# Regional forcing explains local species diversity and turnover on tropical islands

Thomas Ibanez, Gunnar Keppel, Cláudia Baider, Chris Birkinshaw, Heike Culmsee, Susan Cordell, F. Florens, Janet Franklin, Chris Giardina, Thomas Gillespie, et al.

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

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4   Thomas Ibanez[1]*[†], Gunnar Keppel[2,3,†], Cláudia Baider[4], Chris Birkinshaw[5], Heike Culmsee[6],

5   Susan Cordell[7], F. B. Vincent Florens[8], Janet Franklin[9‡], Christian P. Giardina[7], Thomas W.

6   Gillespie[10], Melinda Laidlaw[11], Creighton M. Litton[12], Tara G. Martin[13], Rebecca Ostertag[14],

7   Narayanaswamy Parthasarathy[15], Richard Randrianaivo[16], Miramasoandro

8   Randrianjanahary[16], Muthu Rajkumar[17], Ladan Rasingam[18], Fidy Ratovoson[16], Ludovic

9   Reza[16], Lawren Sack[19], Aiba Shin-ichiro[20], Edward Webb[21], Timothy J. S. Whitfeld[22],

10   Runguo Zang[23], Philippe Birnbaum[1, 24]

11

12   [1] Institut Agronomique néo-Calédonien (IAC), Equipe Sol & Végétation (SolVeg), BPA5,

13   98800 Nouméa, New Caledonia, http://orcid.org/ 0000-0002-3192-1721.

14   [2] School of Natural and Built Environments and Future Industries Institute, University of

15   South Australia, Mawson Lakes Campus, GPO Box 2471, Adelaide, South Australia 5001,

16   Australia, http://orcid.org/0000-0001-7092-6149.

17   [3] Biodiversity, Macroecology and Biogeography Group, Faculty of Forest Sciences and Forest

18   Ecology, Büsgenweg 2, University of Göttingen, Göttingen, D-37077, Germany.

19   [4] The Mauritius Herbarium, Agricultural Services, Ministry of Agro-Industry and Food

20   Security, Réduit, 80835, Mauritius, http://orcid.org/0000-0002-2203-2076.

21   [5] Missouri Botanical Garden - Programme Madagascar, Lot VP 31 Ankadibevava Anjohy, BP

22   3391, Antananarivo 101, Madagascar.

23   [6] DBU Natural Heritage, German Federal Foundation for the Environment, An der Bornau 2,

24   49090 Osnabrück, Germany, http://orcid.org/0000-0003-4577-6307.

25   [7] Institute of Pacific Islands Forestry, USDA Forest Service, 60 Nowelo Street, Hilo HI,

26   96720, USA.

27   [8] Department of Biosciences, Faculty of Science, University of Mauritius, Réduit, 80837,

28   Mauritius, http://orcid.org/0000-0002-1720-5438.

29    [9] School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, AZ

30    85287 USA, http://orcid.org/0000-0003-0314-4598.

31    [10] Department of Geography, University of California Los Angeles, Los Angeles, CA 90095-

32    1524, USA.

33    [11] Queensland Herbarium, Department of Science, Information Technology and Innovation,

34    Toowong, Australia

35    [12] Department of Natural Resources and Environmental Management, University of Hawaii at

36    Manoa, 1910 East-West Rd., Honolulu, HI 96822, USA, http://orcid.org/0000-0001-5521-

37    1188.

38    [13] Department of Forest and Conservation Science, University of British Columbia, 3041 –

39    2424 Main Mall, Vancouver, BC, V6T 1Z4 Canada.

40    [14] Department of Biology, University of Hawaii at Hilo, Hilo, HI  96720, USA.

41    [15] Department of Ecology and Environmental Sciences, Pondicherry University,

42    Puducherry, 605014, India.

43    [16] Missouri Botanical Garden, Madagascar Research and Conservation Program, BP 3391,

44    Antananarivo 101, Madagascar.

45    [17] Tropical Forest Research Institute, Jabalpur, 482021, Madhya Pradesh, India.

46    [18] Botanical Survey of India, Deccan Regional Center, Hyderabad, 500 048 Telangana, India.

