RESEARCH PAPER

Differences in species–area relationships among the major lineages of land plants: a macroecological perspective

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ABSTRACT

Aim Although the increase in species richness with increasing area is considered one of the few laws in ecology, the role of environmental and taxon-specific features in shaping species–area relationships (SARs) remains controversial. Using 421 land-plant floras covering continents, continental islands and oceanic islands, we investigate whether variations in SAR parameters can be interpreted in terms of differences among lineages in speciation mode and dispersal capacities (*TAXON*), or of geological history and geographical isolation between continents and islands (*GEO*).

Location Global.

Methods Linear mixed-effects models describing variation in SARs, depending on the factors *GEO* and *TAXON* and controlling for differences between realms (*REALM*) and biomes (*BIOME*).

Results The best random-effect structure included both random slopes and random intercepts for *GEO*, *TAXON*, *REALM* and *BIOME*. This accounted for 77% of the total variation in species richness, substantially more than the 27% statistically explained by the model with fixed effects only (i.e. the simple SAR). The slopes of the SARs were higher for oceanic islands than for continental islands and continents, and higher in spermatophytes than in pteridophytes and bryophytes. The intercepts largely exhibited the reverse trend. *TAXON* was included in best-fit models restricted to oceanic and continental islands, but not continents. Analysing each plant lineage separately, the intercept of *GEO* was only included in the random structure of spermatophytes.

Main conclusions SAR parameters varied considerably depending on geological history and taxon-specific traits. Such differences in SARs among land plants challenge the neutral theory that the accumulation of species richness on islands is controlled exclusively by extrinsic factors. Taxon-specific differences in SARs were, however, confounded by interactions with geological history and geographical isolation. This highlights the importance of applying integrative frameworks that take both environmental context and taxonomic idiosyncrasies into account in SAR analyses.

Keywords
Bryophytes, carrying capacity, dispersal ability, geographical isolation, pteridophytes, species richness, species turnover, species–area relationship, spermatophytes.

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INTRODUCTION

The increase in species richness (*SR*) with increasing area, known as the species–area relationship (SAR), has been recurrently reported in taxa as diverse as bacteria, plants and animals (Storch *et al.*, 2012, and references therein). The SAR is regarded as one of the few laws in ecology, with fundamental implications for our understanding of global biodiversity patterns (Rosenzweig, 1995). SARs have, for instance, been used to predict the diversity of poorly-surveyed areas, assess extinction rates due to habitat loss, and enhance the design of protected areas (for a review, see Harte *et al.*, 2008). The ecological interpretation of variation in the parameters of the most widely applied power model of the SAR (Arrhenius, 1921) as well as the factors shaping SARs remain, however, areas of controversy (Harte *et al.*, 2008; Šizling *et al.*, 2011; Triantis *et al.*, 2012).

MacArthur & Wilson's (1967, 16) equilibrium theory of island biogeography predicts that, due to the low colonization rates on isolated islands, the slope of the SAR will increase with geographical isolation. Empirical evidence for differences in the shape of SARs in different geological contexts with different degrees of geographical isolation is, however, contradictory (Drakare *et al.*, 2006; Kreft *et al.*, 2008; Sólymos & Lele, 2012; Triantis *et al.*, 2012). Although MacArthur & Wilson (1967) acknowledged the potential role of taxon-specific traits in shaping SARs, the equilibrium theory of island biogeography is a neutral model that relies on the dynamic equilibrium of species richness through colonization and extinction processes, and does not incorporate differences among species. Remote islands may, however, fail to attain the predicted levels of *SR* based on their area because immigration rates are very low on distant archipelagos (Weigelt & Kreft, 2013), especially in taxa with poor dispersal capacities (Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007). In fact, differences in dispersal limitation may alter the SAR by modifying both colonization–extinction–speciation rates and community composition at local and regional scales (Rosenzweig, 1995; Kisel *et al.*, 2011; Ricklefs & Renner, 2012; but see Aranda *et al.*, 2013).

