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Regional forcing explains local species diversity and turnover on tropical islands

Running-title: Regional forcing of diversity and turnover on 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 41 tropical islands of the Indo-Pacific region from Madagascar to Hawai‘i Island

Methods We analysed the diversity (as species density, the number of species per 100 stems) 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 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: area, archipelago, biodiversity hotspot, climate, isolation, geographical distance, species pool, species turnover, Indo-Pacific, woody plants.

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 (MacArthur & Wilson, 1967; Whittaker *et al.*, 2001; Kreft *et al.*, 2008). These biogeographical and environmental forcings, i.e. 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 (Zobel, 1997; Lortie *et al.*, 2004; Santos *et al.*, 2016).

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 (Ricklefs, 1987; Lortie *et al.*, 2004; Harrison & Cornell, 2008). 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 *et al.*, 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 & 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 (Neall & Trewick, 2008; Fernández-Palacios *et al.*, 2016; Weigelt *et al.*, 2016).

Climate affects both species diversity and composition of vegetation (Bellard *et al.*, 2012; Feeley *et al.*, 2013; Cabral *et al.*, 2014), 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 (Webb, 2000; Crisp *et al.*, 2009; 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 (Ricklefs, 1987; Rosenzweig & Ziv, 1999; Karger *et al.*, 2014). 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 MacArthur & Wilson, 1967; Whittaker *et al.*, 2008; Fernández-Palacios *et al.*, 2016).

We know surprisingly little about the origins of and processes maintaining plant diversity in the tropical insular Indo-Pacific, which has eight biodiversity hotspots (Fig. 1). The region is characterized by high biodiversity and intense human impacts (Myers *et al.*, 2000; Shearman & Bryan, 2011; Florens, 2013; Keppel *et al.*, 2014). This area also harbours a wide variety of islands and archipelagos with different origins, sizes, isolation and climatic conditions (Mueller-Dombois & Fosberg, 1998; Mittermeier *et al.*, 2005). 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 geographic 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.

METHODS

Data compilation

We compiled published and unpublished forest inventory data from 165 inventories of plots ≥ 0.1 ha located on 41 islands and 19 archipelagos (Table 1, Fig. 1). Plots located in secondary forests were removed from the analysis. The analysis only considered woody plants (trees and lianas) with a stem diameter ≥ 10 cm at ≈ 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 Table S1 in the Supporting information). 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 *et al.*, 2011). The western-most plot was on Madagascar and the eastern-most plot was on Hawai‘i Island. The final dataset consisted of 60795 woody plants in 3136 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/).

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 Ellinson (2010). Hill numbers (noted ^qD) weigh the number of species (S) by the relative abundance of species (p_i) according to a constant q,

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

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

^{2}D can be interpreted as the effective number of dominant species (also known as Simpson diversity). Hill numbers (q = 0, q = 1 and 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 ≥ 50 inventoried trees were used because extrapolation procedures are not robust below half of the sample size (Chao *et al.*, 2014).

Composition

Variation in community composition was assessed through dissimilarity or β diversity index. β diversity has two components (Baselga, 2010), (i) a nested component that results from a loss (or gain) of taxa, and (ii) 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 *bata.pair* function of the *betapart* R package (Baselga & Orme, 2012),

$$\beta_{sim} = \frac{b}{b + a}$$

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.

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 < 0.70; $p > 0.05$). Latitude was not included because it was strongly correlated with temperature annual range and mean annual precipitation (Spearman's rank correlation coefficients rho = 0.759 and rho = 0.746, respectively; $p < 0.001$). 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 = 0.784, $p < 0.001$). Bioclimatic variables were extracted for plot locations from the WorldClim climatology at a spatial resolution of 30 arc-seconds (≈ 1 km) (Hijmans *et al.*, 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 = -0.774, $p < 0.001$). 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.

Analysis

All analyses were performed using the 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 geographic 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 relationships) with intercepts forced to 0 using the *smatr* R package (Warton *et al.*, 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 *et al.*, 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 generalised 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 AICc (ΔAICc < 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 *et al.*, 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 test (50 permutations per step) to only keep significant predictors (p value < 0.05) using the *gdm.varImp*. 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 *et al.* (2017).

RESULTS

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, $p < 0.001$). 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 (Figure S1 in the Supporting information). Differences among island area and isolation were also strongly correlated with the identity of the archipelago an island belonged to (PERMANOVA, $r^2 = 0.92$, $p < 0.001$). 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).