47    [19] Department of Ecology and Evolutionary Biology, University of California, Los Angeles,

48    CA 90095, USA.

49    [20] Graduate School of Science and Engineering, Kagoshima University, 890-0065 Kagoshima,

50    Japan.

51    [21] Department of Biological Sciences, National University of Singapore, 14 Science Drive 4,

52    Singapore 117543.

53    [22] Department of Ecology and Evolutionary Biology, Brown University, 34 Olive Street, Box

54    G-B225, Providence, Rhode Island, 02912, USA.

55    [23] Institute of Forest Ecology, Environment, and Protection, Chinese Academy of Forestry,

56    Beijing 100091 China.

57   [24] Cirad, UMR AMAP, 34398 Montpellier, France.

58

59   *Correspondence: Thomas Ibanez, Institut Agronomique néo-Calédonien, Equipe SolVeg,

60   BPA5, 98800 Nouméa, New Caledonia.

61   [†]T.I. and G.K. contributed equally to this paper

62   E-mail : ibanez@iac.nc

63   [‡]Present adress: Department of Botany and Plant Sciences, University of California,

64   Riverside, CA 92521 USA

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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).

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

**Data compilation**

173  We compiled published and unpublished forest inventory data from 165 inventories of plots ≥
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 km$^2$. 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

**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,

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

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   $^{2}D$ 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),

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

215

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 ($\approx$ 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 (ΔAICc < 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

## 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.

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

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

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.

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## REFERENCES

Aiba, S.-i., Sawada, Y., Takyu, M., Seino, T., Kitayama, K. & Repin, R. (2015) Structure, floristics and diversity of tropical montane rain forests over ultramafic soils on Mount Kinabalu (Borneo) compared with those on non-ultramafic soils. *Australian Journal of Botany*, **63**, 191-203.

Aiba, S. & Kitayama, K. (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology*, **140**, 139-157.

Bartoń, K. (2016) *{MuMIn}: multi-model inference, {R} package version 1.15.6*.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134-143.

Baselga, A. & Orme, C.D.L. (2012) betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, **3**, 808-812.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 48.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365-377.

Bunnefeld, N. & Phillimore, A.B. (2012) Island, archipelago and taxon effects: mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography*, **35**, 15-22.

Cabral, J.S., Weigelt, P., Kissling, W.D. & Kreft, H. (2014) Biogeographic, climatic and spatial drivers differentially affect $\alpha$-, $\beta$- and $\gamma$-diversities on oceanic archipelagos. *Proceedings of the Royal Society B: Biological Sciences*, **281**

Carvajal-Endara, S., Hendry, A.P., Emery, N.C. & Davies, T.J. (2017) Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. *Ecology Letters*, **20**, 495-504.

Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, **93**, 2533-2547.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. & Ellison, A.M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, **84**, 45-67.

Cowie, R.H. (1995) Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution*, **49**, 1191-1202.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P. & Linder, H.P. (2009) Phylogenetic biome conservatism on a global scale. *Nature*, **458**, 754-756.

Culmsee, H. & Pitopang, R. (2009) Tree diversity in sub-montane and lower montane primary rain forests in Central Sulawesi. *Blumea*, **54**, 119-123.

Culmsee, H., Pitopang, R., Mangopo, H. & Sabir, S. (2011) Tree diversity and phytogeographical patterns of tropical high mountain rain forests in Central Sulawesi, Indonesia. *Biodiversity and Conservation*, **20**, 1103-1123.

Dahl, A.L. (1991) Island Directory. In: *UNEP Regional Seas Directories and Bibliographies*, p. 573, Nairobi.

Ellison, A.M. (2010) Partitioning diversity 1. *Ecology*, **91**, 1962-1963.

Feeley, K.J., Hurtado, J., Saatchi, S., Silman, M.R. & Clark, D.B. (2013) Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biology*, **19**, 3472-3480.

Fernández-Palacios, J.M., Rijsdijk, K.F., Norder, S.J., Otto, R., de Nascimento, L., Fernández-Lugo, S., Tjørve, E. & Whittaker, R.J. (2016) Towards a glacial-sensitive model of island biogeography. *Global Ecology and Biogeography*, **25**, 817-830.

