RESEARCH PAPER

How do different dispersal modes shape the species–area relationship? Evidence for between-group coherence in the Macaronesian flora

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ABSTRACT

Aim We explore the island species–area relationships (ISARs) of several plant groups differing in dispersal ability. We examine whether: (i) the ISAR slope is higher for less dispersive groups (diminishing from not-wind-dispersed seed plants to wind-dispersed seed plants, pteridophytes and bryophytes); and (ii) the regional richness is higher than that predicted by the ISAR of its constituent islands for groups with lower dispersal ability. Additionally, we relate both patterns to the compositional dissimilarity (beta diversity) between islands.

Location The Macaronesian archipelagos of the Azores, Madeira and Canary Islands.

Methods ISARs were estimated using the conventional power model. Differences in slopes among taxa were analysed through ANCOVA tests. We assessed the deviation of the total richness of the Macaronesian flora from that predicted by the ISAR and calculated several measures of beta diversity (turnover, nestedness-resultant dissimilarity and nestedness). Analyses were repeated after excluding the two Canarian islands of Lanzarote and Fuerteventura, which have unique climatic and geological conditions in the region.

Results All ISAR models were significant except for pteridophytes (for which it was significant when excluding Lanzarote and Fuerteventura). ISAR slopes did not differ among taxa. Regional richness followed ISAR predictions for bryophytes and pteridophytes when Lanzarote and Fuerteventura were excluded, while the total number of Macaronesian seed plants (particularly not-wind-dispersed species) always fell above the ISAR. Turnover was higher in seed plants than in bryophytes and pteridophytes, and the opposite occurred with nestedness.

Main conclusions Differences in dispersal ability influence the compositional dissimilarity between these islands, but not the rate of species increase with area. This may be because ISAR slopes are mostly determined by within-island processes of species accumulation, while differences in dispersal generate different between-island patterns. The lack of relationship between the ISAR slope and species replacement or nestedness prevents its use as a proxy for beta diversity.

Keywords

Beta diversity, ferns, *in situ* speciation, liverworts, long-distance dispersal, Macaronesia, mosses, nestedness, turnover, vascular plants.

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INTRODUCTION

The positive and monotonically increasing relationship between the number of species and area is one of the most consistent biogeographical patterns (Rosenzweig, 1995). This phenomenon is so commonly observed that many authors consider the species–area relationship (SAR) as one of the few genuine or canonical laws in ecology (Lawton, 1999), island ecosystems being a special case for model testing. Assuming that species richness (S) increases linearly as a function of island area (A) in a conventional logarithmic form of the power-law model ($\log S = \log c + z \log A$, where c and z are constant parameters), the slope of this relationship (or z-value) tends to vary within a relatively fixed range of values, usually from 0.20 to 0.45 (Rosenzweig, 1995). However, despite its universality, there is still no general agreement on the main processes influencing the SAR, and a number of non-exclusive hypotheses have been put forward to explain this relationship (Whittaker & Fernández-Palacios, 2007). Whatever the mechanism(s) causing the increase in species richness with area, variations in the dispersal ability between taxa and in the degree of isolation among regions are widely recognized as key to explaining differences in the z-value (MacArthur & Wilson, 1963, 1967; Rosenzweig, 1995; but see also Rosindell & Phillimore, 2011). Systems placed further away from their source species pools and taxa with low dispersal capacity are thought to have steeper SARs. This could be because of: (1) higher within-island speciation in larger islands due to higher genetic isolation between populations (e.g. Givnish, 2010), (2) lower connectivity between island biotas that hinders stepping-stone colonization processes (e.g. Diver, 2008), and (3) increasing extinction rates on smaller islands due to the lower prevalence of rescue effects from other islands or the mainland (e.g. Dexter, 2010). Perhaps because both variations in species richness with area and variations in community composition can be related to similar biogeographical processes, differences in the SAR slope are commonly thought to correspond to differences in beta-diversity patterns (e.g. Smith, 2008). In fact, higher SAR slopes have been traditionally assumed to reflect higher rates of community dissimilarity (i.e. higher beta diversity) (Wright, 1981; Drakare *et al.*, 2006; Dexter, 2010).

