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RESEARCH PAPER

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Regional forcing explains local species diversity and turnover on tropical islands

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Abstract

Aim: To determine the role of regional forcing on plot-level species diversity and composition, and to quantify the relative importance of biogeographical and climatic factors in explaining woody plant diversity and composition at the local-, island- and archipelago-scale.

Location: Forty-one tropical islands of the Indo-Pacific region from Madagascar to Hawai'i Island.

Methods: We analysed the diversity and composition of tropical woody plant communities located across 113 plots, 41 islands and 19 archipelagos. We used generalized linear mixed-effects models and generalized dissimilarity models to determine the role of regional forcing at the island and archipelago scale and to assess the relative importance of biogeographical (area and isolation of islands or archipelagos, geographical distance between plots) and climatic factors in explaining differences in local diversity and composition (species turnover). Analyses were conducted at different geographical scales (local, island and archipelago) and taxonomic levels (species, genus and family).

Results: Variation in local (plot-level) diversity (as species density, the number of species per 100 woody plants) was primarily explained by island and archipelago identity. Maximum species density was positively correlated with the area of an island (or archipelago) and negatively correlated with the isolation of an archipelago. Local climatic variability was also a significant predictor of species density, but less important than regional forcing. Climate variables explained $< 20\%$ of the variation in species turnover across all plots. The importance of geographical distance between plots relative to climate in driving species turnover decreased from the species to family level, and from the regional to island level.

Main conclusions: Regional forcing was the key driver of local diversity and composition on islands. Island area and archipelago isolation are likely driving local diversity through their effects on the pool of island species. Geographical distance between plots is the main factor explaining species turnover, while at higher taxonomic levels, climatic factors and niche conservatism are the main drivers.

KEYWORDS
archipelago, area, biodiversity hotspot, climate, geographical distance, Indo-Pacific, isolation, species pool, species turnover, woody plants

1 | INTRODUCTION

Species diversity and composition of island biotas depend on the complex interplay of various processes such as immigration, competition, extinction and speciation. These processes in turn are controlled by biogeographical and environmental factors and processes (Kreft, Jetz, Mutke, Kier, & Barthlott, 2008; MacArthur & Wilson, 1967; Whittaker, Willis, & Field, 2001). These biogeographical and environmental forcings, that is, factors and processes that influence species diversity and composition, can be considered as filters that dictate which species of the total global species pool are present (Lortie et al., 2004; Santos, Field, & Ricklefs, 2016; Zobel, 1997).

The number of species living in a small, ecologically homogeneous area (local or alpha diversity, Ricklefs, 1987) is the product of local (e.g., local climate, competition, topography, resources) and regional (e.g., regional climate, dispersal, species pool) forcing (Harrison & Cornell, 2008; Lortie et al., 2004; Ricklefs, 1987). On islands, regional forcing operating among archipelagos (the archipelago-scale) or islands within an archipelago (island-scale) seems important, as it can explain a considerable proportion of the variation in species diversity at these levels (Gillespie et al., 2013; Keppel, Gillespie, Ormerod, & Fricker, 2016). Island or archipelago area may influence local diversity through its effect on the regional species pool or gamma diversity (Ricklefs, 1987; Rosenzweig & Ziv, 1999), described as the 'echo pattern' by Rosenzweig and Ziv (1999). It is important to note that archipelagos and islands are dynamic systems with complex geological histories, changing size and connectivity with climate-driven sea level changes (Fernández-Palacios et al., 2016; Neall & Trewick, 2008; Weigelt, Steinbauer, Cabral, & Kreft, 2016).

Climate affects both species diversity and composition of vegetation (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Cabral, Weigelt, Kissling, & Kreft, 2014; Feeley, Hurtado, Saatchi, Silman, & Clark, 2013) within and among islands (Gillespie et al., 2013). On islands, the effects of climate on species diversity are presumed to be less pronounced compared to the mainlands because of area and isolation effects (Field et al., 2009). At the local- or plot-scale, climate can have important effects on species diversity (Gillespie et al., 2013). However, it should have even stronger impacts on taxonomic composition because species tend to retain their ancestral ecological characteristics (i.e., niches), a phenomenon known as niche conservatism (Wiens & Graham, 2005). Niche conservatism can result in lineages tending to remain faithful to certain biomes or local environmental conditions (Crisp et al., 2009; Webb, 2000; Wiens et al., 2010).

Quantifying the relative importance of local and regional processes has important implications for explaining patterns of diversity and species composition and, for example, predicting how communities will respond to environmental change, habitat degradation and species loss (Karger et al., 2014; Ricklefs, 1987; Rosenzweig & Ziv, 1999). However, the relative importance of local processes at the stand- or plot-scale and regional processes at the island- and archipelago-scale has received little attention (but see Franklin et al., 2013; Gillespie et al., 2013; Karger et al., 2014). In general, theories seeking to explain species diversity on islands have tended to emphasize regional over local processes (see Fernández-Palacios et al., 2016; MacArthur & Wilson, 1967; Whittaker, Kostas, & Richard, 2008).

We know surprisingly little about the origins of and processes maintaining plant biodiversity in the tropical insular Indo-Pacific, an area characterized by both high biodiversity and intense human threats to that biodiversity (Florens, 2013; Keppel, Morrison, Meyer, & Boehmer, 2014; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Shearman & Bryan, 2011). This area also harbours a wide variety of islands and archipelagos with different origins, sizes, isolation and climatic conditions (Mittermeier et al., 2005; Mueller-Dombois & Fosberg, 1998). In addition, a relatively recent and complex tectonic history (Hall, 2009; Lohman et al., 2011) makes this an ideal study area to analyse how biogeography and climate affect communities at different scales.