532    Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007) Using generalized dissimilarity modelling to
533        analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity*
534        *and Distributions*, **13**, 252-264.
535    Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.F., Kaufman, D.M.,
536        Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial
537        species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132-
538        147.
539    Fitzpatrick, M.C., Sanders, N.J., Normand, S., Svenning, J.-C., Ferrier, S., Gove, A.D. & Dunn, R.R.
540        (2013) Environmental and historical imprints on beta diversity: insights from variation in
541        rates of species turnover along gradients. *Proceedings of the Royal Society B: Biological*
542        *Sciences*, **280**, 1-8.
543    Florens, F.B.V. (2013) Conservation in Mauritus and Rodrigues: Challenges and achievements from
544        two ecologically devastated oceanic islands. *Conservation Biology: Voices from the tropics*
545        (ed. by N.S. Sodhi, L. Gibson and P.H. Raven), pp. 40-50. Wiley Blackwell.
546    Florens, F.B.V., Baider, C., Martin, G.M.N. & Strasberg, D. (2012) Surviving 370 years of human
547        impact: what remains of tree diversity and structure of the lowland wet forests of oceanic
548        island Mauritius? *Biodiversity and Conservation*, **21**, 2139-2167.
549    Franklin, J. (2007) Recovery from clearing, cyclone and fire in rain forests of Tonga, South Pacific:
550        Vegetation dynamics 1995-2005. *Austral Ecology*, **32**, 789-797.
551    Franklin, J. & Steadman, D.W. (2008) Prehistoric species richness of birds on oceanic islands. *Oikos*,
552        **117**, 1885-1891.
553    Franklin, J., Wiser, S.K., Drake, D.R., Burrows, L.E. & Sykes, W.R. (2006) Environment, disturbance
554        history and rain forest composition across the islands of Tonga, Western Polynesia. *Journal of*
555        *Vegetation Science*, **17**, 233-244.
556    Franklin, J., Keppel, G., Webb, E.L., Seamon, J.O., Rey, S.J., Steadman, D.W., Wiser, S.K. & Drake, D.R.
557        (2013) Dispersal limitation, speciation, environmental filtering and niche differentiation
558        influence forest tree communities in West Polynesia. *Journal of Biogeography*, **40**, 988-999.
559    Gillespie, T.W., Keppel, G., Pau, S., Price, J.P., Jaffre, T. & O'Neill, K. (2013) Scaling species richness
560        and endemism of tropical dry forests on oceanic islands. *Diversity and Distributions*, **19**, 896-
561        906.
562    Gray, A. & Cavers, S. (2014) Island biogeography, the effects of taxonomic effort and the importance
563        of island niche diversity to single-island endemic species. *Systematic Biology*, **63**, 55-65.
564    Hall, R. (2009) Southeast Asia's changing palaeogeography. *Blumea*, **54**, 148-161.
565    Hamann, A., Barbon, E.B., Curio, E. & Madulid, D.A. (1999) A botanical inventory of a submontane
566        tropical rainforest on Negros Island, Philippines. *Biodiversity and Conservation*, **8**, 1017-1031.
567    Harmon, L.J. & Harrison, S. (2015) Species Diversity Is Dynamic and Unbounded at Local and
568        Continental Scales. *The American Naturalist*, **185**, 584-593.
569    Harrison, S. & Cornell, H. (2008) Toward a better understanding of the regional causes of local
570        community richness. *Ecology Letters*, **11**, 969-979.
571    Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution
572        interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**,
573        1965-1978.
574    Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427-
575        432.
576    Hurlbert, A.H. & Jetz, W. (2010) More than "More Individuals": the nonequivalence of area and
577        energy in the scaling of species richness. *The American Naturalist*, **176**, E50-E65.
578    Ibanez, T., Blanchard, E., Hequet, V., Keppel, G., Laidlaw, M., Pouteau, R., Vandrot, H. & Birnbaum, P.
579        (in press) High endemism and stem density distinguish New Caledonian from other high-
580        diversity rainforests in the Southwest Pacific. *Annals of Botany*,
581    Jost, L. (2006) Entropy and diversity. *Oikos*, **113**, 363-375.

