



Accounting for data heterogeneity in patterns of biodiversity: an application of linear mixed effect models to the oceanic island biogeography of spore-producing plants

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The general dynamic model of oceanic island biogeography describes the evolution of species diversity properties, including species richness (SR), through time. We investigate the hypothesis that SR in organisms with high dispersal capacities is better predicted by island area and elevation (as a surrogate of habitat diversity) than by time elapsed since island emergence and geographic isolation. Linear mixed effect models (LMMs) subjected to information theoretic model selection were employed to describe moss and liverwort SR patterns from 67 oceanic islands across 12 archipelagos. Random effects, which are used to modulate model parameters to take differences among archipelagos into account, included only a random intercept in the best-fit model for liverworts and in one of the two best-fit models for mosses. In this case, the other coefficients are constant across archipelagos, and we interpret the intercept as a measure of the intrinsic carrying capacity of islands within each archipelago, independently of their size, age, elevation and geographic isolation. The contribution of area and elevation to the models was substantially higher than that of time, with the least contribution made by measures of geographic isolation. This reinforces the idea that oceanic barriers are not a major impediment for migration in bryophytes and, together with the almost complete absence of in situ insular diversification, explains the comparatively limited importance of time in the models. We hence suggest that time per se has little independent role in explaining bryophyte SR and principally features as a variable accounting for the changing area and topographic complexity during the life-cycle of oceanic islands. Simple area models reflecting habitat availability and diversity might hence prevail over more complex temporal models reflecting in-situ speciation and dispersal (time, geographic connectivity) in explaining patterns of biodiversity for exceptionally mobile organisms.

MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography (hereafter ETIB) has long been a keystone in ecology and evolutionary biology. The mathematical expression of the ETIB proposes that island diversity depends upon rates of immigration and extinction, determined by isolation from source populations and island area, respectively. Oceanic islands are, however, dynamic systems, many of which follow a general ontogeny, building to a high cone-shaped form of maximal area and elevation, followed by a period of increasing erosion and maximal topographic complexity, decrease in elevation and size, and eventually complete subsidence into the sea (Stuessy 2007, Fernández-Palacios et al. 2011). This specific ontogeny and

the resulting changes in island carrying capacity are not explicitly taken into account in the ETIB (reviewed by Whittaker and Fernández-Palacios 2007, Lomolino et al. 2010). In a recent development, Whittaker et al. (2008) introduced the general dynamic model of oceanic island biogeography (hereafter, GDM), according to which the carrying capacity of oceanic islands and, hence, their biological diversity, displays a predictable humped trend over time. These expectations were mathematically expressed through the ATT² model:

$$D = b_1 + b_2 \text{AREA} + b_3 \text{TIME} + b_4 \text{TIME}^2 \quad (1)$$

where D is a diversity metric, AREA is the island area, and TIME is time elapsed since island emergence), allowing evaluation of the prediction that island diversity exhibits a positive 'area–time trend' across young islands, a 'hump-shaped trend' across archipelagos with a full range of ontogenic stages, or negative 'area–time trends' in old island groups (Whittaker et al. 2010, Cameron et al. 2012).

The relative importance of time, area, environmental complexity and isolation as drivers for immigration, diversification and extinction is understood to vary, however, among taxonomic or ecological groups (Whittaker et al. 2008, Borges and Hortal 2009). Many organisms such as angiosperms are expected to reach maximum diversity levels when islands reach their highest topographic complexity, which promotes adaptive radiations and within-island allopatric speciation (Whittaker and Fernández-Palacios 2007). By contrast, spore-dispersed plants like bryophytes are a clear example where the contribution of in-situ diversification to patterns of insular diversity is negligible, as evidenced by their extremely low endemism rates (Vanderpoorten et al. 2010). Bryophytes indeed typically do not radiate (Vanderpoorten et al. 2011, but see Wall 2005) and their high dispersal capacities have been suggested to decrease the chances of allopatric speciation (Vanderpoorten et al. 2011). Hence, diversity patterns in such vagile organisms are expected to be controlled by ecological factors rather than by dispersal ability (Borges and Hortal 2009, Aranda et al. 2012, but see Fattorini 2009). Sundberg et al. (2006) indeed concluded that area and habitat type drive diversity patterns of peatmoss species on Baltic Sea islands rather than geographical isolation. The extent to which the low diversification rates and high dispersal capacities of bryophytes affects the validity of biogeographic predictions of models, such as the ETIB, has, however, seldom been tested (Tangney et al. 1990, Sundberg et al. 2006), and the applicability of the GDM in describing diversity patterns in the group has yet to be evaluated.

Because species diversity patterns often vary among archipelagos due to differences in ecological, environmental or historical factors (Whittaker and Fernández-Palacios 2007, Kreft et al. 2010), data sets used in island biogeography are often analysed by archipelago and taxa using regression-based methods. This strategy, however, leads to several methodological issues related to a low sample size, which may: 1) decrease statistical power and hamper the detection of global trends and patterns (type II error or 'false negative'); 2) increase the imprecision of parameter estimation; and 3) cause model overfitting due to the high number of predictors in comparison to the limited number of data points in each analysis (Burnham and Anderson 2002, Zuur et al. 2009, Bunnefeld and Phillimore 2012).

To overcome these statistical shortcomings, we used a mixed effect modelling approach recently promoted by Bunnefeld and Phillimore (2012; see also Cameron et al. 2012), for its suitability to analyse general diversity patterns across archipelagos and taxa. This approach takes advantage of linear mixed effect models (hereafter LMMs) (Zuur et al. 2009) for the analysis of clustered dependent data. LMMs are statistical models that incorporate both fixed (i.e. explanatory factors) and random effects. Random effects are used to control for pseudoreplication in the data while

taking heterogeneity in the relationships between diversity and explanatory factors among archipelagos or taxonomic groups into account. Instead of estimating coefficients separately for each archipelago and taxonomic group, random effects are used to assess the variation of the parameters induced by the particularities of the different archipelagos and/or taxonomic groups under study (Bolker et al. 2009, Bunnefeld and Phillimore 2012).