In addition, area and geographical isolation control both speciation rates and the resulting diversity patterns (Losos & Schluter, 2000; Kisel & Barraclough, 2010; Kisel *et al.*, 2011). On islands, the combined effects of isolation, high levels of environmental heterogeneity and relaxed competition pressure have been identified as key drivers of adaptive radiations in spermatophytes (for review, see Givnish, 2010). Conversely, in more dispersive plants such as bryophytes and to a lesser extent pteridophytes, the substantially lower levels of endemic speciation and, in particular, the almost complete lack of adaptive radiations (Patiño *et al.*, 2014) are expected to result in less species turnover and flatter SARs than in spermatophytes. Consequently, the explanatory power of the SAR may increase considerably when its slope is allowed to vary depending on taxon-specific differences in life-history traits (Franzén *et al.*, 2012). Storch *et al.* (2012) further showed that SARs for various vertebrate classes collapse into a single curve after the axes are rescaled (but see Lazarina *et al.*, 2013), adjusting the area axis to the mean range size of the species and the species axis to the species richness of an area equal to the mean range size. Because dispersal ability has traditionally been perceived as a major driving force in the establishment and maintenance of large range sizes (Lowry & Lester, 2006; but see Iversen *et al.*, 2013), this further implicitly points to the importance of life-history traits in the shape of the SARs (Kisel *et al.*, 2011). The few empirical studies that have explicitly addressed whether SARs vary among organisms that differ in their dispersal capacity (Drakare *et al.*, 2006; Franzén *et al.*, 2012; Aranda *et al.*, 2013) or taxonomic affiliation (Rosenzweig, 1995; Guilhaumon *et al.*, 2008; Triantis *et al.*, 2012) and in whether these differences interact with differences in geological history and geographical isolation (Drakare *et al.*, 2006; Sólymos & Lele, 2012) have reached contradictory conclusions.

Land plants comprise five major lineages: spermatophytes (seed plants; *c.* 300,000 species), pteridophytes (ferns and lycophytes; 9600 spp.), mosses (10,000 spp.), liverworts (5000 spp.) and hornworts (250 spp.). They produce a range of diaspores, the size, number, morphology (Mehltreter *et al.*, 2010; Hintze *et al.*, 2013), stress tolerance (van Zanten & Gradstein, 1988; Löbel & Rydin, 2010) and dispersal mode (Gillespie *et al.*, 2012) of which determine their capacity for long-distance dispersal (LDD). In spermatophytes, seed size ranges from 0.05 mm to a few decimetres, considerably exceeding the average size of spores produced by pteridophytes (0.02–0.13 mm) and bryophytes (0.005–0.1 mm). As a consequence, bryophytes and, to a lesser extent, pteridophytes, exhibit much higher LDD capacities than spermatophytes, explaining the much higher proportion of species shared among continents in the bryophytes and pteridophytes than in spermatophytes (Medina *et al.*, 2011).

Asexual diaspores are produced in great abundance by spore-producing plants, and play a central role in the dispersal and establishment of bryophytes (Medina *et al.*, 2011), although they are relatively unimportant in pteridophytes (Mehltreter *et al.*, 2010). Pteridophyte spores are, on average, larger than those of bryophytes and, for species with only green spores, their viability and tolerance to travel in wind currents are lower than for species with non-green spores (Muñoz *et al.*, 2004; Mehltreter *et al.*, 2010). Within bryophytes, the mechanisms that promote spore release differ substantially among lineages. In liverworts and hornworts, spore dispersal is enhanced by hygroscopic movements of elaters. In mosses, the peristome ensures the gradual release of spores, increasing the likelihood of spores being widely distributed under different climatic conditions.

Based on a global survey of 421 land-plant floras across continents, oceanic islands and continental islands, we determine whether variations in SAR parameters can be interpreted as differences among lineages in terms of speciation mode and LDD capacities, and differences in geological history and geographical isolation between continents and islands. Specifically, we hypothesize: (*H*$_1$) that SARs on islands are characterized by a lower intercept and a higher slope than on continents due to the higher geographical isolation and higher rates of *in situ*

evolution and species turnover in insular environments; (H_2) that SARs in spermatophytes are characterized by higher intercepts and slopes than in pteridophytes and bryophytes due to higher species richness and lower LDD capabilities in the former; (H_3) that differences in SARs among taxonomic lineages are lower on continents than on oceanic islands, where adaptive radiations are much more common in spermatophytes than in spore-producing plants, and where differences in LDD capacities result in substantially different slopes among plant lineages; and (H_4) that geological history and geographical isolation influence SARs in spermatophytes, but less so or not at all in pteridophytes and bryophytes.

