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Research article

From earthquakes to island area: multi-scale effects upon local diversity

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Tropical forests occupy small coral atolls to the vast Amazon basin. They occur across bioregions with different geological and climatic history. Differences in area and bioregional history shape species immigration, extinction and diversification. How this effects local diversity is unclear. The Indonesian archipelago hosts thousands of tree species whose coexistence should depend upon these factors. Using a novel dataset of 215 Indonesian forest plots, across fifteen islands ranging in area from 120 to 785 000 km^2, we apply Gaussian mixed effects models to examine the simultaneous effects of environment, earthquake proximity, island area and bioregion upon tree diversity for trees ≥ 10 cm diameter at breast height. We find that tree diversity declines with precipitation seasonality and increases with island area. Accounting for the effects of environment and island area we show that the westernmost bioregion Sunda has greater local diversity than Wallacea, which in turn has greater local diversity than easternmost Sahul. However, when the model includes geological activity (here proximity to major earthquakes), bioregion differences are reduced. Overall, results indicate that multi-scale, current and historic effects dictate tree diversity. These multi-scale drivers should not be ignored when studying biodiversity gradients and their impacts upon ecosystem function.

Keywords: biodiversity, biogeographic regions, diversity gradients, echo pattern, forest plots, island biogeography

Introduction

The determinants of local species diversity are scale dependent (Willis and Whittaker 2002). Thus, local conditions interplay with large-scale speciation and extinction that controls the number of species that can disperse and persist in a community (Ricklefs and Schluter 1993, Zobel 1997, Spasojevic et al. 2018, Brodie et al. 2022, Trethowan et al. 2023a). In Indonesia and neighbouring countries, we find high plant species richness unmatched in other archipelagoes (Joyce et al. 2020). There are many factors that may influence the country's local diversity (van Steenis 1950, Whitmore 1984). For example, island area and biogeographic history may influence diversification dynamics and thus the number of tree species that locally co-exist (Germain et al. 2016, Blonder et al. 2017, Craven et al. 2019, Kooyman et al. 2019, Herrera-Alsina et al. 2021, McCullough et al. 2022). Climate and local soil conditions, in turn, also influence local tree diversity (Slik et al. 2009, Laumonier and Nasi 2018). So far, however, our understanding of the multi-scale drivers of local plant diversity in tropical archipelagos has been limited (Brambach et al. 2017, Trethowan et al. 2020).

Tropical tree diversity at small spatial scales (e.g. < 10 ha) may be determined by local environmental conditions (Ricklefs 1987). For instance, tree diversity declines with elevation because many species do not tolerate lower temperatures (Slik et al. 2009, Rehm and Feeley 2015, Brambach et al. 2017, Trethowan et al. 2023b). Likewise, seasonally dry forests have lower diversity because fewer species can cope with extended periods of drought (Davidar et al. 2005, Baltzer et al. 2008). Infertile soils, similarly, may remove species with high nutrient requirements (Slik et al. 2009, Cámara-Leret et al. 2017, Draper et al. 2018). Indonesia is part of the largest tropical archipelago in the world and encompasses a wide range of environmental gradients: from mangroves to alpine grasslands and from constantly wet to seasonally dry (Kooyman et al. 2019, Trethowan et al. 2022). Therefore, Indonesia provides a great opportunity to study the relationship between environmental variation and local tree species diversity (Fig. 1a).

Additionally, the impacts of geological activity upon Indonesian diversity require attention. Volcanic eruptions and earthquakes may cause major species turnover events that could have an archipelago-wide impact upon current diversity (Lavigne et al. 2013, Whelley et al. 2015, Sadili et al. 2022).

