

1   **Regional forcing explains local species diversity and turnover on tropical islands**

2   Running-title: Regional forcing of diversity and turnover on islands

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77 **ABSTRACT**

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

82 **Location** 41 tropical islands of the Indo-Pacific region from Madagascar to Hawai‘i Island

83 **Methods** We analysed the diversity (as species density, the number of species per 100 stems)  
84 and composition of tropical woody plant communities located across 113 plots, 41 islands and  
85 19 archipelagos. We used generalized linear mixed-effects models and generalized  
86 dissimilarity models to determine the role of regional forcing at the island and archipelago  
87 scale and to assess the relative importance of biogeographical (area and isolation of islands or  
88 archipelagos, geographical distance between plots) and climatic factors in explaining  
89 differences in local diversity and composition (species turnover). Analyses were conducted at  
90 different geographical scales (local, island and archipelago) and taxonomic levels (species,  
91 genus and family).

92 **Results** Variation in local (plot-level) diversity was primarily explained by island and  
93 archipelago identity. Maximum species density was positively correlated with the area of an  
94 island (or archipelago) and negatively correlated with the isolation of an archipelago. Local  
95 climatic variability was also a significant predictor of species density, but less important than  
96 regional forcing. Climate variables explained < 20% of the variation in species turnover  
97 across all plots. The importance of geographical distance [between plots](#) relative to climate in  
98 driving species turnover decreased from the species to family level, and from the regional to  
99 island level.

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

105

106 **Keywords:** area, archipelago, biodiversity hotspot, climate, isolation, geographical distance,  
107 species pool, species turnover, Indo-Pacific, woody plants.



109 **INTRODUCTION**

110 Species diversity and composition of island biotas depend on the complex interplay of various  
111 processes such as immigration, competition, extinction and speciation. These processes in  
112 turn are controlled by biogeographical and environmental factors and processes (MacArthur  
113 & Wilson, 1967; Whittaker *et al.*, 2001; Kreft *et al.*, 2008). **These biogeographical and**  
114 **environmental forcings, i.e. factors and processes that influence species diversity and**  
115 **composition**, can be considered as filters that dictate which species of the total global species  
116 pool are present (Zobel, 1997; Lortie *et al.*, 2004; Santos *et al.*, 2016).

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

130 Climate affects both species diversity and composition of vegetation (Bellard *et al.*,  
131 2012; Feeley *et al.*, 2013; Cabral *et al.*, 2014), within and among islands (Gillespie *et al.*,  
132 2013). On islands, the effects of climate on species diversity are presumed to be less  
133 pronounced compared to the mainlands because of area and isolation effects (Field *et al.*,  
134 2009). At the local- or plot-scale, climate can have important effects on species diversity  
135 (Gillespie *et al.*, 2013). However, it should have even stronger impacts on taxonomic  
136 composition because species tend to retain their ancestral ecological characteristics (i.e.,  
137 niches), a phenomenon known as niche conservatism (Wiens & Graham, 2005). Niche  
138 conservatism can result in lineages tending to remain faithful to certain biomes or local  
139 environmental conditions (Webb, 2000; Crisp *et al.*, 2009; Wiens *et al.*, 2010).

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

149        We know surprisingly little about the origins of and processes maintaining plant  
150    diversity in the tropical insular Indo-Pacific, which has eight biodiversity hotspots (Fig. 1).  
151    The region is characterized by high biodiversity and intense human impacts (Myers *et al.*,  
152    2000; Shearman & Bryan, 2011; Florens, 2013; Keppel *et al.*, 2014). This area also harbours a  
153    wide variety of islands and archipelagos with different origins, sizes, isolation and climatic  
154    conditions (Mueller-Dombois & Fosberg, 1998; Mittermeier *et al.*, 2005). In addition, a  
155    relatively recent and complex tectonic history (Hall, 2009; Lohman *et al.*, 2011), makes this  
156    an ideal study area to analyse how biogeography and climate affect communities at different  
157    scales.