MATERIALS AND METHODS

Data compilation

The species richness (*SR*) of hornworts, liverworts, mosses, pteridophytes and spermatophytes at different spatial scales ranging from small islands to large political units was obtained from a comprehensive literature survey (Appendix S1 in Supporting Information). Species richness ranged from 0 to 51,220 species of spermatophytes, from 0 to 1500 pteridophytes, from 1 to 990 mosses, and from 0 to 842 liverworts. The inclusion of zero-values may affect the shape of the SAR (Dengler & Oldeland, 2010); the analyses described below were therefore conducted twice, once with and once without the zero-values. Because both approaches returned very similar results, only the analyses excluding the zero-values are presented. To improve the linearity of the relationship between *SR* and *AREA* and the homoscedasticity of the error terms, both variables were log-transformed (power or Arrhenius model of the SAR).

Variation in *SR* was analysed depending on five factors. *AREA* for islands and continental areas was derived from the *Island Directory* of the United Nations Environment Programme (UNEP, 1998) and from encyclopedias when not provided in the references listed in Appendix 1. *AREA* ranged from 0.131 to 8,511,965 km^2 for continents, from 0.071 to 2,166,086 km^2 for continental islands, and from 1.3 to 103,000 km^2 for oceanic islands.

TAXON included the four major lineages of land plants, i.e. spermatophytes, pteridophytes, mosses and liverworts. For phylogenetic consistency, hornworts should have been analysed separately. They are, however, a small group of only about 250 species worldwide whose diversity pales in comparison to the much more diverse liverworts and mosses. The number of hornwort species in our data set did not warrant separate analyses and, because hornworts exhibit a suite of functional vegetative traits and ecological features that are similar to those of thalloid liverworts, the data from the two groups were merged (hereafter referred to as liverworts).

GEO included continents, continental islands (comprising continental-shelf islands and ancient continental fragments) and oceanic islands. The geological origins of islands were extracted from the same sources as for *AREA* (see above). The few cases of island groups with a mixed continental and oceanic origin (e.g. Japan and New Zealand) were included in the continental category. In total, there were 421 operational geographical units (OGUs), including 195 continental OGUs, 100 continental islands, and 126 oceanic islands.

Two additional factors – biome (*BIOME*) and realm (*REALM*) – were also employed to control for differences in SARs caused by variation in macroclimatic conditions and biogeographical history (Drakare *et al.*, 2006; Guilhaumon *et al.*, 2008; Gerstner *et al.*, 2014). Each of the 421 areas was assigned to one of 13 biomes (tundra; boreal forest–taiga; montane grasslands and shrublands; temperate coniferous forests; temperate broad-leaved and mixed forests; tropical and subtropical moist broad-leaved forests; tropical and subtropical dry broad-leaved forests; tropical and subtropical coniferous forests; Mediterranean forests, woodlands and scrub; tropical and subtropical grasslands, savannas and shrublands; temperate grasslands, savannas and shrublands; deserts–xeric shrublands; flooded grasslands and savannas; Olson *et al.*, 2001) and one of seven biogeographical realms (Afrotropics, Indo-Malaya, Nearctic, Neotropics, Palaearctic, Oceania and Australasia; Olson *et al.*, 2001). We excluded the mangrove biome because of its limited extent, azonal character, global scarcity of available data and the almost complete absence of bryophytes and pteridophytes in sea-water environments.

Statistical analyses

Species–area relationships are most commonly described by a power law, $S = cA^z$ (Triantis *et al.*, 2012). When plotted on a log–log scale [$\log(S) = \log(c) + z \log(A)$], the intercept [$\log(c)$] and slope ($z$) have been interpreted as measures of the realized environmental carrying capacity of the system per unit area and the rate of accumulation of species and changes in composition with the increase of area on the logarithmic scale, respectively (Triantis *et al.*, 2012). The application of the power law has, however, been questioned due to the variation of the slope with spatial extent, an issue solved in a maximum-entropy framework (Harte *et al.*, 2008; see also Šizling *et al.*, 2011). Nevertheless, the model of Harte *et al.* (2008) requires data on local abundance that are extremely complicated to derive in clonal organisms like bryophytes and are, in fact, almost never documented for such organisms. The recent finding that variation in spatial scale did not significantly affect the slope of the SAR in a comprehensive meta-analysis across 1918 islands (Sólymos & Lele, 2012) reinforces the notion that the power law remains a good representation of the SAR. We thus used the well-established log–log version of the power-law SAR to make comparisons with previous studies (for a review, see Triantis *et al.*, 2012). Due to the nature of our database, the SAR applied here corresponds to the species–area curve type IV (*sensu* Scheiner, 2003), which is typically constructed from data of species richness extracted from islands (island-type habitats) of irregular shapes and sizes (the 'island species–area relationship' *sensu* Whittaker & Fernández-Palacios, 2007).