Under this statistical framework, the goals of the present study were to investigate whether patterns of bryophyte species richness (SR) across a wide range of archipelagos worldwide can effectively be modelled in a single quantitative analysis under a LMM framework and to discuss particular biological implications of the model parameters. We further evaluate whether SR in organisms with high dispersal capacities might be better predicted by island area and elevation (as a surrogate of habitat diversity) than by time elapsed since island emergence and geographic isolation. In the absence of major limitations for dispersal, larger islands might act as larger targets ('passive traps', Borges and Hortal 2009) that support larger island populations and decrease vulnerability to extinction. In addition, larger islands tend to support greater habitat diversity as a result of greater elevation (ELEV) and topographic complexity. Increased AREA and ELEV are therefore expected to drive high bryophyte SR, whereas TIME per se might be expected to be a variable describing the changing topography of oceanic islands during their life cycle, but one with little independent influence on bryophyte SR patterns.

Methods

Data collection

We selected 67 islands from 12 oceanic archipelagos (Supplementary material Appendix 1) on the basis of the availability of 1) a reasonably robust estimate for maximum geological island age (Table 1 and Supplementary material Appendix 1); and 2) recent, critical and/or updated checklists of bryophytes (Supplementary material Appendix 2). We partitioned the data into mosses and liverworts, as they represent distinct lineages of land plants with different ecological requirements (Vanderpoorten and Goffinet 2009). Hornworts should, for consistency, have been analysed separately. They are, however, a small group of about 150 species whose diversity pales in comparison to liverworts (ca 6000 species) and mosses (ca 10 000 species). The number of hornwort species in our data set did not warrant separate analyses (1–7% of the total liverwort number depending on the archipelago), and since hornworts exhibit a suite of functional vegetative traits and ecological features that are similar to those of liverworts, the data from the two groups were merged (hereafter, liverworts).

For each island, native species richness (SR) was used as the diversity metric (D) in Eq. 1. Bryophytes are almost never deliberately introduced (Vanderpoorten and Goffinet 2009) and so the proportion of alien species in bryophyte floras is very small and does not impede biogeographic analyses. The proportion of native species that are endemic to an island has often been used as an indicator of 'in situ'

Table 1. Geographical features (mean values and range) of the twelve studied archipelagos. For sources, see text and Supplementary material Appendix 1.

	§No. of islands	¶Total area (km ²)	Area (km ²)	#Island age (Ma)	Maximum elevation (m)	Continental isolation (km)	Distance to closest largest island (km)
Azores	9	2341	260 (17–757)	2.5 (0.25–8.1)	1021 (402–2351)	1603.5 (1369–1864)	71.4 (6–219)
Canary Islands	10	7535	753 (1.3–2058)	8.0 (0.035–21)	1337 (256–3718)	232.8 (97–416)	42.3 (9–166)
Cape Verde	8	3716	464 (64–991)	10.2 (3–25.6)	1256 (390–2829)	710.5 (571–836)	67.4 (13–231)
Galapagos	9	7616	846 (5–4588)	1.7 (0.07–4)	851 (340–1707)	1068.9 (927–1167)	22.9 (4–67)
Gulf Guinean	4	2954	738.5 (16–1935)	12.2 (0.1–31)	1658 (654–3008)	208.7 (32–348)	295.1 (207–603)
Hawaii	7	16569	2367 (381–4205)	2.4 (0.6–5.1)	1857 (381–4205)	3760.9 (3675–3920)	45.8 (13–115)
Juan Fernandez	3	100	33 (2–50)	4.2 (2.4–5.8)	890 (374–1380)	508.0 (450–610)	106.7 (160)
Madeira	3	795	265 (15–740)	7.9 (4.6–14)	936 (442–1850)	673.4 (656–690)	21.9 (27–39)
Mascarenes	3	4517	1506 (108–2535)	3.8 (1.5–7.8)	1431 (396–3069)	1979.8 (1658–2436)	324 (176–796)
Society	3	1358	453 (142–1045)	1.9 (1.2–2.7)	1488 (1017–2241)	5657.1 (5569–5713)	72.4 (16–201)
Tristan da Cunha	4	179	45 (4–96)	6.8 (0.2–18)	980 (350–2060)	2713.4 (2561–2781)	116.1 (31–400)
Vanuatu	5	6309	1262 (11–3955)	7.3 (1.1–22)	1028 (643–1879)	1772.4 (1723–1836)	312.9 (222–521)

§Number of islands for each archipelago considered in the present study.

¶Total area as sum of the area of the islands considered in the present study.

#Age of the current emerged islands analysed herein, on the basis of the availability of an appropriate checklist of bryophytes, which does not preclude the existence in the archipelago of older, currently-emerged or submerged islands.

diversification (Emerson and Kolm 2005; but see Witt and Maliakal-Witt 2007, Kisel and Barraclough 2010) and has been considered in previous analyses of the GDM (Whittaker et al. 2008, 2010, Cardoso et al. 2010). However, the extremely low levels of endemism in bryophyte floras (1–11% of the total species number depending on the archipelago, with the particular cases of Hawaii and Juan Fernandez reaching 28 and 23%, respectively), which has been interpreted in terms of the high dispersal ability of the group (Vanderpoorten et al. 2010), precluded any specific analysis of the endemic element in this study.