Going beyond the classical SAR framework, Santos *et al.* (2010a) suggested that the processes determining the assembly of island faunas within an archipelago may influence how much the total number of species in the archipelago departs from what would be expected according to the SAR of its constituent islands (the island species–area relationship, or ISAR). They proposed that the total richness of an archipelago should be similar to the value predicted by the extrapolation of its ISAR for a hypothetical island with an area equivalent to the sum of the area of all their constituent islands (see also Rosenzweig, 2004), unless these islands are not congruent in terms of isolation, geological history and/or the biogeographical origin of their biotas. Deviations from this pattern may be partially due to differences in between- and within-island processes (e.g. allopatric and sympatric speciation, extinction or variation in

colonization rates) which should be reflected by the differential contribution of the two components of beta-diversity patterns, namely species turnover and nestedness (Baselga, 2010, 2012; Almeida-Neto *et al.*, 2012). According to this rationale, it would be expected that the total richness of all the considered islands would be higher than ISAR predictions for taxa with low dispersal ability, because the lower connectivity between islands may promote the existence of more singularities (i.e. species that are island endemics or unique within the archipelago) that will ultimately increase the compositional turnover (species replacement from island to island). Given that ISAR curves are derived from the relationship between island area and island richness, the existence of turnover between islands would cause the total species richness in the archipelago to be higher than expected from the ISAR curve. By contrast, no differences between observed and predicted species richness would indicate that the species communities of smaller islands tend to be spatially nested within those larger islands.

In this study we investigate whether taxa with different dispersal modes – and arguably different dispersal capacities – show contrasting patterns in the ISAR slope, the congruence between the total richness of the archipelago and that predicted by the ISAR of its constituent islands, and the beta diversity between islands. To do this, we analyse the ISAR of the Macaronesian flora, comparing four major plant groups that a priori differ in their dispersal ability: bryophytes (which comprise hornworts, liverworts and mosses), pteridophytes (including ferns and allies), wind-dispersed seed plants and not-wind-dispersed seed plants. Like any group of volcanic islands, the five Macaronesian archipelagos (the Azores, Madeira, the Selvagens, the Canaries and Cape Verde) have been colonized through long-distance dispersal processes (Fernández-Palacios *et al.*, 2011). Although long-distance dispersal events are typically rare, their relevance for the build-up of isolated plant biotas remains a matter of speculation because of the lack of empirical evidence (Longton, 1997; Nathan *et al.*, 2008). Moreover, morphological adaptations of seeds or other diaspores (i.e. dispersal units) that are typically related with their ability to disperse locally within a landscape or environment may not necessarily be associated with the probability of experiencing long-distance dispersal (e.g. Higgins *et al.*, 2003). Despite the problems of determining the role of long-distance dispersal, it can be assumed that the large variations in diaspore traits and dispersal strategies between major plant groups are likely to result in different dispersal abilities, and hence in significantly different relationships between species diversity, occupation of the geographical space and, ultimately, area.

Cryptogams like pteridophytes and bryophytes produce several million spores that are only a few tens of microns in size, thus facilitating passive long-distance dispersal by wind (Frahm, 2008). Most pteridophyte species are homosporous, producing spores of a single size that are larger (30–50 µm, on average) than those of bryophytes (10–20 µm). In addition, there are heterosporous species (including some families of lycophytes and aquatic ferns) that produce both large female megaspores ranging from 200 to 1000 µm and male micro-
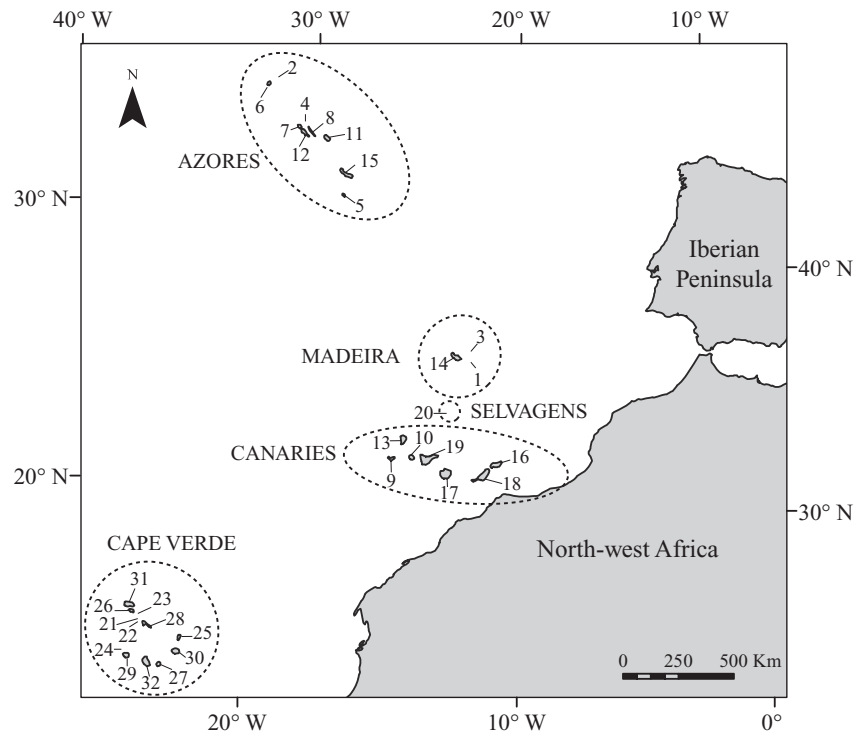
Figure 1 Geographical location of the five Macaronesian archipelagos. See Table 1 for island codes.