The coefficients of the power law are typically derived from linear regression analysis using the log–log formulation.

Species-richness data such as those employed in the present study are, however, highly structured. For instance, islands from the same archipelago are more likely to display similar patterns of species richness than islands from different archipelagos. Such a strong structure in the data violates the key assumption of traditional linear regression models that each data point is independent. Circumventing the issue of non-independence by analysing each taxon and archipelago individually would result in a substantial loss of statistical power. Bunnefeld & Phillimore (2012) therefore promoted the use of linear mixed modelling (LMM) in island biogeography, which allows all the data to be included in a single model, making it further possible to test whether or not trends are general across all taxa and archipelagos while controlling for the structure in the data. LMMs describe the degree to which a response variable is predicted by explanatory variables of two types: fixed and random effects. Fixed effects are predictor variables for which we intend to estimate an effect size (slope). Random effects describe the grouping or the hierarchical structure (e.g. data points within islands within archipelagos) to ensure conditional independence among the observations. They also serve to determine whether or not the slope and intercept coefficients vary across different archipelagos (or taxa) and, if they do, to estimate different coefficients for each archipelago and/or taxon (Bunnefeld & Phillimore, 2012). As pointed out by Sólymos & Lele (2012), extending the mixed-modelling framework to other functional forms of the SAR – including the non-linear mixed-effect models (Pinheiro & Bates, 2000) – would be promising, but is beyond the scope of this study.

The LMM approach was employed here to analyse variation in log(SR) depending on log($AREA$) (fixed effect) while controlling for variation in the factors *GEO*, *TAXON*, *BIOME* and *REALM*, which were included in the random structure (Eqn 1). Following the mathematical expression of Bunnefeld & Phillimore (2012), m and k are the deviations for intercept and slope, respectively, given taxon t, geological context g, realm r and biome b; e_{tgrb} is the deviation of the observation i from the mean prediction for t, g, r and b (the residual or error term).

$$\log(SR_{tgrbi}) = (\log(c) + m_t + m_g + m_r + m_b) + (z + k_t + k_g + k_r + k_b)\log(AREA_{tgrbi}) + e_{tgrb} \quad (1)$$

The model terms m, k and e in Eqn 1 are assumed to follow normal distributions with zero mean and unknown variances to be estimated. The slope and intercept for a given combination of factors can be calculated as the sum of the corresponding fixed-effect [log(c) and z] and random-effect (m and k) terms. We refer to these combined terms as intercept and slope when presenting the effects of the predictors.

We first explored the effects of *GEO*, *TAXON*, *BIOME* and *REALM* together (Analysis I) to test hypotheses H_1 and H_2. We contrasted the performance of competing models including all the possible combinations of varying intercepts and slopes for the random factors considered (*TAXON*, *GEO*, *REALM* and *BIOME*), using the difference (ΔAIC_c) between the Akaike information criterion corrected for small sample size (AIC_c) and the

lowest AIC_c of all models. All models with a ΔAIC_c value below 2.0 were considered to have equivalent support (Burnham & Anderson, 2002). LMMs were computed with the *lmer* function in the LME4 library (Bates *et al.*, 2013) in R 2.12 (R Development Core Team, 2011).

Second, to facilitate the comparisons among plant lineages within each geological context (i.e. continent, continental island or oceanic island) to test H_3, and among geological contexts within each plant lineage (i.e. spermatophytes, pteridophytes, mosses, liverworts) to test H_4, we ran two additional sets of analyses. In Analysis II, we determined the intercept and slope of the SAR within each geological context, keeping *TAXON*, *BIOME* and *REALM* in the random structure. In Analysis III, we determined the SAR parameters within each plant lineage, keeping *GEO*, *BIOME* and *REALM* in the random structure. In analyses II and III, the best combination of factors included in the random structure was determined by the ΔAIC_c among competing models (see above).

