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RESEARCH ARTICLE

Community structure of woody plants on islands along a bioclimatic gradient

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Abstract. Understanding patterns of community structure and the causes for their variation can be furthered by comparative biogeographic analyses of island biotas. We used woody plant data at the local scale to investigate variations in species rarity, alpha, beta, and gamma diversity within and between three islands from the oceanic archipelagoes of Azores, Canaries and Mascarene. We used standardized protocols to sample ten 50 m × 50 m forest plots in each of the three islands with contrasting climate and regional species pools: Terceira (Azores), Tenerife (Canaries), and Reunion (Mascarene Islands). Occupancy frequency distributions and species abundance distributions were used to investigate rarity. The partitioning of beta diversity in a distance-decay framework was used to test for spatial patterns of community composition. Rarity was much more pronounced in the highly diverse islands of Tenerife and Reunion than in the regionally poorer island of Terceira. The number of species rose faster with increasing sample area in both Tenerife and Reunion. The slope of the species rank abundance curve was steeper in Terceira whereas the richer island assemblages approached a lognormal model. Compositional changes according to spatial distance were mostly due to replacement of species in Terceira and Reunion. Our results point to important differences in the community structure of Terceira, which is the less diverse and temperate region in comparison to Tenerife and Reunion which are highly diverse.

Key words: Beta diversity partition, distance-decay, islands, rarity, species abundance distribution (SAD), species area relationship (SAR)

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Introduction

For a given taxonomic group, alpha diversity (i.e., the local species richness), beta diversity (i.e., the spatial turnover in species composition), and gamma diversity (i.e., the overall diversity at the regional scale) are different, albeit interrelated aspects of spatial variation in species numbers and composition (Legendre 2014). These measures of diversity, however, do not consider different aspects of species rarity. It is often the case that researchers only focus on the spatial distribution of species (presence-absence data) due to the difficulty in obtaining standardized abundance data (Gaston 1994). In fact, studying the relationship between alpha, beta, and gamma diversity with species abundance is only recently receiving attention (e.g., Harte et al. 2009, Hubbell 2013, Xu et al. 2015). In this context, due to their spatial isolation and simplified floras and faunas, oceanic islands offer the possibility of performing studies that simultaneously account for variations in several aspects of community structure, namely the relationship between rarity (both in spatial distribution and abundance), alpha, beta, and gamma diversity.

With few exceptions, species assemblages in temperate regions are less diverse than assemblages in comparable tropical regions (Brown 2014) both in terms of local richness (alpha diversity) and beta diversity (Xu et al. 2015). Differences in species community structure between species-poor temperate regions and species-rich tropical regions can arise from multiple processes, including low vs. high incidence of interspecific interactions and speciation rates (but see Schluter 2016) or recent climate history of glacial cycling (e.g., Hewitt 1999). A common observation is that taxonomic diversity in tropical systems is characterized by an excessive number of geographically restricted and low abundant species, a pattern documented at least for trees (Hubbell 2013; Steege et al. 2013).

In this study, we investigated the patterns of variation in diversity and rarity for woody plant communities within and between three distinct oceanic islands: (1) the temperate island of Terceira (Azores), (2) the subtropical island of Tenerife (Canaries), and the (3) tropical island of Reunion (Mascarenes). These three islands can be considered representative of different geographical

