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

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

3

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73

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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 ≥ 10 cm at ≈ 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 km². 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 ^qD) weigh the number of species (S) by
194 the relative abundance of species (p_i) according to a constant q,

$$195 \quad {}^qD = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)}$$

196 When q = 0, all species have the same weight and ⁰D 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 ¹D 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 ²D 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 ≥ 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 β diversity index.
208 β 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 β diversity and only considered its turnover component using the Simpson
213 dissimilarity index β_{sim} using the *bata.pair* function of the *betapart* R package (Baselga &
214 Orme, 2012),

$$215 \quad \beta_{sim} = \frac{b}{b + a}$$

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 β_{sim} dissimilarities on
219 these resampled communities at the species, genus and family levels. This procedure was
220 repeated 100 fold to estimate mean β_{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

229 correlated (Spearman's rank correlation coefficients $\rho < 0.70$; $p > 0.05$). Latitude was not
230 included because it was strongly correlated with temperature annual range and mean annual
231 precipitation (Spearman's rank correlation coefficients $\rho = 0.759$ and $\rho = 0.746$,
232 respectively; $p < 0.001$). Maximum elevation of islands, sometimes used as a proxy of island
233 age and topographical niche diversity (Whittaker *et al.*, 2008), was not retained as an
234 explanatory variable because it was correlated with island area ($\rho = 0.784$, $p < 0.001$).
235 Bioclimatic variables were extracted for plot locations from the WorldClim climatology at a
236 spatial resolution of 30 arc-seconds (≈ 1 km) (Hijmans *et al.*, 2005). WorldClim climatology
237 relies on interpolation using digital elevation models and has strong limitations, especially for
238 precipitation on islands (Hijmans *et al.*, 2005). Islands often display strong climatic variations
239 over distances that are smaller than the resolution of this data. This problem is particularly
240 pronounced in the Pacific, because of the low coverage of climatic stations. Mean annual
241 temperature was correlated with elevation ($\rho = -0.774$, $p < 0.001$). We did not include soil
242 type and island age as explanatory variables because many islands have mixed and complex
243 origins (Neall & Trewick, 2008) and soil typology was often not available at the scale of our
244 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 β_{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
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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.
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713 Humboldt fellowship to work on the effects of environmental heterogeneity on diversity on
714 islands.

715

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.

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 <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/>					
	All				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
<hr/>					
	All				13 (16)
Langkawi	Langkawi (Kohira <i>et al.</i> , 2001)	363	15	Asia	1
Madagascar	Madagascar (Phillips & Miller, 2002, Ratovoson <i>et al.</i> , 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)
<hr/>					

	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)
<hr/>					
	All				2 (8)
Philippine Islands	Luzon (Phillips & Miller, 2002)	109965	600	Asia	1
	Negros (Hamann <i>et al.</i> , 1999)	13075	1450	Asia	1
<hr/>					
	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)
<hr/>					
	All				8 (13)
Sulawesi	Sulawesi (Culmsee & Pitopang, 2009)	180681	1100	Australia	1 (6)
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)
<hr/>					
	All				3 (8)
Taiwan	Taiwan (Phillips & Miller, 2002)	34507	130	Asia	2
Tonga Islands	Kao (Franklin <i>et al.</i> , 2006)	12	3200	Australia	1
	Tofua (Franklin <i>et al.</i> ,	50	3200	Australia	3
<hr/>					

2006)

All

4

720 **Table 2** Best generalized linear mixed models (Δ 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 ²	0.122	0.127
	Conditional R ²	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) \sim 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 ²	0.502	0.534
	Conditional R ²	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(Isolation)	-0.13 (0.02)***
	Temperature annual range	-0.16 (0.04)***
Performance	AICc	157.237
	Pseudo R ²	0.698