spores measuring between 10 and 60 μm (Mehltreter *et al.*, 2010). Apart from the seemingly superior dispersal ability of bryophytes resulting from their smaller spores, they may also be considered better colonizers a priori because they frequently reproduce by means of a large variety of vegetative propagules (plant fragments or specialized structures). By contrast, passive long-distance dispersal seems to be less probable in seed plants, as shown by the lower proportion of disjunct species distributions, smaller distributional ranges and higher number of both endemic and alien species than cryptogams (Medina *et al.*, 2011; Schaefer, 2011; Vanderpoorten *et al.*, 2011). In the case of wind-dispersed species, the number of dispersal units (seeds, fruits and infrutescences) is usually several orders of magnitude smaller than those of bryophytes and pteridophytes. The size of these dispersal units is also typically much larger; for example, the seeds of Ericaceae and orchids – which are among the seed plant families with the smallest seeds – are on average *c.* 1300 μm long and 350 μm wide (Arditti & Ghani, 2000). The arrival of not-wind-dispersed seed plants to distant islands is even more difficult since it relies mainly on dispersion by birds or bats. Given that there are no comparative data about the potential for long-distance transoceanic dispersal between different seed plant groups, here we assume that it may be higher in wind-dispersed than in not-wind-dispersed species, based on the higher rates of wind dispersal observed in open landscapes (Schurr *et al.*, 2005).

Taking into account all these considerations, we examine whether: (i) the ISAR slope varies among groups, following a gradient of increasingly shallower relationships from not-wind-dispersed seed plants to wind-dispersed seed plants, pteridophytes and bryophytes; and (ii) the difference between the total richness of the archipelago and that predicted by the ISAR of its constituent islands is progressively smaller as the dispersive potential increases. In order to determine whether either of these two richness patterns is associated with the compositional dissimilarity (beta diversity) between islands, we also explore the turnover and nestedness patterns of the taxa.

METHODS

Species data

Information on bryophyte, pteridophyte and seed plant species distributions in the Macaronesian islands (Fig. 1) was compiled from the latest published checklists for each archipelago (Arechavaleta *et al.*, 2005, 2010; Borges *et al.*, 2008, 2010), and updated with some recent publications (see Appendix S1 in Supporting Information). However, the cryptogam species lists from Cape Verde and the Selvagens are probably incomplete, because they result from just a few preliminary studies (e.g. Frahm *et al.*, 1996; Lobin *et al.*, 1998). An exploratory evaluation of data quality (following the method proposed by Santos *et al.*, 2010b) also indicated that many (if not all) of these islands are insufficiently sampled for cryptogams (see Appendix S2). Therefore, we excluded both the Cape Verde and Selvagens archipelagos from the analyses, to allow direct comparison between taxa.

After excluding subspecific taxa and exotic species, we pooled all the Macaronesian species available in regional lists and standardized the nomenclature according to Hill *et al.* (2006) for mosses, Ros *et al.* (2007) for liverworts and hornworts (but see Appendix S1 for some exceptions), Silva *et al.* (2010) for pteri-

Table 1 Information on the island area and known species richness of the four major plant groups in Macaronesia. Island inventories from Cape Verde and Selvagens are not reliable for some groups, hence we excluded them from the analyses to allow direct comparison between taxa (see text). Islands are listed in order of size (see also the corresponding codes in Fig. 1).

				Species richness			
Code	Archipelago	Island	Area (km^2)	Bryophytes	Pteridophytes	Wind-dispersed seed plants	Not-wind-dispersed seed plants
Islands included in the analyses (*n* = 19)							
1	MAD	Desertas	15	92	10	46	133
2	AZO	Corvo	17	179	32	26	84
3	MAD	Porto Santo	40	114	12	79	252
4	AZO	Graciosa	62	130	19	20	71
5	AZO	Sta. Maria	97	213	28	33	105
6	AZO	Flores	143	274	43	29	115
7	AZO	Faial	173	283	43	33	117
8	AZO	S. Jorge	246	310	37	34	114
9	CAN	El Hierro	278	198	32	121	362
10	CAN	La Gomera	378	294	38	141	463
11	AZO	Terceira	400	357	44	36	126
12	AZO	Pico	436	281	45	37	123
13	CAN	La Palma	729	351	35	133	458
14	MAD	Madeira	740	513	58	153	468
15	AZO	S. Miguel	750	356	41	39	130
16	CAN	Lanzarote	796	115	14	139	355
17	CAN	Gran Canaria	1532	309	37	207	597
18	CAN	Fuerteventura	1725	132	16	131	380
19	CAN	Tenerife	2058	434	43	235	669
Islands not included in the analyses (*n* = 13)							
20	SEL	Selvagens	3	16	1	21	21
21	VER	Branco	3	0	0	12	39
22	VER	Raso	6	0	0	17	40
23	VER	Sta Luzia	35	0	1	17	43
24	VER	Brava	64	12	12	29	71
25	VER	Sal	216	2	0	21	69
26	VER	S. Vicente	227	25	11	40	106
27	VER	Maio	269	0	1	29	86
28	VER	S. Nicolau	343	73	19	39	101
29	VER	Fogo	476	55	23	44	109
30	VER	Boavista	620	2	12	26	97
31	VER	S. Antão	779	111	25	51	139
32	VER	Santiago	991	35	12	49	134