settings with contrasting climates. Terceira is a young island (3.52 Ma) belonging to the Atlantic archipelago of the Azores (max 8.12 Ma) with low habitat diversity (Borges and Hortal 2009, Triantis et al. 2012). Tenerife is an older island (11 Ma) also part of another Atlantic archipelago (the Canaries) with a longer geological history (max 21 Ma) and a high diversity of climate classifications (see Montoya-Alonso et al. 2016); it has a high biological diversity and is a biodiversity hotspot in the Macaronesian region (Fernández-Palacios and Whittaker 2008). Finally, Reunion (2.1 Ma) belongs to the Mascarene Islands (max 10 Ma), a tropical archipelago located in the southwestern Indian Ocean known for its high level of diversity (Thébaud et al. 2009, Baider et al. 2010). These three islands were sampled using the same methods, giving us the unique opportunity of investigating whether the observed patterns in community structure are consistent with global patterns of variation in plant diversity, i.e., (1) that species assemblages increase in diversity from temperate to tropical regions (Brown 2014, Xu et al. 2015) and (2) that the influence of rare species on taxonomic diversity increases from temperate to tropical regions (Hubbell 2013, Steege et al. 2013). To address these questions, we analysed and compared several important descriptors of community structure: (1) the occupancy-frequency distributions (OFDs) and (2) the species-abundance distribution (SAD) to investigate two forms of rarity (i.e., incidence and abundance); (3) the nested species-area relationship to investigate the spatial scaling of rarity; and (4) the partitioning of beta diversity using a distance-decay framework to test for spatial patterns in community composition.

Methods

Field data collection

Native, wet, and largely undisturbed forest areas across the three study islands were selected. Study sites were located in mostly pristine forests in two of the islands (Terceira and Reunion) and a mixture of pristine and historically logged (many decades old) laurel forest sites in Tenerife. They are dominated by the woody plants *Ilex perado* subsp. *azorica*, *Juniperus breviflora*, *Laurus azorica*, *Myrsine africana*, and *Vaccinium cylindraceum* in Terceira; *Erica arborea*, *Erica*

platycodon, *Ilex canariensis*, *Laurus novocanariensis*, *Morella faya*, *Prunus lusitanica*, and *Viburnum rigidum* in Tenerife; and *Antidesma madagascariense*, *Antirhea borbonica*, *Aphloia theiformis*, *Casearia coriacea*, *Cyathea borbonica*, *Gaertnera vaginata*, *Labourdonnaisia calophylloides*, and *Molinia alternifolia* in Reunion.

Ten 50 m × 50 m square plots were established on each island (see Appendix S1), maximizing the distance between plots within the same mountain chain or continuous forest patch. 50 m × 50 m is the minimum size considered adequate to obtain measures of beta diversity that are independent of gamma diversity for trees (Chao et al. 2009). At each plot corner 5 m × 5 m square subplots were also delimited in which we counted all woody species shoots with a diameter at breast height (DBH) ≥ 1 cm (see for more details Borges et al. 2018).

Data analyses

Unless otherwise stated, all statistical analyses were implemented in R version 3.1.0 (R Core Team 2015). For all sampled plots, the mean as well as the minimum and maximum number of species per plot (alpha richness) were calculated. All analyses were restricted to indigenous species (i.e., endemics plus native non-endemic species), and it excluded exotic species that only represent a small proportion of the overall abundance.

We considered two forms of rarity: incidence (species presences) and abundance (number of individuals). To study incidence-based rarity, the occurrence of unimodal vs. bimodal occupancy frequency distributions (i.e., the frequency histogram of species distributions across plots; OFDs, Gaston 1994) was investigated. Species incidences within an island were measured as the number of plots where a species was recorded (maximum ten). To test for bimodality, we computed the Tokeshi statistical test for bimodality (Tokeshi 1992, Barreto et al. 2003).

To study abundance-based rarity, we focused on the species abundance distributions (SAD). We fitted and compared the following SAD models: the geometric series, the log-series, the Poisson lognormal (non-truncated) model, and the gambin model (Ugland et al. 2007, Matthews et al. 2014). The geometric series is the mathematical model used to express the niche preemption hypothesis in which the sizes of the niche hypervolumes (measured by species relative abundances) are sequentially preempted from the most abundant to the least abundant species. Among all proposed SAD models, the geometric series represents the least equitable distribution, and it is known to provide a good fit for species poor and highly dominated communities (Magurran 2004). The log-series model is also widely used for communities dominated by few species (Matthews and Whittaker 2014). The geometric series and the log-series abundance distributions are interrelated and are essentially two representations of the same underlying abundance distribution (Solé et al. 2004).