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

738

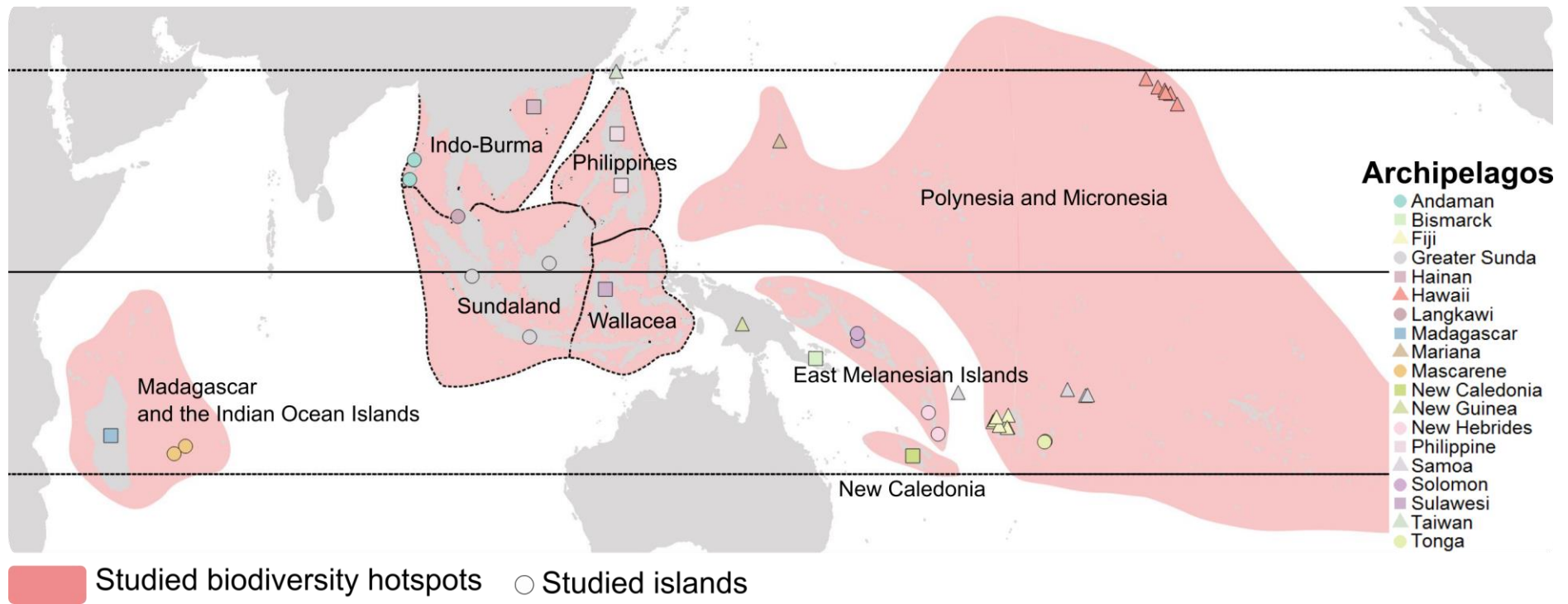


Figure 1 Studied islands and archipelagos in the Indo-Pacific area. The names of the eight biodiversity hotspot surveyed in this study are indicated on the map.