Archipelagos: AZO, Azores; MAD, Madeira; SEL, Selvagens; CAN, Canaries; VER, Cape Verde.

dophytes and The Plant List (http://www.theplantlist.org/, last accessed 26 February 2012) for seed plants. The alien status of bryophytes was established following the most recent literature on this issue (Essl & Lambdon, 2009). In the case of seed plants, we classified the species as either wind-dispersed or not-wind-dispersed taking into account the information provided by different bibliographic sources (mainly Ridley, 1930 and Schaefer *et al.*, 2011; but see Appendix S1 for an additional list of references). In those cases where information was not available to the species level, dispersal mode was assigned taking into consideration data from the closest relatives (mainly other species of the same genus). This allowed the compilation of data for all species known from the Macaronesian islands for each plant group (Fig. 1, Table 1). The small number of endemics in cryptogams (only 27 bryophyte and 16 pteridophyte species endemic to a single archipelago) compared with that of seed plants (724 species) precluded between-taxa comparability related to level of endemism. Hence, we considered all species together for subsequent analyses in this study. The complete list of species (including their occurrence in the different Macaronesian islands, their endemic status and the dispersal character of seed plants) is included in Appendix S3 and is also available at the Azorean Biodiversity Portal (http://www.azoresbioportal.angra.uac.pt/).

Data analysis

We used the logarithmic form of the power model ($\log S = \log c + z \log A$; herein the ISAR model for simplicity) to build the ISAR for the considered plant groups in the whole extent considered. We estimated model parameters through ordinary least-squares regressions and assessed goodness-of-fit by means of the R^2. For statistically significant ISAR models, we examined whether the z-values differed between different taxa using ANCOVA tests.

In order to analyse the deviation of the total species richness of Macaronesia from that predicted by the ISARs, we followed the procedure proposed by Santos *et al.* (2010a). We started by determining the species richness predicted by the ISAR model of each taxon for a large hypothetical island with an area equal to the sum of the area of all the islands considered when building the ISAR. Then, we compared this value with the observed species richness of the whole of Macaronesia (herein the Macaronesian point or S_{MAC}), obtained by combining the species lists of the considered islands. Finally, we determined whether the observed S_{MAC} differs significantly from that predicted by the ISAR ($S_{MACPred}$) using the confidence intervals proposed by Santos *et al.* (2010a). That is, we identified the median absolute value of the residuals of each regression model, and expressed it as a proportion of $S_{MACPred}$ (herein PropMedRes), to then use this proportion to determine whether the difference between S_{MAC} and $S_{MACPred}$ departs from the interval defined by $S_{MACPred} \pm$ PropMedRes.

We used the procedure for partitioning of beta diversity proposed by Baselga (2010, 2012) to estimate both the turnover (β_{SIM}) and nestedness-resultant (β_{NES}) components of beta diversity. Briefly, this method decomposes the overall beta diversity (measured using the Sørensen dissimilarity index) into two additive fractions describing the between-island species turnover (β_{SIM}, the dissimilarity due to species replacement) and the variation in species composition due to richness differences in nested patterns (β_{NES}). We calculated such multiple-site dissimilarity measures in R (version 2.14.1; R Development Core Team, 2011) using the *betapart* R package (Baselga & Orme, 2012). Because β_{NES} is a measure of dissimilarity resulting from nestedness (i.e. accounting for richness differences within nested patterns), we also calculated 'nestedness metric based on overlap and decreasing fill' (NODF) values for rows (NODF$_{sites}$) as a measure of nestedness per se (see Almeida-Neto *et al.*, 2008, 2012; Baselga, 2012), using the *vegan* R package (Oksanen *et al.*, 2011). The significance of the between-taxa differences in β_{SIM}, β_{NES} and NODF$_{sites}$ was measured as the degree of overlap between the parameter distributions estimated through a bootstrapping with replacement procedure, in which groups of 10 islands were randomly sampled 1000 times from the original pool.

Analyses were carried out using all the islands from the Azores, Canaries and Madeira ($n = 19$). We also repeated the analyses considering the same datasets but excluding the two Canary islands of Lanzarote and Fuerteventura ($n = 17$), which present unique climatic conditions (being the driest and warmest islands of the whole Macaronesian region), were connected during glacial maxima forming the so-called island of Mahan, are in an advanced state of subsidence, and are known to deviate from the overall pattern of species accumulation with area (Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008; Fernández-Palacios *et al.*, 2011). Finally, we used data on the islands of Cape Verde and the Selvagens that may be considered sufficiently inventoried for cryptogams to conduct supplementary analyses, as a way to evaluate the robustness of the results obtained (see Appendix S2).