582    Karger, D.N., Weigelt, P., Amoroso, V.B., Darnaedi, D., Hidayat, A., Kreft, H. & Kessler, M. (2014)
583         Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern
584         of fern diversity in the Southeast Asian archipelago. *Journal of Biogeography*, **41**, 250-260.
585    Kartawinata, K., Samsoedin, I., Heriyanto, M. & Afriastini, J.J. (2004) A tree species inventory in a one-
586         hectare plot at the Batang Gadis National Park, North Sumatra, Indonesia. *Reinwardtia*, **12**,
587         145-147.
588    Keppel, G., Buckley, Y.M. & Possingham, H.P. (2010) Drivers of lowland rain forest community
589         assembly, species diversity and forest structure on islands in the tropical South Pacific.
590         *Journal of Ecology*, **98**, 87-95.
591    Keppel, G., Morrison, C., Meyer, J.-Y. & Boehmer, H.J. (2014) Isolated and vulnerable: the history and
592         future of Pacific Island terrestrial biodiversity. *Pacific Conservation Biology*, **20**, 136-145.
593    Keppel, G., Gillespie, T.W., Ormerod, P. & Fricker, G.A. (2016) Habitat diversity predicts orchid
594         diversity in the tropical south-west Pacific. *Journal of Biogeography*, **43**, 2332-2342.
595    Kohira, M., Ninomiya, I., Ibrahim, A.Z. & Latiff, A. (2001) Diversity, diameter structure and spatial
596         pattern of trees in a semi-evergreen rain forest on Langkawi Island, Malaysia. *Journal of*
597         *Tropical Forest Science*, **13**, 460-476.
598    König, C., Weigelt, P. & Kreft, H. (2017) Dissecting global turnover in vascular plants. *Global Ecology*
599         *and Biogeography*, **26**, 228-242.
600    Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008) Global diversity of island floras from a
601         macroecological perspective. *Ecology Letters*, **11**, 116-127.
602    Laidlaw, M., Kitching, R., Goodall, K., Small, A. & Stork, N. (2007) Temporal and spatial variation in an
603         Australian tropical rainforest. *Austral Ecology*, **32**, 10-20.
604    Legendre, P. (2008) Studying beta diversity: ecological variation partitioning by multiple regression
605         and canonical analysis. *Journal of Plant Ecology*, **1**, 3-8.
606    Lohman, D.J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P.K.L., Shih, H.-T., Carvalho, G.R. &
607         von Rintelen, T. (2011) Biogeography of the Indo-Australian Archipelago. *Annual Review of*
608         *Ecology and Systematics*, **42**, 205-226.
609    Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I. & Callaway, R.M. (2004)
610         Rethinking plant community theory. *Oikos*, **107**, 433-438.
611    Lu, X., Zang, R., Ding, Y., Letcher, S.G., Long, W. & Huang, Y. (2014) Variations and trade-offs in
612         functional traits of tree seedlings during secondary succession in a tropical lowland rain
613         forest. *Biotropica*, **46**, 404-414.
614    MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeograpy*. Princeton University Press,
615         Princeton, New Jersey, USA.
616    Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D., Mokany, K. & Fitzpatrick, M.C. (2017) *gdm:*
617         *Generalized Dissimilarity Modeling. R package version 1.3.1. https://CRAN.R-*
618         *project.org/package=gdm*.
619    Meijer, W. (1959) Plant sociological analysis of montane rainforest near Tjibodas, West Java. *Acta*
620         *Botanica Neerlandica*, **8**, 277-291.
621    Mittermeier, R.A., Robles Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoureux,
622         J. & da Fonseca, G.A.B. (2005) *Hotspots revisted*. Chicago University Press, Chicago.
623    Moody, A. (2000) Analysis of plant species diversity with respect to island characteristics on the
624         Channel Islands, California. *Journal of Biogeography*, **27**, 711-723.
625    Mueller-Dombois, D. & Fosberg, F.R. (1998) *Vegetation of the tropical Pacific islands*. Springer, New
626         York.
627    Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity
628         hotspots for conservation priorities. *Nature*, **403**, 853-858.
629    Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining $R^2$ from generalized
630         linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133-142.
631    Neall, V.E. & Trewick, S.A. (2008) The age and origin of the Pacific islands: a geological overview.
632         *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 3293-3308.