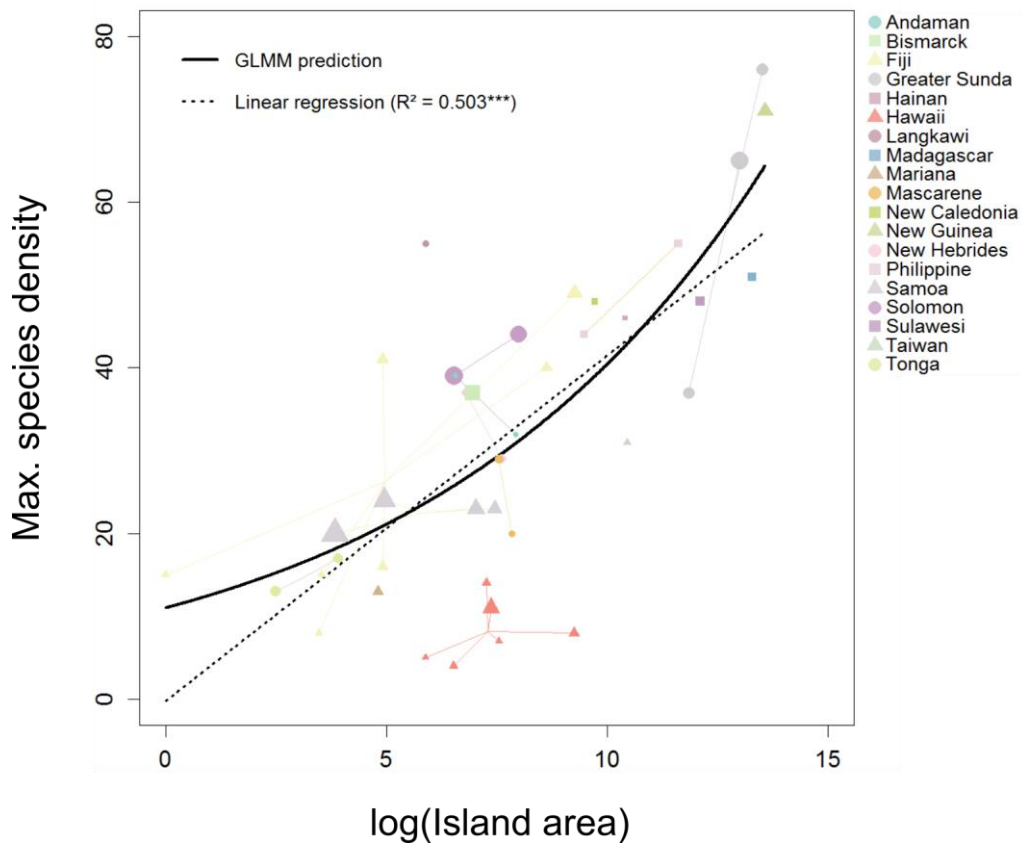


Figure 2 Effect of island area on the maximum species density (controlling for all co-variables in the best GLMM, see Table 2). Point size is proportional to the precipitation during the driest month. “***” p value < 0.001 , “**” p value < 0.01 , “*” p value < 0.05

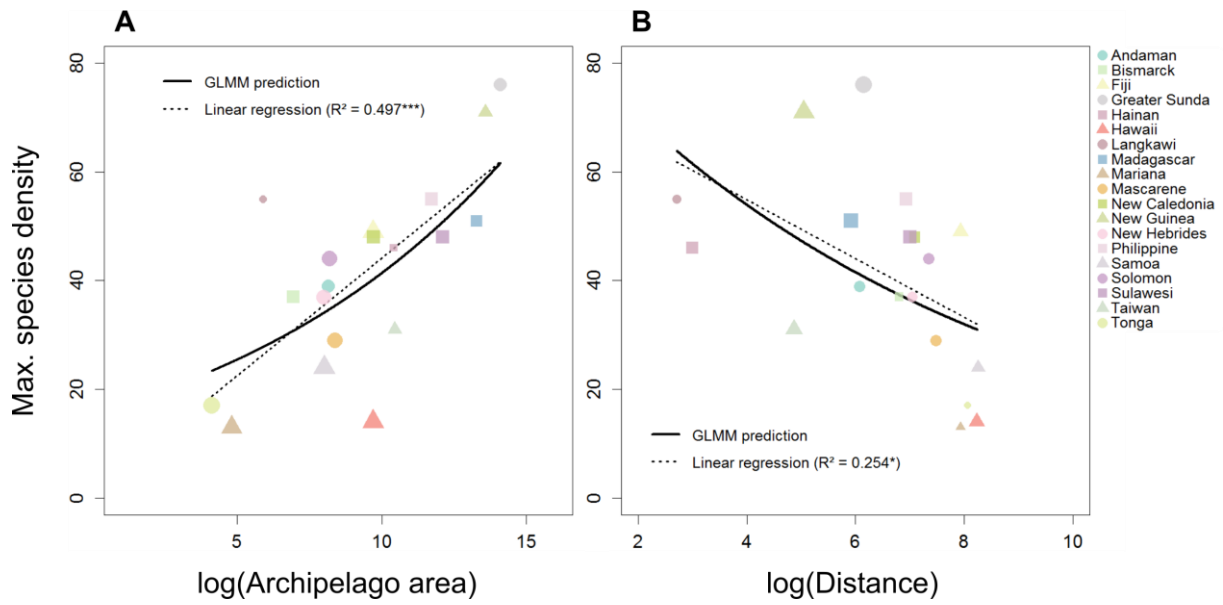


Figure 3 Effects of (A) archipelago area and (B) isolation (distance to the mainland) on the maximum species density (A-B, controlling for all co-variables in the best GLMM, see Table 3). Point size is proportional to the isolation in (A) and to area in (B). “***” p value < 0.001, “**” p value < 0.01,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

