

LETTER

Global diversity of island floras from a macroecological perspective

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Abstract

Islands harbour a significant portion of all plant species worldwide. Their biota are often characterized by narrow distributions and are particularly susceptible to biological invasions and climate change. To date, the global richness pattern of islands is only poorly documented and factors causing differences in species numbers remain controversial. Here, we present the first global analysis of 488 island and 970 mainland floras. We test the relationship between island characteristics (area, isolation, topography, climate and geology) and species richness using traditional and spatial models. Area is the strongest determinant of island species numbers ($R^2 = 0.66$) but a weaker predictor for mainlands ($R^2 = 0.25$). Multivariate analyses reveal that all investigated variables significantly contribute to insular species richness with area being the strongest followed by isolation, temperature and precipitation with about equally strong effects. Elevation and island geology show relatively weak yet significant effects. Together these variables account for 85% of the global variation in species richness.

Keywords

Biodiversity patterns, environmental determinants, equilibrium theory, island biogeography, species richness, species–area relationship, vascular plants, water-energy dynamics.

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INTRODUCTION

A considerable portion of all plant species worldwide is restricted to islands. Around 70 000 vascular plant species are endemic to islands – about one quarter of all known extant species (G. Kier, unpublished data). On the other hand, islands are generally considered as less diverse compared to adjacent mainlands (Whittaker & Fernández-Palacios 2007). However, five of the 20 global centres of plant species richness represent islands or parts of islands (Barthlott *et al.* 2005). Island biota are under severe threat due to habitat loss and climate change and are particularly susceptible to biological invasions (Rejmánek 1989; Sax *et al.* 2002; Pyšek & Richardson 2006; Buckley & Jetz 2007). Because of the high level of endemism of island ecosystems and the considerable degree of threat they face, nine of the 25 global biodiversity hotspots encompass islands or archipelagos (Myers *et al.* 2000).

To date, the global richness pattern of islands is only poorly documented. Recent global-scale studies of plant diversity primarily focus on continental areas and include only a relatively small number of large islands (e.g. Barthlott

et al. 2005; Kreft & Jetz 2007). Consequently, our knowledge about spatial patterns, core determinants and underlying ecological and evolutionary processes of insular plant diversity to date largely depends on local or regional-scale studies (e.g. Johnson & Simberloff 1974; Connor & Simberloff 1978; Price 2004; Cody 2006). However, recent analyses of mainland diversity have highlighted the importance of global-scale approaches to disentangle regional peculiarities from universal global trends (Kreft & Jetz 2007). But the few studies across broader geographic scales to date have been limited by sample sizes (Wright 1983; Hobohm 2000).

After more than two centuries of island research, the core environmental and historical drivers and their respective roles on island species richness remain controversial. Strong relationships between area and richness are generally observed both on islands and mainlands (Arrhenius 1921; Preston 1962; Connor & McCoy 1979; Rosenzweig 1995), but there is considerable disagreement about the general form of the species–area relationship and its mathematical and ecological interpretation (Lomolino 2000; Lomolino & Weiser 2001; Williamson *et al.* 2001; Tjorve 2003). Three

broad categories of potential mechanisms associated with the influence of area can be distinguished. First, larger areas usually harbour a greater number of individuals as they provide more resources and energy which might directly translate into higher species numbers (Preston 1962; MacArthur & Wilson 1967; Wright 1983). Second, larger areas generally contain a greater number of different habitats increasing local and regional turnover of species (Williams 1964). Third, larger areas might have a higher potential for *in situ* speciation (Lomolino 2001). All these mechanisms are not necessarily mutually exclusive but their relative importance or how they may interact is a matter of an ongoing debate.

The most popular model of island species richness is the Equilibrium Theory of Island Biogeography (MacArthur & Wilson 1967), which proposes that the equilibrium number of species on an island is a function of opposing rates of immigration and extinction. These two driving forces in species accumulation and turnover are linked to two major island attributes: area and isolation. The MacArthur and Wilson model has considerably stimulated research on oceanic islands as well as on other island-like systems (e.g. mountain tops, habitat fragments and nature reserves; e.g. Brown 1971; Harris 1984). Among objections that have been raised, a shortfall of the formulation of the Equilibrium Theory is its lack of global applicability (see Whittaker & Fernández-Palacios 2007 for a comprehensive review).

