

Research Article

Biogeographical determinants of pteridophytes and spermatophytes on oceanic archipelagos

ALESSANDRO CHIARUCCI¹, GIOVANNI BACARO¹, KOSTAS A. TRIANTIS^{2,3,4}
& JOSÉ MARIA FERNÁNDEZ-PALACIOS⁵

¹BIOCONNET, Biodiversity and Conservation Network, Department of Environmental Science ‘G. Sarfatti’, University of Siena, Via P.A. Mattioli 4, 53100 Siena, Italy

²Azorean Biodiversity Group CITA-A, Universidade dos Açores, Terra-Chã, 9700-851 Angra do Heroísmo, Terceira, Açores, Portugal

³Biodiversity Research Group, Oxford University, Centre for the Environment, South Parks Road, Oxford OX1 3QY, UK

⁴Department of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University of Athens, Athens GR-15784, Greece

⁵Department of Ecology, La Laguna University, La Laguna 38206, Tenerife, Spain

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Using the data from six oceanic archipelagos, we investigated the species richness patterns on islands for all natives, archipelagic endemics and single-island endemics of pteridophytes and spermatophytes. We tested the hypothesis that the descriptive ability of biogeographical factors for species is reduced as we move from native species, to archipelagic endemics and to single island endemics, because of the increasing importance of island ‘idiosyncrasies’ (i.e. unique features of each island shaping its biota, such as catastrophic volcanic eruptions, random colonization events, mega-landslides) in controlling the species richness of endemic species. This hypothesis was addressed using two approaches: (1) the island species–area relationships (ISARs), and (2) a multiple regression approach with variable selection based on permutation, to test the combined effects of island area with other biogeographical factors. Area was an effective predictor of species richness for all native species ($R^2 = 0.568$ and $R^2 = 0.624$ for pteridophytes and spermatophytes respectively), but its predictive capacity decreased for archipelagic endemics ($R^2 = 0.261$ and $R^2 = 0.531$) and single-island endemics ($R^2 = 0.084$ and $R^2 = 0.438$). The reduction of R^2 from all native species, to archipelagic endemics and to single-island endemics was attributed to the increasing effects of the ‘idiosyncrasies’ of each island. The predictive capacity of multiple regression models increased with respect to ISARs, ranging from 27.3% (for single-island endemic pteridophytes) to 83.3% (all native pteridophytes), and included three to five predictors. Island area remained the most important variable for spermatophytes but was less important for pteridophytes. For pteridophytes, elevation was the most important predictor for native species, while isolation-related variables were the most important predictors for archipelagic endemics and single-island endemics. Our results support the hypothesis that as we move from native, to archipelagic endemic and to single-island endemic species the predictive ability of models is reduced, indicating an increased effect of the ‘idiosyncratic’ character of islands.

Key words: Azores, Canaries, Cape Verde, flora, Galápagos, Hawaii, island biogeography, Marquesas, predictive models, species richness

Introduction

Oceanic archipelagos are composed by islands that have never been connected to the mainland and share a common geological history. These islands originated because of volcanic activity and, on geological time scales, disappear because of erosion and subsidence, possibly remaining as atolls in tropical seas. Despite the relative simplicity of the geological history of some oceanic archipelagos, most arise through complex processes and their origins are dif-

ficult to disentangle (Courtilot *et al.*, 2003; Clouard & Bonneville, 2005). Oceanic islands may differ in the type of volcanism they experience, resulting in different geological structures, even within the same island (Carracedo & Tilling, 2003). The prevalence of different types of volcanic activity in shaping the configuration of an island together with the frequency of volcanic activity can have profound effects on the islands’ biota, extinguishing a number of terrestrial clades (see Geldmacher *et al.*, 2005; Holm *et al.*, 2006; Whittaker & Fernández-Palacios, 2007; Anderson *et al.*, 2009). Nevertheless, oceanic archipelagos share a number of common features, such as a volcanic origin and

Correspondence to: Alessandro Chiarucci. E-mail: alessandro.chiarucci@unisi.it

never having been connected to continental landmasses (Whittaker & Fernández-Palacios, 2007). These islands have a typical developmental life cycle from youth, through maturity, to old age and eventual loss (Whittaker *et al.*, 2008). In addition to the volcanic activity, other catastrophic events, such as landslides and tsunamis, can partly or totally destroy the biota of these islands making them available for new processes of colonization, succession and evolution (Thornton, 2007; Whittaker & Fernández-Palacios, 2007).

The features of oceanic islands make their biota a unique product of ecological and evolutionary dynamics (Wagner & Funk, 1995; Grant & Grant, 2008), inhabited by species arriving via long-distance dispersal or evolving by *in-situ* speciation (Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008; Losos & Ricklefs, 2009). Speciation processes are particularly important in these systems and usually result in high numbers of endemic taxa (Carlquist, 1974; Williamson, 1981; Kier *et al.*, 2009): some taxa can be shared by some or all the islands of an archipelago (Multiple Island Endemics, MIEs hereafter) or can be exclusive to a single island (Single-Island Endemics, SIEs hereafter). These groups of species can be used as simple metrics of evolutionary dynamics of the island systems, as each can be influenced by speciation, extinction and migration events (Emerson & Kolm, 2005; Triantis *et al.*, 2008a; Whittaker *et al.*, 2008).