The key factors of the GDM, namely, time elapsed since island formation (TIME, in Ma), and its quadratic product (TIME²), log-transformed island size (AREA), maximum elevation (ELEV), continental isolation (ISOL; measured as the distance from the nearest continent), and distance to the nearest largest island within each archipelago (DIST), were employed as explanatory variables. Data on AREA, ELEV, ISOL and DIST were mainly obtained from the United Nations Environment Program (UNEP) online Island Directory database. Island data missing from the UNEP database were compiled from primary literature. Information for each archipelago is provided in Table 1, Supplementary material Appendix 1, Fig. A1.

We may anticipate collinearity among these variables, allowing the exclusion of less powerful pairs of variables within model selection (Borges and Hortal 2009). Here, we only observed significant correlation between AREA and ELEV (Spearman rank correlation coefficient = 0.681, $p < 0.001$). However, since 1) oceanic islands do not all achieve analogous geomorphological features across the different ontogenic stages (e.g. they might vary significantly in area and elevation at a comparable ontogenic phase), and 2) island ontogeny in practice is rarely as simple as the GDM assumes (Whittaker et al. 2008, 2010), we compensated for collinearity shortcomings by applying the LMMs approach

to evaluate models containing all possible combinations of variables.

Statistical analyses

Following Bunnfeld and Phillimore (2012), the diversity metrics here considered (i.e. moss and liverwort SR) were log-transformed ($\log(n+1)$ because of the presence of zero values in the liverwort data set). Using the log-transformation of diversity metric values (and area values, see above), we assumed a ‘log–log power law’ modelling of the species–area component of the GDM (Fattorini 2009, Triantis et al. 2012). We performed regression analyses to determine which models (i.e. what combinations of explanatory factors) best-fit moss and liverwort SR. To facilitate the interpretation of the results and to decrease the complexity of the analyses, we ran independent LMM analyses for mosses and liverworts. The grouping factor considered as random effects was hence the archipelago to which each of the studied islands belongs.

We employed a top-down strategy for model selection (Diggle et al. 2002, Zuur et al. 2009, Bunnfeld and Phillimore 2012). First, the best random effect structures, with all fixed effects considered, were selected using the small-sample corrected Akaike’s information criterion (AICc) (Burnham and Anderson 2002). The difference between the AICc of each model and the lowest AICc of all models, ΔAICc , as well as the Akaike weights derived from the AICc (AICc-w) (Burnham and Anderson 2002), were used to identify the best model(s) for mosses and liverworts. All models with a ΔAICc value < 2 were considered as having effectively equivalent levels of support (Burnham and Anderson 2002). We ran models allowing or not for a varying intercept across archipelagos and all possible combinations of varying slopes across archipelagos for the

different predictors considered (i.e. AREA, TIME, TIME², ELEV, ISOL, DIST). In the models including a random intercept, some baseline variation in the diversity metric is assumed between the groups (i.e. archipelagos), and the variation in the effects remaining (i.e. slopes) is subsequently investigated. In the models fitting random slopes without a random intercept, no baseline variation in the diversity metric is assumed between the archipelagos, all the inter-archipelagic variability is estimated only around the slopes. Models were fit with the 'lmer' function in the 'lme4' library (ver. 0.999375-39) in R (R 2.12, R Development Core Team), using restricted maximum likelihood (REML).

After finding the best random effect structures, the best combinations of fixed effects were selected using maximum likelihood (ML) methods and model selection based on AICc. We used the dredge function in the MuMIn package in R (ver. 0.13.17) to run a complete set of models with all possible combinations of the fixed effects and to identify the set of 'best models' according to the criterion of $\Delta AICc < 2$ (Burnham and Anderson 2002). For each random structure, the Akaike weights (AICc-w) were employed, following Cameron et al. (2012), to estimate the relative importance of each variable (fixed effects) by summing the AICc-w across the models in which they were included. Variable importance was estimated both on the full set of models and on the set of 'best models' (i.e. $\Delta AICc < 2$).

Following Bunnefeld and Phillimore (2012), we also examined graphical displays of the models generated for all the archipelagos separately, with a particular focus on the GDM pattern.

Comparable R² values (with the same meaning as in simple or multiple linear regression) are not easy to obtain for LMMs (Zuur et al. 2009). We thus used a R² measure that compares the deviance of the LMM with the deviance of a linear intercept-only model (Kvalseth 1985):

$$R^2 = 1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2} \quad (2)$$

We used these R² values as indicators of the proportion of the total variation among islands in bryophyte SR that is explained (accounted for) by selected LMMs.

Results

Based on the $\Delta AICc$ and AICc-w, the best random effect structure included either a random slope of AREA or a random intercept for moss SR, and a random intercept for liverwort SR (Table 2, see Supplementary material Appendix 3 for complete results of the random effect structure model selection procedure). Using these random structures, several competing models were included in the

Table 2. Coefficients for the fixed (geographical) factors included in the best random effect models used to predict moss and liverwort species richness of 67 oceanic islands from 12 archipelagos. The random structure (variables allowed to vary across archipelagos, see Statistical analyses), the number of parameters in the model (k), the AICc, AICc difference ($\Delta AICc$) and Akaike weights derived from the AICc (AICc-w) are given for each model. The best-fit models ($\Delta AICc < 2$) are presented. The contribution of each variable to those models is estimated by summing the AICc-w of the models in which it was included; values in parentheses correspond to the contribution of each variable calculated over the full set of models, regardless of the $\Delta AICc$ scores. The proportion of the total variation in bryophyte SR among islands (R²) that is accounted for by selected LMMs is indicated.