RESULTS

All ISAR models for the whole extent considered were statistically significant, accounting for between 31 and 46% of data variance, except in the case of pteridophytes, which was close to significant (Fig. 2, Table 2). The ISAR slopes did not differ significantly between taxa ($F_{2,51} = 1.12$, $P = 0.33$). Although seed plants appear to show two different ISAR curves (one for Azorean islands and another for the remaining islands; see Fig. S2.2 in Appendix S2 for the distinction of archipelagos), their slopes were not statistically different from those of bryophytes and pteridophytes (not shown). The species richness of the whole of Macaronesia (S_{MAC} or the Macaronesian point) was slightly higher than the upper bound predicted by the ISAR of its constituent islands ($S_{MACPred}$ + PropMedRes, herein $S_{MACPredUB}$) for both bryophytes ($S_{MAC} = 725$; $S_{MACPredUB} = 636$) and not-wind-dispersed seed plants ($S_{MAC} = 1253$; $S_{MACPredUB} = 1233$; see Fig. 2).

When excluding Lanzarote and Fuerteventura from the analyses, the ISAR slopes remained similar, although the explanatory power of area increased importantly. The ISAR of pteridophytes became statistically significant and that of bryophytes accounted for 75% of data variation (Table 2). Again, there were no statistical differences between the slopes of the models of the four plant groups ($F_{3,60} = 0.37$, $P = 0.77$), whose values (between 0.24 and 0.35) fell within the range typically reported for islands (Table 2). Contrary to the results obtained for all islands, the Macaronesian point fell within the ISAR for bryophytes (Fig. 2). Similar results were found when including Cape Verde and the Selvagens archipelagos in the analyses (Appendix S2).

Species turnover (β_{SIM}) was significantly higher in seed plants than in bryophytes and pteridophytes (Fig. 3a); no significant differences were found between the two latter groups, nor between wind-dispersed and not-wind-dispersed seed plants [see Appendix S4 for raw (non-bootstrapped) values of all between-group comparisons]. Compositional dissimilarity due to nestedness (β_{NES}) did not differ significantly between any of the considered plant groups (Fig. 3b). In contrast, both bryophytes and pteridophytes showed significantly higher nestedness (NODF$_{sites}$) than seed plants (Fig. 3c). Similar findings were obtained when excluding Lanzarote and Fuerteventura (Appendix S4) and when including the islands from Cape Verde and the Selvagens whose inventories could be considered reliable (not shown).
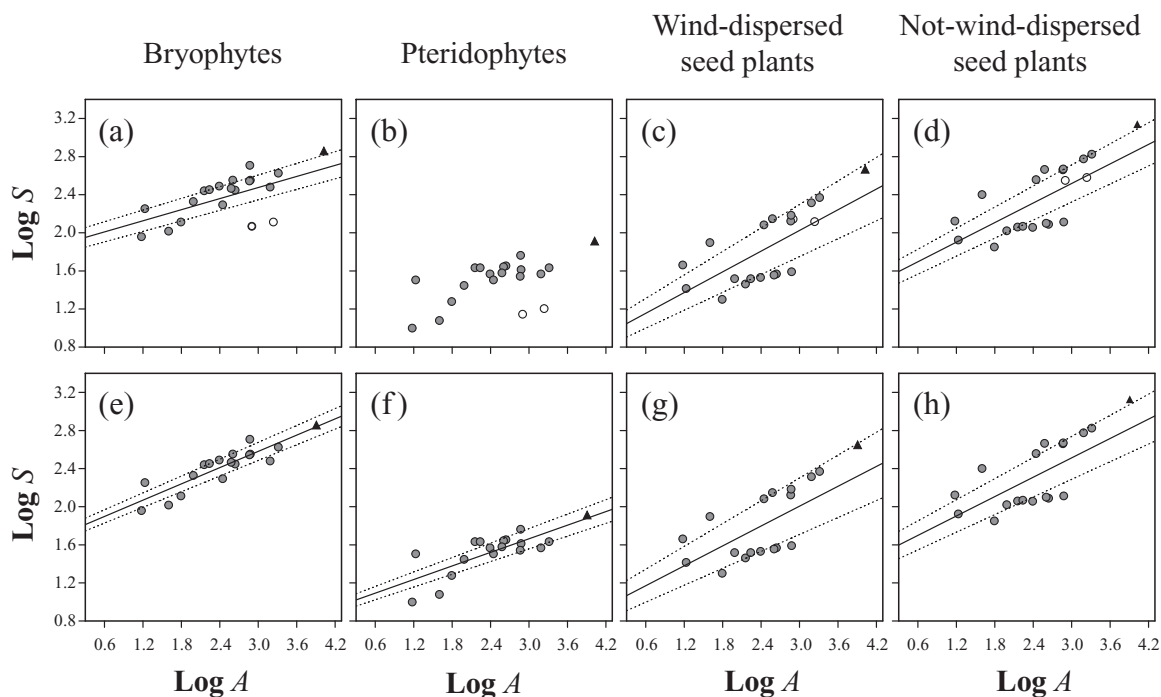
Figure 2 Island species–area relationships (ISAR) for the four considered plant groups. Analyses were carried out including (a–d) or excluding (e–h) Lanzarote and Fuerteventura islands (open circles). The species richness of the whole Macaronesia (that is, the Macaronesian point; dark triangles) and the species richness of each individual island (solid circles) are shown in all cases. For significant relationships (continuous line), the dashed lines show the intervals where the Macaronesian point should fall if it follows the same ISAR as its constituent islands (see text). Both species richness and area were $\log_{10}$-transformed (see Table 1 for non-transformed values). Regression parameters and goodness-of-fit of the power-law models are shown in Table 2.