The lognormal is one of the most commonly used models for describing SADs (McGill 2003), and it assumes that the logarithmic abundances are distributed normally. In the gambin model, based on the gamma distribution, parameter α determines the distribution's shape. A small α indicates a distribution with a positive skew, (i.e., a high density at small abundance values) whereas a high α indicates a distribution closer to

normal at a log scale of abundance (Ugland et al. 2007, Matthews et al. 2014, Matthews and Whittaker 2014).

Two main methods were employed to plot and model the SADs: (1) histograms (frequency distributions) of the species' abundances in which data were binned into abundance octaves and (2) rank–abundance plots in which abundances were plotted against rank order; rank one corresponds to the species with the highest abundance, rank two corresponding to the species with the second highest abundance, and so on. As a method to determine the best SAD model for any given data set, rank–abundance plots are not as intuitive as histograms, but they are useful for highlighting differences in evenness between datasets because steeper curves indicate lower evenness. The rank-abundance plot is also particularly appropriate for modelling the geometric series because if a log scale is used for abundance, the species fall exactly along a straight line, according to the equation: $\log(a) = b_0 + b_1 r$, where a is the species abundance, r is the respective rank, and b_0 (the intercept) and b_1 (the slope) are optimized fitting parameters (Fattorini 2005). With this approach, it is possible to use the regression slope to compare different species assemblages that follow the same rank-abundance distribution. For these reasons, we modelled the geometric series using un-binned “species rank abundance plots”. However, the three datasets cannot be directly compared because they exhibit a large variation in the total number of individuals (sample size) and SADs change as a function of sample size (Borda-de-Água et al. 2017). To compare datasets, a rarefaction procedure was carried out by resampling each dataset without replacement 1000 times to a fixed number of 715 individuals, which corresponds to the minimum number of individuals in Tenerife. An OLS regression model was fitted to each rarefied run and the 95% confidence limits for the slopes (defined as the 0.025 and 0.975 percentiles) were constructed for comparison between islands. Regression comparisons were assessed by performing an overall analysis of covariance (ANCOVA) (Fattorini et al. 2016) followed by multiple comparisons tests with adjusted probability values using the R package multcomp (Hothorn et al. 2017).

Gambin can only be fitted to binned data; therefore, to fairly compare the other three competing models (logseries, PLN, and gambin) they were all fitted to binned data. Bins were constructed using base 2 logs. Various model-selection statistics can be used to compare competing models (Matthews and Whittaker 2014). Following current best practices, we used the Akaike information criterion corrected for small sample size (Matthews and Whittaker 2014). The model with the lowest AIC_c value was considered the best fitting model; all models within two AIC_c values of the lowest AIC_c were considered to have equivalent support (Burnham and Anderson 2002). The Poisson lognormal (non-truncated; PLN) model was fitted using the ‘poilog’ R package (Grøtan and Engen 2009), and the gambin model was fitted using the ‘gambin’ R package (version 1.4 Matthews et al. 2014).

Nested (cumulative) species–area relationships (SARs) were computed using the ten sampling plots as sampling units. Our nested SARs are similar to the Type IIIB arrangement of Scheiner (2003), with no explicit spatial information. Firstly, we constructed random species accumulation curves (SACs) using the EstimateS program v. 9.1.0 (Colwell 2013), with 100 runs. We then applied a log-log transformation to model a

classic nested SAR as a power function (Rosenzweig 1995, Scheiner 2003). Concerns regarding the spatial effect of plot location in generating different levels of beta diversity in Reunion, which can impact on the value of the slope, led us to restrict the analyses for Reunion to only four plots located within a 12 km range, similar to the range covered by the 10 plots in Terceira and Tenerife. Thus, when we compared the slopes between the three islands, we avoided potential biases due to the large spatial distances between plots in Reunion. The ten plots in Reunion were also analysed and the results were qualitatively similar (not shown).