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

169

170    **METHODS**

171

172 **Data compilation**

173 We compiled published and unpublished forest inventory data from 165 inventories of plots  $\geq$   
174 0.1 ha located on 41 islands and 19 archipelagos (Table 1, Fig. 1). Plots located in secondary  
175 forests were removed from the analysis. The analysis only considered woody plants (trees and  
176 lianas) with a stem diameter  $\geq 10$  cm at  $\approx 1.3$  m above the base (DBH, diameter at breast  
177 height). Plots located in close proximity (within 1 km) were pooled (considered as a single  
178 plot) to avoid pseudoreplication, resulting in 113 plots (see Table S1 in the Supporting  
179 information). All plots were located in lowland tropical forests in the Indo-Pacific region on  
180 islands larger than 1 km<sup>2</sup>. Montane **forest** plots (as defined by authors of source data) were not  
181 considered in the analysis (e.g. Aiba & Kitayama, 1999; Culmsee *et al.*, 2011). The western-  
182 most plot was on Madagascar and the eastern-most plot was on Hawai‘i Island. The final  
183 dataset consisted of 60795 woody plants in 3136 species, 769 genera and 148 families.  
184 Nomenclature followed the Taxonomic Name Resolution Service v4.0  
185 (<http://tnrs.iplantcollaborative.org/>). For taxa without resolution we referred to The Plant List  
186 website (<http://www.theplantlist.org/>).

187

188 **Diversity**

189 Because plots differed in their sampling sizes (from 0.1 to 4 ha), we used rarefaction and  
190 extrapolation curves to produce diversity indices for a sample size of 100 woody plants per  
191 plot using the *iNEXT* R package (Chao & Jost, 2012; Chao *et al.*, 2014). We used Hill  
192 numbers or effective number of species (Hill, 1973) as diversity indices, as recommended by  
193 Jost (2006) and Ellinson (2010). Hill numbers (noted <sup>q</sup>D) weigh the number of species (S) by  
194 the relative abundance of species (p<sub>i</sub>) according to a constant q,

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

196 When q = 0, all species have the same weight and <sup>0</sup>D corresponds to the **number of species**  
197 **per 100 woody plants (i.e., species density)**. When q = 1, species are weighted by their  
198 relative abundance and <sup>1</sup>D can be interpreted as the effective number of abundant species  
199 (also known as Shannon diversity). When q = 2, less abundant species have little weight and

200  $D^2$  can be interpreted as the effective number of dominant species (also known as Simpson  
201 diversity). Hill numbers ( $q = 0$ ,  $q = 1$  and  $q = 2$ ) were estimated at species, genus and family  
202 levels for 100 woody plants as the mean value of 50 bootstrap iterations. Only plots with  $\geq 50$   
203 inventoried trees were used because extrapolation procedures are not robust below half of the  
204 sample size (Chao *et al.*, 2014).

205

## 206 **Composition**

207 Variation in community composition was assessed through dissimilarity or  $\beta$  diversity index.  
208  $\beta$  diversity has two components (Baselga, 2010), (i) a nested component that results from a  
209 loss (or gain) of taxa, and (ii) a turnover component that results from a replacement of taxa  
210 due to environmental sorting or spatial and historical constraints. To assess taxonomic  
211 dissimilarities independently of differences in taxonomic diversity, we removed the nested  
212 component of the  $\beta$  diversity and only considered its turnover component using the Simpson  
213 dissimilarity index  $\beta_{sim}$  using the *bata.pair* function of the *betapart* R package (Baselga &  
214 Orme, 2012),

215

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

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

221

## 222 **Explanatory variables**

223 After variable selection, we retained two biogeographic variables – island area (Area), and  
224 distance to nearest mainland (**Isolation**) – extracted from the Island Directory website  
225 (<http://islands.unep.ch>, Dahl, 1991) or estimated using the ruler and polygon tool on *Google*  
226 *Earth*. Four bioclimatic variables (mean annual temperature, temperature annual range, mean  
227 annual precipitation and the precipitation of the driest month) were investigated as potential  
228 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 ( $\approx 1$  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.

245

## 246 Analysis

247 All analyses were performed using the R.3.3.0 (R Core Team, 2016). We first ordinated plots  
248 according to their climate, and islands according to their geographical features, using  
249 principal component analysis (PCA). We used permutational analysis of variance  
250 (PERMANOVA) to test whether climatic and geographic differences were due to plots or  
251 islands belonging to different islands and/or archipelagos. We also tested the relationships  
252 between Hill numbers using standard major axes applied to log-transformed data (i.e.,  
253 modelling power law relationships) with intercepts forced to 0 using the *smatr* R package  
254 (Warton *et al.*, 2012).