Random structure	Intercept	AREA	TIME	TIME ²	ELEV	ISOL	DIST	k	AICc	$\Delta AICc$	AICc-w	R ²
Mosses												
Slope of AREA	1.6313	0.2967	0.0733	-0.0036	0.0005	N	N	7	181.168	0	0.2168	0.7619
	1.7755	0.3257	N	-0.0011	0.0005	N	N	6	181.212	0.0445	0.2120	0.7525
	1.7757	0.2912	N	N	0.0006	N	N	5	181.838	0.6703	0.1551	0.7404
	1.5488	0.3051	N	-0.0010	0.0005	0.0002	N	7	181.978	0.8104	0.1445	0.7639
	1.4253	0.2756	0.0717	-0.0035	0.0006	0.0002	N	8	182.064	0.8964	0.1384	0.7703
	1.5296	0.2698	N	N	0.0006	0.0002	N	6	182.145	0.9767	0.1330	0.7526
Variable contribution to the model	1 (0.98)	0.35 (0.42)	0.76 (0.67)	1 (0.98)	0.42 (0.41)	0 (0.26)						
Intercept	1.6971	0.2552	0.0821	-0.0039	0.0006	N	N	7	180.487	0.0000	0.4642	0.7659
	1.8306	0.2925	N	-0.0011	0.0005	N	N	6	181.368	0.8805	0.2989	0.7534
	1.8492	0.2549	N	N	0.0006	N	N	5	181.832	1.3450	0.2369	0.7406
Variable contribution to the model	1 (0.98)	0.46 (0.50)	0.76 (0.67)	1 (0.99)	0 (0.24)	0 (0.25)						
Liverworts												
Intercept	1.1913	0.2364	0.1234	-0.0048	0.0006	N	N	7	209.377	0.0000	0.4447	0.7225
	1.4120	0.2705	N	N	0.0006	N	N	5	209.844	0.4677	0.3519	0.6907
	0.8444	0.2293	0.1301	-0.0049	0.0007	0.0002	N	8	210.941	1.5644	0.2034	0.7255
Variable contribution to the model	1 (0.92)	0.64 (0.54)	0.64 (0.56)	1 (0.98)	0.2 (0.3)	0 (0.27)						

TIME: time elapsed since the island emergence; ELEV: elevation above the sea level; ISOL: continental isolation; DIST: distance to the closest largest island within each archipelago; N indicates that the variable was not included in the model. The mathematical expression of the general dynamic model (ATT²) is highlighted in bold. 12 oceanic archipelagos were considered: Azores, Canaries, Cape Verde, Galápagos, Gulf Guinean, Hawaii, Juan Fernández, Madeira, Mascarenes, Society, Tristan da Cunha, and Vanuatu.

group of best fixed-effect models for the two diversity metrics considered (Table 2). AREA and ELEV were always included in the models selected for moss and liverwort SR. TIME and TIME² were included in the overall best (lowest AICc) model selected for mosses (both random structures) and liverworts. Fitting a random slope of AREA, ISOL was further included in three of the six competing models selected for mosses. AREA, TIME, ELEV and ISOL positively contributed to both moss and liverwort SR, whereas the coefficient of TIME² was negative, implying a humped trend of diversity over time as predicted by the GDM (Table 2).

The relative contribution of each variable to the models based on the AICc-w and taking into account the set of best models ($\Delta\text{AICc} < 2$) is presented in Table 2. AREA and ELEV contributed most to the description of moss and liverwort SR patterns, with an AICc-w of 1 in the best-fit models for the two groups. By comparison, the contribution of TIME and TIME² was only of 0.35 and 0.76, respectively, in the best-fit model for mosses with a random intercept; 0.46 and 0.76 in the best-fit model for mosses with a random slope for AREA; and 0.64 and 0.64 in the best liverwort model. DIST and ISOL were the least important variables, with AICc-w values ranging between 0.00 and 0.42 across best-fit models for mosses and liverworts for ISOL and 0.00 for DIST. Similar patterns were obtained when the AICc-w summation was carried out over the full set of models (Table 2). In the set of best models ($\Delta\text{AICc} < 2$), the explanatory variables accounted for (see R²-values, Table 2) 74–76% (random intercept for mosses), 69–72% (random intercept for liverworts) and 74–77% (random slope of island area for mosses) of the total variation in SR among islands.

The fitted ATT² models (Eq. 1) described an increase in SR with island area (the species–area relationship) (Table 2). Although the overall ‘best’ model for each taxon involves a humped relationship with time elapsed (Table 2), the shape of the SR–TIME relationships varied among archipelagos in relation to the range of ontogenetic stages exhibited by the particular archipelagos (Fig. 1, 2). In archipelagos displaying a comparatively limited range of island ages (e.g. the Azores, Hawaii and Galápagos, Table 1, Supplementary material Appendix 4, Fig. A1), the available island ages span the phase in which SR increases more or less linearly with elapsed time (Fig. 1, 2). In comparison, SR exhibits a hump-shaped relationship with island age for those archipelagos spanning a broader range of island ages, such as the Canaries, Cape Verde, Gulf Guinean islands, Tristan da Cunha and Vanuatu (Fig. 1, Supplementary material Appendix 4, Fig. A1). The Azores, Madeira, Society Islands, Mascarenes and Tristan da Cunha showed highest intercept values, while the lowest values were observed for Cape Verde, Galápagos, Hawaii, Canaries and Vanuatu (Fig. 1 and Supplementary material Appendix 4).

To check the robustness of these results to archipelagic sample size, we re-ran all the analyses, including only those archipelagos with more than five islands. The results were completely consistent in terms of the best random effect structures, as well as the group of best fixed-effect models for both mosses and liverworts (results not shown).

Discussion

Implementation of LMMs to model species richness in heterogeneous datasets

Despite the large heterogeneity of the dataset explored here, including a wide range of archipelagos worldwide, patterns of bryophyte SR could effectively be modelled in a single quantitative analysis owing to two interesting features of LMMs analysed in an information-theoretic model selection framework. First, the analyses presented here resulted in the selection of several models equally supported by the data. Such an uncertainty linked to the selection of a variety of equivalently supported combinations of best-fixed effects parallels previous reports on the implementation of the GDM using LMMs (Bunnefeld and Phillimore 2012, Cameron et al. 2012). The consideration of several competing models emphasizes the capacity to discuss actual data complexity rather than focusing on a single best solution, which may result in a loss of information (Johnson and Omland 2004, Spitale et al. 2009).