Species diversity patterns on islands have been widely studied, and in many cases comparable approaches across different archipelagos have been applied (Wagner & Funk, 1995; Price & Clague, 2002; Willerslev *et al.*, 2002; Price, 2004; Duarte *et al.*, 2008; Triantis *et al.*, 2008a, 2008b; Whittaker *et al.*, 2008; Carine & Schaefer, 2010). Nevertheless, studies including islands belonging to different archipelagos are scarce. Furthermore, despite the availability of species richness data, few global analyses have been performed on the diversity patterns of native and endemic plants of oceanic archipelagos. Hobohm (2000) analysed the species richness of 57 islands and archipelagos worldwide, concluding that neither the distance to the mainland nor the proportion of endemics is significantly correlated with the species diversity. Kreft *et al.* (2008) analysed the species richness of 488 island and 970 mainland floras, highlighting the striking importance of area as a determinant of species richness in islands. They noted that the global patterns of plant species richness on islands are still poorly documented, and factors controlling species richness remain controversial. Kier *et al.* (2009) showed that islands have a number of endemic species exceeding that of continents by almost an order of magnitude. Although Kier *et al.* (2009) included islands from across the globe, they didn't separate the oceanic archipelagos from other types of islands, such as continental fragments or land-bridge islands. Recently, Chiarucci *et al.* (2010), using a dataset of plants from six oceanic archipelagos, concluded that

species diversity partitioning across islands differs between pteridophytes and spermatophytes and across archipelagos.

We aim to explain the species richness patterns of plants on oceanic islands for different chorological groups (i.e. all native, archipelagic endemic and SIE species) of pteridophytes and spermatophytes on various oceanic archipelagos. We separately analysed spermatophytes and pteridophytes because of the pronounced differences in their biological and ecological attributes (see e.g. Kreft *et al.*, 2010).

Our main hypothesis is that the descriptive ability of various biogeographical factors for species richness will gradually be reduced as we move from native species, to archipelagic endemics and to single-island endemics, because of the increasing importance of island 'idiosyncrasies' (factors which can hardly be included in a deterministic model, e.g. catastrophic volcanic eruptions, random colonization events, mega-landslides) in setting up the richness of endemic species. To test this hypothesis we used the data from six oceanic archipelagos (Azores, Canaries, Cape Verde, Galápagos, Hawaii and Marquesas) to: (a) fit the classic island species–area models (ISARs) and (b) test more complex models with additional geographical, topographical and geological variables about the islands and archipelagos. Separate tests were performed for pteridophytes and spermatophytes, two groups of plants with different biological and ecological features.

Materials and methods

Study areas

The six oceanic archipelagos used, i.e. Azores, Canaries, Cape Verde, Galápagos, Hawaii and Marquesas, are positioned across the globe and represent the most well-studied oceanic groups in terms of their biota. A synthetic description of these archipelagos can be found in Chiarucci *et al.* (2010). Only islands larger than 1 km² were included in the analyses, because good quality data were not available for the smaller islets. The geographical and biological features of the six studied archipelagos are presented in Table 1 and Appendix 1 (see supplementary material which is available on the Supplementary tab of the article's Informaworld page at <http://dx.doi.org/10.1080/14772000.2011.603381>).

Data collection

We used the available checklists of native pteridophytes and spermatophytes for the six archipelagos: the Azores (Borges *et al.*, 2005), the Canary Islands (Kunkel, 1980; this source and not the checklist by Izquierdo *et al.*, 2004 was used, since the latter lacks data for the islands Alegranza, Montaña Clara, La Graciosa and Lobos), Cape

Table 1. Geographical and biological features of the six studied archipelagos. For some features the name of the corresponding island is also indicated. *Age of the oldest emerged island, which does not preclude the existence in the archipelago of older, now submerged islands.

	Azores	Canaries	Cape Verde	Galápagos	Hawaii	Marquesas
N° islands > 1 km ²	9	11	12	17	8	9
Total area (km ²)	2764	7445	4033	7876	16 759	1049
Maximum elevation (m)	2351 (Pico)	3718 (Tenerife)	2835 (Fogo)	1707 (Isabela)	4205 (Hawaii)	1230 (Ua Pou)
Continental isolation (km)	1369 (Sao Miguel)	97 (Fuerteventura)	571 (Boavista)	927 (San Cristóbal)	3675 (Hawaii)	4737 (Hatutaa)
Mean intra-archipelago isolation (km)	220.0	196.5	140.8	140.1	168.8	146.5
Latitudinal extent (°)	37–40 N	27–29 N	15–17 N	1N–1S	19–23 N	7–11 S
Age (My)	8 (Santa María)	20*(Fuerteventura)	16 (Sal)	6.3* (San Cristóbal)	5.1* (Niihau)	7 (Eiao)
Last volcanic eruption	1957 (Faial)	1971 (La Palma)	1995 (Fogo)	2008 (Isabela)	2008 (Hawaii)	Pleistocene (?)
Number of native fern species	48	50	33	110	161	102
Number of endemic fern species	7	3	1	5	119	31
Number of native spermatophyte species	164	1204	209	439	1003	229
Number of endemic spermatophyte species	61	582	65	141	905	130