Global-scale understanding of species numbers on islands was significantly advanced by Wright (1983) who analysed angiosperm diversity of 24 island floras covering a range in area size from 12 000 to 7 million km². He replaced the variable area in the power model of the species–area relationship by a measure of total available energy and found remarkably high correlations with species richness. His seminal work has strongly influenced many other studies on macro-scale relationships between contemporary climate and species richness of mainlands (e.g. Currie 1991; Hawkins *et al.* 2003; Currie *et al.* 2004; Krefr & Jetz 2007), but had surprisingly little impact on island biogeography (but compare Kalmar & Currie 2006). Contemporary climate may constrain the number of individuals and thus the number of species or may alternatively limit the number of successful colonizers from nearby continents. Interestingly, to date no attempt has been made to incorporate the role of climate, area and isolation in a globally consistent model of plant richness on islands. Recently, Kalmar & Currie (2006) presented a model of avian diversity that combines aspects of the MacArthur and Wilson theory with species-energy theory. Analysing relationships between abiotic island characteristics and avian richness of some 346 islands worldwide, their global model accounted for 85–90% of the observed variation in species richness.

In this study, we analyse the native species richness of vascular plants of 488 islands worldwide and its relationship

with abiotic island characteristics. To identify differential effects of putative diversity determinants between islands and mainlands, we compare the species richness of island floras with a global data set of 970 mainland floras. Specifically, we scrutinize the respective influence of area, geographic isolation, contemporary climate, topography and island geology using non-spatial and spatial modelling techniques.

METHODS

Diversity data

Based on an exhaustive literature review, we assembled species richness data for vascular plants (ferns, gymnosperms and angiosperms) for 488 islands worldwide (Fig. 1a). Sources for species richness were island floras, checklists and compilations. Islands were defined as landmasses smaller than Australia surrounded by an ocean. Islands of freshwater bodies were not included. We considered only the number of native species per island and excluded cultivated or invasive species. If we encountered differing species numbers for one and the same island, we usually used the more recent reference hypothesizing that younger references reflect a more complete floristic and taxonomic state of knowledge. The islands assembled in this data set encompass a wide range of different area sizes, climates, geological types and different degrees of geographic isolation. The majority of islands represent single landmasses. Only in some cases, mostly for atolls, islands may consist of numerous islets sharing a common geological origin.

To analyse putative differences in the effects of different abiotic determinants on the species richness of islands and mainlands, we compared the island data with a data set consisting of 970 non-overlapping mainland regions (Fig. 1b). The original data set consists of diversity information referring to more than 1800 geographic units and is described in more detail in Kier *et al.* (2005). The mainland data set has been used to document global patterns of vascular plant diversity (Barthlott *et al.* 2005; Kier *et al.* 2005), to analyse global latitudinal gradients of plant species richness (Mutke & Barthlott 2005), and for a global-scale analysis of core drivers of plant species richness of mainlands (Krefr & Jetz 2007). To estimate area size and environmental variables, boundaries of all 970 mainland regions were digitized according to the primary references in a geographical information system (Krefr & Jetz 2007).

Abiotic data

Six abiotic island characteristics were investigated as putative determinants of plant species richness: area, distance to the nearest continent, climate (mean annual temperature and

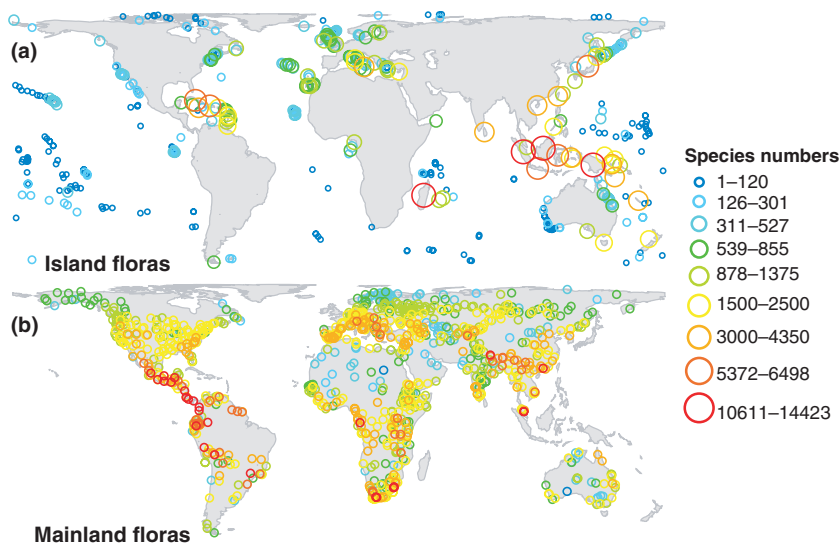


Figure 1 Spatial distribution of (a) 488 island and (b) 970 mainland floras investigated in this study. The number of vascular plant species is shown for the mass centroid of the geographic region. Natural breaks classification, Behrmann projection.