Here we determine the role of area, isolation and climate on diversity and composition of tropical Indo-Pacific island woody plant communities at the local- (among plots on the same island), island- and archipelago-scale using forest inventory data from 41 islands and 19 archipelagos. We expect that regional-scale forcing, specifically the area and isolation of islands or archipelagos, will be the predominant drivers of species diversity by determining the regional species pool and thus the potential maximum local species diversity. We also test the importance of climate relative to geographical distance (i.e., isolation of islands or archipelagos and distances between plots) in determining species diversity and composition. We expect that, because of niche conservatism, climatic variables will have a stronger impact on composition than on diversity, with their relative importance increasing at higher taxonomic levels, which are less affected by local speciation.

2 | METHODS

2.1 | Data compilation

We compiled published and unpublished forest inventory data from 165 inventories of plots $\geq$ 0.1 ha located on 41 islands and 19 archipelagos covering eight biodiversity hotspots (Table 1, Figure 1). Plots located in secondary forests were removed from the analysis. The analysis only considered woody plants (trees and lianas) with a stem diameter $\geq$ 10 cm at *c.* 1.3 m above the base (DBH, diameter at breast height). Plots located in close proximity (within 1 km) were pooled (considered as a single plot) to avoid pseudoreplication, resulting in 113 plots (see Supporting Information Table S1). All plots were located in lowland tropical forests in the Indo-Pacific region on islands larger than 1 km^2. Montane forest plots (as defined by authors of source data) were not considered in the analysis (e.g., Aiba & Kitayama, 1999; Culmsee, Pitopang, Mangopo, & Sabir, 2011). The western-most plot was on Madagascar and the eastern-most plot was on Hawai'i Island. The final dataset consisted of 60,795 woody plants in 3,136 species, 769 genera and 148 families. Nomenclature followed the Taxonomic Name Resolution Service v4.0 (http://tnrs.iplantcollaborative.org/). For taxa without resolution we referred to The Plant List website (http://www.theplantlist.org/).

2.2 | Diversity

Because plots differed in their sampling sizes (from 0.1 to 4 ha), we used rarefaction and extrapolation curves to produce diversity indices for a sample size of 100 woody plants per plot using the *iNEXT* R package (Chao & Jost, 2012; Chao et al., 2014). We used Hill numbers or effective number of species (Hill, 1973) as diversity indices, as recommended by Jost (2006) and Ellison (2010). Hill numbers (noted ^qD) weight the number of species (S) by the relative abundance of species (p_i) according to a constant q:

$$^qD=\left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)} \tag{1}$$

When $q = 0$, all species have the same weight and ^0D corresponds to the number of species per 100 woody plants (i.e., species density). When $q = 1$, species are weighted by their relative abundance and ^1D can be interpreted as the effective number of abundant species (also known as Shannon diversity). When $q = 2$, less abundant species have little weight and ^2D can be interpreted as the effective number of dominant species (also known as Simpson diversity). Hill numbers ($q = 0$, $q = 1$, $q = 2$) were estimated at species, genus and family levels for 100 woody plants as the mean value of 50 bootstrap iterations. Only plots with $\geq$ 50 inventoried woody plants were used because extrapolation procedures are not robust below half of the sample size (Chao et al., 2014).

2.3 | Composition

Variation in community composition was assessed through dissimilarity or β diversity index. β diversity has two components (Baselga, 2010), (a) a nested component that results from a loss (or gain) of taxa, and (b) a turnover component that results from a replacement of taxa due to environmental sorting or spatial and historical constraints. To assess taxonomic dissimilarities independently of differences in taxonomic diversity, we removed the nested component of the β diversity and only considered its turnover component using the Simpson dissimilarity index β_{sim} using the *beta.pair* function of the *betapart* R package (Baselga & Orme, 2012):

TABLE 1 Dataset description (Area = island area, Isolation = distance to nearest mainland)