We used the data-cloning (DC) algorithm (Lele *et al.*, 2010) to obtain maximum-likelihood estimates and asymptotic Wald-type confidence intervals for the model hyperparameters and random effects similarly to Sólymos & Lele (2012). We checked the convergence of the posterior distribution using the DCLONE R package (Sólymos, 2010), built on JAGS 1.0.3 (Plummer, 2009). We used the maximum-likelihood estimates and the inverse of the Fisher information matrix from the LMM obtained in Analysis I. Random effects and residual standard deviation (SD) parameters were log-transformed to enable multivariate normal parametrization, but untransformed SD values are presented below.

We used an R^2 measure (Eqn 2) that compares the deviance of the LMM with the deviance of a linear intercept-only model (Kvålseth, 1985). Residual sums of squares were calculated based on squared differences between log(SR) and fitted values. We used the log–log model of the SAR (i.e. linear model) as a benchmark for evaluating the fit of the selected LMMs.

$$R^2 = 1 - \sum(y - \hat{y})^2 \big/ (y - \overline{y})^2 \quad (2)$$

RESULTS

In Analysis I, the set of best-fitting models ($\Delta AIC_c < 2$) included a single model with intercepts and slopes for each of the factors *TAXON*, *GEO*, *REALM* and *BIOME* in the random structure ($AIC_c = 1116.4$; $\Delta AIC_c = 0$; see Fig. 1). The mean intercept log(c) was 1.211 with 95% confidence limits (CL) of 0.731–1.690, and the mean slope (z) was 0.246 with 95% CL of 0.130–0.362 (Table 1). The linear model of the SAR (with fixed effects only) accounted for 27% (R^2), whereas the LMM accounted for 77% of the total variation in *SR*.

Variation in the SAR among the main lineages of land plants in the different geological contexts is illustrated in Figure 1. The mean z-values of marginal *GEO* distributions increased from continents to continental islands and oceanic islands, whereas the c-values decreased from continents to continental islands
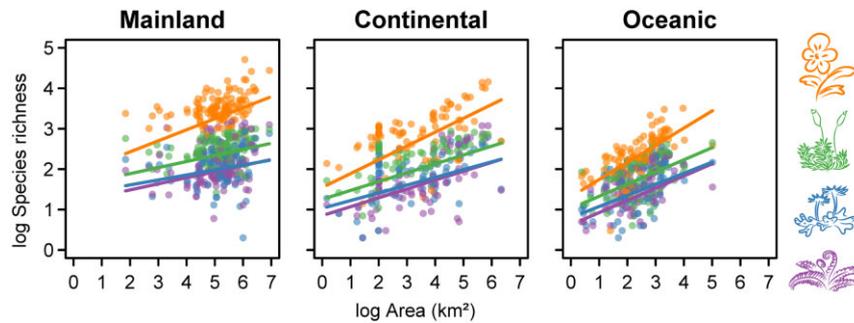
Figure 1 Relationships between species richness [log(*SR*)] and area [log(*AREA*), km²] in spermatophytes (orange), pteridophytes (violet), liverworts (blue) and mosses (green) on continents, continental islands and oceanic islands (Analysis I). The regression lines are derived from linear mixed-effects models accounting for variation among geological contexts (*GEO*), lineages of land plants (*TAXON*), biomes (*BIOME*) and realms (*REALM*).

Table 1 Linear mixed-model analysis of the power-law species–area relationship (Analysis I) model on a log–log scale describing variation in species richness of land plants depending on area (*AREA*) while controlling for variation among factors considered as random effects (SD: standard deviation of normally distributed random effects with zero mean), including geological context (*GEO*), lineage of land plants (*TAXON*), realm (*REALM*) and biome (*BIOME*). The best-supported random effect structure is shown for the linear mixed model based on AIC$_c$ model comparisons. Estimates were obtained based on the data cloning procedure; CL$_{2.5\%}$ and CL$_{97.5\%}$ represent asymptotic confidence limits for 95% nominal coverage.