precipitation), topography and island geology. Other variables of interest, such as island age, are unfortunately not available for a sufficient number of islands and with a satisfying accuracy and therefore could not be included in the analyses. Island area was adopted from the original reference if stated by the authors. Otherwise, area was derived from the UNEP Island Directory (UNEP 1998) or from encyclopaedias. Geographic isolation and remoteness is thought to be a primary driver of species composition and richness of islands (MacArthur & Wilson 1967; Whittaker & Fernández-Palacios 2007). We thus included the distance to the nearest continent as an independent variable in our analyses hypothesizing that mainland floras are the most important sources for island colonizations. Furthermore, ecological and historical processes might be strongly influenced by island geology (Mueller-Dombois 2002; Whittaker & Fernández-Palacios 2007). We thus investigated the effect of this factor on species richness. Three main types of geological origins were recognized: continental, volcanic and atolls. Continental islands are either part of the continental shelf (e.g. Great Britain) or were once connected to continental landmasses but became separated by tectonic movement (e.g. Madagascar and New Caledonia), eustatic sea level rise or subsidence of the continental shelf. Oceanic islands of volcanic origin have arisen as newly formed land from the sea floor. In contrast to continental islands, these islands must have been newly colonized from nearby continents or surrounding islands. The third geological type are atolls representing flat coral islands that are usually formed around submerged or eroded volcanic islands or on low lying reefs (Whittaker & Fernández-Palacios 2007). Information on island geology was derived from the original references, the UNEP Islands Directory (UNEP 1998) or encyclopaedias.

We found that climatic and environmental characteristics were much harder to determine for islands than for mainland regions, because smaller islands are not well represented in most global environmental data sets that are frequently used in macroecological studies. For the mainland data set, we could show in an earlier study that, for instance, the water–energy relationship of plant diversity is best described by a combination of potential evapotranspiration, as a measure of ambient energy, and the annual number of days with precipitation (Kreft & Jetz 2007), a variable that encapsulates amount and seasonality of precipitation. Because such data are not available for most islands, the set of potential variables was limited and we used the most frequently reported climatic measures, mean annual temperature and precipitation, for our analyses.

Climate data were derived from the WORLDCLIM 1.4 data set (Hijmans *et al.* 2006), a global data set with a spatial resolution of *c.* 1 km². In some cases, values had to be estimated from nearby islands or from weather station data. We also included the maximum elevational range of an island which is regarded to be a surrogate of topographic complexity and habitat diversity (Kerr & Packer 1997; Rahbek & Graves 2001; Jetz & Rahbek 2002; Kreft & Jetz 2007). Maximum elevation was adopted from the original reference when stated. Otherwise, it was derived from the WORLDCLIM data set (Hijmans *et al.* 2006) or from encyclopaedias. Species richness and all continuous predictor variables (except for distance) were log₁₀-transformed to approximate normally distributed residuals. Distance did not show a log–log relationship with species richness and alternative models (e.g. exponential) also yielded a poorer fit. Therefore, distance was not transformed for the analyses.

Statistical analysis

We first investigated univariate relationships between abiotic variables and species richness on islands, mainlands and in the combined data set. In a second step, we tested interaction models of all independent variables. Finally, we developed a combined multi-predictor model of island species richness.

Correlative studies of insular species richness have generally applied traditional statistical methods – most frequently ordinary least-square regression (OLS). An underlying assumption of OLS is that observations are independent. Indeed, in most macroecological data sets both the response variable (e.g. species richness) and the predictor variables (e.g. environmental covariates) are spatially autocorrelated. Spatial autocorrelation in turn might inflate Type I errors and might bias parameter estimates (Legendre 1993; Dormann 2007). Moreover, ignoring spatial autocorrelation might even invert obtained statistical relationships (Kühn 2007). As expected, spatial autocorrelation is present in the data analysed here. We thus performed traditional, non-spatial generalized linear models (GLMs; Gaussian error distribution and identity link function) as well as spatial linear models (SLMs) of the Simultaneous Autoregressive Model type (SAR). SARs have proven to be a powerful approach for macroecological analyses (e.g. Tognelli & Kelt 2004; Kissling & Carl 2008; Kreft & Jetz 2007). As residuals show an approximately normal distribution after transformation, GLM results equal those of OLS. Parameters of GLMs and SARs are estimated in a maximum likelihood framework which produces directly comparable results.

As there is no theory-based selection strategy for SLMs or SARs in ecology, we applied a data-driven approach to parameterize SARs. The selection of an appropriate neighbourhood structure and weighting was based on model fit and successful removal of spatial autocorrelation in model residuals (following Kissling & Carl 2008). A SAR of the error type was chosen and a lag distance of $d = 1000$ km with weighted neighbourhood structure showed best model fits and was able to remove spatial autocorrelation from the residuals. We used Moran's I correlograms and global Moran's I values to evaluate patterns and levels of spatial autocorrelation in the model residuals (Fortin & Dale 2005). Moran's I might be considered as a spatial equivalent to Pearson's r and generally varies between 1 (indicating positive autocorrelation) and -1 (negative autocorrelation) (Fortin & Dale 2005).