Island area is often cited as a key driver of the number of species that can coexist locally (MacArthur and Wilson 1963, Karger et al. 2014, Ibanez et al. 2018, Schrader et al. 2019a, b). Larger islands support a larger species pool for local communities, which therefore have more potential species (Ricklefs 1987). This 'echo pattern' coined by Rosenzweig and Ziv (1999) also accounts for the fact that on larger islands species that go locally extinct may, over time, re-establish because they survived in neighbouring populations. Larger islands also have higher immigration rates (Brown and Kodric-Brown 1977) and are more likely to

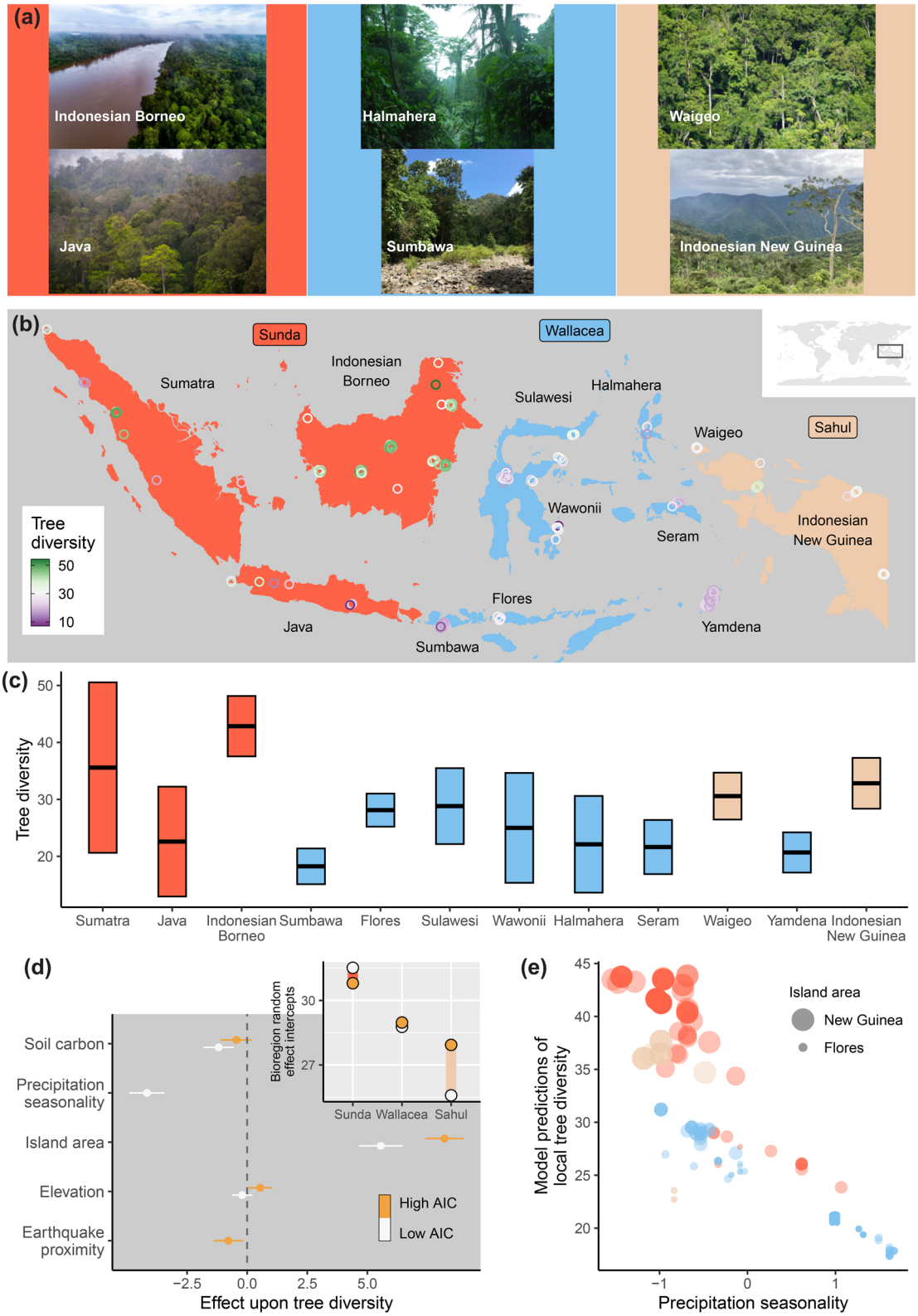

Figure 1. (a) Forests across Indonesia's three bioregions. Top left wet lowland Central Kalimantan. Top middle wet lowland Halmahera. Top right wet lowland Waigeo. Bottom left Mount Salak, Java. Bottom middle seasonally dry forest West Sumbawa. Bottom right Arfak mountains, Indonesian New Guinea. (b) Map of Indonesian rarefied forest plot tree diversity and their global position (inset). (c) Rarefied tree diversity per island. Islands with single plots not shown. Boxplots represent island mean and SD diversity. (d) +/− 1 SE (horizontal lines) for effects (points) of environmental variables, earthquake proximity and island area on local tree diversity in Indonesia. Both models either

Figure 1. (Continued)

with precipitation seasonality or earthquake proximity parameters are shown, hence single effects shown for these two parameters. Inset shows the random effect intercepts for bioregion across our two models. Point colour shows model prediction error as measured by the Aikake Information Criterion (AIC). (e) Mixed effect model predictions for local tree diversity in plots along the precipitation seasonality gradient, on islands of varying area, across three bioregions. Point opaqueness shows overlapping points. Photographers for (a): top left Nanang Sujana, CIFOR; top middle JS; top right JS; bottom left Mokhamad Edliadi, CIFOR; bottom middle LAT; bottom right LAT.

witness in situ speciation, increasing the pool of species available at local scales (Ricklefs 2004, Borges and Hortal 2009). Unlike tropical continental forests, island area effects could be prominent in tropical archipelagoes like Indonesia where there are numerous islands with considerable variation in size (Roos et al. 2004, Schrader et al. 2019b, Sin et al. 2022).