255 The relative importance of various processes in driving local diversity was  
256 investigated at multiple scales with mixed-effect models that can partition the total variation  
257 in a dataset into different levels, and are especially relevant when looking at species diversity  
258 on different islands and archipelagos (Bunnefeld & Phillimore, 2012). At the plot-scale, we  
259 tested the effects of climate on diversity using generalized linear mixed-effects models  
260 (GLMMs) with Poisson distribution using the *glmer* function from the *lme4* R package (Bates

261 *et al.*, 2015), including the identity of the island and archipelago as random effects. At the  
262 island- and archipelago-scale, we selected the species density of the most species diverse plot  
263 as a response variable that provided the best estimate of maximum diversity of the  
264 island/archipelago. At the island-scale, we used the log-area of the island as well as the  
265 climatic variables of the most diverse plot as fixed effects, with the identity of the archipelago  
266 set as a random effect. At the archipelago scale, we used generalised linear models with the  
267 log-area of the archipelago (sum of the values for islands belonging to the same archipelago),  
268 the log-distance between the archipelago and mainland (mean of the values for islands  
269 belonging to the same archipelago) and the climate variables of the most diverse plot as  
270 explanatory variables. Note that climatic variables were centred and scaled before fitting the  
271 models to make their effects directly comparable.

272 We used the *MuMIn* R package (Bartoń, 2016) and the *dredge* function to generate  
273 different sets of models representing all possible combinations and subsets of fixed effects.  
274 We then selected the best models based on their AICc ( $\Delta\text{AICc} < 2$  from the best models,  
275 Bunnefeld & Phillimore, 2012). We used marginal- $r^2$  (without random effects) and  
276 conditional- $r^2$  (with random effects) to assess the relative importance of fixed and random  
277 effects in *GLMMs* (Nakagawa & Schielzeth, 2013).

278 We then investigated the relative importance of climate and geographical distance  
279 **between plots** in driving community composition turnover (beta-diversity) using generalized  
280 dissimilarity modelling (GDM, Ferrier *et al.*, 2007) computed with the *gdm* function of the  
281 *gdm* R package (Manion *et al.*, 2017). We used geographical distance **between plots** as well as  
282 climate (mean annual temperature, temperature annual range, mean annual precipitation and  
283 the precipitation of the driest month) as predictors and  $\beta_{sim}$  distances in composition as  
284 response variables. We performed stepwise backward procedures with matrix permutation test  
285 (50 permutations per step) to only keep significant predictors ( $p$  value  $< 0.05$ ) using the  
286 *gdm.varImp*. The proportion of variance explained by climate and geographical distance  
287 **between plots** was then estimated by comparing the variance explained by different models  
288 computed with both climate and geographical distance as predictors and with only  
289 environmental or geographical distance as predictors (Legendre, 2008). We also computed the  
290 relative importance of each individual predictor following Fitzpatrick *et al.* (2013) and König  
291 *et al.* (2017).

292

293 **RESULTS**

294

295 **Climate and geography**

296 Climate was intrinsically linked with geography, such that the identity of the island and  
297 archipelago explained 84% and 75% of the observed differences in climate, respectively  
298 (PERMANOVA,  $p < 0.001$ ). For instance, plots located on islands of the Greater Sunda  
299 Island close to the equator tend to receive more rainfall with a less pronounced dry season  
300 than plots located on islands at higher latitudes, such as Madagascar or New Caledonia  
301 (Figure S1 in the Supporting information). Differences among island area and isolation were  
302 also strongly correlated with the identity of the archipelago an island belonged to  
303 (PERMANOVA,  $r^2 = 0.92$ ,  $p < 0.001$ ). Large islands, such as those of the Greater Sunda  
304 Islands, tended to be closer to the continent (and the equator) and less isolated than small  
305 islands such those of the Polynesian Archipelagos (e.g. Samoa and Tonga Islands).

306

307 **Diversity**

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

316 Among plots, local climate together with the identity of the island and archipelago  
317 explained 85% of the variation in species density (Table 2). Species density tended to increase  
318 with increasing mean annual precipitation and decreasing mean annual temperature. However,  
319 differences among plots (within the same island) in climate variables (i.e. local climatic  
320 variability), explained only 12% (marginal  $r^2$ ) of this variation. About 73% (conditional  $r^2 -$   
321 marginal  $r^2$ ) of the variation in species density among plots was explained by the identity of  
322 islands and archipelagos (random effects). Therefore, almost 75% of the variation in species

323 density among plots was explained by regional processes, mostly at archipelago scale (the  
324 standard deviation of the intercept among archipelagos and islands in the best model being  
325 0.537 and 0.344, respectively).

