086/368223>
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, 405, 220–227. <https://doi.org/10.1038/35012228>
- Gentry, A.H. (1992) Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos*, 63, 19. <https://doi.org/10.2307/3545512>
- Goodman, S.M. & Jungers, W.L. (2014) *Extinct Madagascar: picturing the island's past*. University of Chicago Press, Chicago and London.
- Gould, S.J. (1979) An allometric interpretation of species-area curves: the meaning of the coefficient. *The American Naturalist* 114, 335–343. <https://doi.org/10.1086/283482>
- Gupta, A. ed. (2005) *The physical geography of Southeast Asia*. Oxford University Press, Oxford. <https://doi.org/10.1093/oso/9780199248025.001.0001>
- Hagen, O., Skeels, A., Onstein, R.E., Jetz, W. & Pellissier, L. (2021) Earth history events shaped the evolution of uneven biodiversity across tropical moist forests. *Proceedings of the National Academy of Sciences USA*, 118, e2026347118. <https://doi.org/10.1073/pnas.2026347118>
- Hawkins, B.A., Field, R., Cornell, H. V., et al. (2003) Energy, water and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117. <https://doi.org/10.1890/03-8006>
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163, 192–211. <https://doi.org/10.1086/381004>

- Hopper, S.D. (2009) OCBIL theory: Towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil*, 322, 49–86. <https://doi.org/10.1007/s11104-009-0068-0>
- Hopper, S.D. & Gioia, P. (2004) The Southwest Australian Floristic Region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 35, 623–650. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130201>
- Huntley, B., Allen, J.R.M., Forrest, M., Hickler, T., Ohlemüller, R., Singarayer, J.S., Valdes, P.J. & Williams, J. (2021) Projected climatic changes lead to biome changes in areas of previously constant biome. *Journal of Biogeography*, 48, 2418–2428. <https://doi.org/10.1111/jbi.14213>
- Jansson, R. & Dynesius, M. (2002) The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. *Annual Review of Ecology and Systematics*, 33, 741–777. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150520>
- Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA*, 104, 5925–5930. <https://doi.org/10.1073/pnas.0608361104>
- Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008) Global diversity of island floras from a macroecological perspective. *Ecology Letters*, 11, 116–127. <https://doi.org/10.1111/j.1461-0248.2007.01129.x>
- Lamont, B.B., Downes, S. & Fox, J.E.D. (1977) Importance–value curves and diversity indices applied to a species-rich heathland in Western Australia. *Nature*, 265, 438–441. <https://doi.org/10.1038/265438a0>
- Lamont, B.B. & He, T. (2017) When did a Mediterranean-type climate originate in southwestern Australia? *Global and Planetary Change*, 156, 46–58. <https://doi.org/10.1016/j.gloplacha.2017.08.004>
- Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, 67, 325. <https://doi.org/10.2307/3545479>
- Latimer, A.M., Silander, J.A. & Cowling, R.M. (2005) Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science*, 309, 1722–1725. <https://doi.org/10.1126/science.1115576>
- Lomolino, M. V (2000) Ecology’s most general, yet protean pattern: the species-area relationship. *Journal of Biogeography*, 27, 17–26.
- Lüttge, U. (1997) *Physiological Ecology of Tropical Plants*. Springer Berlin Heidelberg, Berlin, Heidelberg. <https://doi.org/10.1007/978-3-662-03340-1>
- Manning, J.C. & Goldblatt, P. eds. (2012) *Plants of the Greater Cape Floristic Region, Vol. 1: the Core Cape Flora*. South African National Biodiversity Institute, Pretoria.