As a goodness-of-fit criterion we used Akaike's Information Criterion (AIC; Johnson & Omland 2004). AIC has two components: twice the negative log-likelihood of the model and a bias correction factor that penalizes models with greater complexity by adding twice the number of param-

eters included in the model. Additionally, we report likelihood-based R^2 -values after Nagelkerke (in Lichstein *et al.* 2002). For GLMs, Nagelkerke's R^2 is identical to the adjusted R^2 of multiple OLS regressions. For the calculation of Nagelkerke's R^2 for SARs, spatial autocorrelation is ignored to fit the null model (compare Lichstein *et al.* 2002). Statistical analyses were performed in R using the SPDEP package for spatial models (Bivand 2006).

RESULTS

Collinearity among predictor variables in the island data set is generally low, with absolute Pearson correlations of 0.10–0.38 (Supplementary Table S1). The only strong correlation exists between island size and elevational range ($r = 0.69$), i.e. larger islands reach a higher maximum elevation. Furthermore, we find significant differences in the abiotic conditions among the three geological island types (Supplementary Table S1). For instance, atolls are significantly smaller, warmer, more remote, flatter and wetter than continental or volcanic islands. Significant differences also exist between volcanic and continental islands. Volcanic islands differ from continental ones in having a higher mean elevational range, warmer temperatures and in being more remote.

Global species numbers of vascular plants on islands vary by five orders of magnitude ranging from zero species on, e.g. some sub-Antarctic islands up to the island of Borneo which harbours more than 14 000 species of vascular plants (Fig. 1a). The geographic distribution of insular species richness shows clear spatial patterns. This observation is also supported by the fact that species richness is spatially autocorrelated up to distances of $c. 3500$ km (Supplementary Fig. S1).

Univariate analyses reveal that, among all investigated variables, island area is by far the strongest predictor of the island species richness and explains a remarkable amount of variation (66% in SAR and 50% in GLM; Fig. 2b, Table 1). The predictive power of area size is much stronger for islands than for mainland regions, where it explains only 25% in SAR and 8% in GLM, respectively. The slope of the species–area relationship is clearly steeper for islands (SAR: 0.33 ± 0.01 ; estimate \pm confidence intervals) than for mainland regions (SAR: 0.17 ± 0.01 ; Fig. 3a, Table 1). This apparent difference remains robust when the selection of islands is restricted to the same data range and frequency distribution as mainlands. In contrast to prevalent hypotheses claiming that different slopes are influenced by different environmental conditions or different degrees of isolation (Connor & McCoy 1979; Rosenzweig 1995; Whittaker & Fernández-Palacios 2007), we find that the remarkable island–mainland difference remains after controlling for core environmental predictors in the context of a