Geological history has left an imprint upon current diversity patterns across the world's biogeographic regions or 'bioregions' which we use here for brevity (Ricklefs and He 2016, Hagen et al. 2021, Herrera-Alsina et al. 2021). Indonesia straddles three island-dominated bioregions that differ in their histories of uplift, persistence above sea level and climate (Morley 2018a, Kooyman et al. 2019, Ali and Heaney 2021). Mesozoic emergence of the backbone of Sunda, the westernmost bioregion, preceded Java formed during the Pliocene (Hall 2009). Wet tropical forest became widespread across Sunda by the Miocene (Morley 2018b, Wilf et al. 2022). Sunda's land area fluctuated during the Quaternary when island connections increased during glacials and decreased during interglacials (Voris 2000, Cannon et al. 2009, Husson et al. 2020). The easternmost region of Sahul began to emerge in the Oligocene but formation of most of New Guinea's land area and central mountain range occurred in the late Miocene and Pliocene (Ufford and Cloos 2005, Toussaint et al. 2014). During Pleistocene glacial maxima, lower sea levels resulted in land connections between New Guinea and Australia, although Sahul was largely characterized by dry desert (Hope 1994, Byrne et al. 2008, Lohman et al. 2011, Toon et al. 2017). Sulawesi, the largest island in the central Wallacean region, amalgamated from a number of small islands in the Pliocene and Pleistocene, this was likely when Halmahera formed its current configuration (Hall et al. 1988, Nugraha and Hall 2018). Other Wallacean islands are even younger; Timor, Yamdena and Seram's uplift occurring in the late Pliocene (Hall 2009). Previous palynological and phylogenetic studies have mainly concerned the presence of lineages (Crayn et al. 2015, Morley 2018b, Yap et al. 2018, Hamilton et al. 2019, Kooyman et al. 2019). Here, we propose hypotheses that consider the impact of geological and climatic histories on diversity. The rapid recent formation of Wallacea and Sahul's environmental gradients could have promoted diversification and resulted in greater local diversity (Toussaint et al. 2014, Rowe et al. 2019, Kennedy et al. 2022, McCullough et al. 2022, Roycroft et al. 2022, Struebig et al. 2022). More likely, the longer residence time of terrestrial areas in Sunda may have resulted in the build-up of greater regional diversity, increasing the possible number of species able to coexist locally (de Bruyn et al. 2014, O'Connell et al. 2018). Added to that, widespread drought during glacial maxima except for equatorial Sunda likely caused the extinction of many tropical species in Wallacea and Sahul (Morley 1981, Cannon and Manos 2003, Cannon et al. 2009, Byrne et al. 2011, Hamilton et al. 2019, Wurster et al. 2019). Whilst the legacy of paleoclimate and bioregion has recently been shown to influence vertebrate distributions (Skeels et al. 2023), we do not have a clear idea of effects upon local diversity.