Verde Islands (Arechavaleta *et al.*, 2005); Galápagos (Lawesson *et al.*, 1987); Hawaii (Price, 2004); the Marquesas Islands [Wagner & Lorence (2002) by the Smithsonian Institution]. The islands included in the analyses, their geographical and geological properties, as well as species richness data of pteridophytes and spermatophytes are the same as in Chiarucci *et al.* (2010). For each island the species richness of all native species (*Nat*), archipelagic endemics (*End*, given by MIEs + SIEs) and SIEs of both pteridophytes (S_{P-Nat} , S_{P-End} and S_{P-SIE}) and spermatophytes (S_{S-Nat} , S_{S-End} and S_{S-SIE}) were calculated.

The main biogeographical factors considered, corresponding to the geographical, topographical and geological attributes of the islands, were: (1) island area (measured as planar area); (2) maximum elevation; (3) island age; (4) archipelago's age (measured as the age of the oldest island); (5) continental isolation (measured as the distance from the nearest continent); (6) distance to the nearest larger island (this was 0 for the largest island of the archipelago); (7) relative island age (calculated as the ratio of the age of a specific island divided by the age of the oldest island of the archipelago); (8) distance to the nearest older island (this was 0 for the oldest island of the archipelago); (9) distance from the Equator. Data about geological age of islands and archipelagos were obtained from França *et al.* (2003) for Azores; Carracedo *et al.* (2002) for the seven larger Canaries; de la Nuez *et al.* (1997) and Carracedo *et al.* (2001) for the smaller Canaries; Duarte *et al.* (2008) for Cape Verde; Price (2004) for Hawaii; Peck (2005) for Galápagos; and Clouard & Bonneville (2005) for Marquesas.

Data analyses

The determinants of the six species richness metrics (S_{P-Nat} , S_{P-End} , S_{P-SIE} , S_{S-Nat} , S_{S-End} and S_{S-SIE}) were modelled by two complementary approaches: (1) the island species–area relationships (ISARs), and (2) a multiple regression approach with variable selection based on permutation, to test the combined effects of island area with the other geographical, topographical and geological factors.

ISARs were investigated by fitting, for 66 islands from six archipelagos, the linearized version of the Arrhenius (1921) power model, $\text{Log}(S) = c + z \cdot \text{Log}(A)$, and the Gleason (1922) exponential model, $S = k + z \cdot \text{Log}(A)$, where S is the value for one of the diversity metrics used, A is the area of the respective island in km² and c , k and z the fitted parameters. A value of 1 was added to all the pteridophytes and spermatophyte SIEs, before log transformation, since zero values were reported for some islands. As the two models have the same number of fitted parameters, they were compared by using the proportion of explained variance (R^2) as a measure of their goodness of fit (Triantis *et al.*, 2003). More sophisticated ISAR models, with a higher number of parameters (see e.g. those reported by Tjørve, 2003, 2009; Dengler, 2009; Williams *et al.*, 2009) were not tested here due to the lack of comparability with previous studies.

To test the combined effects of the nine biogeographical factors considered to the six species richness metrics (S_{P-Nat} , S_{P-End} , S_{P-SIE} and S_{S-Nat} , S_{S-End} , S_{S-SIE}) we applied a stepwise regression. Since all the response variables consist of count data, they were normalized by using the Box–Cox family of transformations (Box & Cox, 1964). The Box–Cox transformation is a useful normalization procedure defined

by:

$$T(Y) = (Y^\lambda - 1)/\lambda \quad (1)$$

where Y is the response variable and λ is the transformation parameter. For $\lambda = 0$, the natural log of the data is taken instead of using the above formula.

Once normalized, the response variables were fitted to the linear, log-transformed and 2nd order polynomial transformation of each predictor variables. The transformation able to maximize the amount of variation explained in the response variable was then included in the model. In order to detect multicollinearity in the set of predictor variables, a general explorative analysis of pairwise variable correlations (using Pearson's correlation coefficient) was carried out (Appendix 2, see supplementary material which is available online). Multicollinearity represents a factor which can strongly influence model development and the selection of predictor variables during stepwise modelling (Fox, 2008), leading to the potential exclusion of important predictors from the model (i.e. with strong collinearity, the inclusion/exclusion of a variable in the final model is mainly due to the order that variable is added to the model).