	Estimate	CL$_{2.5\%}$	CL$_{97.5\%}$
Intercept [log(*c*)]	1.211	0.731	1.690
Slope (*z*)	0.246	0.130	0.362
Random intercept SD			
GEO	0.271	0.004	0.538
TAXON	0.297	0.069	0.525
REALM	0.229	0.064	0.395
BIOME	0.176	0.071	0.280
Random slope SD			
GEO	0.070	0.003	0.137
TAXON	0.065	0.015	0.115
REALM	0.060	0.018	0.102
BIOME	0.036	0.011	0.061
Residual SD	0.362	0.347	0.377

Table 2 Intercept and slope of the power-law species–area relationship (Analysis I) model on the log–log scale depending on the geological context (*GEO*) and land plant group (*TAXON*). 95% confidence limits (CL$_{2.5\%}$ and CL$_{97.5}$) of the SAR model parameters based on the linear mixed model are shown.

		Intercept			Slope		
	n	Estimate	CL$_{2.5\%}$	CL$_{97.5\%}$	Estimate	CL$_{2.5\%}$	CL$_{97.5\%}$
GEO							
Continent	195	1.659	0.887	2.462	0.171	0.027	0.383
Continental island	100	1.325	0.565	2.095	0.242	0.103	0.454
Oceanic island	126	1.108	0.354	1.884	0.317	0.172	0.531
TAXON							
Liverworts	404	1.272	0.531	2.036	0.182	0.013	0.377
Mosses	418	1.502	0.743	2.256	0.207	0.042	0.406
Pteridophytes	354	1.076	0.322	1.839	0.213	0.046	0.413
Spermatophytes	410	1.796	1.037	2.544	0.331	0.168	0.532

and oceanic islands (Table 2). The mean slopes of marginal *TAXON* distributions increased from liverworts to mosses, pteridophytes and spermatophytes, whereas the intercepts increased from pteridophytes to liverworts, mosses and spermatophytes (Table 2).

In analyses performed independently at the scale of continents, continental islands and oceanic islands (Analysis II), a random intercept for *TAXON* was included in all of the best-fitting models. In contrast, a random slope for *TAXON* was only included in the best random-effect structure for continental islands and oceanic islands (ΔAIC$_c$ < 2; Appendix S2). A signifi-

cant SAR (non-zero slope) was observed for all plant lineages on continents, on continental islands and on oceanic islands (results not shown). For each *GEO* category (continents, continental islands and oceanic islands), pteridophytes showed the lowest intercepts, followed by liverworts, mosses and spermatophytes, whereas the slope values gradually decreased from spermatophytes to pteridophytes, mosses and then liverworts (Table 3; see also Fig. 1). Differences in slopes between mosses and pteridophytes were negligible in most cases. In line with Analysis I, the mean intercept values for each lineage progressively decreased (from spermatophytes to mosses, liverworts and then pteridophytes), whereas the mean slope values increased from continents to continental islands to oceanic islands (Table 3; see also Fig. 1).

In analyses performed separately for each of the lineages (Analysis III), a random slope for *GEO* was included in all of the best-fitting models, but a random intercept was only included for spermatophytes (Appendix S3).

DISCUSSION

In line with hypotheses H_1 and H_2, the best model in Analysis I included the factors *GEO*, *TAXON*, *REALM* and *BIOME* in the

Table 3 Intercept and slope of the power-law species–area relationship (Analysis II) model on the log–log scale performed depending on the land plant group (*TAXON*) on continents, continental islands and oceanic islands, respectively. 95% confidence limits (CL) of the SAR model parameters based on the linear mixed model are shown.

			Intercept			Slope		
GEO	*TAXON*	*n*	Estimate	$CL_{2.5\%}$	$CL_{97.5\%}$	Estimate	$CL_{2.5\%}$	$CL_{97.5\%}$
Continent	Liverworts	186	1.535	0.906	2.082	0.118	0.008	0.290
	Mosses	194	1.770	1.143	2.335	0.142	0.028	0.315
	Pteridophytes	142	1.360	0.707	1.906	0.145	0.030	0.322
	Spermatophytes	187	2.066	1.417	2.605	0.265	0.155	0.445
Continental island	Liverworts	92	1.191	0.584	1.678	0.189	0.082	0.357
	Mosses	100	1.410	0.818	1.908	0.216	0.109	0.386
	Pteridophytes	93	0.999	0.395	1.492	0.219	0.110	0.391
	Spermatophytes	98	1.704	1.107	2.197	0.340	0.234	0.512
Oceanic island	Liverworts	126	0.981	0.393	1.479	0.263	0.144	0.437
	Mosses	124	1.213	0.615	1.714	0.288	0.169	0.462
	Pteridophytes	119	0.777	0.165	1.272	0.300	0.181	0.476
	Spermatophytes	125	1.482	0.898	1.983	0.418	0.301	0.590