633 Ostertag, R., Inman-Narahari, F., Cordell, S., Giardina, C.P. & Sack, L. (2014) Forest structure in low-
634     diversity tropical forests: A study of Hawaiian wet and dry forests. *Plos One*, **9**, e103268.
635     https://doi.org/10.1371/journal.pone.0103268.
636 Phillips, O. & Miller, J.S. (2002) *Global patterns of plant diversity: Alwyn H. Gentry's forest transect*
637     *data set*. MBG press, Missouri Botanical Garden, St. Louis.
638 Preston, F.W. (1962) Canonical distribution of commonness and rarity Part I. *Ecology*, **43**, 185-215.
639 Price, J.P. (2004) Floristic biogeography of the Hawaiian Islands: influences of area, environment and
640     paleogeography. *Journal of Biogeography*, **31**, 487-500.
641 R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for
642     Statistical Computing.
643 Rajkumar, M. & Parthasarathy, N. (2008) Tree diversity and structure of Andaman giant evergreen
644     forests,India. *Taiwania*, **53**, 356-358.
645 Rasingam, L. & Parthasarathy, N. (2009) Tree species diversity and population structure across major
646     forest formations and disturbance categories in Little Andaman Island, India. *Tropical*
647     *Ecology*, **50**, 89-102.
648 Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**,
649     167-171.
650 Ricklefs, R.E. & He, F.L. (2016) Region effects influence local tree species diversity. *Proceedings of the*
651     *National Academy of Sciences of the United States of America*, **113**, 674-679.
652 Rosenzweig, M.L. & Ziv, Y. (1999) The echo pattern of species diversity: pattern and processes.
653     *Ecography*, **22**, 614-628.
654 Santos, A.M.C., Field, R. & Ricklefs, R.E. (2016) New directions in island biogeography. *Global Ecology*
655     *and Biogeography*, **25**, 751-768.
656 Shearman, P. & Bryan, J. (2011) A bioregional analysis of the distribution of rainforest cover,
657     deforestation and degradation in Papua New Guinea. *Austral Ecology*, **36**, 9-24.
658 Simberloff, D. (1976) Experimental Zoogeography of Islands: Effects of Island Size. *Ecology*, **57**, 629-
659     648.
660 Small, A., Martin, T.G., Kitching, R.L. & Wong, K.M. (2004) Contribution of tree species to the
661     biodiversity of a 1 ha Old World rainforest in Brunei, Borneo. *Biodiversity and Conservation*,
662     **13**, 2067-2088.
663 Strasberg, D. (1996) Diversity, size composition and spatial aggregation among trees on a 1-ha rain
664     forest plot at La Reunion. *Biodiversity and Conservation*, **5**, 825-840.
665 Triantis, K.A., Economo, E.P., Guilhaumon, F. & Ricklefs, R.E. (2015) Diversity regulation at macro-
666     scales: species richness on oceanic archipelagos. *Global Ecology and Biogeography*, **24**, 594-
667     605.
668 Warton, D.I., Duursma, R.A., Falster, D.S. & Taskinen, S. (2012) smatr 3 - an R package for estimation
669     and inference about allometric lines. *Methods in Ecology and Evolution*, **3**, 257-259.
670 Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for
671     rain forest trees. *The American Naturalist*, **156**, 145-155.
672 Webb, E.L. & Fa'aumu, S. (1999) Diversity and structure of tropical rain forest of Tutuila, American
673     Samoa: effects of site age and substrate. *Plant Ecology*, **144**, 257-274.
674 Webb, E.L., Seamon, J.O. & Fa'aumu, S. (2011) Frequent, low-amplitude disturbances drive high tree
675     turnover rates on a remote, cyclone-prone Polynesian island. *Journal of Biogeography*, **38**,
676     1240-1252.
677 Webb, E.L., Van de Bult, M., Chutipong, W. & Kabir, M.E. (2006) Composition and structure of
678     lowland rain-forest tree communities on Ta'u, American Samoa. *Pacific Science*, **60**, 333-354.
679 Weigelt, P. & Kreft, H. (2013) Quantifying island isolation: insights from global patterns of insular
680     plant species richness. *Ecography*, **36**, 417-429.
681 Weigelt, P., Steinbauer, M.J., Cabral, J.S. & Kreft, H. (2016) Late Quaternary climate change shapes
682     island biodiversity. *Nature*, **532**, 99-102.

683 Whitfeld, T.J.S., Lasky, J.R., Damas, K., Sosanika, G., Molem, K. & Montgomery, R.A. (2014) Species
684       richness, forest structure, and functional diversity during succession in the New Guinea
685       lowlands. *Biotropica*, **46**, 538-548.
686 Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general,
687       hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.
688 Whittaker, R.J., Kostas, A.T. & Richard, J.L. (2008) A general dynamic theory of oceanic island
689       biogeography. *Journal of Biogeography*, **35**, 977-994.
690 Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology and
691       conservation biology. *Annual Review of Ecology, Evolution and Systematics*, **36**, 519-539.
692 Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I.,
693       Jonathan Davies, T., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M. &
694       Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and
695       conservation biology. *Ecology Letters*, **13**, 1310-1324.
696 Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496-506.
697 Zobel, M. (1997) The relative of species pools in determining plant species richness: an alternative
698       explanation of species coexistence? *Trends in Ecology & Evolution*, **12**, 266-269.

699

## SUPPORTING INFORMATION

701 Appendix Table S1 Plot data

702 Appendix Figure S1-4 Additional figures

703

## 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.

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.