By fitting this full model, the (total) adjusted coefficient of multiple determination (R^2_{adj}) was assessed. In order to select a minimal adequate (parsimonious) model and to avoid multicollinearity in selected predictor variables, a forward variable selection criterion based upon permutations and parametric tests was used (Blanchet *et al.*, 2008). Classic forward selection of ecological variables presents two well-known problems: (1) an inflated rate of Type I error and (2) an overestimation of the amount of variance explained. The forward procedure proposed by Blanchet *et al.* (2008) overcomes these problems as the selection of predictors is done by applying a permutation of residuals under a reduced model. The proposed forward selection has to be carried out with two stopping criteria: (1) the usual alpha significance level (significance level selected = 0.05) and (2) the adjusted coefficient of multiple determination (R^2_{Adj}) calculated using all explanatory variables. When forward selection identifies a variable that brings one or the other criterion over the fixed threshold, that variable is rejected, and the procedure is stopped. The most important advantage of such a method is that selection of unimportant variables is less likely to occur. Moreover, this method is highly conservative, selecting fewer and more biologically meaningful variables. Other methods for selecting variables in stepwise procedures are more subject to problems, with predictor variables which present multicollinearity; methods such as the Akaike Information Criterion could provide a number of different models with quite similar values (usually within the range of two AIC units) on the basis of the order of variable introduction (Burnham & Anderson, 2002). For each analysis 1000 permutations

were performed. The R software and the 'packfor' package (version 0.0–7) were used for the regression analyses.

Results

Species–area relationships

In general, the Arrhenius ISAR model had a better fit for all the species richness metrics than the Gleason model and both ISAR models explained a higher proportion of variance for spermatophytes than for pteridophytes (Table 2). The explained variance in richness was higher for all native species (Nat) than for archipelagic endemics (End) or SIEs (Table 2, Figure 1). The z parameters of the linearized Arrhenius ISAR models for pteridophytes were 0.597 for S_{P-Nat} , 0.332 for S_{P-End} and 0.069 for S_{P-SIE} (Figure 1, Table 3). The respective values of the z parameter for the spermatophytes' species metrics were 0.326 for S_{S-Nat} , 0.392 for S_{S-End} and 0.503 for S_{S-SIE} (Figure 1, Table 3). The c values were much smaller for pteridophytes than for spermatophytes and showed that no ferns are expected on islands with an area of 1 km² or less. The combined results for the z and c values indicated that native pteridophytes were almost absent in small islands. However the richness of native pteridophytes increased with increasing area more steeply than the richness of native spermatophytes. The z -values of the linearized Arrhenius ISARs revealed a contrasting pattern for pteridophytes and spermatophytes, showing a reduction for the former and an increase for the latter, passing from all native species to archipelagic endemics and to SIEs. Thus, for spermatophytes the increase in species richness with increasing island area (i.e. the z value) was higher for SIE than for archipelagic endemic and for native species, while the opposite pattern was observed for pteridophytes, even given the lower descriptive power of the ISAR models for pteridophyte endemics and SIEs (Table 2; Figure 1).

Table 2. Model fitting (R^2 and P -level) of the Arrhenius and Gleason ISAR models for the total data set (66 islands belonging to the six oceanic archipelagos) for the four groups of plants considered in the analyses. * $P < 0.01$, *** $P < 0.001$; $n = 66$ for the six data sets.

	Arrhenius	Gleason
Pteridophytes		
All native species	0.568***	0.409***
Archipelagic endemic species	0.261***	0.171***
SIEs	0.084*	0.066*
Spermatophytes		
All native species	0.624***	0.434***
Archipelagic endemic species	0.531***	0.351***
SIEs	0.438***	0.225***