random structure. That this model accounted for so much more of the variation in species richness (77%) than the simple SAR (fixed effects only, 27%) suggests that differences between the main lineages of land plants and among areas with contrasting geological origins, climatic histories and levels of geographical isolation have substantial impacts on the shape (intercept and slope) of the SAR. This result reinforces the idea that variation in SARs is attributable to a suite of factors that operate in combination, including taxon-specific life-history traits, speciation mode, climate and historical biogeography (Drakare *et al.*, 2006; Guilhaumon *et al.*, 2008; Losos & Parent, 2010; Hortal, 2011; Franzén *et al.*, 2012; Triantis *et al.*, 2012; Gerstner *et al.*, 2014).

The slope of the SAR increased progressively from continents through continental islands to oceanic islands, whereas the intercept exhibited the reverse trend for all the taxa considered. These findings support previous studies pointing to lower values of log(*c*) on islands than on continents due to their geographical isolation (Kreft *et al.*, 2008; Sólymos & Lele, 2012; Triantis *et al.*, 2012). This is also consistent with the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) and, in particular, with the expectation that species richness decreases with geographical isolation due to lower colonization rates (Weigelt & Kreft, 2013). The increase in slope from continents to islands is much more controversial (Drakare *et al.*, 2006; Kreft *et al.*, 2008; Triantis *et al.*, 2012), but is consistent with the lower rates of local extinction on continents (for review see Rosenzweig, 1995) and the comparatively high rates of adaptive radiations and species turnover displayed by island biotas (Losos & Schluter, 2000; Whittaker & Fernández-Palacios, 2007; Losos & Parent, 2010). The observation that the SAR parameters on continental islands are intermediate between those observed on continents and oceanic islands (Table 2, Fig. 1) suggests that continental-island floras might have different origins, reflecting ancient continental connections or subsequent dispersal events.

Phylogenetic evidence does indeed point to a complex mixture of fragmentation of a formerly common species pool prior to the isolation of the island (vicariance) and LDD events in continental island biotas (e.g. Goldberg *et al.*, 2008).

The inclusion of the factor *TAXON* in the best-fitting model across all geological contexts demonstrated, in agreement with hypothesis H_2, the existence of taxon-specific patterns in the SAR parameters. This contrasts with the only previous comparison of SARs among all major lineages of land plants on oceanic islands, which we interpret as a result of the biogeographical region analysed in that study and its lack of statistical power ($n = 19$, for a set of non-independent islands from three archipelagos; Aranda *et al.*, 2013). Our findings are in line with other studies stressing the importance of non-neutral mechanisms in SAR variation (Kisel *et al.*, 2011; Sólymos & Lele, 2012; Triantis *et al.*, 2012). Altogether, these observations are not consistent with dispersal-neutral theoretical models, which attempt to explain species richness in terms of common extrinsic immigration–speciation–extinction mechanisms.

In line with H_2, bryophytes (mosses and liverworts) and pteridophytes exhibited lower intercepts than spermatophytes, whereas the slope increased from bryophytes to pteridophytes and spermatophytes. The higher intercept observed in spermatophytes is consistent with their much higher global diversity and regional species richness per unit area than the other groups. The shape of the SAR in bryophytes, and in particular, their low *z*-values in liverworts, parallels that reported in microbes, which typically have flatter SARs than macrobes (reviewed by Hortal, 2011). Bryophytes and, to a lesser extent, pteridophytes display a high wind-LDD capacity (Medina *et al.*, 2011; Schaefer, 2011). This condition results in larger range sizes, lower compositional turnover, more homogenous community composition (Drakare *et al.*, 2006; Lowry & Lester, 2006) and hence flatter SARs than in spermatophytes.