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

| Archipelago | Island (data sources) | Area (km²) | 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

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 (Δ 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 $R^2$ | 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
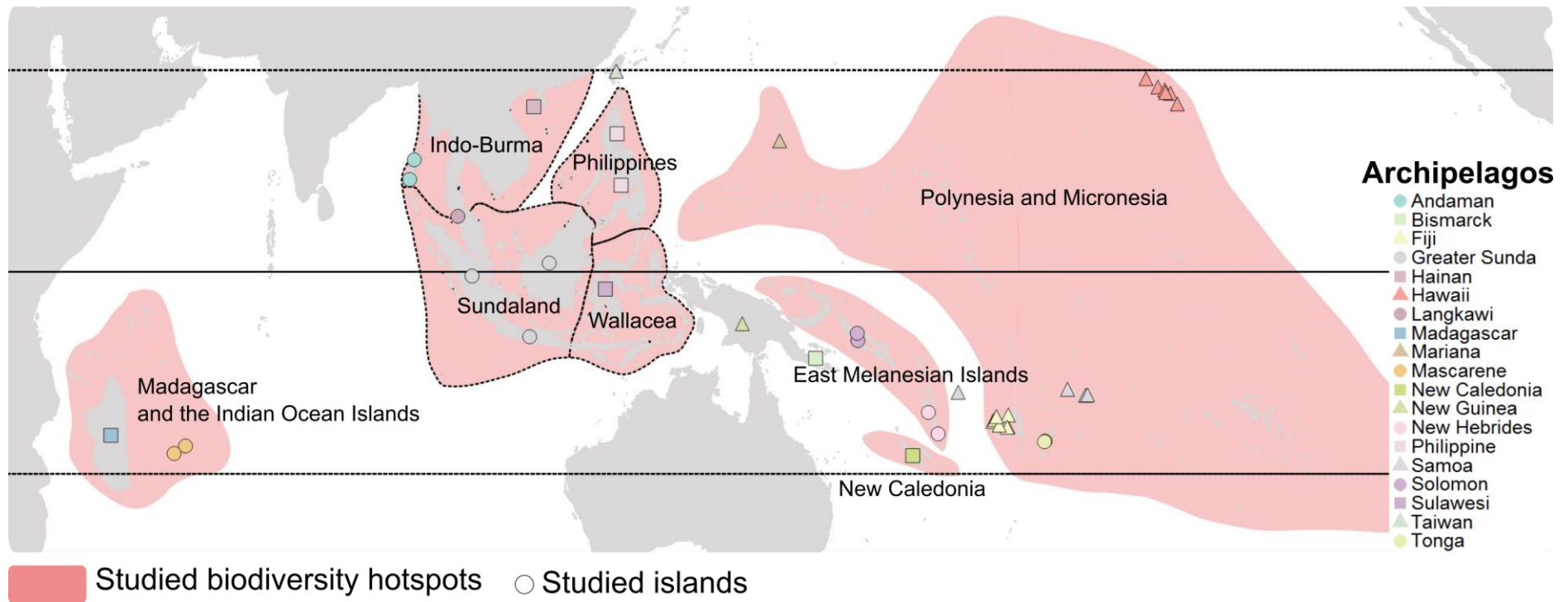
738