We evaluated beta diversity patterns at different scales. To study the spatial distribution of species, as well as test the hypothesis that species aggregation should be stronger in the islands with more species richness than the species poor island (Terceira), two complementary statistics were computed. First, individual species distributions per island were tested for significant aggregation. Average pairwise geographical distance between both populations (plots where each species was present) and individuals (distances between individuals collected in the same plot were considered as 0) were calculated. These observed distances were compared with 999 null distributions where populations were randomly distributed among the ten studied sites on each island. A species was considered to be spatially aggregated if the observed average distance was below the 0.025 percentile of the average distances obtained from the null models, and it was spatially overdispersed if it was above the 0.975 percentile for both incidence and abundance data.

To express variation in species composition between plots, we calculated pairwise dissimilarities using the complement Jaccard index (1-Jaccard) as a measure of total beta diversity (β_{total}). This measure of total differentiation between every two plots was divided into its species replacement (β_{repl}) and species richness differences (β_{rich}) components (Carvalho et al. 2012). β_{total} , β_{repl} , and β_{rich} were calculated using the R package BAT (Cardoso et al. 2015). To investigate how beta diversity varies spatially, each measure was regressed against the geographical distance between the plots. The distance-decay relationship assumes that similarity in species composition decreases with distance due to either a decrease in environmental similarity or by limits to dispersal and niche width differences among species (Nekola and White 1999). Based on these assumptions, we expected that beta diversity measures should be correlated positively with distance. Thus, we correlated beta diversity with inter-plot geographical distances. The correlation between inter-plot values of beta diversity and geographical distances was tested with Mantel tests using the R package vegan (Oksanen et al. 2015). The statistical significance of the difference between the relationship of beta diversity measures and distance was tested using the R Package simba (Jurasinski and Retzer 2012).

Results

Alpha, beta and gamma diversity patterns

93 woody plant species were sampled across thirty 50 m x 50 m plots (Appendix S2). Both Terceira and Tenerife had very similar values of average alpha diversity

per plot, but beta diversity was more than two times higher for Tenerife (Table 1). Average alpha diversity was more than three times higher in Reunion than in the other two islands. Beta diversity in Reunion was three times higher than in Terceira, as well as higher than Tenerife. The density of woody plants in Terceira was three times higher than in Tenerife. Beta and gamma diversity in Terceira were the lowest of the three islands (Table 1).

Table 1. Diversity metrics for woody vascular plants for the three study islands: Terceira (Azores), Tenerife (Canaries), and Reunion (Mascarene Islands). Gamma is the accumulated total number of species in the ten plots. Alpha is the mean number of species in the ten plots. Max and Min alpha is the maximum and minimum number of species found in the ten plots, respectively. Beta diversity was calculated as $\text{Beta} = (\text{Gamma}/\text{Alpha}) - 1$. N is the number of individuals.

	Terceira	Tenerife	Reunion
N	2186	715	1497
Gamma	11	17	67
Alpha	7.3	7.4	25.6
Beta	0.51	1.16	1.61
Max alpha	9	9	33
Min alpha	5	5	16

Rarity

The three islands studied showed contrasting patterns of wood plant rarity. In Terceira, only 18% of woody plant species occur in one plot whilst 45% occur in all ten plots (Tokeshi test $P_{\text{right}} = 0.002$), thus showing a strong right unimodal species distribution. In Tenerife, 38% of the species only occur in one plot whereas only 13% are common to all plots, following a left unimodal species distribution (Tokeshi test $P_{\text{left}} = 0.0005$). Finally, in Reunion, a left unimodal species distribution is also followed, with 25% of the plant species occurring in only one plot and 3% occurring in all 10 plots (Tokeshi test $P_{\text{left}} < 0.0001$; (Fig. 1).