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 (Appendix SC and SD). The estimated number of species, genera and families for 100 woody plants ranged from 2 for all taxonomic levels for a Hawaiian dry forest plot to 76, 51 and 31 for a Bornean rainforest. Species density was highly correlated with genus and family density (Figure S2 in the Supporting information). The number of species, genera and families (Hill number, q=0) were also highly correlated with the number of abundant (Hill number, q=1) and dominant (Hill number, q=2) taxa at different taxonomic levels (Figure S3 in the Supporting information).

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 (Fig. 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 (Fig. 2). Precipitation during the 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 (Fig. 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 (Fig. 3B), having greater species density than expected with respect to their isolation from the mainland.

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 (Fig. 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 (Figure S4 in the Supporting information), 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.

DISCUSSION

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. Preston, 1962; MacArthur & Wilson, 1967; Moody, 2000; Price, 2004) or global scale (Kreft *et al.*, 2008; Triantis *et al.*, 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 (Santos et al. 2010; Triantis et al. 2015; Gillespie et al. 2013), island (Whittaker et al. 2008, Kreft et al. 2008; Gillespie et al. 2013) and plot.

The underlying processes causing the high predictive power of area for species diversity remain controversial. MacArthur and Wilson (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 MacArthur & Wilson, 1967; Wright, 1983; Cowie, 1995; Whittaker *et al.*, 2008; Hurlbert & Jetz, 2010; Keppel *et al.*, 2016). 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 (~3800 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 *et al.*, 2001). Ricklefs and He (2016) also found that local species diversity is significantly lower on islands in comparison with mainland 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 make 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 mainland) are by definition more likely to have been connected or closer to the mainland during past sea level.

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

Composition

Species turnover was driven by similar factors as species density. Geographic 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 *et al.*, 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 geographic distance at higher taxonomic levels. We found that the relative importance of climate versus geographic 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.

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 islands and thus the regional species pool (i.e. the set of species that is capable to coexist 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 geographic 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., Webb & Fa'aumu, 1999; Franklin *et al.*, 2006; Aiba *et al.*, 2015) and disturbance history (e.g., Franklin, 2007; Webb *et al.*, 2011; Florens *et al.*, 2012). The effect of human disturbances 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 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.

Conclusion

To our knowledge this is the first time that the effects of biogeographic 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 provided meaningful estimators of species diversity on islands, validating previous studies that used plot data (Keppel *et al.*, 2010; Gillespie *et al.*, 2013). 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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SUPPORTING INFORMATION

Appendix Table S1 Plot data

Appendix Figure S1-4 Additional figures

BIOSKETCH

Thomas Ibanez is a postdoctoral researcher at the Agronomic Institute of New Caledonia (Nouméa, New Caledonia) and associate researcher at the UMR AMAP (Montpellier, France). He is interested in the assemblage and dynamics of forest communities as well as the distribution of diversity. His research mainly focuses on tropical rainforests in the islands of the southwest Pacific, and more specifically in New Caledonia.

Gunnar Keppel is interested the biogeography and assembly of island communities, the conservation of biodiversity and the impacts of environmental change on natural ecosystems. He is currently based at the University of Göttingen as part of a 12-month Alexander von Humboldt fellowship to work on the effects of environmental heterogeneity on diversity on islands.

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.

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

Archipelago	Island (data sources)	Area (km^2)	Isolation (km)	Nearest mainland	# Plots (sub-plots)
Andaman Islands	Little Andaman (Rasingam & Parthasarathy, 2009)	710	610	Asia	4
	Middle Andaman (Rajkumar & Parthasarathy, 2008)	2781	260	Asia	2
	All				6
Bismarck Archipelago	Normanby (Keppel *et al.*, 2010)	1040	900	Australia	1 (4)
Fiji Islands	Gau (Keppel *et al.*, 2010)	136	2800	Australia	2 (4)
	Macuata (Gillespie *et al.*, 2013)	136	2850	Australia	1
	Monu (Gillespie *et al.*, 2013)	1	2650	Australia	1
	Naviti (Gillespie *et al.*, 2013)	34	2800	Australia	1
	Vanua Levu (Keppel *et al.*, 2010)	5587	2900	Australia	1 (4)