Archipelago	Island (data sources)	Area (km^2)	Isolation (km)	Nearest mainland	No. plots (sub-plots)
Andaman Islands	Little Andaman (Rasingam & Parthasarathy, 2009)	710	610	Asia	4
	Middle Andaman (Rajkumar & Parthasarathy, 2008)	2,781	260	Asia	2
	All				6
Bismarck Archipelago	Normanby (Keppel et al., 2010)	1,040	900	Australia	1 (4)
Fiji Islands	Gau (Keppel et al., 2010)	136	2,800	Australia	2 (4)
	Macuata (Gillespie et al., 2013)	136	2,850	Australia	1
	Monu (Gillespie et al., 2013)	1	2,650	Australia	1
	Naviti (Gillespie et al., 2013)	34	2,800	Australia	1
	Vanua Levu (Keppel et al., 2010)	5,587	2,900	Australia	1 (4)
	Viti Levu (Gillespie et al., 2013)	10,531	2,700	Australia	3 (6)
	Yasawa (Gillespie et al., 2013)	32	2,800	Australia	1
	All				11 (19)
Greater Sunda Islands	Borneo (Aiba & Kitayama, 1999; Aiba et al., 2015; Phillips & Miller, 2002; Small, Martin, Kitching, & Wong, 2004)	748,168	550	Asia	5
	Java (Meijer, 1959)	138,794	800	Asia	1
	Sumatra (Kartawinata, Samsoedin, Heriyanto, & Afriastini, 2004)	443,066	60	Asia	1
					7
Hainan	Hainan (Lu et al., 2014)	33,210	20	Asia	1 (2)
Hawaiian Islands	Hawaii (Gillespie et al., 2013; Ostertag et al., 2014)	10,434	3,750	North America	4 (5)
	Kauai (Gillespie et al., 2013)	1,435	3,800	North America	4
	Lanai (Gillespie et al., 2013)	358	3,750	North America	1 (3)
	Maui (Gillespie et al., 2013)	1,903	3,700	North America	1
	Molokai (Gillespie et al., 2013)	678	3,750	North America	1
	Oahu (Gillespie et al., 2013)	1,583	3,800	North America	2
	All				13 (16)
Langkawi	Langkawi (Kohira et al., 2001)	363	15	Asia	1
Madagascar	Madagascar (Phillips & Miller, 2002, Birkinshaw, Randrianaivo, Randrianjanahary, Ratovoson and Reza, 2017, unpublished)	587,713	370	Africa	18 (27)
Mariana Islands	Saipan (Gillespie et al., 2013)	123	2,800	Asia	2 (3)
Mascarene Archipelago	La Réunion (Strasberg, 1996)	2,535	1,700	Africa	1
	Mauritius (Florens & Baider, unpublished)	1,874	1,800		4 (5)
	All				5 (6)
New Caledonia	Grande Terre (Phillips & Miller, 2002; Gillespie et al., 2013; Ibanez et al., 2017)	16,648	1,200	Australia	22 (24)
New Guinea	New Guinea (Phillips & Miller, 2002; Laidlaw, Kitching, Goodall, Small, & Stork, 2007; Whitfeld et al., 2014)	785,753	155	Australia	5 (8)
New Hebrides	Erromango (Keppel et al., 2010)	888	1,100	Australia	1 (4)
	Malakula (Keppel et al., 2010)	2,041	1,200	Australia	1 (4)
	All				2 (8)
Philippine Islands	Luzon (Phillips & Miller, 2002)	109,965	600	Asia	1
	Negros (Hamann, Barbon, Curio, & Madulid, 1999)	13,075	1,450	Asia	1
	All				2
Samoa Islands	Savaii (Keppel et al., 2010)	1,718	3,800	Australia	1 (3)
	Ta'u (Webb, Van de Bult, Chutipong, & Kabir, 2006)	46	3,900	Australia	2
	Tutuila (Webb & Fa'aumu, 1999)	142	3,900	Australia	4
	Upolu (Keppel et al., 2010)	1,125	3,800	Australia	1 (4)
	All				8 (13)
Sulawesi	Sulawesi (Culmsee & Pitopang, 2009)	180,681	1,100	Australia	1 (6)
Solomon Islands	Choiseul (Keppel et al., 2010)	2,971	1,600	Australia	2 (4)
	Kolombangara (Keppel et al., 2010)	688	1,500	Australia	1 (4)
	All				3 (8)

(Continues)

TABLE 1 (Continued)

Archipelago	Island (data sources)	Area (km^2)	Isolation (km)	Nearest mainland	No. plots (sub-plots)
Taiwan	Taiwan (Phillips & Miller, 2002)	34,507	130	Asia	2
Tonga Islands	Kao (Franklin et al., 2006)	12	3,200	Australia	1
	Tofua (Franklin et al., 2006)	50	3,200	Australia	3
	All				4

$$\beta_{\mathrm{sim}} = \frac{b}{b+a} \qquad (2)$$

Where *a* is the number of shared taxa between two plots and *b* is the number of taxa unique to the plot with the least unique taxa. To compare plots with different sample sizes, we randomly sampled 50 woody plants per plot (with replacement) and computed β_{sim} dissimilarities on these resampled communities at the species, genus and family levels. This procedure was repeated 100-fold to estimate mean β_{sim} dissimilarities.

2.4 | Explanatory variables

After variable selection, we retained two biogeographic variables – island area (Area), and distance to nearest mainland (Isolation) – extracted from the Island Directory website (http://islands.unep.ch, Dahl, 1991) or estimated using the ruler and polygon tool on Google Earth. Four bioclimatic variables mean annual temperature, temperature annual range, mean annual precipitation and the precipitation of the driest month were investigated as potential predictors of local diversity and composition. None of these explanatory variables were correlated (Spearman's rank correlation coefficients rho $< .70$; $p > .05$). Latitude was not included because it was strongly correlated with temperature annual range and mean annual precipitation (Spearman's rank correlation coefficients rho $= .759$ and rho $= .746$, respectively; $p < .001$). Maximum elevation of islands, sometimes used as a proxy of island age and topographical niche diversity (Whittaker et al., 2008), was not retained as an explanatory variable because it was correlated with island area (rho $= .784$, $p < .001$). Bioclimatic variables were extracted for plot locations from the WorldClim climatology at a spatial resolution of 30 arc-seconds (*c.* 1 km) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). WorldClim climatology relies on interpolation using digital elevation models and has strong limitations especially for precipitation on islands (Hijmans et al., 2005). Islands often display strong climatic variations over distances that are smaller than the resolution of this data. This problem is particularly pronounced in the Pacific, because of the low coverage of climatic stations. Mean annual temperature was correlated with elevation (rho $= -.774$, $p < .001$). We did not include soil type and island age as explanatory variables because many islands have mixed and complex origins (Neall & Trewick, 2008) and soil typology was often not available at the scale of our study.