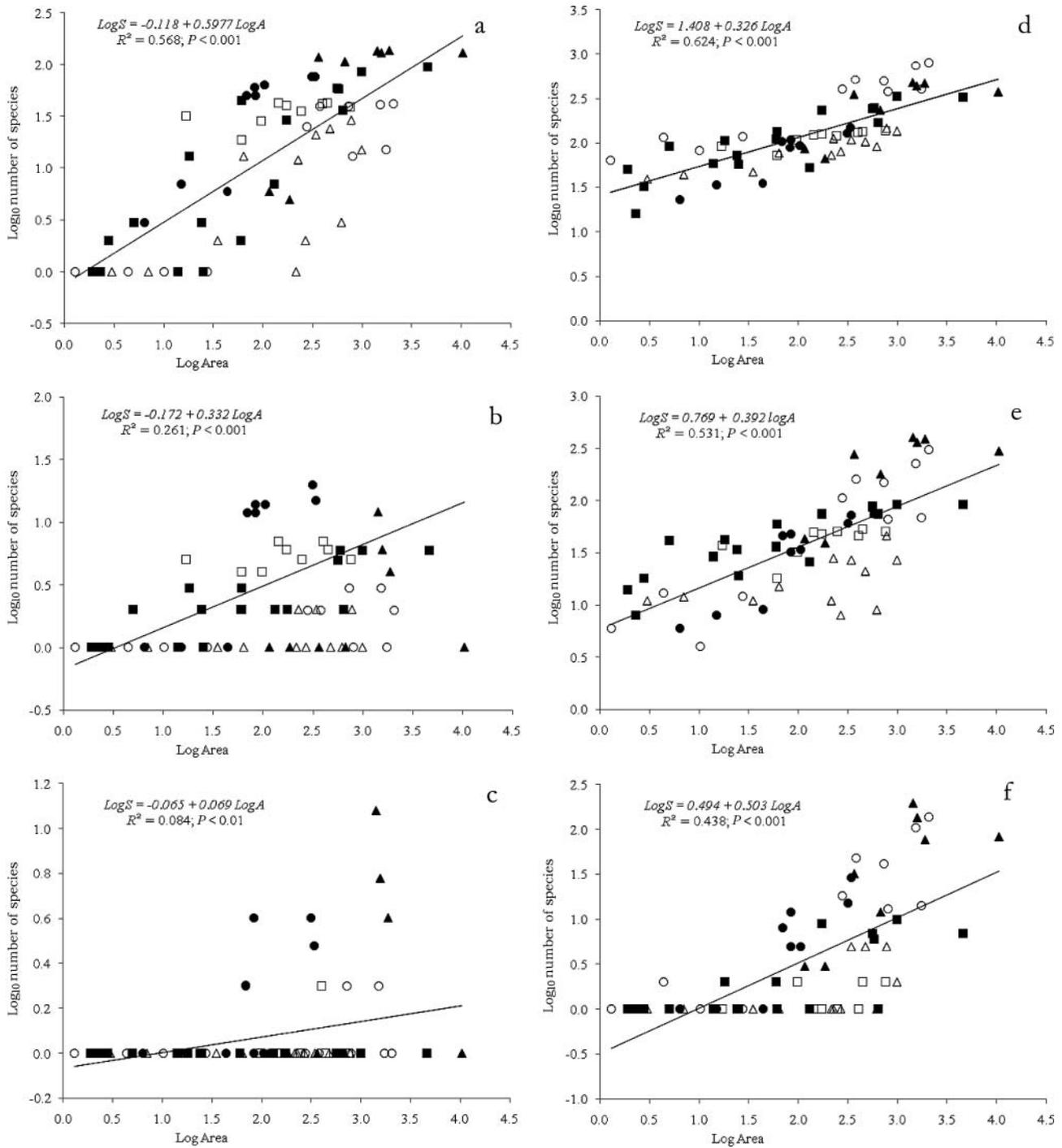


Fig. 1. Species–area relationships according to the Arrhenius ISAR model for (a) all native pteridophytes; (b) archipelagic endemic pteridophytes; (c) SIE pteridophytes; (d) all native spermatophytes; (e) archipelagic endemic spermatophytes and (f) SIE spermatophytes. The labels for each archipelago are as follows: Azores (white squares); Canaries (white circles); Cape Verde (white triangles); Galápagos (black squares); Hawaii (black triangles); Marquesas (black circles).

Predictive modelling

Multicollinearity among the whole set of predictor variables was practically absent (the highest correlation coefficient being 0.66 between elevation and island area). Further

diagnostic analyses to detect collinearity were therefore excluded.

For the predictive modelling of pteridophytes, the normalization procedure returned estimated *lambda*

Table 3. Slope (z) and intercept (c) parameters of the linearized Arrhenius ISAR model ($\text{Log}(S) = c + z \cdot \text{Log}(A)$) fitted for the 66 islands belonging to the six oceanic archipelagos for the three groups of plants included in the analyses. $n = 66$ for the three data sets. Note that the c parameters of some ISAR (evidenced by an asterisk) were affected by the addition of a constant (+1) to the original values, as needed for the log-transformation. The last column reports the values of the k parameter, corresponding to the untransformed value of c parameter of the Arrhenius model, to indicate the number of species of each group expected by the ISAR model in an island of unit area (1 km^2).

ISAR model	z	c	k
Pteridophytes			
All native species	0.597	-0.118*	-0.2
Archipelagic endemic species	0.332	-0.172*	-0.3
SIEs	0.069	-0.065*	-0.1
Spermatophytes			
All native species	0.326	1.408	25.6
Archipelagic endemic species	0.392	0.769	5.9
SIEs	0.503	0.494*	2.1

parameters of 0.216 for S_{P-Nat} , -0.436 for S_{P-End} and -4.856 for S_{P-SIE} . The percentage of explained variance ranged from 27.3% for S_{P-SIE} to 73.1% for S_{P-End} and to 83.3% for S_{P-Nat} . (Table 4). The three models for pteridophyte species richness showed a higher predictive capacity than the simple ISAR models, however, the proportion of explained variance remained low for S_{P-SIE} (likely due to the non-normal distribution of data even after the Box-Cox transformation). Elevation was the most important predictor explaining S_{P-Nat} , while continental isolation was the most important predictor variable for S_{P-End} and S_{P-SIE} (Table 4). The additional predictor

variables retained in the models for the three species richness metrics of pteridophytes are presented in Table 4.

For the predictive modelling of spermatophytes, the normalization procedure returned estimated λ parameters of -0.039 for S_{S-Nat} , -0.046 for S_{S-End} and -0.402 for S_{P-SIE} . The percentage of explained variance ranged from 65.6% for S_{S-SIE} to 67.6% for S_{S-End} and to 78.1% for S_{S-Nat} , (Table 5). The predictive power of the models showed an increased explanatory power with respect to ISAR models and island area was the most important predictor variable in explaining the species richness of the three species richness metrics. The additional predictor variables retained in the models for the three species richness metrics of spermatophytes are presented in Table 5.