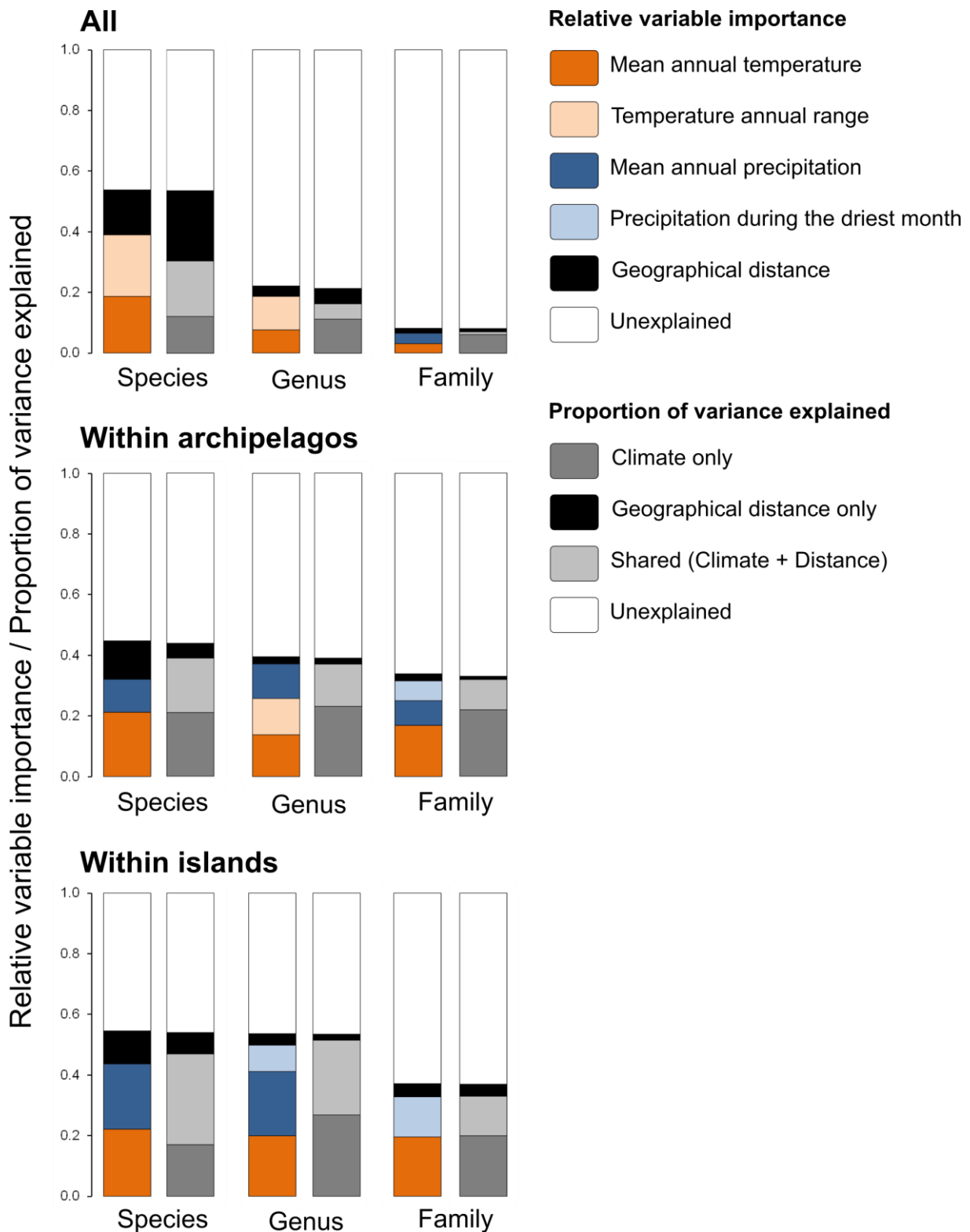


Figure 4 Turnover partitioning for taxonomic composition (β_{sim}) using generalized dissimilarity modeling (*GDM*). Results are shown for different taxonomic levels (species, genus and family) and for different subsets: All = all pairs of plots ($N = 6555$ pairs), within islands = only pair of plots 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.