2.5 | Analysis

All analyses were performed using R 3.3.0 (R Core Team, 2016). We first ordinated plots according to their climate, and islands according to their geographical features, using principal component analysis (PCA). We used permutational analysis of variance (PERMANOVA) to test whether climatic and geographical differences were due to plots or islands belonging to different islands and/or archipelagos. We also tested the relationships between Hill numbers using standard major axes applied to log-transformed data (i.e., modelling power law

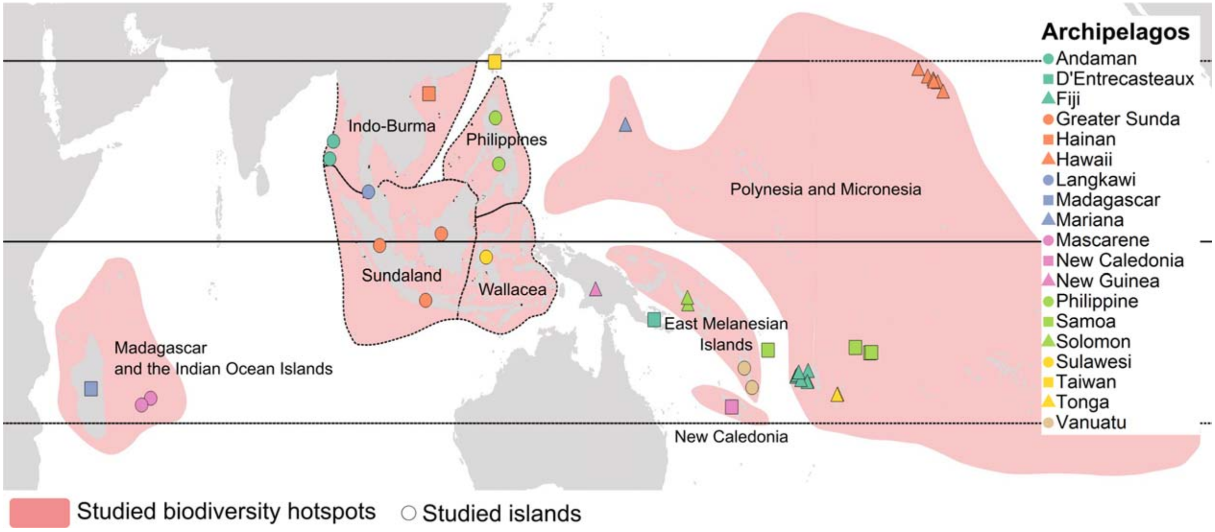

FIGURE 1 Studied islands and archipelagos in the Indo-Pacific area. The names of the eight biodiversity hotspots surveyed in this study are indicated on the map

relationships) with intercepts forced to 0 using the *smatr* R package (Warton, Duursma, Falster, & Taskinen, 2012).

The relative importance of various processes in driving local diversity was investigated at multiple scales with mixed-effect models that can partition the total variation in a dataset into different levels, and are especially relevant when looking at species diversity on different islands and archipelagos (Bunnefeld & Phillimore, 2012). At the plot-scale, we tested the effects of climate on diversity using generalized linear mixed-effects models (GLMMs) with Poisson distribution using the *glmer* function from the *lme4* R package (Bates, Mächler, Bolker, & Walker, 2015), including the identity of the island and archipelago as random effects. At the island- and archipelago-scale, we selected the species density of the most species diverse plot as a response variable that provided the best estimate of maximum diversity of the island/archipelago. At the island-scale, we used the log-area of the island as well as the climatic variables of the most diverse plot as fixed effects, with the identity of the archipelago set as a random effect. At the archipelago scale, we used generalized linear models with the log-area of the archipelago (sum of the values for islands belonging to the same archipelago), the log-distance between the archipelago and mainland (mean of the values for islands belonging to the same archipelago) and the climate variables of the most diverse plot as explanatory variables. Note that climatic variables were centred and scaled before fitting the models to make their effects directly comparable.

We used the *MuMIn* R package (Bartoń, 2016) and the *dredge* function to generate different sets of models representing all possible combinations and subsets of fixed effects. We then selected the best models based on their corrected Akaike information criterion (AICc), which express the quality of a model as a function of the goodness of fit (maximum likelihood) and the number of parameters ($\Delta\text{AICc} < 2$ from the best models, Bunnefeld & Phillimore, 2012). We used marginal R^2 (without random effects) and conditional R^2 (with random effects) to assess the relative importance of fixed and random effects in GLMMs (Nakagawa & Schielzeth, 2013).

We then investigated the relative importance of climate and geographical distance between plots in driving community composition turnover (beta-diversity) using generalized dissimilarity modelling (GDM, Ferrier, Manion, Elith, & Richardson, 2007) computed with the *gdm* function of the *gdm* R package (Manion et al., 2017). We used geographical distance between plots as well as climate (mean annual temperature, temperature annual range, mean annual precipitation and the precipitation of the driest month) as predictors and β_{sim} distances in composition as response variables. We performed stepwise backward procedures with matrix permutation tests (50 permutations per step) to only keep significant predictors (p-value $< .05$) using the *gdm.varImp* function. The proportion of variance explained by climate and geographical distance between plots was then estimated by comparing the variance explained by different models computed with both climate and geographical distance as predictors and with only environmental or geographical distance as predictors (Legendre, 2008). We also computed the relative importance of each individual predictor following Fitzpatrick et al. (2013) and König, Weigelt, and Kreft (2017).

3 | RESULTS

3.1 | Climate and geography

Climate was intrinsically linked with geography, such that the identity of the island and archipelago explained 84 and 75% of the observed differences in climate, respectively (PERMANOVA, $p < .001$). For instance, plots located on islands of the Greater Sunda Island close to the equator tend to receive more rainfall with a less pronounced dry season than plots located on islands at higher latitudes, such as Madagascar or New Caledonia (Supporting Information Figure S1). Differences among island area and isolation were also strongly correlated with the identity of the archipelago an island belonged to (PERMANOVA, $R^2 = .92$, $p < .001$). Large islands, such as those of the Greater Sunda Islands, tended to be closer to the continent (and the equator) and less isolated than small islands such those of the Polynesian Archipelagos (e.g., Samoa and Tonga Islands).