Discussion

Island species–area relationships

The analysis of 66 oceanic islands from six archipelagos confirmed area as the most powerful single explanatory variable of species richness in islands (MacArthur & Wilson, 1967; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2008a). The Arrhenius (1921) model had a predictive capacity of more than 62% for spermatophyte and about 57% for pteridophyte species richness for the oceanic islands considered. These values are in line with the results of Kreft *et al.* (2008), who reported an $R^2 = 0.66$ for the ISAR fitted by the Arrhenius model on the total flora (spermatophytes and pteridophytes) of 488 islands across the globe. Note that considering spermatophytes and pteridophytes together for our dataset we get the same value, i.e. $R^2 = 0.66$ (results not shown).

Table 4. Summary statistics for predictive models of species richness of all native pteridophytes (S_{P-Nat}), archipelagic endemic pteridophytes (S_{P-End}), and SIE pteridophytes (S_{P-SIE}). log = logarithmic transformation; 2nd ord. = predictor was included in the model as a second order polynomial term; UT = untransformed. For each significant predictor included in the minimal model after forward stepwise variable selection (10 000 permutations, see text for details), the following data were reported: the transformation adopted (for polynomials, significant orders are reported in parentheses), the explained variance expressed by means of the coefficient of determination R^2 and the sign of the estimated relationship between the response and the predictor. Total variance explained by each model was calculated using the R^2 adjusted statistics (see text for details).

Variable	Transformation	Coefficient sign	R^2_{Cum}	Cumulative R^2_{adj}	F	P
(1) S_{P-Nat}						
Elevation	log	+	0.630	0.624	104.18	< 0.001
Archipelagos age	2 nd (1)	-	0.814	0.807	59.24	< 0.001
Island area	log	+	0.841	0.833	10.03	0.002
(2) S_{P-End}						
Continental isolation	2 nd (1,2)	+, -	0.370	0.358	26.10	< 0.001
Island area	log	+	0.594	0.578	29.74	< 0.001
Island age	UT	-	0.726	0.708	24.21	< 0.001
Archipelago age	2 nd (1)	-	0.752	0.731	5.91	0.018
(3) S_{P-SIE}						
Continental isolation	UT	+	0.159	0.145	11.55	0.001
Island area	log	+	0.254	0.229	7.66	0.010
Elevation	2 nd (2)	-	0.308	0.273	4.577	0.038

Table 5. Summary statistics for predictive models of species richness of all native spermatophytes (SS-Nat), archipelagic endemic spermatophytes (SS-End), and SIE spermatophytes (SF-SIE). log = logarithmic transformation; 2nd ord. = predictor was included in the model as a second order polynomial term; UT = untransformed. For each significant predictor included in the minimal model after forward stepwise variable selection (10 000 permutations, see text for details), the following data were reported: the transformation adopted (for polynomials, significant orders are reported in parentheses), the explained variance expressed by means of the coefficient of determination R^2 and the sign of the estimated relationship between the response and the predictor. Total variance explained by each model was calculated using the R^2 adjusted statistics (see text for details).

Variable	Transformation	Coefficient sign	R^2_{Cum}	Cumulative R^2_{adj}	F	P
(1) S_{P-Nat}						
Island area	log	+	0.647	0.641	112.02	<0.001
Continental isolation	log	-	0.697	0.687	9.92	0.002
Archipelago age	2 nd (1)	+	0.733	0.719	7.96	0.007
Elevation	log	+	0.783	0.768	13.27	0.001
Distance to the nearest larger island	log	+	0.798	0.780	4.30	0.043
(2) S_{S-End}						
Island area	log	+	0.519	0.511	65.96	<0.001
Archipelago age	UT	-	0.641	0.629	20.35	<0.001
Elevation	2 nd (1)	+	0.691	0.675	9.61	0.03
(3) S_{S-SIE}						
Island area	log	+	0.462	0.453	52.40	<0.001
Distance to the nearest larger island	2 nd (2)	-	0.524	0.508	7.83	0.006
Archipelago age	UT	-	0.611	0.591	13.23	<0.001
Elevation	log	+	0.646	0.622	5.77	0.018
Continental isolation	UT	+	0.683	0.655	6.63	0.014

Area is a very powerful single explanatory variable for species richness, especially in islands, since it can effectively describe the available ecological space for species to be established (e.g. Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2008b; Losos & Ricklefs, 2009). The main role of area in controlling species richness has been the subject of many theoretical and empirical studies in island biogeography (e.g. MacArthur & Wilson, 1967; Williamson, 1988; Rosenzweig, 1995; Lomolino, 2001; Price, 2004; Whittaker & Fernández-Palacios, 2007; Triantis *et al.*, 2008a) and many authors attempted to find the best model to fit insular ISARs. The discussion over the best model and the exact shape of the ISARs, as well as the possibility to generalize this pattern into a general function (Williamson, 1988; Lomolino, 2000, 2001; Lomolino & Weiser, 2001; Scheiner, 2003; Tjorve, 2003, 2009; Dengler, 2009) remain a source of debate. Although ISAR is considered one of the few real laws in both ecology and biogeography (Rosenzweig, 1995), it is unlikely that a single unifying model will ever be found and interpreted, because this is a simple attempt of explanation for a complex phenomenon (Williamson, 1988; Triantis *et al.*, 2008b). However, our results confirmed that the Arrhenius model remains an effective model to-date.