Here we test predictions that local tree diversity 1) declines with elevation, precipitation seasonality, soil infertility and geological activity, 2) increases with island area and 3) is greater in the older geological and climatically stable setting of Sunda compared to Wallacea and Sahul. We therefore test the fine-scale effects of prediction (1) and large-scale, historic, species-pool effects of predictions (2) and (3): allowing examination of these predictions, in cohort, for the first time across a megadiverse region.

Material and methods

Species/morphospecies abundance lists were compiled for trees ≥ 10 cm diameter, from 215 georeferenced plots (Fig. 1b), ranging in size from 0.2 to 10.5 ha (plot metadata and reference list in the Supporting information) across Weh (1 plot), Sumatra (8), Bangka (1), Java (10), Indonesian Borneo (42), Sumbawa (14), Flores (4), Sulawesi (22), Buton (1), Wawonii (6), Halmahera (2), Seram (5), Yamdena (64), Waigeo (4) and Indonesian New Guinea (11) (Brearley et al. 2019). Accepted species names followed the world checklist of vascular plants (Govaerts et al. 2021, Walker 2021). Our diversity metric was rarefied Hill diversity akin to species richness (Chao et al. 2014). The rarefied metric was equivalent to the diversity we would expect if plots had the same number of individuals as the plot with the fewest, in this case 60. Rarefaction allowed us to account for differences in numbers of individuals per plot and therefore compare plots of different sizes (Hsieh et al. 2016). This rarefied diversity metric is henceforth termed 'diversity'. To determine if rarefaction impacted our results we also calculated diversity indices equivalent to that found for 100, 200 and 300 individuals across all plots and repeated analyses below using these data as response variables (Hsieh et al. 2016).

We examined the drivers of local tree diversity in Indonesia with a Gaussian mixed effects model and an identity link function. Tree diversity was modelled as a function of island area (total island area used for Borneo and New Guinea as these differ from the Indonesian border) and environmental variables (elevation, precipitation seasonality and soil carbon). These environmental variables were chosen because they have been shown to influence tropical tree diversity (Baltzer et al.

2008, Brambach et al. 2017, Draper et al. 2018) and were the largest independent contributors (Supporting information) to the three principal component axes that represented 85% variability in mean annual temperature, temperature range, elevation, mean annual precipitation, precipitation seasonality, soil nitrogen, soil carbon and soil cation exchange capacity taken from SRTM, WorldClim and SoilGrids databases (Farr et al. 2007, Exposito-Alonso 2017, Hengl et al. 2017). When the three selected variables, elevation, precipitation seasonality and soil carbon were included in the model, alongside island area, all predictor variance inflation factors (VIFs) were below 1.7 (Supporting information), indicating a lack of covariation amongst predictors. Given that we also wanted to test how geological activity affected diversity, we also built a model where precipitation seasonality was replaced with earthquake proximity, as parameters for this model had VIFs below 1.7 (Supporting information). We used proximity to earthquakes rather than volcanoes, as VIFs for the model parameterised with volcano proximity exceeded 1.7. All predictors were scaled, as z-scores, prior to analysis to allow effect score comparison. Proximity to earthquakes (> 7.5 Richter magnitude since 2150 BC) and volcanoes was calculated from the NGDC/WDS databases (Service 2023a, b). Volcano data were expanded with data from Whelley et al. (2015). We also included a random intercept for bioregions (Sunda, Wallacea or Sahul). Bioregions follow the concept first outlined by Heilprin and Darlington (Fig. 1b, Ali and Heaney 2021). This reflected the different climatic and geological histories found between bioregions (Supporting information). Model residuals did not show spatial dependence (Moran's I test both $p > 0.5$, Hartig 2021). Finally, prediction error, using the Akaike Information Criterion, was compared between models parameterised either by precipitation seasonality and earthquake proximity.