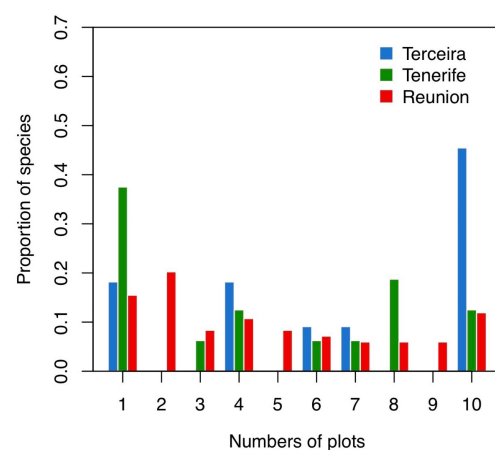


Figure 1. Frequency histograms showing the proportion of woody plants occupying the 10 plots in Terceira (Azores), Tenerife (Canaries), and Reunion (Mascarenes) islands.

The gambin model provided the best fit for the Tenerife and Reunion binned datasets whereas the PLN model provided the best fit for Terceira data (Table 2). The PLN and gambin models always provided a better fit for the binned data than the logseries model (Fig. 2). When plotted using the rank-abundance approach, the SADs for Terceira and Tenerife were characterised by steep curves (with $z = -0.304$ and $z = -0.150$, respectively) whereas the SAD for Reunion displayed a shallower curve (with $z = -0.031$) (Fig. 3). The three regression lines showed significantly different slopes (equality of slopes: $F_{(2,88)} = 312.280$, $P < 0.0001$). Post-hoc tests for differences between slopes indicated significant differences in all pairwise comparisons ($P < 0.0001$).

Table 2. AIC_c values for the SAD model selection for the three SAD models (logseries, Poisson lognormal-PLN, and gambin) fitted to indigenous woody plants in each island (Terceira, Tenerife, and Reunion). The model comparison was undertaken using binned abundance data. The best fitting model is highlighted in bold. Gambin's alpha parameter values ("Alpha") are also shown.

	Terceira	Tenerife	Reunion
Logseries	67.69	88.59	317.64
PLN	64.54	76	277.66
Gambin	65.46	75.31	274.36
Alpha	13.41	6.67	2.24

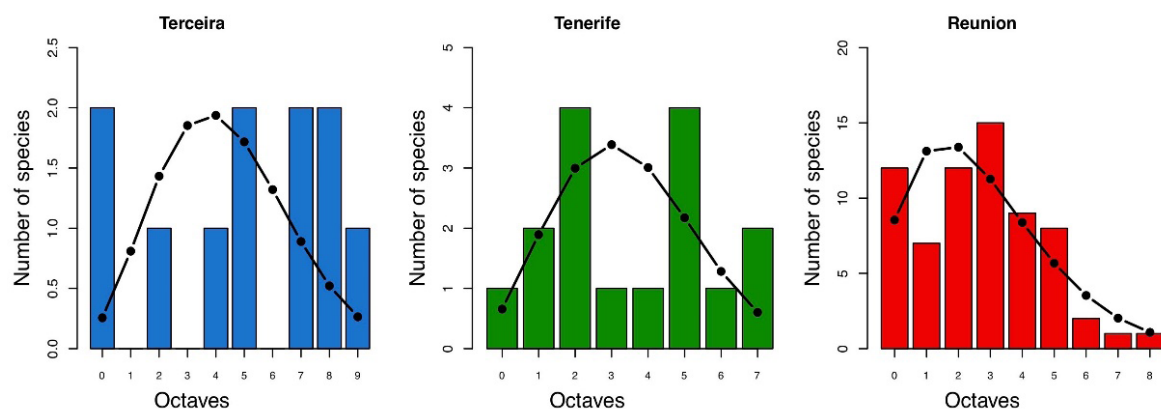


Figure 2. Species abundance distribution (SADs) histograms for woody plants in Terceira (a), Tenerife (b), and Reunion (c). The following binning system was used: 0 corresponds to the number of species with 1 individual per species, bin 1 corresponds to the number of species with 2-3 individuals per species, bin 2 corresponds to the number of species with 4-7 individuals per species, etc. The curve represents the best fit model (Gambin).