	Viti Levu (Gillespie *et al.*, 2013)	10531	2700	Australia	3 (6)
	Yasawa (Gillespie *et al.*, 2013)	32	2800	Australia	1
	All				11 (19)
Greater Sunda Islands	Borneo (Aiba & Kitayama, 1999; Phillips & Miller, 2002; Small *et al.*, 2004; Aiba *et al.*, 2015)	748168	550	Asia	5
	Java (Meijer, 1959)	138794	800	Asia	1
	Sumatra (Kartawinata *et al.*, 2004)	443066	60	Asia	1
					7
Hainan	Hainan (Lu *et al.*, 2014)	33210	20	Asia	1 (2)
Hawaiian Islands	Hawaii (Gillespie *et al.*, 2013; Ostertag *et al.*, 2014)	10434	3750	North America	4 (5)
	Kauai (Gillespie *et al.*, 2013)	1435	3800	North America	4
	Lanai (Gillespie *et al.*,	358	3750	North	1 (3)

	2013)			America	
	Maui (Gillespie *et al.*, 2013)	1903	3700	North America	1
	Molokai (Gillespie *et al.*, 2013)	678	3750	North America	1
	Oahu (Gillespie *et al.*, 2013)	1583	3800	North America	2
	All				13 (16)
Langkawi	Langkawi (Kohira *et al.*, 2001)	363	15	Asia	1
Madagascar	Madagascar (Phillips & Miller, 2002, Ratovoson et al., unpublished)	587713	370	Africa	18 (27)
Mariana Islands	Saipan (Gillespie *et al.*, 2013)	123	2800	Asia	2 (3)
Mascarene Archipelago	La Réunion (Strasberg, 1996)	2535	1700	Africa	1
	Mauritius (Florens & Baider, unpublished)	1874	1800		4 (5)

	All				5 (6)
New Caledonia	Grande Terre (Phillips & Miller, 2002; Gillespie *et al.*, 2013; Ibanez *et al.*, in press)	16648	1200	Australia	22 (24)
New Guinea	New Guinea (Phillips & Miller, 2002; Laidlaw *et al.*, 2007; Whitfeld *et al.*, 2014)	785753	155	Australia	5 (8)
New Hebrides	Erromango (Keppel *et al.*, 2010)	888	1100	Australia	1 (4)
	Malakula (Keppel *et al.*, 2010)	2041	1200	Australia	1 (4)
	All				2 (8)
Philippine Islands	Luzon (Phillips & Miller, 2002)	109965	600	Asia	1
	Negros (Hamann *et al.*, 1999)	13075	1450	Asia	1
	All				2

Samoa Islands	Savaii (Keppel *et al.*, 2010)	1718	3800	Australia	1 (3)
	Ta'u (Webb *et al.*, 2006)	46	3900	Australia	2
	Tutuila (Webb & Fa'aumu, 1999)	142	3900	Australia	4
	Upolu (Keppel *et al.*, 2010)	1125	3800	Australia	1 (4)
	All				8 (13)
Sulawesi	Sulawesi (Culmsee & Pitopang, 2009)	180681	1100	Australia	1 (6)
Solomon Islands	Choiseul (Keppel *et al.*, 2010)	2971	1600	Australia	2 (4)
	Kolombangara (Keppel *et al.*, 2010)	688	1500	Australia	1 (4)
	All				3 (8)
Taiwan	Taiwan (Phillips & Miller, 2002)	34507	130	Asia	2
Tonga Islands	Kao (Franklin *et al.*, 2006)	12	3200	Australia	1
	Tofua (Franklin *et al.*,	50	3200	Australia	3

	2006)	
	All	4

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. 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)].

		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	0.122	0.127
	Conditional R^2	0.848	0.852

“***” *p* value < 0.001, “**” *p* value < 0.01, “*” *p* value < 0.05

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. 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)].

		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	0.502	0.534
	Conditional R^2	0.853	0.828

"***" *p* value < 0.001, "**" *p* value < 0.01, "*" *p* value < 0.05

Table 4 Generalized linear model explaining maximum woody plant species density (i.e. max number of species / 100 woody plant, Poisson distribution) across the 19 archipelagos [Full model = max(species density) ~ log(Area) + log (Isolation) + Mean annual temperature + Temperature annual range + Precipitation of the driest month].