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

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

341

## 342 Composition

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

353

354 **DISCUSSION**

355 **Diversity**

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

363 The area of an island or archipelago was strongly and positively correlated with  
364 maximum species density recorded in a plot, explaining 50% of the variation. While it is well  
365 known that area of an island explains a significant proportion of the variability in the number  
366 of species on an island at a regional (e.g. Preston, 1962; MacArthur & Wilson, 1967; Moody,  
367 2000; Price, 2004) or global scale (Kreft *et al.*, 2008; Triantis *et al.*, 2015), few studies have  
368 explored the relationship between area of an island and the local, plot-level species density  
369 (but see Gillespie *et al.*, 2013; Karger *et al.*, 2014). Our results therefore suggest that area is  
370 an important predictor of species diversity at all scales investigated, including archipelago  
371 (Santos *et al.* 2010; Triantis *et al.* 2015; Gillespie *et al.* 2013), island (Whittaker *et al.* 2008,  
372 Kreft *et al.* 2008; Gillespie *et al.* 2013) and plot.

373 The underlying processes causing the high predictive power of area for species  
374 diversity remain controversial. MacArthur and Wilson (1967) suggested that the “area effect”  
375 is due to increasing extinction rate with decreasing island area because smaller population  
376 sizes on smaller islands would result in higher extinction probabilities. However, area is also  
377 often correlated with habitat diversity (e.g. island elevation and topographical complexity),  
378 energy availability and island age (on oceanic islands), which would exert a more direct effect  
379 on species number through immigration, extinction and speciation rates as well as  
380 determining the carrying capacity of islands (see MacArthur & Wilson, 1967; Wright, 1983;  
381 Cowie, 1995; Whittaker *et al.*, 2008; Hurlbert & Jetz, 2010; Keppel *et al.*, 2016). However,  
382 Simberloff (1976) also determined an independent effect of island area on species diversity by  
383 experimentally controlling for environmental heterogeneity.

384        The isolation of an archipelago (i.e., the distance to the closest mainland) also  
385    constituted an important negative predictor of species diversity. For instance, the isolated  
386    archipelago of Hawaii (~3800 km west of North America) exhibits low species density with  
387    respect to its size (see Ostertag *et al.*, 2014), while the small archipelago of Langkawi, which  
388    is located only 15 km from the Malay Peninsula, exhibits a relatively high species density  
389    (Kohira *et al.*, 2001). Ricklefs and He (2016) also found that local species diversity is  
390    significantly lower on islands in comparison with mainland due to isolation effects. Similarly,  
391    Gillespie *et al.* (2013) and Karger *et al.* (2014) found isolation of an island from the closest  
392    source of propagules from the global species pool to be particularly important at the  
393    archipelago-scale. It has been suggested that the effect of isolation is weaker for large and / or  
394    continental islands (Weigelt & Kreft, 2013), as was the case in our study. However,  
395    continental islands in the Indo-Pacific tend to be larger and closer to the continent than  
396    oceanic islands, which make it difficult to disentangle the effects of isolation and area. Indeed,  
397    this issue is likely to be a global issue as continental islands (i.e. islands that are pieces of land  
398    connected by the continental shelf to mainland) are by definition more likely to have been  
399    connected or closer to the mainland during past sea level.

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

410

## 411    **Composition**

412    Species turnover was driven by similar factors as species density. [Geographic distance](#)  
413    [between plots](#) had the strongest effect at the largest scale, suggesting that regional forcing had  
414    a strong impact on determining the regional species pool. The relative importance of  
415    geographical distance (with respect to climate) in driving species turnover decreased from the

416 species to family level, and from the archipelago to the plot level. These patterns are likely the  
417 result of high island/archipelago species endemism in the region (Kier et al. 2009), being the  
418 result of local speciation.

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

431

### 432 **Regional versus local processes**

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

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

451        While regional processes determine the regional species pool, local processes also  
452        contribute to stand-level species composition and diversity. Here we used local climate to  
453        represent local processes, ignoring other factors that drive diversity and species composition  
454        at the plot scale such as topography and soil type (e.g., Webb & Fa'aumu, 1999; Franklin *et*  
455        *al.*, 2006; Aiba *et al.*, 2015) and disturbance history (e.g., Franklin, 2007; Webb *et al.*, 2011;  
456        Florens *et al.*, 2012). The effect of human disturbances on species composition and diversity  
457        is also likely greater on smaller and or more isolated islands (e.g., Franklin & Steadman,  
458        2008). Local climate explained about 13% of the total variation in our dataset, despite known  
459        uncertainties of WorldClim for islands (Hijmans *et al.* 2005). The importance of climate and,  
460        notably, of water availability are very likely underestimated because of the poor quality of  
461        climatic data available for islands. Factors such as soil, disturbance history, and uncertainty in  
462        the climate data may also account for the large proportion of variation in species diversity and  
463        composition that remained unexplained by our models.