	n	$c \pm SE$	$z \pm SE$	R^2	F	P
Bryophytes						
All islands	19	1.90 ± 0.17	0.19 ± 0.07	0.31	7.80	0.012
Excluding Lan, Fue	17	1.73 ± 0.10	0.28 ± 0.04	0.75	43.91	< 0.001
Pteridophytes						
All islands	19	1.11 ± 0.19	0.15 ± 0.08	0.18	3.82	0.067
Excluding Lan, Fue	17	0.95 ± 0.14	0.24 ± 0.06	0.53	16.89	< 0.001
Wind-dispersed seed plants						
All islands	19	0.94 ± 0.25	0.36 ± 0.10	0.44	13.27	0.002
Excluding Lan, Fue	17	0.96 ± 0.27	0.35 ± 0.11	0.39	9.55	0.007
Not-wind-dispersed seed plants						
All islands	19	1.49 ± 0.22	0.34 ± 0.09	0.46	14.59	0.001
Excluding Lan, Fue	17	1.50 ± 0.25	0.34 ± 0.10	0.42	10.99	0.005

Table 2 Parameters and goodness-of-fit of the log–log power-law models of the island species–area relationship for each plant group. c, z and R^2 are the intercept, slope and coefficient of determination of the regression equations, respectively. The standard error (SE) is shown for both model parameters. Analyses were carried out both considering all the islands and excluding Lanzarote (Lan) and Fuerteventura (Fue) islands (see text).

DISCUSSION

Although other studies have shown that bryophytes, pteridophytes and seed plants respond differently to area on islands and in fragmented landscapes (e.g. Virtanen & Oksanen, 2007; Kreft *et al.*, 2010), to our knowledge this is the first cross-taxon comparison using the entire flora of an extensive biogeographical region encompassing several oceanic archipelagos. This comprehensive approach has allowed us to evaluate whether both the species–area relationship and the compositional differences between islands can be associated with the (assumed) different dispersal capacities of four plant groups. Our results show that the slope of the ISAR is not sufficient to represent the differences in the biogeographical patterns associated with the varying dispersal capacity of the organisms and/or the degree of island isolation. On the contrary, the diversity of regional biotas seems to be progressively higher than predicted by the ISAR for less dispersive groups such as seed plants, which also show
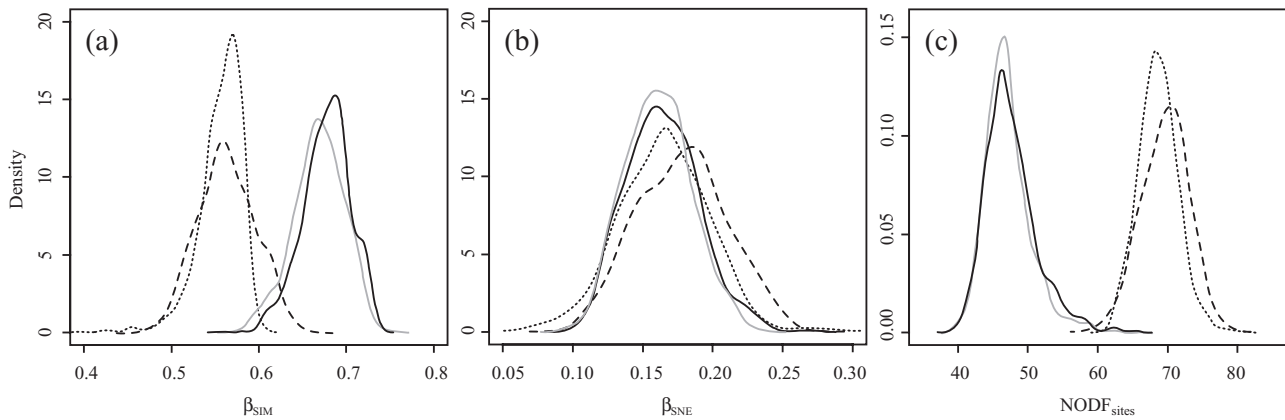
Figure 3 Differences of (a) species turnover, (b) nestedness-resultant dissimilarity and (c) nestedness between bryophytes (dashed line), pteridophytes (dotted line), wind-dispersed seed plants (black solid line) and not-wind-dispersed seed plants (grey line). Results of statistical significance (see text) were assessed by the degree of overlap between the parameter distributions estimated through a bootstrapping with replacement procedure, in which groups of 10 islands were randomly sampled 1000 times from the original pool ($n = 19$). Note that beta-diversity indices (β_{SIM} and β_{NES}) range from 0 to 1, while $NODF_{sites}$ oscillates between 0 and 100, hence the different scales of the density function axis.