		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	0.698

“***” *p* value < 0.001, “**” *p* value < 0.01, “*” *p* value < 0

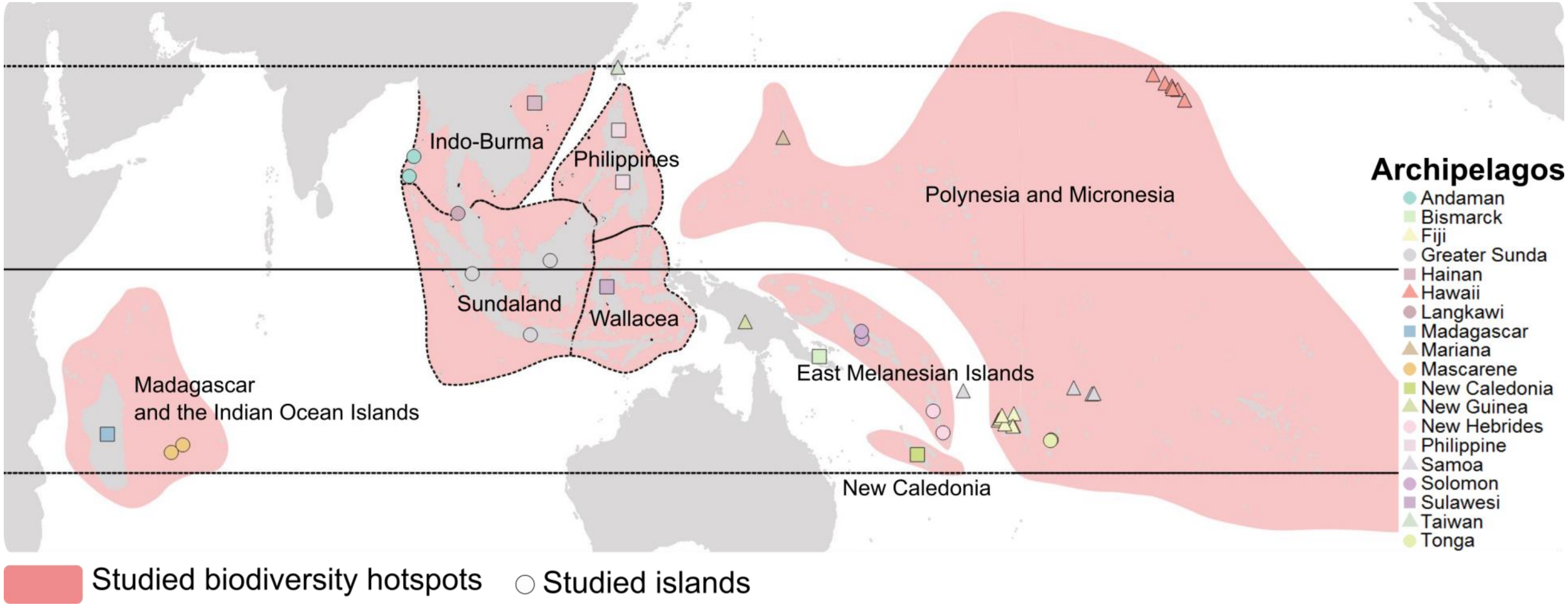

Figure 1 Studied islands and archipelagos in the Indo-Pacific area. The names of the eight biodiversity hotspot surveyed in this study are indicated on the map.