3.2 | Diversity

Plots differed considerably in species density (number of species per 100 woody plants), which was a good estimator of taxonomic diversity in our plots (Supporting Information Figure S2 and S3). The estimated number of species, genera and families for 100 woody plants ranged from two for all taxonomic levels for a Hawaiian dry forest plot to 76, 51 and 31, respectively, for a Bornean rainforest. Species density was highly correlated with genus and family density (Supporting Information Figure S2). The numbers of species, genera and families (Hill number, $q = 0$) were also highly correlated with the numbers of abundant (Hill number, $q = 1$) and dominant (Hill number, $q = 2$) taxa at different taxonomic levels (Supporting Information Figure S3).

Among plots, local climate together with the identity of the island and archipelago explained 85% of the variation in species density (Table 2). Species density tended to increase with increasing mean annual precipitation and decreasing mean annual temperature. However, differences among plots (within the same island) in climate variables (i.e., local climatic variability) explained only 12% (marginal r^2) of this variation. About 73% (conditional r^2 – marginal r^2) of the variation in species density among plots was explained by the identity of islands and archipelagos (random effects). Therefore, almost 75% of the variation in species density among plots was explained by regional processes, mostly at archipelago scale (the standard deviation of the intercept among archipelagos and islands in the best model being 0.537 and 0.344, respectively).

At the island scale, maximum (highest recorded for the island) species density was mainly driven by island area (Table 3). In the best model, island area together with precipitation during the driest month explained 50% of the variance, with an additional 35% explained by the identity of archipelagos. Maximum species density increased with the log-transformed area of the islands (Figure 2). Plots on the small islands of the Hawaiian and Langkawi archipelagos were notable outliers in having respectively lesser and greater species density than expected with respect to their sizes (Figure 2). Precipitation during the

TABLE 2 Best generalized linear mixed models (Δ AICc < 2) explaining woody plant species density (number of species/100 woody plants, Poisson distribution) across the 113 studied plots

		Model 1	Model 2
Parameters (*SE*)	Mean annual temperature	−0.25 (0.04)***	−0.26 (0.04)***
	Temperature annual range	0.11 (0.04)*	0.11 (0.05)*
	Mean annual precipitation	0.31 (0.04)***	0.27 (0.06)***
	Precipitation of the driest month		0.06 (0.07)
Performance	AICc	891.174	892.804
	Marginal R^2	.122	.127
	Conditional R^2	.848	.852

Islands (*n* = 41) and archipelagos (*n* = 19) were considered as random effects [Full model: Species density ~ Mean annual temperature + Temperature annual range + Mean annual precipitation + Precipitation of the driest month + (1|Island) + (1|Archipelago)]. AICc = corrected Akaike information criterion

***$p < .001$, *$p < .05$.

driest month also had a positive, but weak, effect on maximum species density.

At the archipelago scale, area was also a key driver of maximum species density (Table 4). Together with the distance to the nearest continent and the annual temperature range, archipelago area explained 70% of the variance. Maximum species density increased with the log-transformed area of the archipelago (Figure 3a) but decreased with the log-distance between archipelago and mainland (i.e., isolation). The Greater Sunda Islands and New Guinea archipelagos were noticeable outliers (Figure 3b), having greater species density than expected with respect to their isolation from the mainland.

3.3 | Composition

Overall, climate and geographical distance explained about 55% of the turnover in species composition, and geographical distance between plots alone explained about twice as much variance as climate (Figure 4). However, the sole effect of geographical distance decreased with increasing taxonomic levels (species level: 23%; genus: 5%; family: 1%), while the sole effect of climate changed comparatively little (species level: 12%; genus: 11%; family: 6%). Mean annual temperature and annual temperature range were the most important variables in driving floristic dissimilarities (Supporting Information Figure S4), but the sole effect of climate did not exceed 20% at any scale. Considering only plots located in the same archipelago (island-scale) or island (plot-scale), the sole effect of geographical distance was smaller and the sole effect of climate was larger than for the complete dataset.

TABLE 3 Best generalized linear mixed models (Δ AICc < 2) explaining maximum woody plant species density (i.e., number of species/100 woody plants, Poisson distribution) across the 41 studied islands

		Model 1	Model 2
Parameters (*SE*)	log(Area)	0.13 (0.02)***	0.13 (0.02)***
	Mean annual temperature		0.06 (0.06)
	Precipitation of the driest month	0.14 (0.05)**	0.13 (0.05)**
Performance	AICc	319.003	320.446
	Marginal R^2	.502	.534
	Conditional R^2	.853	.828

Archipelagos (*n* = 19) were considered as random effects [Full model = max(species density) ~ log(Area) + Mean annual temperature + Temperature annual range + Mean annual precipitation + Precipitation of the driest month + (1|Archipelago)]. AICc = corrected Akaike information criterion

***$p < .001$, **$p < .01$.

4 | DISCUSSION

4.1 | Diversity

While local climatic conditions had a significant influence on local-scale diversity, regional forcing explained the most of its variation. Similar to a study by Ricklefs and He (2016), regional forcing explained 70–75% of the variation in woody plant species diversity among plots. These findings highlight the key role of regional forcing in determining local species diversity, likely by limiting the regional species pool through dispersal limitation, habitat availability and environmental filtering, which are linked to the isolation, area and regional climate of islands and archipelagos.