Within spore-producing plants, the slope of the SAR for liverworts was lower than that observed in mosses and pteridophytes. The spores of most liverworts directly germinate into gametophytes without first passing through the extremely sensitive protonemal phase characteristic of both mosses and pteridophytes. In addition, liverworts produce more specialized asexual diaspores than mosses or pteridophytes (Mehltreter *et al.*, 2010; Patiño *et al.*, 2013a). In the British flora, for example, 46% of liverwort species but only 18% of moss species produce specialized asexual diaspores (Algar-Hedderson *et al.*, 2013). Compared with spores, asexual diaspores allow for higher rates of successful establishment due to their lower sensitivity to habitat quality and, importantly, earlier and higher germination rates (Löbel & Rydin, 2010). Altogether, these features may promote higher rates of establishment following dispersal in liverworts than in mosses and pteridophytes. Such a hypothesis, which calls for comparative analyses of spore germination and development across spore-producing plants exposed to a range of environmental conditions, would explain why liverworts exhibited the lowest SAR slopes among land plants.

In agreement with H_3 (Analysis II), a random slope for the factor *TAXON* was included in the best-fitting model in analyses performed at the level of islands (both continental and oceanic), but not of continents. The exacerbation of lineage-specific differences of community turnover on islands, especially on oceanic islands (Fig. 1, Table 3), can be interpreted in terms of the substantially higher LDD capacities of bryophytes and – to a lesser extent – pteridophytes than of spermatophytes. Low levels of diversification in oceanic-island bryophytes and pteridophytes may further contribute to their lower z-values than spermatophytes. In fact, a comparative analysis of the land-plant floras on oceanic archipelagos revealed that anagenetic speciation (i.e. the gradual evolution of a new species after a founder event) contributed up to 49% of bryophyte and 40% of endemic pteridophyte species, but only 17% of seed-plant species (Patiño *et al.*, 2014).

When the four plant groups were analysed separately (H_4, Analysis III), the factor *GEO* was only included in the random structure for the intercept of spermatophytes. This finding suggests that, in pteridophytes and bryophytes, the realized island carrying capacity does not decrease with geographical isolation because of declining colonization rates. This is consistent with previous studies (De Groot *et al.*, 2012; Patiño *et al.*, 2013b), in which the contribution of geographical remoteness to explaining spatial patterns of species richness was substantially lower than that of factors accounting for environmental heterogeneity. These observations, along with the widespread distributions of bryophyte and pteridophyte species among islands within archipelagos (Mehltreter *et al.*, 2010; Vanderpoorten *et al.*, 2011), their extremely reduced levels of endemism (Patiño *et al.*, 2014) and substantial allele sharing between islands and continents (Shepherd *et al.*, 2009; Hutsemékers *et al.*, 2011), reinforce the idea that oceanic barriers are not a major impediment for gene flow in these two groups of plants (Mehltreter *et al.*, 2010; Patiño *et al.*, 2013b). This is also consistent with the idea that, once airborne, spores randomly travel across a wide range of distances (Sundberg, 2013).

Our results demonstrate that SARs in land plants are shaped by extrinsic and intrinsic factors, challenging purely neutral models such as the mathematical expression of MacArthur & Wilson's (1967) theory. This highlights the importance of applying integrative frameworks that take both geological histories and taxonomic idiosyncrasies into account in SAR studies, which has critical consequences for the use of the SAR in conservation biology (Guilhaumon *et al.*, 2008; Sólymos & Lele, 2012). Recent theories suggest, however, that taxon-specific curves collapse if z-values are plotted against local values of the total abundance: species richness ratio, pointing to the existence of a universal SAR (Harte *et al.*, 2013; Šizling *et al.*, 2013). Testing this hypothesis would require extensive data on local abundance, which is currently missing for pteridophytes and bryophytes. Altogether, our results suggest a need for experimental studies in plants, especially in spore-producing plants, to document basic patterns of reproductive biology and ecology.

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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 References used to compile the species lists for each lineage of land plants.

Appendix S2 Factors included in the random structure of the linear mixed model controlling for variation in the species–area relationships of land plants due to differences among lineages of land plants (*TAXON*), realms (*REALM*) and biomes (*BIOME*) at the scale of continents, continental islands and oceanic islands.

Appendix S3 Factors included in the random structure of the linear mixed model controlling for variation in the species–area relationships of land plants due to differences among geological contexts (*GEO*), realms (*REALM*) and biomes (*BIOME*) within each lineage of land plants.

BIOSKETCH

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