Results

Mean diversity per island was lowest in the seasonally dry forests of Sumbawa (diversity = 18.24 and SE = 0.44) and highest in the wet forests of Kalimantan (diversity = 42.85 and SE = 6.00) (Fig. 1c). The model parameterised by precipitation seasonality found a negative effect of precipitation seasonality and soil carbon and a positive effect of island area on local tree diversity (precipitation seasonality effect = −4.17 and SE = 0.74, soil carbon effect = −1.19 and SE = 0.64, island area effect = 5.56 and SE = 0.92, Fig. 1d). There was no effect of elevation (effect = −0.21 and SE = 0.43). The model parameterised by earthquake proximity showed a small negative effect of soil carbon and a positive effect of island area upon local tree diversity (soil carbon effect = −0.45 and SE = 0.66, island area effect = 8.21 and SE = 0.8, Fig. 1d). Elevation had a small positive effect on local tree diversity, whereas earthquake proximity had a small negative effect (elevation effect = 0.55 and SE = 0.49, earthquake proximity effect = −0.79 and SE = 0.61).

Random effect intercepts for the precipitation seasonality model suggested that bioregion was strongly associated with tree diversity. The highest effects were in Sunda (intercept = 31.52) followed by Wallacea (28.78) and then Sahul (25.59, Fig. 1d inset). This suggests that in Sahul diversity is lower than would be predicted by environmental variables and island area alone (Fig. 1e). Likewise, for a given value of island area and environmental variable, Wallacea has lower diversity than Sunda (but higher than Sahul). The bioregion random effect explained approx. 19% of variation in tree diversity. However, when earthquake proximity was included in the model, differences amongst bioregions were reduced (7% variation in diversity explained, Fig. 1d inset).

The model parameterised by precipitation seasonality that also had larger differences between bioregions according to random effect intercepts was more precise than the model that showed smaller differences between bioregions and was parameterised by earthquake proximity (precipitation seasonality model AIC 29 less than earthquake proximity model, Fig. 1d).

Results repeated with diversity metrics equivalent to 100, 200 and 300 did not show large differences from that calculated from 60 individuals (Supporting information).

Discussion

Here, we have analysed 215 forest plots across fifteen major islands of the Indonesian archipelago and shown that local tree diversity appears to be influenced by fine-scale local environment and proximity to earthquakes, and by large-scale drivers of island area and bioregion.

The physiological limits imposed by drought should be detrimental to the number of tropical trees able to co-exist locally (Baltzer et al. 2008, Baltzer and Davies 2012). Our results showing declining diversity with precipitation seasonality indicate that drought effects are relevant across large scales.

We did not find a clear relationship between elevation and diversity, perhaps caused by our plots not spanning sufficiently high elevations to detect diversity tail-off. Alternatively, it may be due to differing mountain topography, where dependent upon how/if mountains taper, large-scale diversity-elevation relationships can differ from monotonic decline in richness to an increase (Elsen and Tingley 2015). For instance, the central New Guinea highlands have a 'diamond' shaped topography where area is greatest at mid-elevations (Elsen and Tingley 2015). Similarly, mountain species pools may not necessarily decline linearly with elevation (Bachman et al. 2004, Whitman et al. 2021). Our results suggest that mountain species pools, rather than elevation per se, could be a major driver of local diversity (Rosenzweig 1995). This could also be reflected across different habitats. For instance, in the Amazon low soil nutrient habitats are locally rich if that habitat is widely distributed and vice versa high nutrient habitat with a small species pool can show low diversity (ter Steege et al. 2023).