The area of an island or archipelago was strongly and positively correlated with maximum species density recorded in a plot, explaining 50% of the variation. While it is well known that area of an island explains a significant proportion of the variability in the number of species on an island at a regional (e.g., MacArthur & Wilson, 1967; Moody, 2000; Preston, 1962; Price, 2004) or global scale (Kreft et al., 2008; Triantis, Economo, Guilhaumon, & Ricklefs, 2015), few studies have explored the relationship between area of an island and the local, plot-level species density (but see Gillespie et al., 2013; Karger et al., 2014). Our results therefore suggest that area is an important predictor of species diversity at all scales investigated, including archipelago (Gillespie et al., 2013; Santos et al., 2010; Triantis et al., 2015), island (Kreft et al., 2008; Gillespie et al., 2013; Whittaker et al., 2008) and plot.

The underlying processes causing the high predictive power of area for species diversity remain controversial. MacArthur and Wilson

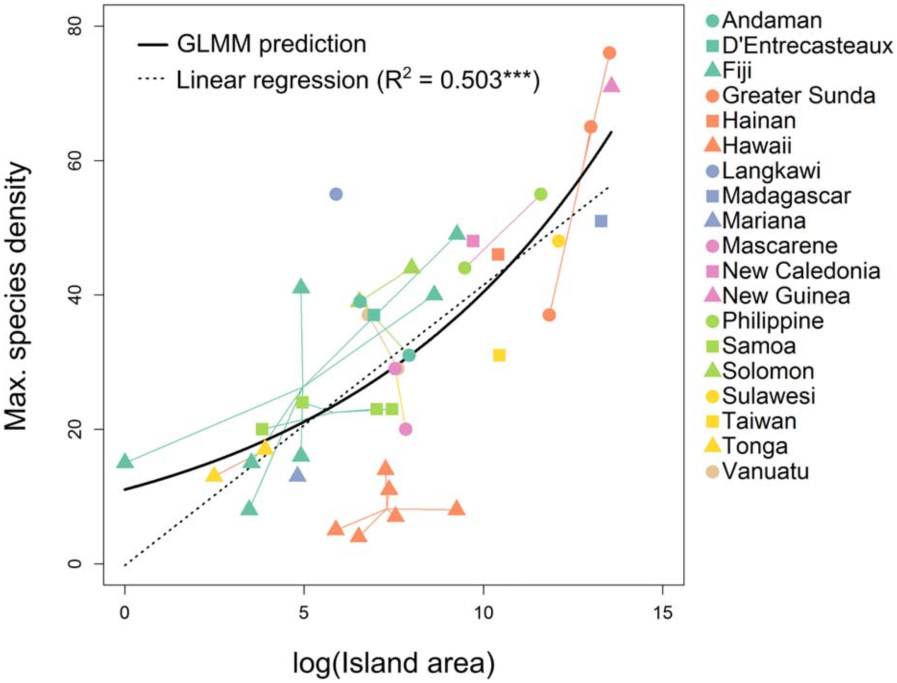

FIGURE 2 Effect of island area on the maximum species density [controlling for all covariables in the best generalized linear mixed-effects model (GLMM), see Table 2]. ***$p < .001$

(1967) suggested that the 'area effect' is due to increasing extinction rate with decreasing island area because smaller population sizes on smaller islands would result in higher extinction probabilities. However, area is also often correlated with habitat diversity (e.g., island elevation and topographical complexity), energy availability and island age (on oceanic islands), which would exert a more direct effect on species number through immigration, extinction and speciation rates as well as determining the carrying capacity of islands (see Cowie, 1995; Hurlbert & Jetz, 2010; Keppel et al., 2016; MacArthur & Wilson, 1967; Wright, 1983; Whittaker et al., 2008). However, Simberloff (1976) also determined an independent effect of island area on species diversity by experimentally controlling for environmental heterogeneity.

The isolation of an archipelago (i.e., the distance to the closest mainland) also constituted an important negative predictor of species diversity. For instance, the isolated archipelago of Hawaii (*c.* 3,800 km west of North America) exhibits low species density with respect to its size (see Ostertag et al., 2014), while the small archipelago of Langkawi, which is located only 15 km from the Malay Peninsula, exhibits a relatively high species density (Kohira, Ninomiya, Ibrahim, & Latiff, 2001). Ricklefs and He (2016) also found that local species diversity is significantly lower on islands in comparison with mainlands due to isolation effects. Similarly, Gillespie et al. (2013) and Karger et al. (2014) found isolation of an island from the closest source of propagules from the global species pool to be particularly important at the archipelago-scale. It has been suggested that the effect of isolation is weaker for large and/or continental islands (Weigelt & Kreft, 2013), as was the case in our study. However, continental islands in the Indo-Pacific tend to be larger and closer to the continent than oceanic islands, which makes it difficult to disentangle the effects of isolation and area. Indeed, this issue is likely to be a global issue as continental islands (i.e., islands that are pieces of land connected by the continental shelf to the mainland) are by definition more likely to have been connected or closer to the mainland during past sea level variations.

While we did not consider variation in sea level in our analysis, its variation during the last glacial maximum (LGM) is known to have played an important role in shaping present biodiversity (see Fernández-Palacios et al., 2016; Weigelt et al., 2016). Past sea-level changes could explain the greater maximum species densities observed in Greater Sunda Islands and New Guinea, which were about twice the expected value based on isolation from the mainland. Both islands were connected to the mainland during the LGM. Indeed, the Greater Sunda Islands (Borneo, Sumatra and Java) formed a single landmass (Sundaland), twice their current combined land area and connected to the Malay Peninsula. Similarly, New Guinea,

TABLE 4 Generalized linear model explaining maximum woody plant species density (i.e., maximum number of species/100 woody plant, Poisson distribution) across the 19 archipelagos

		Model 1
Parameters (*SE*)	log(Area)	0.10 (0.01)***
	log(Isolation)	−0.13 (0.02)***
	Temperature annual range	−0.16 (0.04)***
Performance	AICc	157.237
	Pseudo R^2	.698

[Full model = max(species density) ~ log(Area) + log (Isolation) + Mean annual temperature + Temperature annual range + Precipitation of the driest month]. AICc = corrected Akaike information criterion
***$p < .001$.