The capacity to model the species richness of archipelagic endemics and SIEs by the same ISAR approach was much lower than for all native species, especially for pteridophytes. The sequential reduction of R^2 from all native species, to archipelagic endemics and to SIEs can be explained by the increasing effect of the 'idiosyncrasies'

of each island on its evolutionary dynamics (cf. Triantis *et al.*, 2010a). Tryon (1970) and Kisel & Barraclogh (2010) showed that the speciation rate of pteridophytes does not scale with island area, since they exhibit high frequencies of polyploid and hybrid speciation, which are not expected to be so area dependent. Kisel & Barraclogh (2010) suggested that ferns speciation on islands is apparently unrelated to island size. Hence, although area can approximate the overall carrying capacity of an island in terms of native species, it is a less powerful predictor of the island's richness in terms of archipelagic or SIE species, which can be more dependent on the evolutionary dynamics than on area itself. Despite this there are cases where area remains a strong predictor of endemic species richness (see Willerslev *et al.*, 2002).

One of the main reasons for the prevalence of the Arrhenius' function in the application of the ISAR is that its parameters have been interpreted with ecological or biogeographic significance (e.g. MacArthur & Wilson, 1967; Rosenzweig, 1995; Lomolino, 2000; Triantis *et al.*, 2008a; but see Connor & McCoy, 1979). Although the values of the z parameter observed in the present study fall within the range reported by Williamson (1988), a large variability was observed. The pattern of the z values showed that the increase in island area is less important for the increase in species richness of archipelagic endemics and SIEs than for all species in spermatophytes while an opposite pattern exists for pteridophytes, but the reduced predictive power for the latter groups of species suggest some caution. In the present set of archipelagos, pteridophytes appeared to be less adapted to colonize or persist in smaller islands than

spermatophytes, needing larger islands with more specialized habitats. The sequential decrease in the z value in pteridophytes from all native species, to archipelagic endemics and SIEs, suggest that the area factor is more important for the widely distributed pteridophyte taxa, and thus reflects more a colonization issue than a speciation one (Triantis *et al.*, 2008a). On the other hand, the increase of the z value in spermatophytes when we move from native to archipelagic endemics and to SIEs suggest that speciation assumes an increasing importance for species addition as a function of island area for spermatophytes (Rosenzweig, 1995; Triantis *et al.*, 2008a). This evidence is consistent with the results of Birand & Howard (2008) and Vilenkin *et al.* (2008), who reported an exponential increase in endemic species richness as a function of the non-endemic species richness (and thus a higher z rate for endemics than for all native species; see also Triantis *et al.*, 2008a), as expected under a random process of endemic speciation. A higher speciation rate can be expected in spermatophytes than in pteridophytes, given their major limitations in pollination and diaspore dispersal, which reduce gene flux among islands.

Species diversity may be mediated by other factors which cannot be effectively measured by area, such as geological or habitat diversity (Triantis *et al.*, 2003; Whittaker & Fernández-Palacios, 2007; Kreft *et al.*, 2008; Whittaker *et al.*, 2008). In addition, extremely rigorous tests are not possible, due to the amount of noise in species richness data obtained from different sources and under different taxonomic treatments. Moreover, the real area of an island can differ from the standard planar projection and this may affect the model fit (Fattorini, 2007), although available tests considering topographically diverse oceanic islands, have shown no significant differences (Triantis *et al.*, 2008b). Our results show that even under such limitations, using ISARs can describe about 60% of the variance in the species richness of all native pteridophytes and spermatophytes in islands of different oceanic archipelagos across the globe, confirming area as the most basic, intuitive model for the explanation of island biological diversity.

Predictive modelling

The predictive power of the regressive models shows a high variability, but it was overall higher than the simple ISAR models. Models for the richness of all native species (both pteridophytes and spermatophytes) resulted in a predictive capacity close to or even higher than 80%, a high value in comparison with the typical outputs of such models at the regional and continental extents (e.g. Pausas, 1994; Ohmann & Spies, 1998; Pausas *et al.*, 2003; Bacaro *et al.*, 2008). The models developed here did not account for spatial autocorrelation in the species richness data. The effect of spatial autocorrelation on the interpretation of ordinary statistical methodology has been assessed several times (Lennon, 2000; Dale & Fortin, 2002) and its role

in influencing both coefficients and inference in statistical analyses has been shown (Dormann, 2007). From an ecological and biogeographical point of view, spatial autocorrelation contains information one might not want to 'correct for' in the analysis and many studies have not found any evidence for spatial autocorrelation in model residuals when models with the adequate set of covariates have been developed (see Dormann, 2007 for a review). Moreover, Diniz-Filho *et al.* (2003) showed the loss of importance of spatial autocorrelation when large-scale datasets are used, since spatial variation occurs at a much larger scale than the ecological processes of dispersal and biotic interactions.