We have shown how important island area and linked species pool size variation (Zobel 1997) are for local tropical tree diversity. These patterns are therefore key to understanding

drivers of diversity of the tropical ecosystems where most global diversity exists. Larger islands have more species and can therefore support more species at local scales (Rosenzweig and Ziv 1999, Roos et al. 2004). To examine this further we require more baseline floristic data from Indonesia and neighbouring countries. First, we need to accelerate the production of expert-led species checklists and taxonomic revisions across the region (Cámara-Leret et al. 2020, Joyce et al. 2020, Rustiami et al. 2020). Despite taxonomic information being critical to identify tree individuals from forest plots, many big tropical genera still remain taxonomically neglected (Frodin 2004). Second, better interdisciplinary collaboration among ecologists and taxonomists is needed. This will be important for ecologists who want to have high-grade vouchers (Baker et al. 2017), and for systematists who seek to understand what drives trait variation across the archipelago. The growth of dual expert-verified data would allow examination of island species–area relationships and their dependence upon environmental variation between and within islands.

Here we have assumed that larger islands have larger species pools. However, equally species-rich pools may differ in the diversity of traits that they support (Spasojevic et al. 2018). Traits determine species ability to persist in an environment so the trait pool should better reflect the number of species that can occur at small scales (Spasojevic et al. 2018, Schrader et al. 2021). Likewise, the overall dispersal capacity of pools should shape how many species can disperse into and occur at sites (Xie et al. 2023). Exploration of these potential patterns would require the collation and analysis of trait data linked to dispersal and adaptation to environment, such as height, leaf and fruit size (Wright et al. 2017, Olson et al. 2018, Brodie et al. 2022, Trethowan et al. 2022, 2023a).

Our results suggest an influence of biogeographic history upon local tropical tree diversity. We find a decrease with longitude from Sunda to Sahul rather than clear differences between the ancient geological region of Sunda and younger Wallacea and Sahul. This could reflect increasing distance from the wet tropical source pool of mainland Southeast Asia, as opposed to Australia where Neogene aridification drove widespread extinction of rainforest taxa (Byrne et al. 2011, Kooyman et al. 2019). Heightened diversity with closer proximity to the western source pool suggests that dispersal distances have been crucial for the formation of modern diversity in Indonesia (MacArthur and Wilson 1963). Greater chance of tropical lineage dispersal, from the western source pool, also promotes their opportunities for diversification (Crayn et al. 2015, Morley 2018b, Atkins et al. 2019, Kooyman et al. 2019). In the western bioregions, this presumably increased the proportion of species adapted to tropical conditions. Here, these species that are pre-adapted to modern conditions are less likely to be outcompeted, and potentially a greater number of species can coexist (Harrison and Cornell 2008, Swenson et al. 2023). However, our model incorporating geological activity showed reduced differences in local diversity explained by bioregion. Regional geology causing non-climatic differences between bioregions, e.g. via earthquake frequency, is therefore likely important for local diversity.

We have shown, for the first time, how local tree diversity varies across Indonesia. With this new Indonesian plot-based data, future global studies of local tree diversity will have an opportunity to better cover the entirety of the tropics (Parmentier et al. 2007, Sullivan et al. 2017, Cazzolla Gatti et al. 2022, ter Steege et al. 2023). Local and indigenous groups in Indonesia have interacted with plants for millennia and still use thousands of species (Sheil and Salim 2012, Sheil et al. 2012, Cámara-Leret and Dennehy 2019), so further studies of humankind's ecological legacies on the archipelago's forests are warranted (Hamilton et al. 2021). However, more forest plot-based data are still needed. Sampling of the large, forested areas in southeast Sulawesi, Flores, Sumba and Indonesian New Guinea should remain a priority, including coverage of high elevations and extreme ultramafic and karstic soils (Galey et al. 2017, Geekiyanage et al. 2019, Brambach et al. 2020).

Diversity is key for the functioning of ecosystems (Jucker et al. 2014, van der Plas et al. 2018). We have highlighted here how for a megadiverse tree flora the parameters of diversity vary from the fine-scale and modern to the large-scale and historic. Therefore, studies that forecast diversity, including those that use the results to predict alteration of ecosystem function, should integrate relevant multi-scale parameters across space and time.

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Author contributions

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Transparent peer review

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Data availability statement

Plot diversity metrics, coordinates and an Rmarkdown to recreate the manuscript and analysis are available from the Zenodo Digital Repository: https://zenodo.org/doi/10.5281/zenodo.7989963 (Trethowan et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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