Second, random effects are used to modulate model parameters and fit the particularities of different archipelagos. Among the variables investigated, the data only supported the inclusion of a random slope of island area and only for moss SR. Such a difference might, to some extent, reflect the differences in ecological range displayed by mosses and liverworts. Leafy liverworts, which represent the bulk of species diversity among liverworts and influence the global diversity patterns of the group, indeed prevail in moist and cool habitats, rendering the niche of the group as a whole more homogeneous than that of mosses. Consequently, while mosses were reported from all of the investigated islands, some of the most xeric ones harboured no liverworts (Fig. 2c), potentially resulting in a higher influence of environmental heterogeneity in explaining differences in moss SR patterns.

The inclusion of only island area among the investigated factors in the random structure suggests that the effect of other predictors for describing patterns of moss and liverwort SR does not vary greatly across the twelve archipelagos considered. The other best random effect structures for moss and liverwort SR only included the intercept. The biological meaning of this parameter has hitherto scarcely been discussed. The intercept can be considered as a measure of the expected number of species per unit area in the logarithmic implementation of the power model of the species–area relationship (Gould 1979, Triantis et al. 2012). In the ATT², however, such an interpretation does not apply directly because the intercept is associated with both the area and time factors (Fattorini 2009). Accordingly, Fattorini (2009) proposed an index (‘colonization ability’) measuring the expected number of species (per unit area at equilibrium) per unit time. In an LMM framework, the ‘colonization ability’ index is reduced, when the random structure only includes an intercept, to the intercept value of the model, as the other coefficients are constant across archipelagos. We therefore interpret the intercept in this case as a measure of the intrinsic carrying capacity of islands within each archipelago, independently of their size and age.

The intercept range observed here suggests that the investigated archipelagos display different carrying capacities. Bryophytes are poikylhydric, which means that they have the ability to dry out to equilibrium with air that is moderately to extremely dry and resume normal metabolic activity after rehydration. A positive carbon balance (i.e. a positive net photosynthesis) is, however, difficult or impossible to achieve in areas where bryophyte patches are hydrated for insufficient periods of time, which would help to explain the scarcity of bryophytes in arid areas. Climatic variation, and precipitation in particular, hence plays a key role in bryophyte distributions (Bjerke et al. 2011, Lloret and González-Mancebo 2011, Preston et al. 2011), and might explain the contrasting carrying capacities observed here, for example, between Cape Verde (intercept values for mosses and liverworts of 0.5031 and -0.7344 , respectively) and Azores (2.7862, 2.3259), which experience a subtropical arid vs an oceanic temperate climate with extremely high levels of atmospheric humidity.

While fair amounts of variation in bryophyte SR were taken into account by the models considered here (R^2 values of >0.70), their performance is difficult to compare with previous applications because of potential issues of model overfitting in previous studies that partitioned data per archipelago (Bunnfeld and Phillimore 2012). However, visual inspection of the fit of the models to actual observations (Fig. 1, 2) suggests that substantial differences between observed and predicted SR values occasionally exist for some of the archipelagos. While the random structure can control for differences among archipelagos, such departures of SR patterns from predictions are likely caused by differences among islands within archipelagos, pointing to two potential limitations. First, island-specific features ('intra-island idiosyncratic' processes, Chiarucci et al. 2011, Aranda et al. 2012), and in particular, recent recurrent volcanic activities might, at least partially, explain the comparatively low SR observed for instance in Sao Miguel (4 Ma) and Sao Tomé (13 Ma), so that most of their land area is