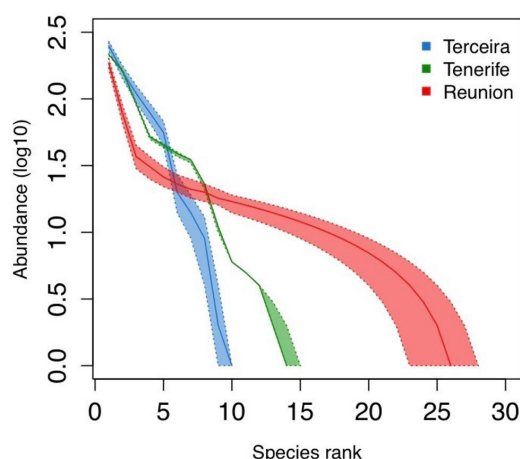


Figure 3. Geometric series rank-abundance plots for woody plants in Terceira, Tenerife, and Reunion. Rarefaction with 1000 randomizations was performed to the same number of individuals as in the island with a lower overall abundance. Averages and 95% confidence limits envelopes for curves (a) and 95% confidence limits for slopes (b) are presented. OLS regression equations and goodness-of-fit values: Terceira: $y = -0.304x + 2.999$, $R^2 = 0.937$; Tenerife: $y = -0.150x + 2.459$, $R^2 = 0.985$; Reunion: $y = -0.031x + 1.630$, $R^2 = 0.960$.

Species Area Relationships

The analyses of nested SARs confirmed the expectation that the number of species rises more rapidly as sampling area increases in the two islands with the highest species richness (higher z -values) compared to the species poor and temperate island of Terceira (Fig. 4; equality of slopes: $F_{(2,18)} = 282.090$, $P < 0.0001$). Post-hoc tests for differences between slopes indicated significant differences in all pairwise comparisons ($P < 0.0001$).

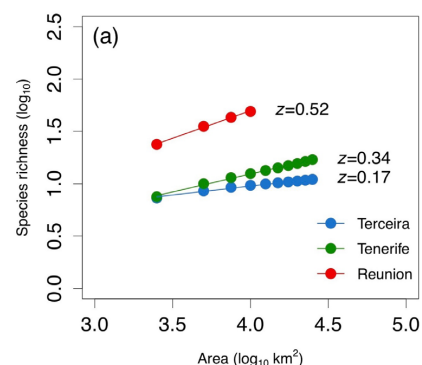


Figure 4. Species-area relationships (SARs) based on species accumulation curves (SACs) in Terceira (Azores), Tenerife (Canaries), and Reunion (Mascarenes).

Spatial distribution

A high proportion of spatially aggregated species were found in Terceira whereas overdispersion was uncommon, involving only a very small fraction of species, in Reunion (Table 3). A significant pattern of distance decay was found in Terceira and Reunion, mostly driven by species replacement in both cases although this was stronger in Terceira (Table 4). Slopes of decay relationships for Terceira and Reunion were significantly different for both the replacement curves ($P < 0.014$) and for the β_{total} ($P = 0.001$).

Table 3. Number and percentage of species with significant aggregation or overdispersion considering incidence and abundance data.

	Terceira	Tenerife	Reunion
Significant Aggregation			
Incidence	2(18%)	1(6%)	1(2%)
Abundance	3(27%)	0	0
Significant Overdispersion			
Incidence	0	0	1(2%)
Abundance	0	0	3(5%)

Table 4. Distance decay slopes and respective P values (* $P < 0.05$) per island.