464

## 465        **Conclusion**

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

473        Our study also highlights that plot-level diversity provided meaningful estimators of  
474        species diversity on islands, validating previous studies that used plot data (Keppel *et al.*,  
475        2010; Gillespie *et al.*, 2013). Plot-based estimates of diversity do not suffer from collection  
476        bias, an important problem for estimates of species diversity on islands based on collected

477 specimens (Gray & Cavers, 2014; Keppel *et al.*, 2016). Furthermore, the plots provided  
478 information about the composition and diversity of particular locations and islands, allowing  
479 identification of within-island drivers of species distributions a major gap in island  
480 biogeographical knowledge (Santos *et al.*, 2016). In addition to providing information on  
481 local processes, comparing plot-scale diversity within and among islands and among  
482 archipelagos facilitated disentanglement of local and regional effects on species diversity.

483

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699

## 700 SUPPORTING INFORMATION

701 Appendix Table S1 Plot data

702 Appendix Figure S1-4 Additional figures

703

## 704 BIOSKETCH

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

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

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716 Author contributions: T.I. and G.K. conceived of the idea, analysed and interpreted the data  
717 and drafted the paper. T.I. collated the data. All authors contributed to the collection of data  
718 and the writing of the paper.

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

Archipelago	Island (data sources)	Area (km <sup>2</sup> )	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 <i>et al.</i> , 2010)	1040	900	Australia	1 (4)
Fiji Islands	Gau (Keppel <i>et al.</i> , 2010)	136	2800	Australia	2 (4)
	Macuata (Gillespie <i>et al.</i> , 2013)	136	2850	Australia	1
	Monu (Gillespie <i>et al.</i> , 2013)	1	2650	Australia	1
	Naviti (Gillespie <i>et al.</i> , 2013)	34	2800	Australia	1
	Vanua Levu (Keppel <i>et al.</i> , 2010)	5587	2900	Australia	1 (4)

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

	2013)			America	
	Maui (Gillespie <i>et al.</i> , 2013)	1903	3700	North America	1
	Molokai (Gillespie <i>et al.</i> , 2013)	678	3750	North America	1
	Oahu (Gillespie <i>et al.</i> , 2013)	1583	3800	North America	2
	All				13 (16)
Langkawi	Langkawi (Kohira <i>et al.</i> , 2001)	363	15	Asia	1
Madagascar	Madagascar (Phillips & Miller, 2002, Ratovoson et al., unpublished)	587713	370	Africa	18 (27)
Mariana Islands	Saipan (Gillespie <i>et al.</i> , 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 <i>et al.</i> , 2013; Ibanez <i>et al.</i> , in press)	16648	1200	Australia	22 (24)
New Guinea	New Guinea (Phillips & Miller, 2002; Laidlaw <i>et al.</i> , 2007; Whitfeld <i>et al.</i> , 2014)	785753	155	Australia	5 (8)
New Hebrides	Erromango (Keppel <i>et al.</i> , 2010)	888	1100	Australia	1 (4)
	Malakula (Keppel <i>et al.</i> , 2010)	2041	1200	Australia	1 (4)
All					2 (8)
Philippine Islands	Luzon (Phillips & Miller, 2002)	109965	600	Asia	1
	Negros (Hamann <i>et al.</i> , 1999)	13075	1450	Asia	1
All					2

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

2006)

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All

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720 **Table 2** Best generalized linear mixed models ( $\Delta \text{AICc} < 2$ ) explaining woody plant species  
 721 density (number of species / 100 woody plants, Poisson distribution) across the 113 studied  
 722 plots. Islands (N=41) and archipelagos (N = 19) were considered as random effects [Full  
 723 model: Species density ~ Mean annual temperature + Temperature annual range + Mean  
 724 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 <sup>2</sup>	0.122	0.127
	Conditional R <sup>2</sup>	0.848	0.852