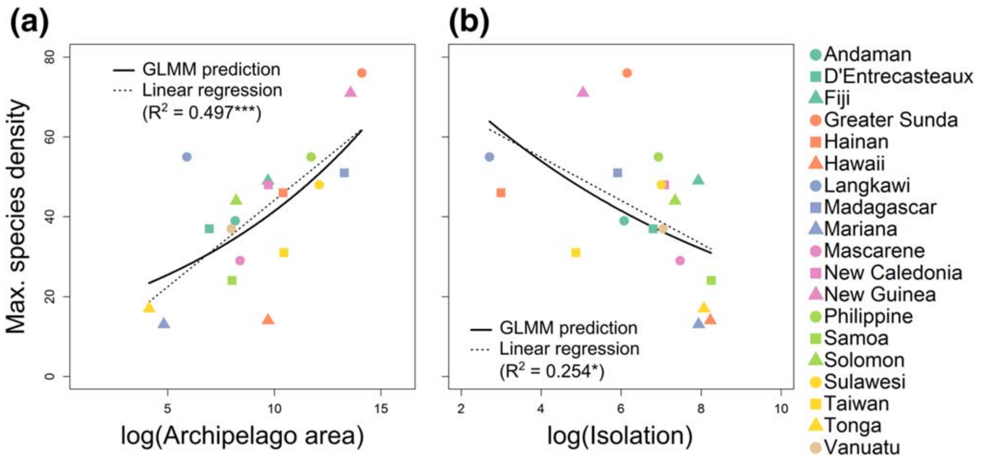

FIGURE 3 Effects of (a) archipelago area and (b) isolation (distance to the mainland) on the maximum species density [a, b, controlling for all covariables in the best generalized linear mixed-effects model (GLMM), see Table 3]. ***$p < .001$, *$p < .05$

Australia and Tasmania were connected during the LGM, forming the Sahul continent (Fernández-Palacios et al., 2016).

4.2 | Composition

Species turnover was driven by similar factors as species density. Geographical distance between plots had the strongest effect at the largest scale, suggesting that regional forcing had a strong impact on determining the regional species pool. The relative importance of geographical distance (with respect to climate) in driving species turnover decreased from the species to family level, and from the archipelago to the plot level. These patterns are likely the result of high island/archipelago species endemism in the region (Kier et al., 2009), being the result of local speciation.

It has been recently suggested that habitat filtering can be more important than dispersal limitation in determining species composition at the archipelago- and island-scale (Carvajal-Endara, Hendry, Emery, Davies, & Regan, 2017). Our study suggests that niche conservatism and environmental filtering also play an important role in determining local species composition. If niche conservatism was important, its effect on composition should be more pronounced at higher taxonomic levels (genus and family) because species that evolved within archipelagos and islands would not impact composition at larger scales. Hence we would expect that climate played a more important role relative to geographical distance at higher taxonomic levels. We found that the relative importance of climate versus geographical distance did indeed increase at higher taxonomic levels from 12% versus 23% (ratio = 0.5) at species, to 11% versus 5% (ratio = 2.2) at genus and 6% versus 1% (ratio = 6.0) at family level. Niche conservatism also impacts species diversity (Wiens et al., 2010) but our study did not define this effect.

4.3 | Regional versus local processes

Regional forcing (biogeography and climate) plays a key role in determining both species diversity and composition on islands in the Indo-Pacific region. Following the 'regional enrichment model' of Ricklefs (1987), we suggest that island area (through the effects of habitat availability and population size of resident species) and archipelago isolation (through dispersal limitation) drive local species diversity by determining the number of successful immigrants to an island, and hence bounding the potential maximum species density. As described above, island area indirectly affects the number of species on the whole island and thus the regional species pool (i.e., the set of species that is capable of coexisting in a community, see Zobel 1997), which in turn bound the maximum local species diversity (Ricklefs, 1987). This pattern has been described as the 'echo pattern' by Rosenzweig and Ziv (1999). While our study strongly supports the importance of regional factors in bounding local species density by determining the regional species pool on islands and archipelagos, this mechanism remains contentious in continental systems (e.g., Harmon & Harrison, 2015).

Regional processes also strongly impact species composition. This is suggested by the strong effect of geographical distance between plots on species compositional turnover among all plots (but not at the local scale within islands), although we cannot quantify the variation explained by local versus regional effects. This further supports that dispersal limitation and habitat availability are likely important filters for determining the local species pool.