**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.
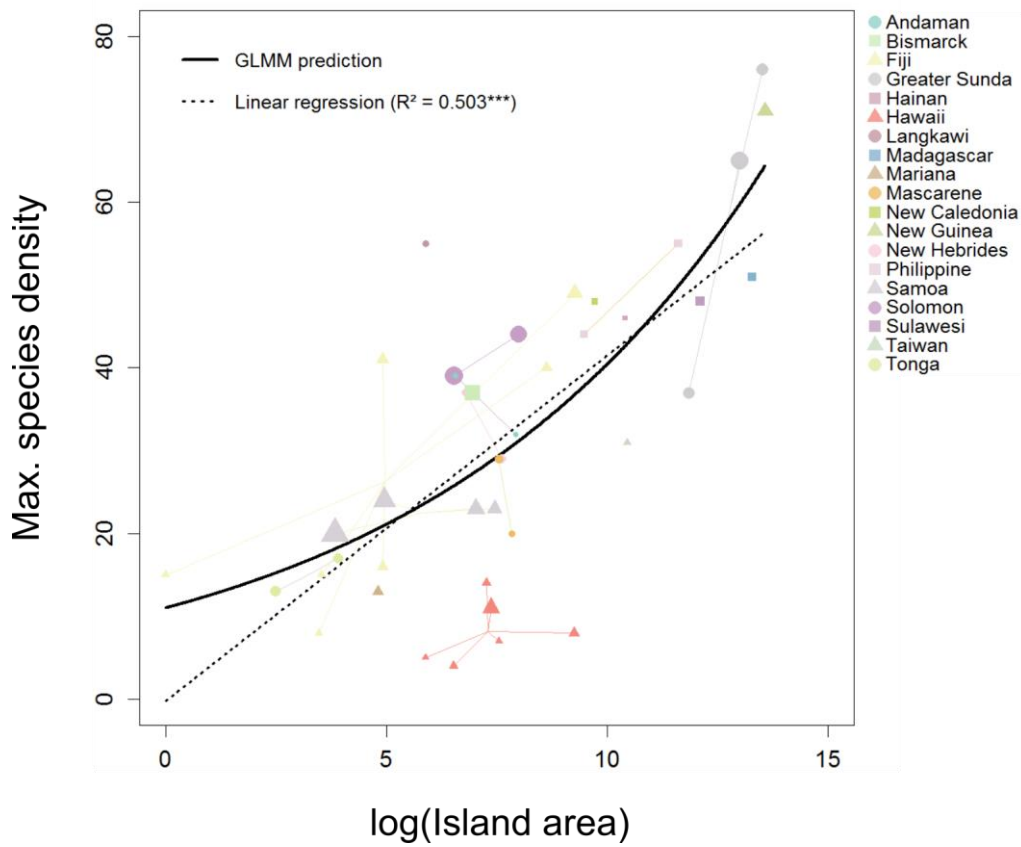
**Figure 2** Effect of island area on the maximum species density (controlling for all co-variables in the best GLMM, see Table 2). Point size is proportional to the precipitation during the driest month. "***" *p* value < 0.001, "**" *p* value < 0.01, "*" *p* value < 0.05
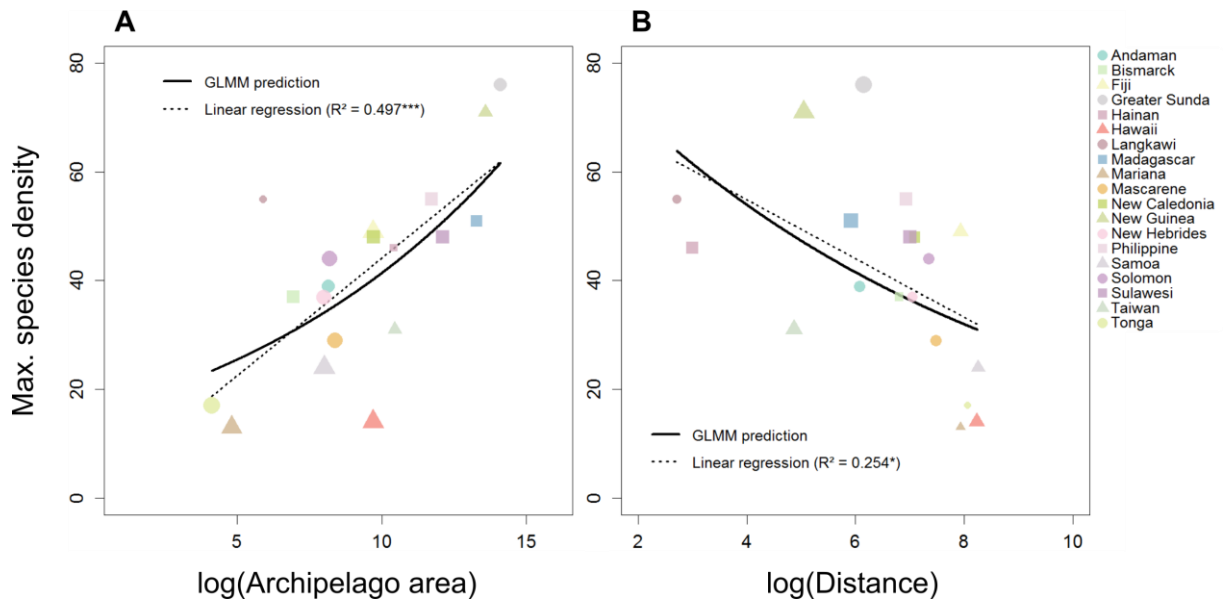
**Figure 3** Effects of (A) archipelago area and (B) isolation (distance to the mainland) on the maximum species density (A-B, controlling for all co-variables