725 \*\*\* p value < 0.001, \*\* p value < 0.01, \* p value < 0.05

726

727 **Table 3** Best generalized linear mixed models ( $\Delta \text{AICc} < 2$ ) explaining maximum woody  
 728 plant species density (i.e. number of species / 100 woody plants, Poisson distribution) across  
 729 the 41 studied islands. Archipelagos ( $N = 19$ ) were considered as random effects [Full model  
 730 = max(species density) ~ log(Area) + Mean annual temperature + Temperature annual range  
 731 + 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 <sup>2</sup>	0.502	0.534
	Conditional R <sup>2</sup>	0.853	0.828

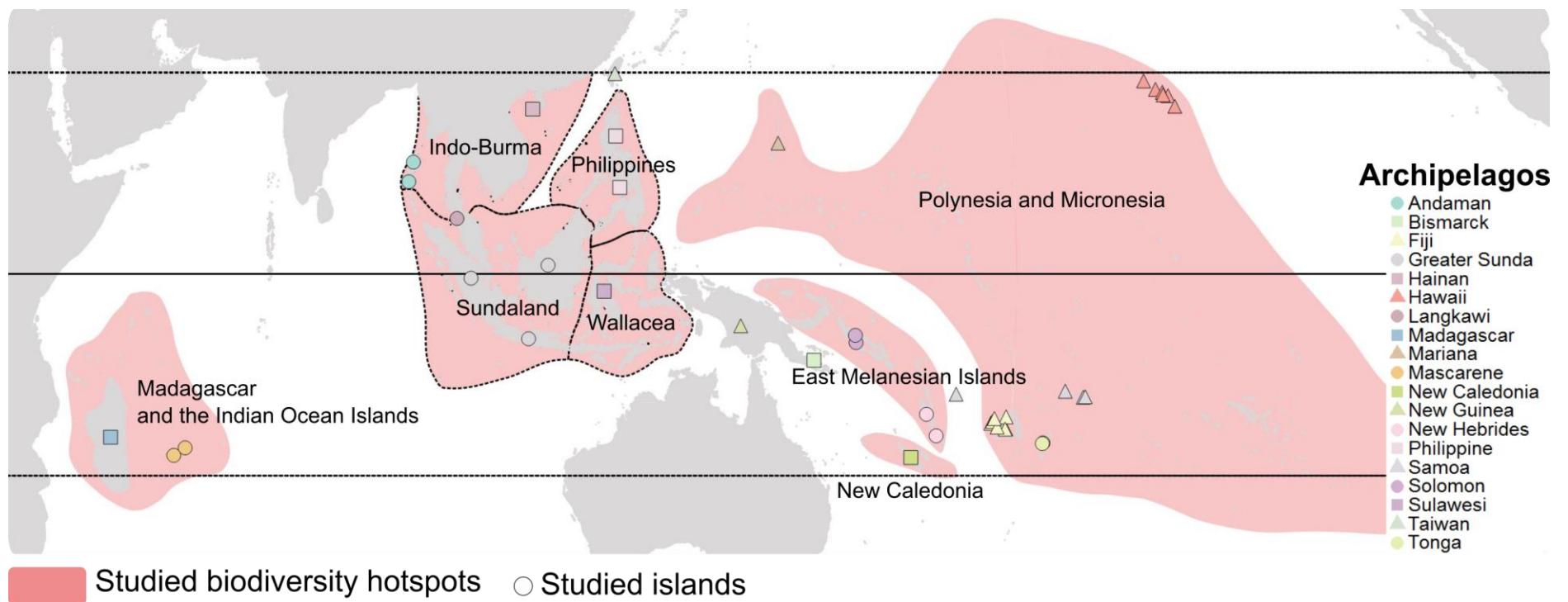
732 \*\*\*  $p$  value  $< 0.001$ , \*\*  $p$  value  $< 0.01$ , \*  $p$  value  $< 0.05$