	Terceira	Tenerife	Reunion
Btotal	0.00764*	0.00242	0.00316*
Brepl	0.01091*	-0.00090	0.00400*
Brich	-0.00330	0.00334	-0.00080

Discussion

We have investigated the patterns of variation in the levels of diversity and species abundance distributions (SADs) within and between islands using standardized methodological protocols in pristine or near-pristine forests across different oceanic archipelagoes. Differences in alpha and beta diversity among the local communities echoed the differences in gamma diversity between islands, further demonstrating that regions differed in local richness, spatial aggregation of species, and the way in which the communities are assembled; the latter being revealed by the analysis of SADs. Our results indicated that local communities in the temperate island of Terceira are species poor and are dominated by widespread taxa whereas the tropical island of Reunion is richer and with only a few species that can be considered common.

According to Raunkiaer's law, occupancy frequency distributions (OFDs) within homogenous plant formations should follow bimodal patterns, indicating that the species in a community are either rare or common (Papp and Izsák 1997). According to Tokeshi (1992), however, bimodal distributions occurred in about 27% of investigated communities whereas approximately 46% of observations showed a right-skewed unimodal

shape and 27% were uniform. Similarly, Hui (2012) found that 24% of investigated communities had bimodal OFDs.

The Azorean woody plants showed an uncommon left-skewed (right unimodal) OFD, which can be explained by the high compositional uniformity of the Azorean extant native forest (Sjögren 1973). In fact, all Terceira plots were placed in *Juniperus-Ilex* forests, which are now the dominant natural forests of the Azores, unlike pre-settlement times where other types of forest communities were abundant, namely Laurel forests (Elias et al. 2016). The extreme right unimodal OFD for the woody plants at this small scale is also characteristic of other taxa in the Azores (bryophytes, other vascular plants, mollusks, and vertebrates) at broader scales (Carine and Schaefer 2010, Borges et al. 2011) as a result of the large proportion of both indigenous and endemic species occurring in most islands.

Finally, wood plants in Tenerife and Reunion showed a right-skewed unimodal shape, which is the most commonly observed OFD pattern. In our case, this may be generated by two possible, mutually non-exclusive, causes among those discussed by Gaston (1994): (1) species of low abundance have a low probability of being recorded at any one sampling unit (plots in our case) because they are often more difficult to find; and (2) species adapted to the sampled habitat tend to occupy most (if not all) sampled plots, while species adapted to other habitats tend to occupy only a few plots, hence inflating the left-hand mode at this scale.

Because z -values in SACs are a measure of species replacement, highly isolated areas tend to share fewer species, and, hence, have higher z -values than less isolated areas (Rosenzweig 1995). Assuming that species can potentially disperse freely among plots within each island, we should expect shallower slopes (z -values) for within-island SARs in comparison to classical nested SARs that use true isolates (Rosenzweig 1995, Matthews et al. 2016). The very low z -value observed for Terceira plots, which was the shallowest slope among the three analysed islands, is in line with this assumption. The very small z -value found for the Terceira plots is also consistent with the widespread distribution of woody plants in the Azores and the uniform interplot distribution highlighted by the OFD, which means that spatial turnover in species composition is necessarily low. This is the consequence of the overall poor native species richness (gamma diversity) and the large ecological amplitude of many species (Schaefer 2003).

The other two SACs exhibit z -values close to those commonly found for true isolates (Matthews et al. 2016), which is an unexpected result. However, species with narrow environmental tolerances and limited dispersal ability may violate the assumption that species can potentially disperse freely among plots within a given island, if sampled plots exist within a variable environmental matrix where interplot distances traverse unfavourable ecological conditions that make it difficult for a species to move from one plot to another. The very high z -value for Reunion, coupled with the

observed OFD, suggests the occurrence of many rare species with scattered distributions as expected for tropical systems and further exacerbated by the steep elevational gradient, which increased habitat heterogeneity in our transect. The high z -value for Tenerife may be explained by the presence of both very rare species and species that are rare in the sampled plots because they are more strictly associated with other unsampled habitat types.