While regional processes determine the regional species pool, local processes also contribute to stand-level species composition and diversity. Here we used local climate to represent local processes, ignoring other factors that drive diversity and species composition at the plot-scale such as topography and soil type (e.g., Aiba et al., 2015; Franklin, Wiser, Drake, Burrows, & Sykes, 2006; Webb & Fa'Aumu, 1999) and disturbance history (e.g., Florens, Baider, Martin, & Strasberg, 2012; Franklin, 2007; Webb, Seamon, & Fa'Aumu, 2011). The effect of human disturbance on species composition and diversity is also likely greater on smaller and or more isolated islands (e.g., Franklin & Steadman, 2008). Local climate explained about 13% of the total variation in our dataset, despite known uncertainties of WorldClim for islands (Hijmans et al., 2005). The importance of climate and, notably, of water availability are very likely underestimated because of the poor quality of climatic data available for islands. Factors such as soil, disturbance

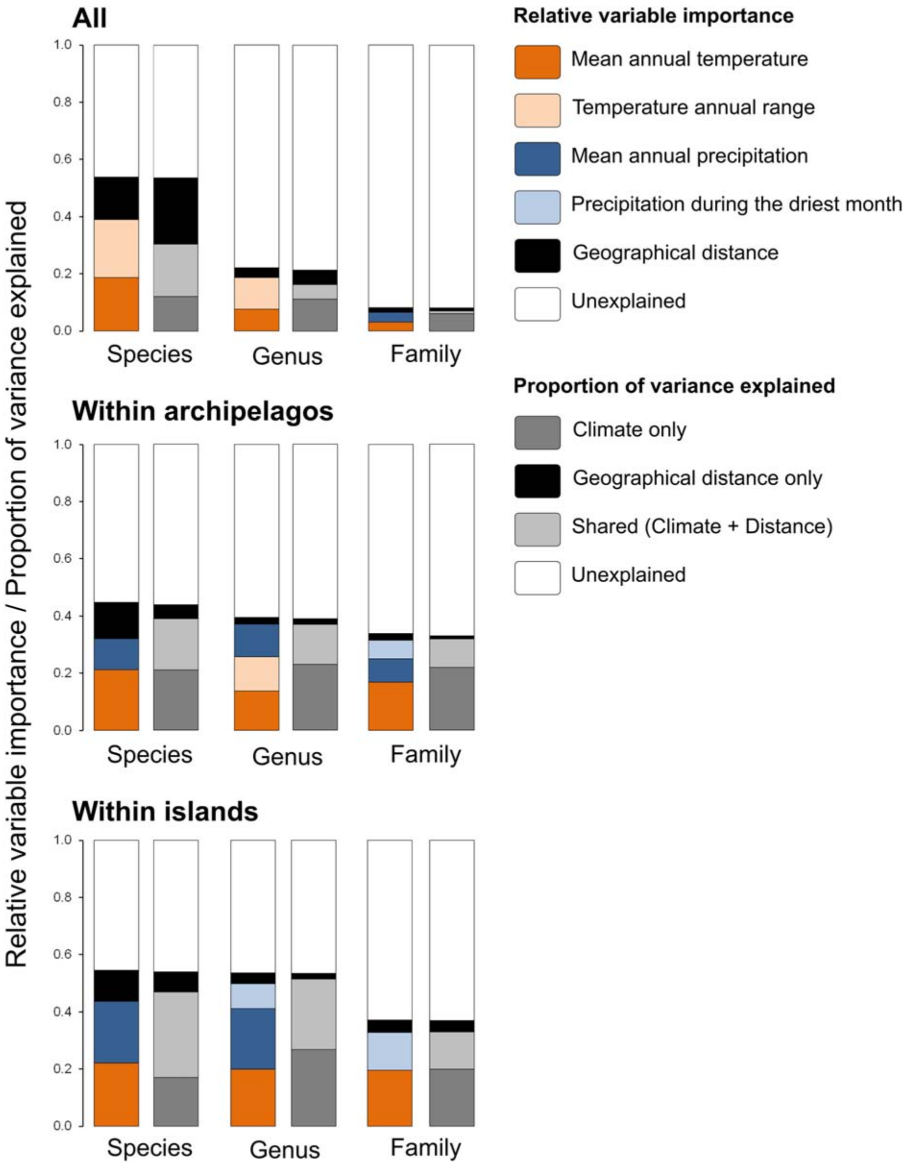

FIGURE 4 Turnover partitioning for taxonomic composition (β_{sim}) using generalized dissimilarity modelling (GDM). Results are shown for different taxonomic levels (species, genus and family) and for different subsets: All = all pairs of plots (*n* = 6555 pairs), within islands = only pairs of plots located on the same archipelago (*n* = 627), within islands = only pairs of plots located on the same island (*n* = 452). For each taxonomic level and subset the left-hand bar represents the relative importance of each individual variable and the right-hand bar represents the proportion of variance explained either by climate, geographical distances between plots or both

history, and uncertainty in the climate data may also account for the large proportion of variation in species diversity and composition that remained unexplained by our models.

5 | CONCLUSION

To our knowledge this is the first time that the effects of biogeographical and climatic variables on patterns of both diversity (represented by taxon density) and composition (represented by turnover measures) of communities have been investigated at different taxonomic levels. This is also the first time that a study has attempted to specifically disentangle local (within islands) and regional (among islands and archipelagos) drivers of species diversity and composition. Our results demonstrate the importance of regional forcing on local, plot-level patterns of biodiversity.

Our study also highlights that plot-level diversity provides meaningful estimators of species diversity on islands, validating previous studies that used plot data (Gillespie et al., 2013; Keppel, Buckley, & Possingham, 2010). Plot-based estimates of diversity do not suffer from collection bias, an important problem for estimates of species diversity on islands based on collected specimens (Gray & Cavers, 2014; Keppel et al., 2016). Furthermore, the plots provided information about the composition and diversity of particular locations and islands, allowing identification of within-island drivers of species distributions, a major gap in island biogeographical knowledge (Santos et al., 2016). In addition to providing information on local processes, comparing plot-scale diversity within and among islands and among archipelagos facilitated disentanglement of local and regional effects on species diversity.

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AUTHOR CONTRIBUTIONS

T.I. and G.K. conceived of the idea, analysed and interpreted the data and drafted the paper. T.I. collated the data. All authors contributed to the collection of data and the writing of the paper

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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