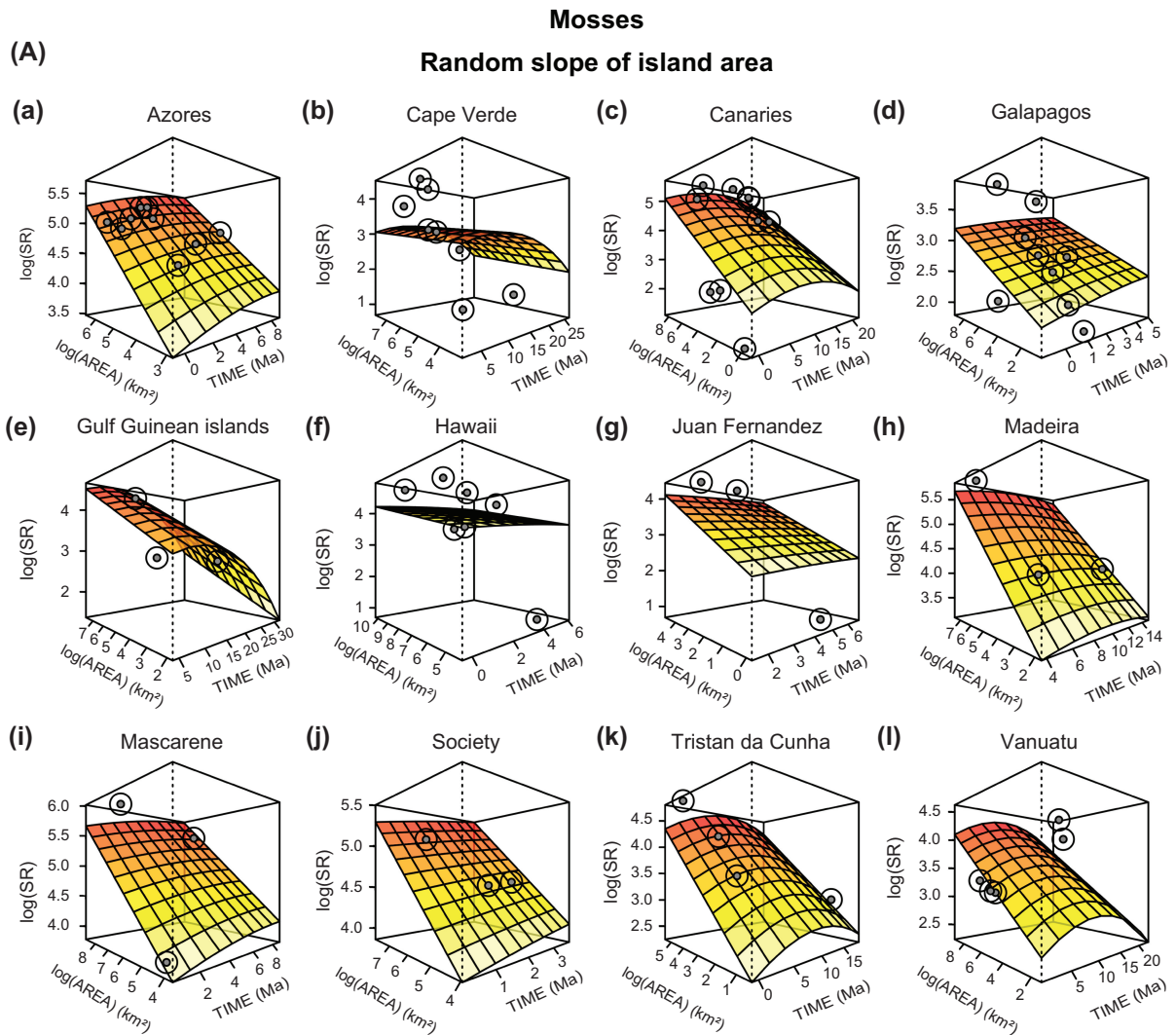


Figure 1. Species–area (km^2)–time (Ma) relationships for species richness of mosses (A) and liverworts (B) in eight archipelagos. Species richness (SR) and area were log-transformed. The surface is the prediction from the mixed effect model including a random slope of AREA for mosses and a random intercept among archipelagos for both mosses and liverworts (Table 2). The effect of elevation was also included, using the mean elevation of each archipelago. The colour shading indicates the SR predicted by the models (from white [low SR] to red [high SR]).

Random intercept

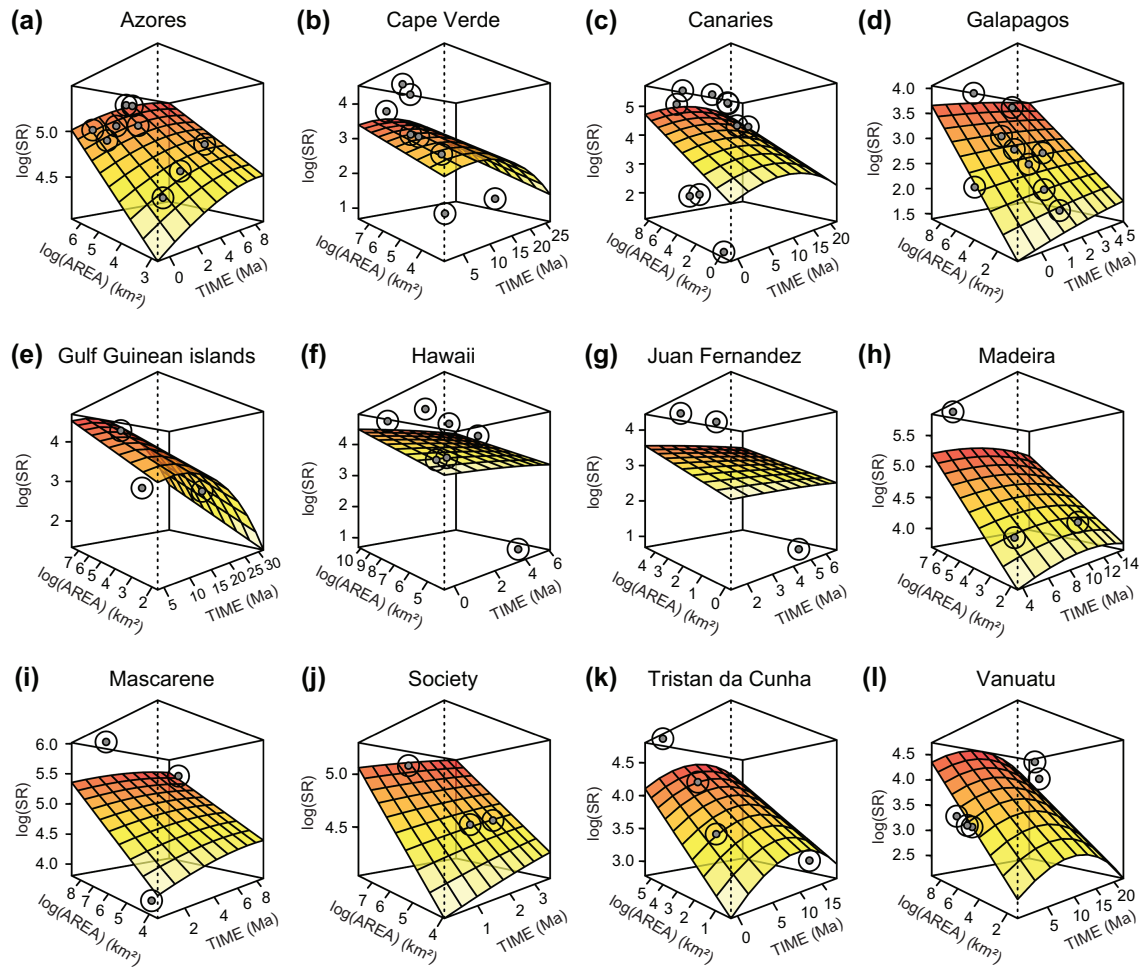


Figure 1. Continued.