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

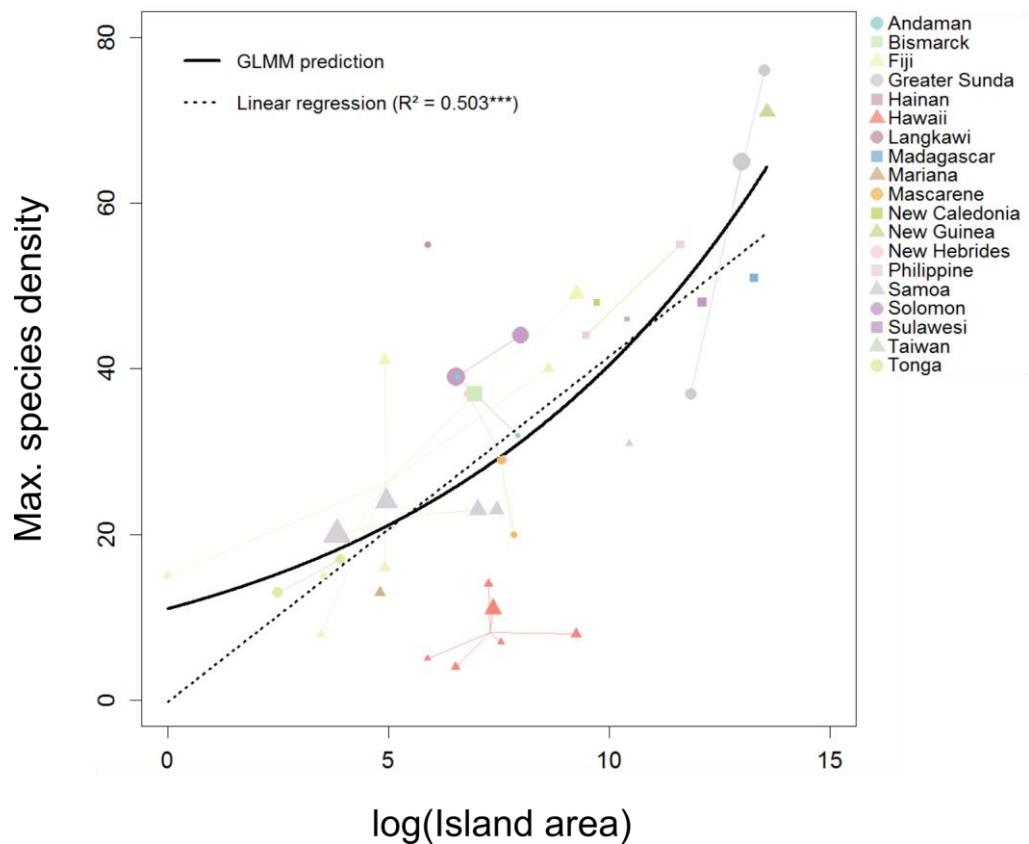
Model 1		
Parameters (SE)	log(Area)	0.10 (0.01)***
	log( <a href="#">Isolation</a> )	-0.13 (0.02)***
	Temperature annual range	-0.16 (0.04)***
Performance	AICc	157.237
	Pseudo R <sup>2</sup>	0.698