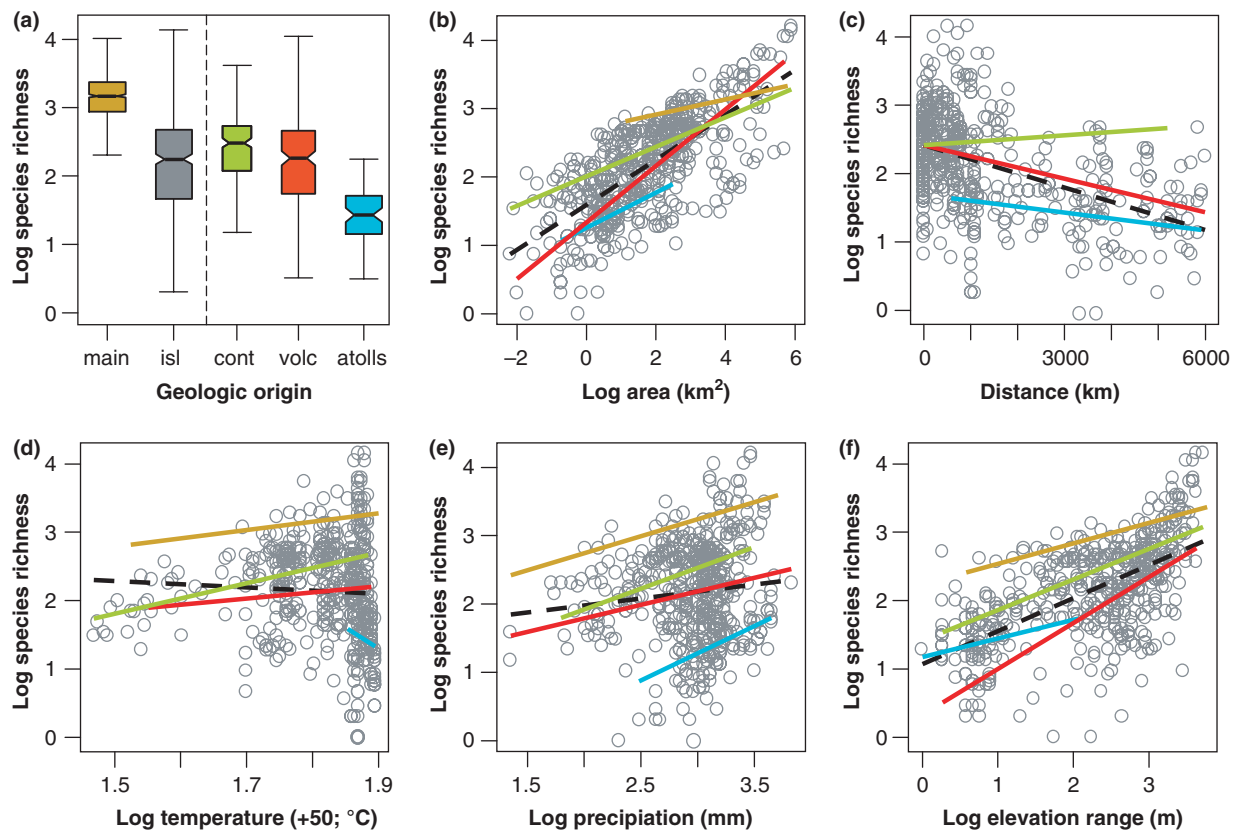


Figure 2 Relationship between different abiotic variables and vascular plant species richness of 488 island floras worldwide. Lines give linear fits. Black, hatched lines mark overall fits of all island floras; coloured lines give individual fits for islands of different geological origin: continental islands (green), volcanic islands (red), atolls (blue). Brown lines indicate regression lines for 970 mainland floras (points not shown). (a) Geological origin (abbreviations: main – mainland, isl – islands, cont – continental islands, volc – volcanic islands); (b) area (\log_{10} ; km^2); (c) distance to next continent (km); (d) mean annual temperature ($\log_{10} x + 50$; $^{\circ}\text{C}$); (e) mean annual precipitation (\log_{10} ; mm per year) and (f) elevation range (\log_{10} ; m).

multi-predictor model (Fig. 3b). Another noteworthy observation is that continental islands have shallower slopes than atolls and especially than volcanic islands (0.21 ± 0.03 , 0.24 ± 0.12 and 0.41 ± 0.05 , respectively). Continental islands, on the other hand, are characterized by much higher species richness per unit area (intercept; Fig. 2b).

The second strongest predictor is elevational range which explains some 40% of the variation in species richness. The predictive power of this variable is somewhat weaker for mainland regions (SAR: $R^2 = 0.27$; GLM: $R^2 = 0.21$), but slopes are similar among the two groups (Fig. 2f, Table 1). Distance to the nearest mainland has a significant negative effect on species richness and explains a substantial amount of variance in a GLM framework ($R^2 = 0.23$). However, it accounts for only 7% if spatial autocorrelation is explicitly modelled. The comparison of the individual effect of distance on island species richness exhibits a remarkable difference between islands of continental and oceanic origin. Whereas significant negative effects of geographic isolation

on species richness are observed for atolls (SAR: $\hat{\alpha} = -2.31$, $P = 0.02$, $n = 79$) and volcanic islands (SAR: $\hat{\alpha} = -3.1$, $P = 0.002$, $n = 202$), this relationship is altogether non-significant for continental islands (SAR: $\hat{\alpha} = -0.76$, $P = 0.45$, $n = 207$; Fig. 2c). This difference may potentially arise as an artefact because the distances to the mainland for continental and oceanic islands show different data ranges and frequency distributions with continental islands being generally less remote than oceanic islands (Supplementary Table S3). We thus repeated the analysis limiting volcanic and continental islands to the same data range (50–1870 km). We then adjusted both frequency distributions by deleting records from distance classes which were comparatively overrepresented in the volcanic island subsample, i.e. records for more remote islands. We find that the relationship between distance and species richness remains significantly negative for volcanic islands (SAR: $\hat{\alpha} = -2.49$, $P = 0.013$; $n = 141$) and remains non-significant for continental islands (SAR: $\hat{\alpha} = 0.41$, $P = 0.68$; $n = 122$).