<1 Myr old (Johnson et al. 1998, Munhá et al. 2002). Second, biological inventories, especially for inconspicuous and taxonomically challenging organisms like bryophytes, are never complete. Thus, for example, we cannot entirely rule out the hypothesis that differences in SR between Sal and S. Vicente, which are of approximately the same size, are due to inventory shortcomings (Aranda et al. 2012).

Bryophytes and the general dynamic model of oceanic island biogeography

Our results show that 67% of the competing models included time elapsed since island emergence as an explanatory factor ($\text{TIME} + \text{TIME}^2$ or TIME^2 ; Table 2), indicating that the ATT² may be applied even to bryophytes, a highly vagile group of organisms, thus extending the wide range of applications of the model (Borges and Hortal 2009, Fattorini 2009, Bunnefeld and Phillimore 2012, Cameron et al. 2012). SR exhibited, as predicted by the GDM, either a positive monotonic (Azores and Galapagos) or a unimodal (Canaries, Cape Verde, Madeira, Mascarenes,

Tristan da Cunha and Vanuatu) relationship with time depending on the range of island ontogenic stages (Fig. 1, 2).

TIME, however, contributed substantially less to explain the observed SR patterns as compared to other factors such as area and elevation. In fact, all of the models included area and elevation. These two factors therefore exhibited higher AICc-w's than time (TIME , TIME^2), which was not sampled in 33% of the competing models. The positive relationship between bryophyte SR and habitat diversity has long been evidenced by the high species turnover along elevational (Ah-Peng et al. 2007, Grau et al. 2007, Lloret and González-Mancebo 2011), geological and pedological (Vanderpoorten and Engels 2002, Bates 2009, Spitale et al. 2009), climatic (Hedenäs 2007, Mota de Oliveira et al. 2009, Patiño and González-Mancebo 2011) and land use gradients (Gradstein and Sporn 2010). The fact that ELEV was consistently included in the competing models reinforces the idea that habitat diversity plays a key role in the establishment and assembly of island bryophyte biotas (Sundberg et al. 2006). In addition, the inclusion of AREA in all of the models is consistent with the idea that larger islands might act as larger 'passive traps'

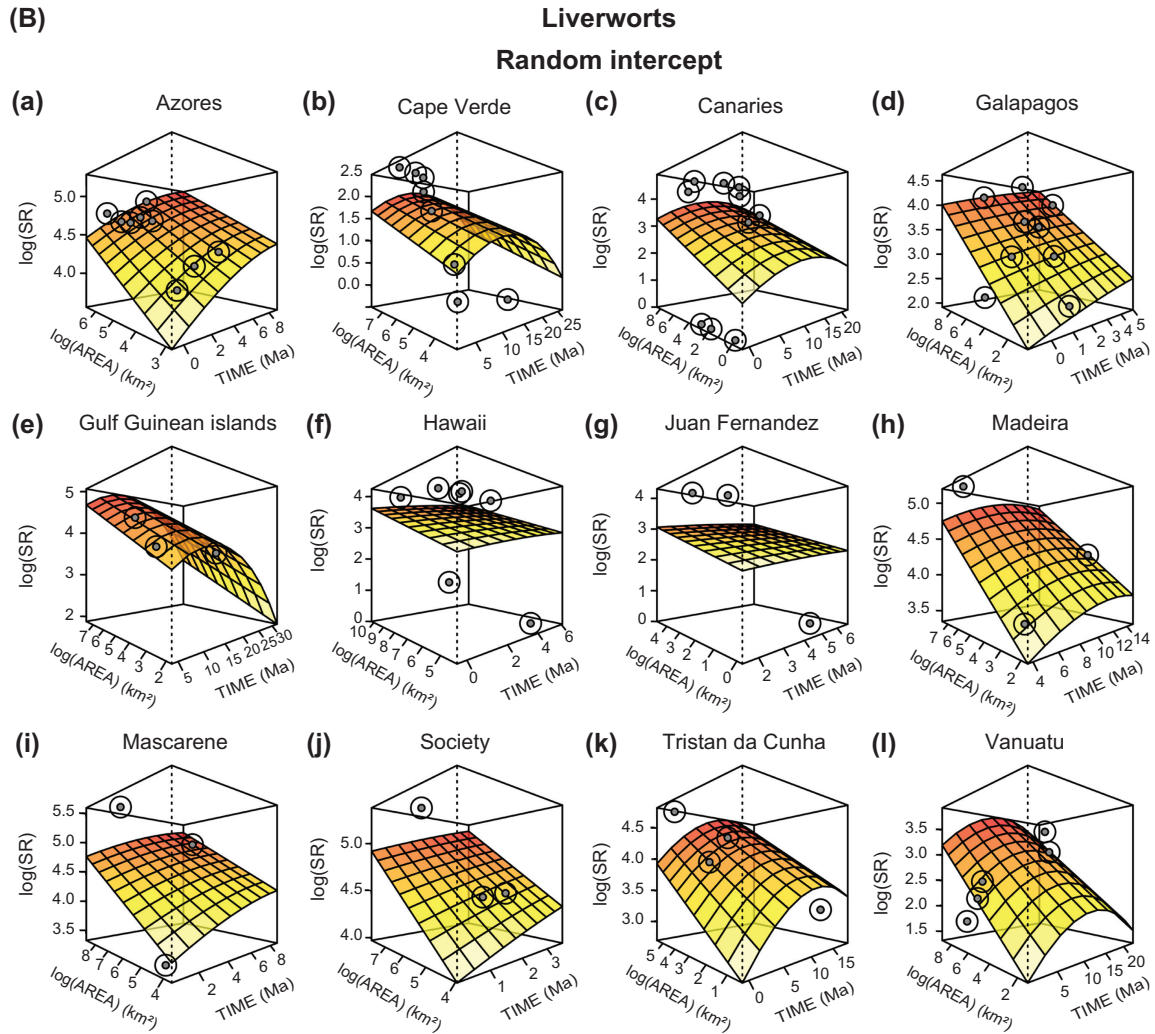


Figure 1. Continued.