Island area was retained as a significant predictor in all the six models, but it was the best predictor only for the three models explaining the species richness of the different groups of spermatophytes, confirming the higher predictive capacity of ISARs for the species richness of spermatophytes than for those of pteridophytes. So, even if the ISARs provided good predictive capacity of pteridophyte and spermatophyte species richness, the effect of island area has a primary role in controlling the species richness of spermatophytes and only a secondary role on that of pteridophytes. This confirms the findings of Kreft *et al.* (2010) that area has a limited effect on pteridophyte species richness. Kreft *et al.* (2010) also reported that area did not have a significant effect on the proportion of pteridophytes in the flora. Our data (results not shown) showed that the proportion of pteridophytes in the overall flora of the islands significantly increased with island area, confirming the major negative effects of small island area for this group of plants.

Elevation was retained as a significant predictor in five out of six models (all but archipelagic endemic pteridophytes) and it was selected as the most important variable for the species richness of all native pteridophytes. This simple topographic variable is considered a good proxy for habitat diversity in island ecosystems, since it contributes to the variation in ecological factors such as air pressure, temperature, solar radiation, rainfall, wind velocity and seasonality (Körner, 2007). However, the correlation between habitat diversity and elevation may vary, depending on the elevation gradient and the approach taken for defining habitat types, calling for caution in the use of elevation as a surrogate of habitat diversity (Triantis *et al.*, 2008b). Our results offer significant support for the primary role of elevation as one of the major determinants of species richness of native and endemic taxa. This is in agreement with the findings of the positive link between pteridophyte species richness and topographic heterogeneity (Kreft *et al.*, 2010).

Both island and archipelago ages significantly contributed to the predictions made by the models, though with different scaling (logarithmic or unimodal) and different importance for pteridophytes vs. spermatophytes and for all the species richness metrics. The alternative selection of the variable 'elevation' (see above) instead of 'island

age' (Whittaker *et al.*, 2008) could be the cause for the non-inclusion of the latter in some of the models. The geological age of islands and archipelagos has been considered as one of the major determinants of species richness, since it controls colonization and speciation processes (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008), even if some studies failed to include the island geological age into models explaining plant species richness at the within-archipelago scale, probably because of the problems related to age estimation (Willerslev *et al.*, 2002; see discussion in Whittaker *et al.*, 2008). The results of the present investigation, based on a much larger dataset than the one used by Willerslev *et al.* (2002), confirm geological age of islands and archipelagos as one of the significant predictor variables for modelling plant species richness on islands. The failure to find a significant effect of age variables may be due to the bias involved in obtaining age estimates (e.g. in islands with limited geochronological information) or to the limited variability of age ranges in the dataset (e.g. within archipelagos made up of islands of similar age). The present modelling approach allows us to deconstruct the age factor into two different parts, i.e. island age and archipelago age, and these were retained in the models for the different groups of species with varying importance.

The variables related to isolation (i.e. continental isolation, distance to the nearest older island and distance to the nearest larger island) were selected for some of the models and were included in the model for the species richness of pteridophyte archipelagic endemics and SIEs and for spermatophytes all natives and SIEs. In pteridophytes, continental isolation had a positive effect on the number of SIEs and a mixed (positive for lower distances and negative for higher distances) effect for archipelagic endemics, while the distance to nearest island was negatively related to the number of SIEs. This general picture is in agreement with the low speciation rates associated to pteridophytes in island ecosystems (Tryon, 1970; Kreft *et al.*, 2010). In spermatophytes, the negative effect of continental isolation on the species richness of native species confirmed the expectations due to the reduced genetic flux with continental biotas, and the positive effect on both archipelagic endemics and SIEs confirmed the expectations from the evolutionary dynamics associated with isolation.

Conclusions

The origin of species diversity on oceanic islands is a long-standing question in ecology and biogeography. The present paper confirms the major role of area as an effective predictor of species richness for all native species of pteridophytes and spermatophytes, but its predictive capacity decreased for archipelagic endemics and single-island endemics for both pteridophytes and spermatophytes, compared with the overall native species richness. This is likely to be due to the increasing effects of the 'idiosyncrasies' of each island

on its evolutionary dynamics. On the other hand, the predictive capacity of multiple regression modelling increased with respect to ISARs, by including two to five predictor variables, with different importance. Island area remained the most important variable for spermatophytes but only had a secondary importance for pteridophytes. For pteridophytes, elevation was the most important predictor of the species richness of all native species, while continental isolation variables were the most important predictor variables for the species richness of archipelagic endemic and single island endemic species.

Comparative studies, such as the present one, considering islands from various oceanic archipelagos and additional taxa with different life histories, dispersal abilities and ecological requirements, could offer a new perspective on the way diversity is established and preserved on the most vulnerable systems of the Earth, oceanic islands (e.g. Triantis *et al.*, 2010b).

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