significantly higher turnover and lower nestedness values. These results suggest that the a priori differential dispersal capacities of the analysed taxa, and the differential isolation character of the Macaronesian islands for each of these plant groups, have a decisive influence in the compositional singularity of each island and archipelago, but not on the rate of species increase with island area.

Other studies have shown non-significant or weak relationships between species richness and area for spore-dispersed organisms (e.g. Kimmerer & Driscoll, 2000; Sundberg *et al.*, 2006), although steep SARs have also been found for bryophytes (e.g. Tangney *et al.*, 1990; Virtanen & Oksanen, 2007). The slopes obtained in this study are within the range of values commonly found for isolated patches or islands for many groups of both micro- and macroorganisms (see Hortal, 2011; Triantis *et al.*, 2012). Fungi, lichens, bryophytes and pteridophytes are usually included with microorganisms in terms of their biogeographical characteristics, because of their reliance on microscopic dispersal stages. Although microbes show distinct biogeographical patterns from those of macroorganisms, usually involving fundamentally different scaling relationships, several patterns and processes are also congruent between the two groups (Fontaneto & Hortal, 2012). This is the case for the slope of the SAR, which seems to be similar across many taxa, regardless of their dispersal ability (see Hortal, 2011 and references therein). Perhaps more interestingly, the lack of empirical evidence confirming both the existence of between-group differences of dispersal ability in plants and its effect over the ISAR slope casts doubt on the influence of long-distance dispersal processes over a biogeographical pattern as fundamental as the increase of species with area. The similarity (or difficulty of finding significant differences) we found in the ISAR slopes of different groups could thus indicate: (1) that the capacity for long-distance dispersal is not significantly different between the considered groups (Higgins *et al.*, 2003); (2) the existence of

relatively similar colonization processes in spite of major differences in dispersal mode; or (3) the inappropriateness of ISAR slopes to reflect consistent beta-diversity patterns between islands caused by the differences in dispersal capacities (see below).

In contrast to the similarity in the slopes of the species–area relationships, the departure of the total Macaronesian richness from the ISAR predictions and the results obtained from beta diversity and nestedness analyses reveal between-group differences that could be associated with their different dispersal modes. The tendency for seed plants (and in particular not-wind-dispersed ones) to show higher regional richness than what would be expected from the ISAR should thus be associated with their higher rates of turnover between island assemblages, as suggested by Santos *et al.* (2010a). This may indicate that within-island processes regulating immigration and diversification rates – and thus the compositional dissimilarity of species between different islands – could increase in importance in those groups with lower dispersal ability. For these groups the floras of some islands (and/or island groups) will have a higher tendency to behave idiosyncratically, owing to their internal ecological dynamics, singular geographical characteristics or geological histories and the concurrence of multiple colonization sources (see Chiarucci *et al.*, 2011).

An important component of such higher island (or archipelago) idiosyncrasy may be the smaller gene flow among seed plant populations between and within different islands that might occur as a result of their dispersal limitations. This may lead to allopatric and even sympatric speciation, causing both the divergence and diversification of local floras, and ultimately resulting in higher rates of species turnover across the archipelago. This is illustrated by the existence of more than 80 endemic species distributed across several seed plant genera of the Crassulaceae and Asteraceae families (e.g. *Aeonium*, *Aichryson*, *Argyranthemum*, *Sonchus*), all of which radiated within

Macaronesia (Whittaker & Fernández-Palacios, 2007; see also Appendix S3). The accumulation of these island-idiosyncratic processes will produce a regional accumulation of species exceeding the predictions of the ISAR. By contrast, the congruence between the Macaronesian point and the ISAR predictions for both cryptogam groups (but see below) suggests that their higher dispersal capacity – or, at least, the higher frequency of long-distance dispersal – results in more similar and compositionally nested island floras. Hence, the Macaronesian bryophyte and pteridophyte island floras are more nested than those of seed plants despite the known repeated colonization of many bryophyte species back and forth between the Azores – a known glacial refuge for many European species – and mainland Europe, and the high genetic singularity of the Azorean bryoflora (Hutsemékers *et al.*, 2011; Laenen *et al.*, 2011).