in the best GLMM, see Table 3). Point size is proportional to the isolation in (A) and to area in (B). "***" *p* value < 0.001, "**" *p* value < 0.01, "*" *p* value < 0.05.
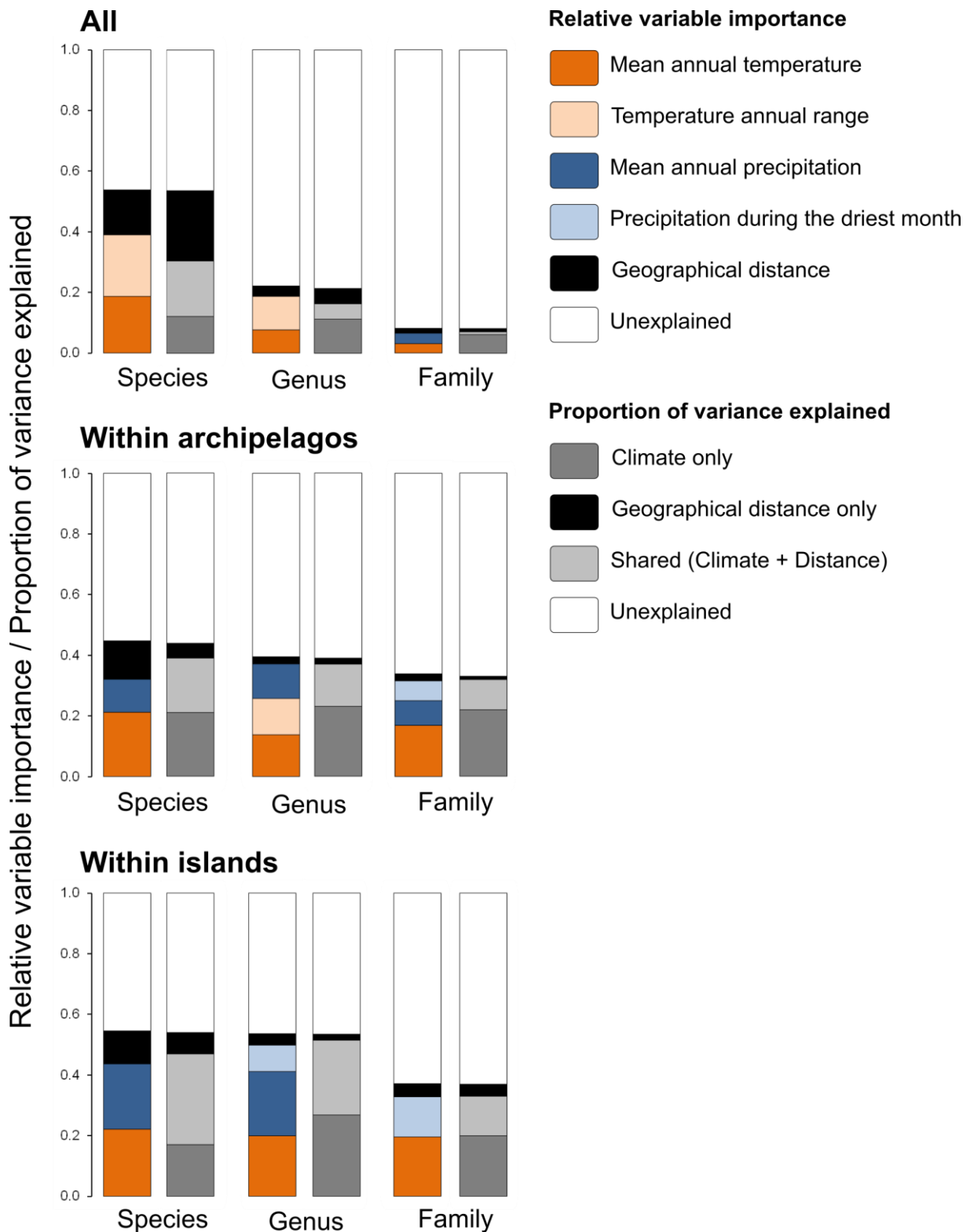
**Figure 4** Turnover partitioning for taxonomic composition ($\beta_{sim}$) using generalized dissimilarity modeling (*GDM*). Results are shown for different taxonomic levels (species, genus and family) and for different subsets: All = all pairs of plots (N = 6555 pairs), within islands = only pair 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.