(Borges and Hortal 2009) for highly vagile groups like bryophytes.

The idea that bryophytes might successfully colonize all the islands of an archipelago at a rapid pace, provided that suitable ecological conditions are met, is further supported by the fact that distance from the mainland and distance among islands within archipelagos were seldom or never selected as an explanatory factor of bryophyte diversity. This is consistent with previous observations reporting a lack of relationship between species richness on islands and distance from the mainland (Sundberg et al. 2006). These observations, along with the widespread distributions of bryophyte species among islands within archipelagos (Gradstein and Weber 1982, Vanderpoorten et al. 2011), extremely reduced levels of endemism (Vanderpoorten et al. 2010), and substantial allele sharing between islands and continents (Grundmann et al. 2007, Szövényi et al. 2008, Vanderpoorten et al. 2008, Hutsemékers et al. 2011, Stenøien et al. 2011), reinforce the idea that oceanic barriers are not a major impediment for migration in the group.

The weakness of the migration filter in bryophytes, together with their extremely low rates of endemism, explains

the comparatively limited importance of time in the models. Thus, time per se appears to have, as hypothesised, little independent role in explaining SR and principally features as a variable accounting for the changing area and topographic complexity during the life-cycle of oceanic islands. We interpret these results as suggesting that bryophyte SR intimately follows the evolution of island carrying capacity, peaking at the earliest stages of erosion and substantially decreasing on old islands with decreasing habitat diversity and elevation, and associated increased drought, as best exemplified by Porto Santo in Madeira and Lanzarote and Fuerteventura in the Canaries. This parallels observations made on colonization patterns of artificial substrates, wherein SR patterns over time represent a trade-off between increasing habitat complexity and heterogeneity on the one hand, and increased niche saturation and competition on the other (Hutsemékers et al. 2008). As a result, while patterns of species richness in angiosperms (Whittaker et al. 2008, Bunnefeld and Phillimore 2012) and bryophytes on islands conform to a large extent to the predictions of the GDM, the balance of the evolutionary mechanisms (migration/immigration and speciation) accounting for this

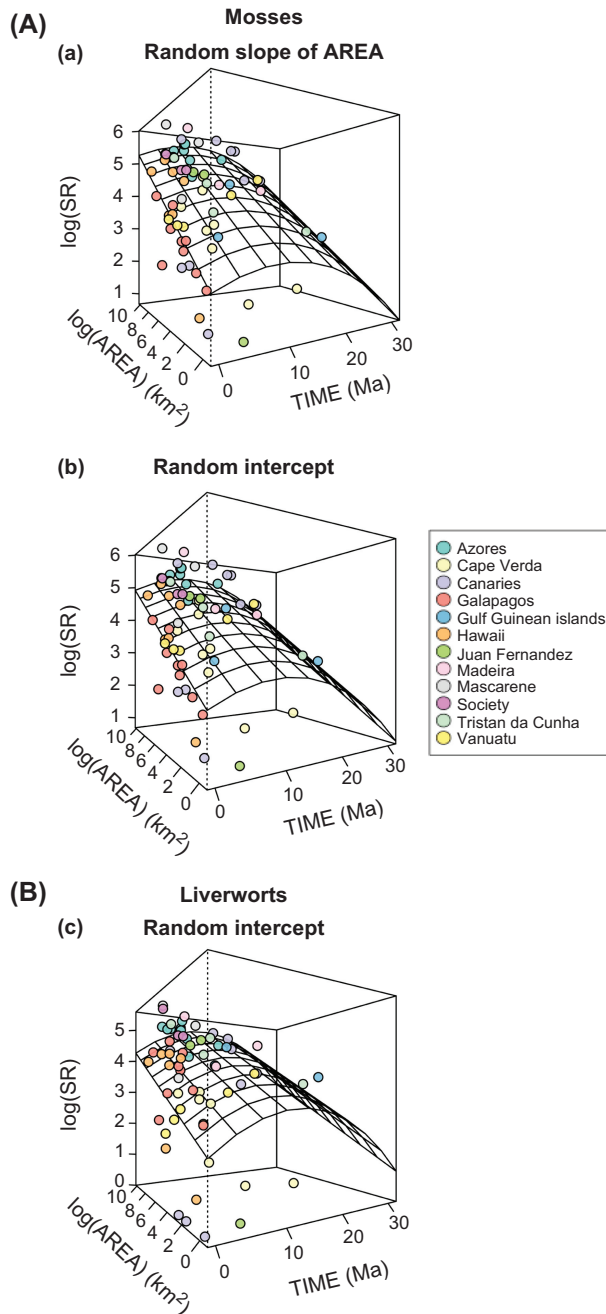


Figure 2. Species–area–time (Ma) relationships for moss (A) and liverwort (B) SR with all the archipelagos considered together. Species richness (SR) and area were log-transformed. The surface is the prediction from the mixed effect model including a random slope of AREA for mosses (a) and a random intercept among archipelagos for both mosses (b) and liverworts (c) (Table 2).

pattern substantially differ between these two groups of plants. This further suggests, in agreement with Borges and Hortal (2009), that simple models including island area and elevation as a surrogate of habitat diversity perform equally well or even better than the ATT^2 model and its variants in explaining diversity patterns of highly mobile organisms across oceanic archipelagos.

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Supplementary material (Appendix ECOG-00020 at <www.oikosoffice.lu.se/appendix>). Appendix 1–4.