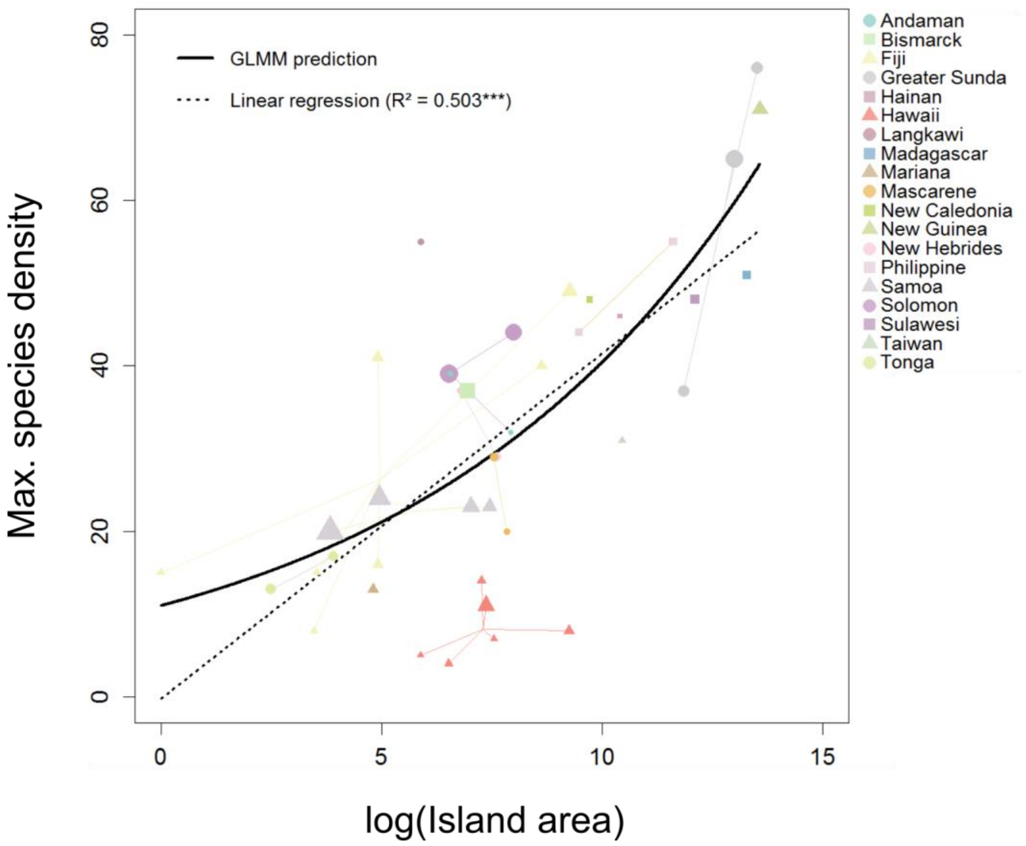

Figure 2 Effect of island area on the maximum species density (controlling for all co-variables in the best GLMM, see Table 2). Point size is proportional to the precipitation during the driest month. "***" *p* value < 0.001, "**" *p* value < 0.01, "*" *p* value < 0.05

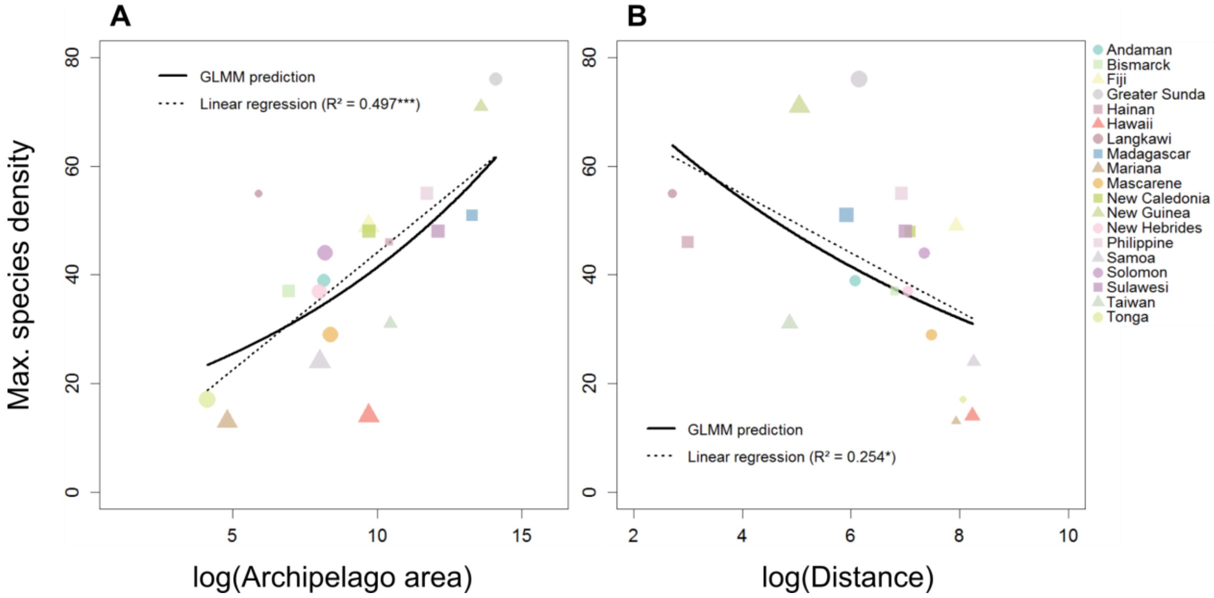

Figure 3 Effects of (A) archipelago area and (B) isolation (distance to the mainland) on the maximum species density (A-B, controlling for all co-variables in the best GLMM, see Table 3). Point size is proportional to the isolation in (A) and to area in (B). “***” *p* value < 0.001, “**” *p* value < 0.01, “*” *p* value < 0.05.