- Matthews, T.J., Triantis, K.A. & Whittaker, R.J. (2021) The species–area relationship: both general and protean? In: *The Species–Area Relationship*. (ed. by T.J. Matthews, K.A. Triantis, and R.J. Whittaker), pp. 3–19, Cambridge University Press, Cambridge. <https://doi.org/10.1017/9781108569422.004>
- Mazijk, R., Cramer, M.D. & Verboom, G.A. (2021) Environmental heterogeneity explains contrasting plant species richness between the South African Cape and southwestern Australia. *Journal of Biogeography*, jbi.14118. <https://doi.org/10.1111/jbi.14118>
- McGlone, M.S. (1996) When history matters: scale, time, climate and tree diversity. *Global Ecology and Biogeography Letters*, 5, 309. <https://doi.org/10.2307/2997586>
- Middleton, D.J., Armstrong, K., Baba, Y., et al. (2019) Progress on Southeast Asia’s flora projects. *Gardens’ Bulletin Singapore*, 71, 267–319. [https://doi.org/10.26492/gbs71\(2\).2019-02](https://doi.org/10.26492/gbs71(2).2019-02)
- Mittelbach, G.G., Schemske, D.W., Cornell, H. V., et al. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10, 315–331. <https://doi.org/10.1111/j.1461-0248.2007.01020.x>
- Muellner-Riehl, A.N., Schnitzler, J., Kissling, W.D., Mosbrugger, V., Rijdsdijk, K.F., Seijmonsbergen, A.C., Versteegh, H. & Favre, A. (2019) Origins of global mountain plant biodiversity: testing the ‘mountain-geobiodiversity hypothesis.’ *Journal of Biogeography*, 46, 2826–2838. <https://doi.org/10.1111/jbi.13715>

- Mutke, J. & Barthlott, W. (2005) Patterns of vascular plant diversity at continental to global scales. *Biologische Skrifter*, 55, 521–531.
- O'Brien, E. (1998) Water–energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography*, 25, 379–398. <https://doi.org/10.1046/j.1365-2699.1998.252166.x>
- O'Brien, E.M. (2006) Biological relativity to water–energy dynamics. *Journal of Biogeography*, 33, 1868–1888. <https://doi.org/10.1111/j.1365-2699.2006.01534.x>
- O'Brien, E.M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography*, 20, 181. <https://doi.org/10.2307/2845670>
- Onstein, R.E., Baker, W.J., Couvreur, T.L.P., Faurby, S., Svenning, J.-C. & Kissling, W.D. (2017) Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution*, 1, 1903–1911. <https://doi.org/10.1038/s41559-017-0348-7>
- Parmentier, I., Malhi, Y., Senterre, B., et al. (2007) The odd man out? Might climate explain the lower tree α -diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology*, 95, 1058–1071. <https://doi.org/10.1111/j.1365-2745.2007.01273.x>
- Pedersen, T.L. (2020) patchwork: The Composer of Plots. <https://patchwork.data-imaginist.com/>
- Pelser, P.B., Barcelona, J.F. & Nickrent, D.L. (2011) Co's Digital Flora of the Philippines. <https://www.philippineplants.org>
- 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>
- Qian, H. & Ricklefs, R.E. (2004) Taxon richness and climate in angiosperms: is there a globally consistent relationship that precludes region effects? *The American Naturalist*, 163, 773–779. <https://doi.org/10.1086/383097>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <https://www.Rproject.org/>
- 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>
- Richards, P.W. (1973) Africa, the “odd man out.” In: *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*. (ed. by B.J. Meggers, E.S. Ayensu, and W.D. Duckworth), pp. 21–26, Smithsonian Institution Press, Washington, DC.
- Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, 87, S3–S13. [https://doi.org/10.1890/0012-9658\(2006\)87\[3:EDATOO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[3:EDATOO]2.0.CO;2)
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, New York.