Regarding our SAD analyses, it is well known that they exhibit very different patterns in different ecosystems. Steege et al. (2013) predicted that 1.4% of tree species in the Amazon account for half of all individuals, and Hubbell (2013) found that in the Barro Colorado Island the nine most abundant species, out of a total of 306 (2.9% of the species), make up half of the individuals. These figures are in accordance with the observation of Ulrich et al. (2016): tropical trees follow a logseries SAD. Our data for the tropical island of Reunion showed a different pattern that may be related to the fact that we were dealing with islands rather than continental floras. In Reunion, approximately 8% of woody species make up 50% of individual trees, and the SAD follows an approximate lognormal distribution, not a logseries. This pattern is thus not completely in accordance with an expectation of hyper-dominance and an excess of rare species typically found in continental tropical forests (Hubbell 2013, Steege et al. 2013). Assuming that Reunion is a more productive system, our SAD results are more in accordance with James Brown's (2014) view, who argued that high productivity generates a lognormal SAD which is contrary to the recent findings of Ulrich et al. (2016). An alternative explanation is that our use of binned data influenced the SAD model selection results. The SADs in the two other islands were best approximated by models that have more uneven patterns, with Terceira being characterized by a very high dominance effect (steeper curve in the rank-abundance plot), which is consistent with the compositional uniformity and poor richness of this island.

Regarding the gambin model, communities dominated by rare species are expected to have low alpha values as in the case of Reunion (see Table 2) whereas communities with relatively few rare species, many of intermediate abundance and some additional abundant species, should have higher gambin α values as in the case of Terceira. In contrast, Tenerife, which has a few more species and lower impact of the most dominant ones, has an intermediate value of α (see Ugland et al. 2007 and Matthews et al. 2014 for further discussion on the interpretation of the α value parameter),

In Terceira and Reunion, plant species compositional changes according to spatial distance were mostly due to species replacement whereas no significant correlation was found between distance and differences in richness. This means that, overall, the more distant plots do not differ much in the number of species than those closer, but they do differ more in terms of species composition. This pattern indicates that

the variation in values of species richness are not geographically structured. This may result from the fact that sampling areas are ecologically uniform regarding the main factors that influence richness (such as elevation). However, species composition is spatially structured, suggesting that the factors that control species composition are not uniformly distributed within an island. On the contrary, in Tenerife we did not find any significant relationship between beta diversity and distance, which may be a consequence of the complex orography of Anaga.

Finally, regarding the spatial aggregation results, we found a high proportion of spatially aggregated species in Terceira. Elias et al. (2011) have shown that the spatial distribution of tree species may be explained by factors such as disturbance regimes, species regeneration strategies or habitat-related patchiness. The last explanation seems to fit particularly well for Terceira, where native forests have been largely destroyed, which probably contributed to some species representing the extreme range of their distribution after the disappearance of middle and low elevation forests in the Azores.

To conclude, our results point to important differences in the woody plant community structure of the regionally less diverse temperate island (Terceira) versus the two regionally highly diverse islands (Tenerife and Reunion). High regional diversity of species in Tenerife and Reunion is a consequence of comparably long eco-evolutionary history that has promoted high levels of diversity which are not comparable to the relatively species-poor biota of the Azores, constrained by recent geological history and low environmental diversity.

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PAVB, PC, BCE, CT, PO, DS, RBE, JMFP and JCC conceived the study design and sampling program. RBE, AJP, JMFP, RO, SFL, LN, JCC, AMS and DS performed plant sampling and identification. PC, PAVB, FR, SF, LBA, TM analyzed the data. PAVB, PC and SF led the writing with the help of FR, LDB, LBD, TM, IRA, MF, JCC, RBE, JMFP, PO, CT, DS, BCE. All authors commented on the final version of the manuscript.

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Supporting Information

Additional Supporting Information may be found online with this article:

Appendix S1 – Information about the sites.

Appendix S2 – Dataset.