Table 1 Single-predictor relationships between vascular plant species numbers on islands, in mainland regions and in the combined data set

	SAR					
	Estimate	SE	χ^2	<i>P</i> -value	<i>R</i> ²	AIC
Island floras						
Area	0.33	0.01	31.28	***	0.66	279
Precipitation	0.35	0.11	3.33	***	0.02	796
Temperature	−1.00	0.84	−1.19	n.s.	0.003	805
Elevation	0.49	0.04	18.24	***	0.40	553
Distance	−2.20e ^{−04}	3.46e ^{−05}	−6.34	***	0.07	773
Geology					0.14	735
Atoll	—	—	—	—		
Continental	1.04	0.11	9.04	***		
Volcanic	0.64	0.11	6.12	***		
Mainland floras						
Area	0.17	0.01	18.45	***	0.25	32
Precipitation	0.41	0.04	11.03	***	0.11	206
Temperature	0.37	0.30	1.25	n.s.	0.001	314
Elevation	0.35	0.02	18.93	***	0.27	13
All (islands and mainlands)						
Area	0.26	0.01	42.65	***	0.56	513
Precipitation	0.39	0.05	7.81	***	0.04	1635
Temperature	−1.60	0.46	−3.46	***	0.01	1682
Elevation	0.48	0.02	30.64	***	0.39	970
Distance	−3.71e ^{−04}	3.47e ^{−05}	−10.71	***	0.06	1610
Geology					0.23	1317
Atoll	—	—	—	—		
Continental	0.89	0.09	10.11	***		
Volcanic	0.65	0.08	7.92	***		
Mainland	1.48	0.09	17.04	***		
Island (yes/no)	0.66	0.04	18.47	***	0.18	1405

Results of spatial Simultaneous Autoregressive Models (SAR) are reported (for GLM results compare Supplementary Table S2). Species richness (response) and all continuous predictor variables (except for distance) were log10 transformed.

Significance: ****P* < 0.001; ***P* < 0.01; **P* < 0.05. n.s., not significant.

Temperature and precipitation show insignificant or weak effects on island species richness as single predictors but show moderate positive effects for mainland regions. The strength, however, increases if variation of species richness

is additionally controlled for area and isolation (Table 2). Absolute geographic latitude shows insignificant relationship with species richness both as a single predictor (SAR: *P* = 0.26) and when additionally controlling for area and

Figure 3 Species–area relationships of island and mainland floras. (a) Log-transformed raw richness plotted against log-transformed area size. (b) Species–area relationship after richness is controlled for core environmental predictors (compare multivariate models in Table 2). Regression lines indicate linear fits (a) and partial fits (b); blue – island, brown – mainland floras.

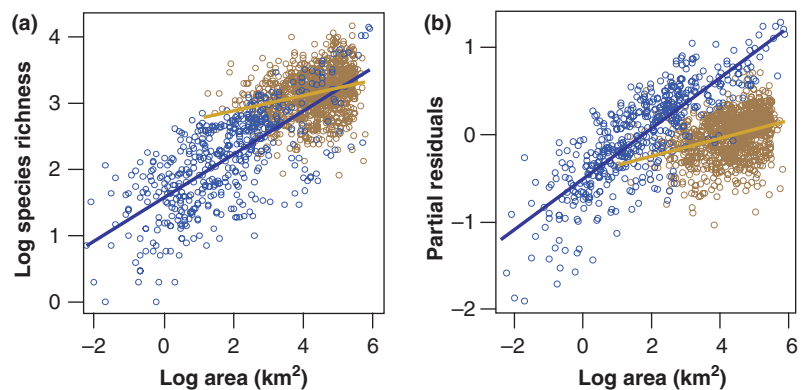


Table 2 Multi-predictor models of vascular plant species richness for island and mainland floras and for the combined data set

	SAR					
	Estimate	SE	$\hat{\tau}$	<i>P</i> -value	R^2	AIC
Island floras						
Full model					0.85	156
Area	0.29	0.01	21.2	***		
Elevation	0.09	0.03	3.1	**		
Distance	-1.43e^{-04}	2.12e^{-05}	-6.8	***		
Precipitation	0.37	0.05	6.8	***		
Temperature	2.38	0.39	6.0	***		
Geology						
Atoll	—	—	—	—		
Continental	0.41	0.07	5.5	***		
Volcanic	0.24	0.07	3.5	***		
Mainland floras						
Full model					0.64	-300
Area	0.13	0.01	14.5	***		
Elevation	0.23	0.02	12.6	***		
Precipitation	0.40	0.03	13.1	***		
Temperature	1.13	0.23	5.0	***		
All floras						
Full model					0.87	74
Area	0.20	0.01	26.1	***		
Elevation	0.19	0.02	11.6	***		
Distance	-1.49e^{-04}	2.10e^{-05}	-7.1	***		
Precipitation	0.43	0.03	15.1	***		
Temperature	1.22	0.23	5.4	***		
Geology						
Atoll	—	—	—	—		
Mainland	0.34	0.07	5.0	***		
Continental	0.33	0.06	5.2	***		
Volcanic	0.14	0.06	2.3	*		

Results of spatial Simultaneous Autoregressive Models (SARs; for results of non-spatial GLMs compare Supplementary Table S4). SARs leave no significant spatial autocorrelation in model residuals and are thus able to adequately deal with the spatial autocorrelation (compare Supplementary Figs S1 and S2).

Significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

n.s., not significant.

isolation effects (SAR: $P = 0.11$). As biological inference is limited for this variable (Hawkins & Diniz-Filho 2004), we did not examine it further. Island geology also emerges as a strong predictor of island species richness (SAR: $R^2 = 0.14$; GLM: $R^2 = 0.25$), with continental islands showing greatest mean species richness, followed by volcanic islands and atolls (Fig. 2a; species richness differs significantly among all geological island types; Tukey's HSD all $P < 0.0001$).

Whereas island area shows a clearly linear relationship with plant richness (Figs 2b and 3a), restrictive relationships

(i.e. points fall into a triangular space with a distinct upper boundary) are observed for temperature, precipitation, elevation and isolation pointing at a constraining effect of these variables (Fig. 2c–f). Different variables are also likely to show interactive effects rather than acting merely additive. We tested for these effects by investigating two-way interaction terms among all predictor variables (Supplementary Table S3). Five of the 15 possible two-variable interaction terms provided stronger relative support for the interaction than for the main effect model (area : temperature, area : distance, area : geology, temperature : elevation and distance : precipitation).

We then proceeded to construct a multivariate *ad hoc* model including all above-mentioned variables as well as significant two-way interactions (Table 2). Whereas main effects of all variables remain significant in a multivariate context, none of the previously asserted interaction terms show significant effects. Consisting of six variables, the full model explains 85% of the global variation in island richness in SAR and 80% in GLM, respectively (Table 2, Fig. 4). Again, area shows strongest effects followed by distance, temperature and precipitation with about equally strong effects. Elevational range and island geology, on the other hand, show relatively weak yet significant effects on island species richness (Fig. 4).

Islands are generally thought to contain fewer species than mainland regions (e.g. Whittaker & Fernández-Palacios 2007). We also clearly notice this important difference across all 1458 investigated floras (Table 1, Fig. 2a). After controlling for the effect of area, the difference in island and mainland species richness decreases, but significant residual differences remain (Tukey's HSD; $P = 0.0016$). After additionally controlling for differences in climate, topography and geographic isolation, no significant difference remains between island and mainland richness (Tukey's HSD; $P = 0.43$).

Very few island biogeographical studies have so far considered the spatial structure and associated methodological issues of the data. We note that while residuals from non-spatial GLMs show significant levels of spatial autocorrelation, SARs are able to fully reduce spatial autocorrelation (Supplementary Figs S1 and S2). Visual inspection of the spatial pattern of residual variation reveals strong regional patterns for GLM but not for SAR residuals (Supplementary Fig. S2). Furthermore, SARs improve model fits (compare AIC and R^2 values in Tables 1 and 2 with Supplementary Tables S2 and S3). The spatial structure of the data also strongly affects parameter estimates. A comparison of all coefficients reveals a mean difference of 29.99% between GLM and SLM estimates (median = 16.16%, 39 pairs of GLM and SLM coefficients). This value is very close to misestimations reported from a recent meta-analysis of non-spatial and spatial analyses in ecology (Dormann 2007).