- Rundel, P.W., Arroyo, M.T.K., Cowling, R.M., Keeley, J.E., Lamont, B.B., Pausas, J.G. & Vargas, P. (2018) Fire and plant diversification in Mediterranean-climate regions. *Frontiers in Plant Science*, 9, 851. <https://doi.org/10.3389/fpls.2018.00851>
- Rundel, P.W., Arroyo, M.T.K., Cowling, R.M., Keeley, J.E., Lamont, B.B. & Vargas, P. (2016) Mediterranean biomes: evolution of their vegetation, floras, and climate. *Annual Review of Ecology, Evolution, and Systematics*, 47, 383–407. <https://doi.org/10.1146/annurev-ecolsys-121415-032330>
- Schluter, D. (2016) Speciation, ecological opportunity, and latitude. *The American Naturalist*, 187, 1–18. <https://doi.org/10.1086/684193>
- Scotese, C.R., Song, H., Mills, B.J.W. & van der Meer, D.G. (2021) Phanerozoic paleotemperatures: the earth's changing climate during the last 540 million years. *Earth-Science Reviews*, 215, 103503. <https://doi.org/10.1016/j.earscirev.2021.103503>
- Silva de Miranda, P.L., Dexter, K.G., Swaine, M.D., de Oliveira-Filho, A.T., Hardy, O.J. & Fayolle, A. (2022) Dissecting the difference in tree species richness between Africa and South America. *Proceedings of the National Academy of Sciences USA*, 119, e2112336119. <https://doi.org/10.1073/pnas.2112336119>
- Sosef, M.S.M., Dauby, G., Blach-Overgaard, A., et al. (2017) Exploring the floristic diversity of

- tropical Africa. *BMC Biology*, 15, 15. <https://doi.org/10.1186/s12915-017-0356-8>
- Suissa, J.S., Sundue, M.A. & Testo, W.L. (2021) Mountains, climate and niche heterogeneity explain global patterns of fern diversity. *Journal of Biogeography*, 48, 1296–1308. <https://doi.org/10.1111/jbi.14076>
- Svenning, J.-C., Eiserhardt, W.L., Normand, S., Ordonez, A. & Sandel, B. (2015) The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 46, 551–572. <https://doi.org/10.1146/annurev-ecolsys-112414-054314>
- Treurnicht, M., Colville, J.F., Joppa, L.N., Huysen, O. & Manning, J. (2017) Counting complete? Finalising the plant inventory of a global biodiversity hotspot. *PeerJ*, 5, e2984. <https://doi.org/10.7717/peerj.2984>
- Ulloa Ulloa, C., Acevedo-Rodríguez, P., Beck, S., et al. (2017) An integrated assessment of the vascular plant species of the Americas. *Science*, 358, 1614–1617. <https://doi.org/10.1126/science.aao0398>
- Veblen, T., Young, K. & Orme, A. eds. (2007) *The Physical Geography of South America*. Oxford University Press, Oxford. <https://doi.org/10.1093/oso/9780195313413.001.0001>
- Vences, M., Wollenberg, K.C., Vieites, D.R. & Lees, D.C. (2009) Madagascar as a model region of species diversification. *Trends in Ecology and Evolution*, 24, 456–465. <https://doi.org/10.1016/j.tree.2009.03.011>
- Wang, G., Ives, A.R., Zhu, H., Tan, Y., Chen, S., Yang, J. & Wang, B. (2022) Phylogenetic conservatism explains why plants are more likely to produce fleshy fruits in the tropics. *Ecology*, 103. <https://doi.org/10.1002/ecy.3555>
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, 21, 213–251. <https://doi.org/10.2307/1218190>
- Whittaker, R.J. & Triantis, K.A. (2012) The species-area relationship: an exploration of that ‘most general, yet protean pattern.’ *Journal of Biogeography*, 39, 623–626. <https://doi.org/10.1111/j.1365-2699.2012.02692.x>
- Wickham, H., Averick, M., Bryan, J., et al. (2019) Welcome to the Tidyverse. *Journal of Open Source Software*, 4, 1686. <https://doi.org/10.21105/joss.01686>
- Woodward, J. ed. (2009) *The physical geography of the Mediterranean*. Oxford University Press, Oxford. <https://doi.org/10.1093/oso/9780199268030.001.0001>
- Yang, B., Deng, M., Zhang, M.-X., Moe, A.Z., Ding, H.-B., Maw, M.B., Win, P.P., Corlett, R.T. & Tan, Y.-H. (2020) Contributions to the flora of Myanmar from 2000 to 2019. *Plant Diversity*, 42, 292–301. <https://doi.org/10.1016/j.pld.2020.06.005>
- Zhang, Y., Xiao, X., Wu, X., Zhou, S., Zhang, G., Qin, Y. & Dong, J. (2017) A global moderate resolution dataset of gross primary production of vegetation for 2000–2016. *Scientific Data*, 4, 170165. <https://doi.org/10.1038/sdata.2017.165>
- Zhu, H. (2016) Biogeographical evidences help revealing the origin of Hainan Island. *PLOS ONE*, 11, e0151941. <https://doi.org/10.1371/journal.pone.0151941>

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