Here it is important to notice that while NODF$_{sites}$ identifies significantly higher degrees of nestedness for spore-forming plants, there were no between-group differences in nestedness-resultant dissimilarity (β_{NES}). This means that the lower overall differences in species richness between islands compensate for the higher nestedness in the case of cryptogam communities, while the opposite pattern occurs for seed plants (see Almeida-Neto *et al.*, 2012; Baselga, 2012). However, despite the only two measures that show no between-group variation (ISAR slope and β_{NES}) depend on differences in species richness between islands, it cannot be established from our analyses whether there is any meaningful correlation between them or if their similar behaviour in this particular case is a matter of chance. We therefore suggest that, at least at this scale (i.e. island biotas), the ISAR slope measures no more than richness variations and is insensitive to any compositional patterns (turnover or nestedness) between islands. This implies that the ISAR slope is not a good proxy for the archipelago's beta diversity. Our results highlight the difficulty of using ISAR slopes to demonstrate the existence of biogeographical processes that affect islands' biotas differently. This may be because ISAR slopes are mostly determined by within-island processes of species accumulation, while different dispersal abilities – as well as other factors affecting the biogeographical relationships between island assemblages – generate different patterns of between-island dissimilarity in species composition.

There are three main sources of uncertainty that should be taken into consideration while interpreting the results of this study. First, there is a large array of fitting functions for the species–area relationship, and the power model may not always provide the best fit (see Rosindell & Phillimore, 2011). In our case, we used the power-law fit not because of its long-standing tradition in this kind of research but rather because it is among the best and simplest models and its parameters can be interpreted biologically (see Sólymos & Lele, 2012; Triantis *et al.*, 2012). Second, sample size limitations may lead to Type II errors, hence giving the false impression of no effect of dispersal on the ISAR slope and, ultimately, on the regional species accumulation with area. This possibility remains to be confirmed until new studies extend our approach to a wider range of taxa

and biogeographical regions; this task may, however, be hampered by the fact that it is not always feasible to obtain good-quality data on island floras like those used here. Finally, it could be argued that our results may depend on the particular set of islands used for the analysis. However, the analyses conducted excluding Lanzarote and Fuerteventura or including Cape Verde and the Selvagens show similar results (see Appendix S2), with the exception of changes in the statistical significance of ISAR slopes. Although bryophytes depart from the ISAR when all islands are considered, a careful examination of Fig. 2(a,e) shows that such a departure is due to the excessive influence of the anomalously low richness values of Lanzarote and Fuerteventura. As commented before, these islands are climatically and geologically distinct from the rest of the Macaronesian islands considered, so it is common practice to discard them in analyses of the relationship between species richness and area (see Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008; Santos *et al.*, 2010a). Given the well-known influence of the availability of water on bryophyte diversity, it seems sound to base our conclusions on the dataset that discards these anomalously dry low-altitude islands. This is supported by the extra analyses presented in the Appendix S2, which also show that the ISAR model for bryophytes is not significant when including the island inventories from the drier Cape Verde archipelago. However, additional evidence is needed to evaluate whether the effects of climatic gradients on species richness might be so important as to obscure those of area in the Macaronesian region.

CONCLUSIONS

In spite of the caution that should be used when interpreting and inferring processes from simple correlations such as ISARs, our results allow us to hypothesize that differences in dispersal modes may have a significant effect on the compositional dissimilarity of species within a region, but not on the increase of species richness with area. This supports the usefulness of the approach proposed by Rosenzweig (2004), and followed by Santos *et al.* (2010a), for widening the descriptive capacity of species–area relationships to study biogeographical processes that may remain undetected when considering only the ISAR slopes. Here, the study of the relationships between ISAR curves and measures of different aspects of between-island compositional differences has opened up new research opportunities. In the specific case of the Macaronesian region, further research – including detailed studies on floristic differences between islands and more detailed inventories of the Cape Verde and Selvagens archipelagos – is needed to disentangle the effects of geographical factors, climatic differences or habitat diversity on the species richness of bryophytes, pteridophytes and seed plants.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Additional references used to build the species lists and to establish the dispersal mode of seed plant species.

Appendix S2 Additional island species–area relationship analyses incorporating the Cape Verde and Selvagens archipelagos, accounting also for the selection of islands with comparable inventories.

Appendix S3 Bryophyte, pteridophyte and seed plant species distribution in the Macaronesian islands.

Appendix S4 Multi-site species turnover (β_{SIM}), nestedness-resultant dissimilarity (β_{NES}) and nestedness ($NODF_{sites}$) of the Macaronesian bryophytes, pteridophytes, wind-dispersed seed plants and not-wind-dispersed seed plants. The indices were calculated including ($n = 19$) and excluding ($n = 17$) Lanzarote and Fuerteventura islands.

BIOSKETCH

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