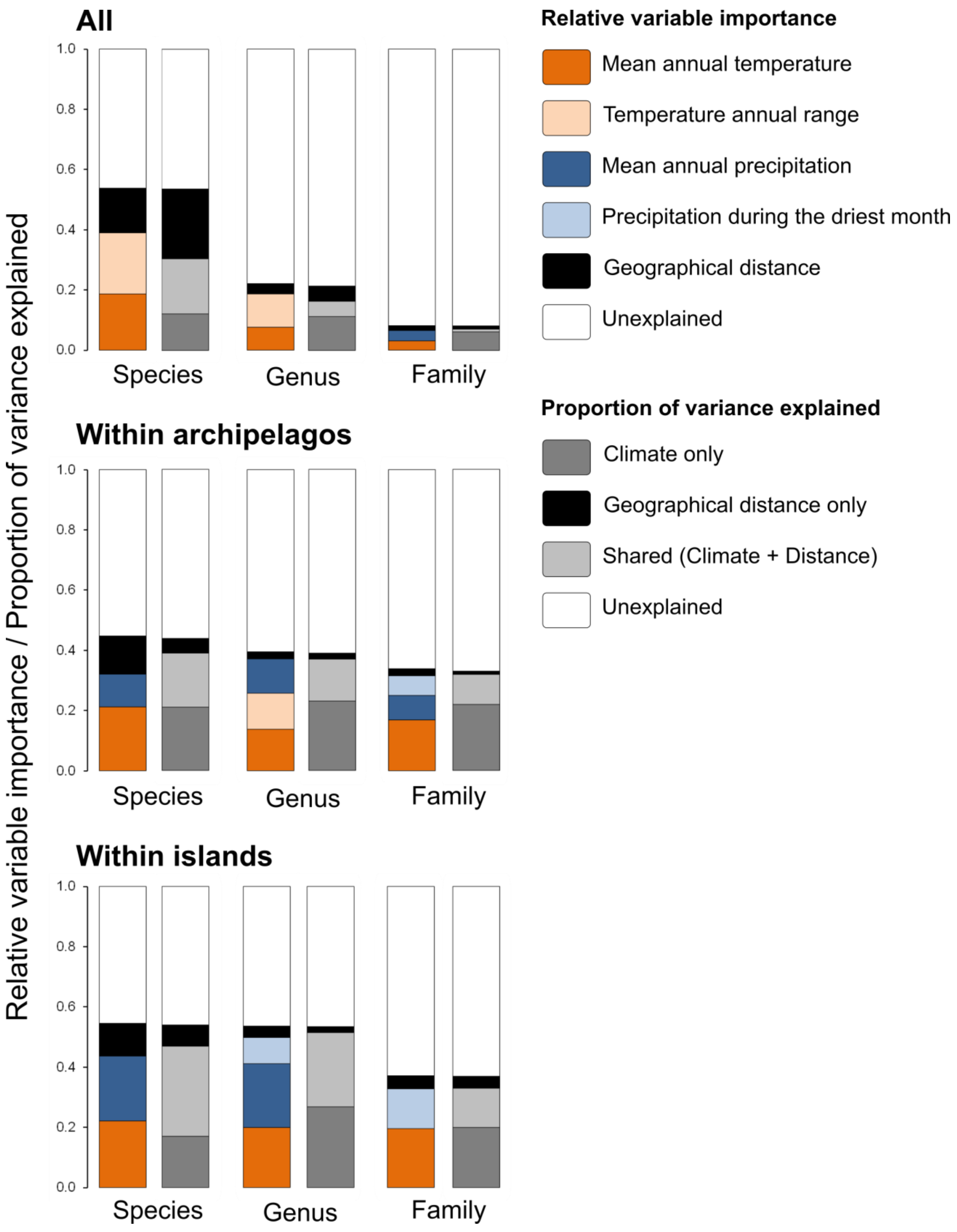

Figure 4 Turnover partitioning for taxonomic composition (β_{sim}) using generalized dissimilarity modeling (*GDM*). Results are shown for different taxonomic levels (species, genus and family) and for different subsets: All = all pairs of plots (N = 6555 pairs), within islands = only pair of plots located on the same archipelago (N = 627), within islands = only pair of plots located on the same island (N = 452). For each taxonomic level and subsets 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 distance between plots or both.