737 \*\*\* p value < 0.001, \*\* p value < 0.01, \* p value < 0

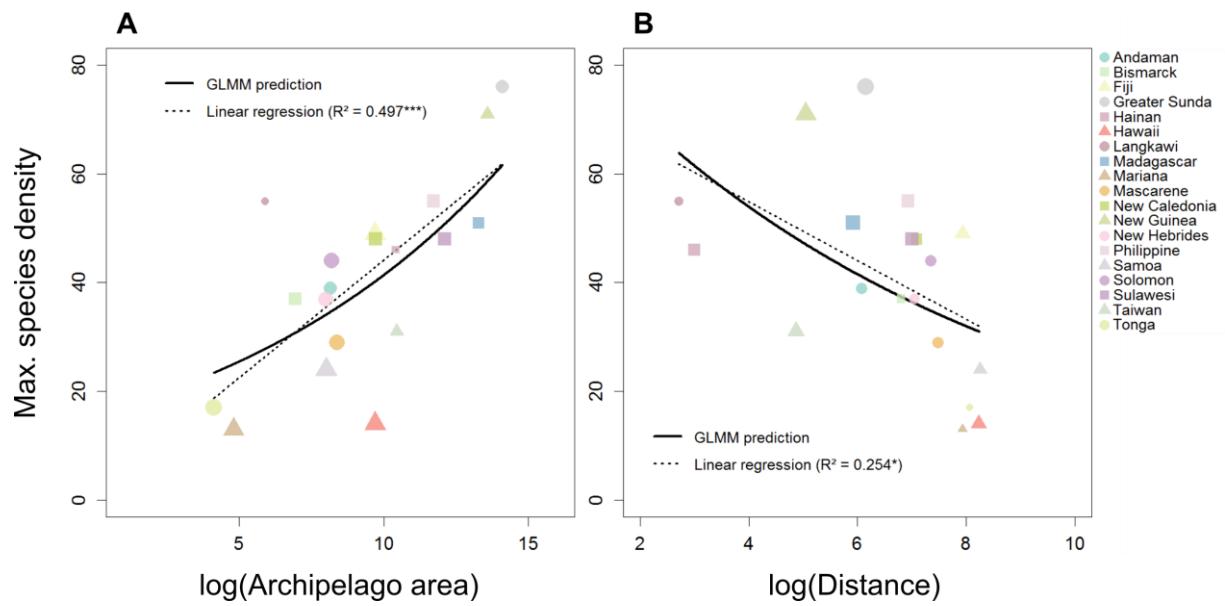
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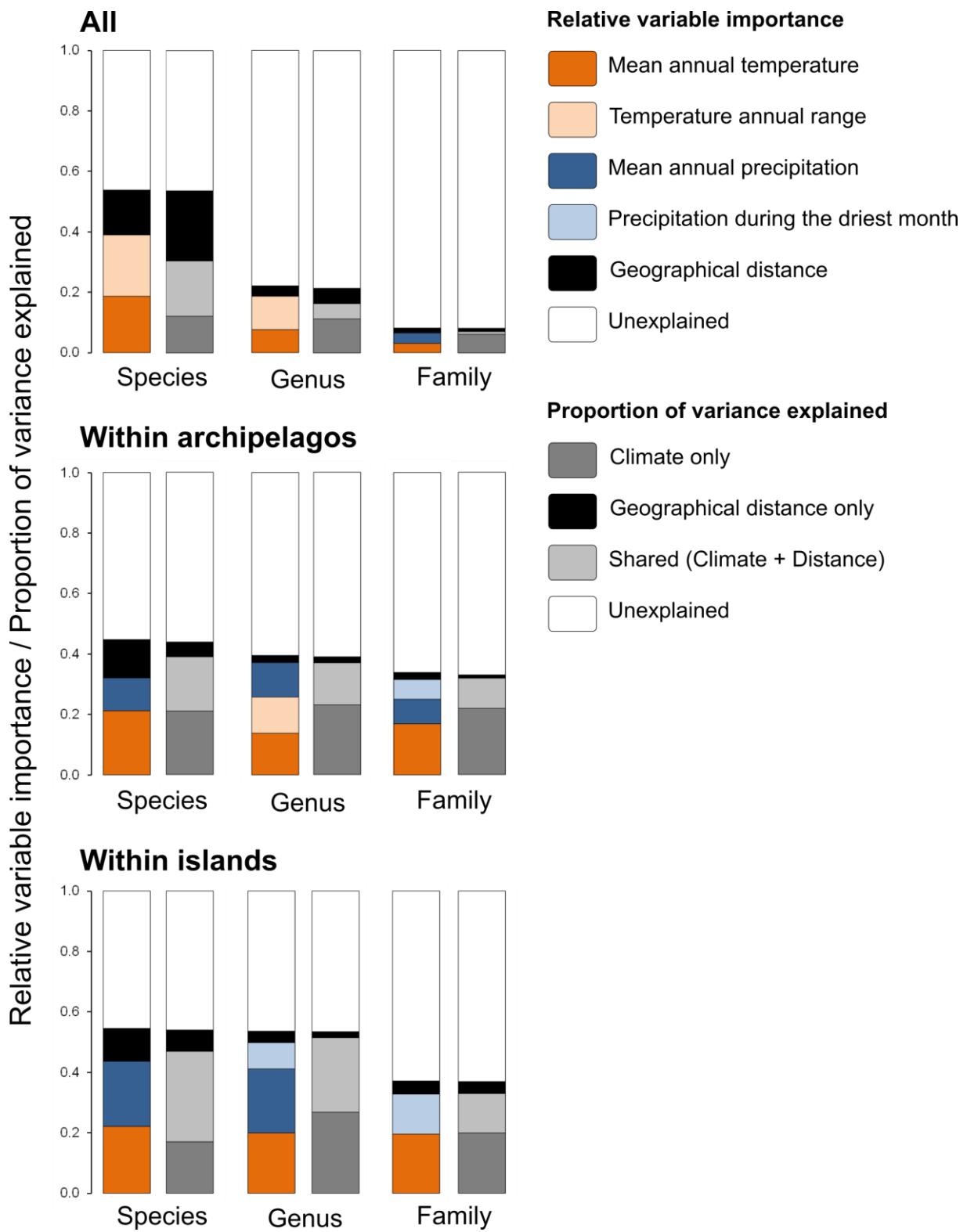
**Figure 1** Studied islands and archipelagos in the Indo-Pacific area. The names of the eight biodiversity hotspot surveyed in this study are indicated on the map.



**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 ( $\beta_{sim}$ ) 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.