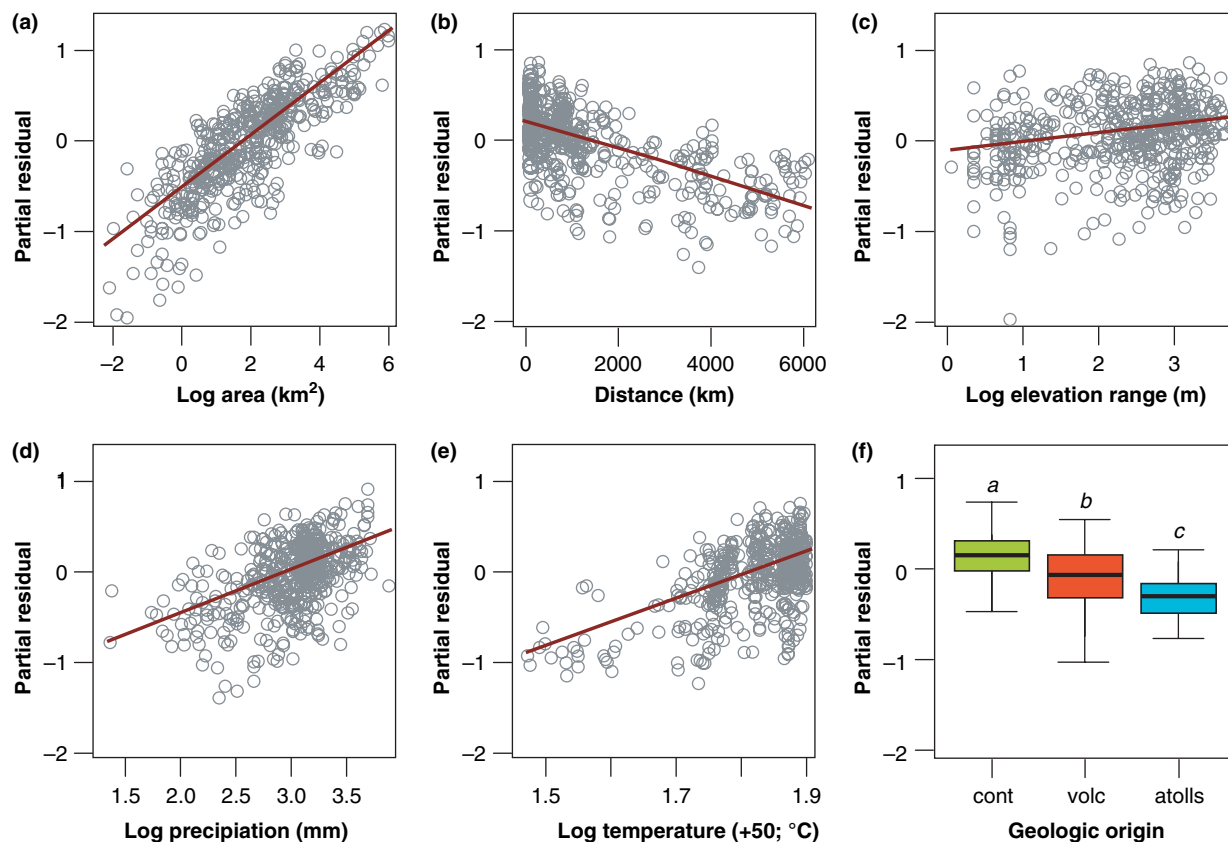


Figure 4 Partial residual plots for the six predictors of the multi-predictor model of global island species richness. Plots show the individual effects of (a) area, (b) distance to the next continent, (c) elevational range, (d) mean annual precipitation, (e) mean annual temperature and (f) islands of different geological origin. A partial residual plot is a plot of $r_i + b_k \cdot x_{ik}$ vs. x_{ik} , where r_i is the ordinary residual for the i -th observation, x_{ik} is the i -th observation of the k -th predictor and b_k is the regression coefficient estimate for the k -th predictor. Regression lines indicate partial fits. Abbreviations: cont – continental islands, volc – volcanic islands.

DISCUSSION

The number of vascular plant species on a given island is highly predictable from a set of a few and relatively simple island characteristics. These core determinants explain a remarkable amount of the global variation in species richness which is particularly noteworthy as the island data set covers such a broad spectrum of different area sizes, climates, vegetation types, as well different degrees of isolation and colonization histories. The great explanatory power of the multi-predictor model of island richness may suggest that other potential drivers are either strongly collinear with these core predictors or altogether less important – at least at a global scale. The overall model fit might have even further improved if ecologically more meaningful climatic variables instead of mean annual temperature and precipitation had been available. For mainland regions, it has been demonstrated that the water-energy dynamics are best described by a combination of potential evapotranspiration and wet day frequency (Kreft & Jetz 2007).

Island area emerges as the strongest predictor among all investigated variables. This is especially glaring compared to the relatively low predictive power of this variable for mainland floras (Kreft & Jetz 2007). Generally, the species–area relationship has only been considered to show strong correlations within climatically homogenous regions (MacArthur & Wilson 1967). This view has received multiple support from many regional-scale island biogeographical studies (e.g. Price 2004; Cody 2006; but see Whittaker & Fernández-Palacios 2007 for noteworthy exceptions). Our results, however, show that even at a global scale, i.e. across climatic and biogeographic zones, area is the primary determinant of insular species numbers. Indeed, area has been regarded as the most troublesome of all variables (Whittaker 2006) and has thus received particular attention in island biogeography (e.g. MacArthur & Wilson 1967; Rosenzweig 1995; Whittaker & Fernández-Palacios 2007). There is still much controversy about the most fundamental issues of its effect on diversity, e.g. the general form of the species–area relationship or the interpretation of the various

parameters of its mathematical formulation (Rosenzweig 1995; Lomolino 2000; Lomolino & Weiser 2001; Williamson *et al.* 2001; Scheiner 2003; Tjorve 2003). The comparison between island and mainland floras exhibits some noteworthy differences which point to differential effects of the variable area on mainland and island species richness. For mainland floras, the area effect is mostly replaced if variables describing topographical complexity or the number of ecosystems enter a statistical model suggesting that the species–area relationship for mainland floras is largely driven by factors related to habitat heterogeneity (Kreft & Jetz 2007). Like for mainland regions, island area is likely to act via an increase of habitat heterogeneity and thus regional species turnover. And, the positive effect of elevational range, a variable that is generally interpreted as a suitable proxy for habitat heterogeneity (Rahbek & Graves 2001; Kreft & Jetz 2007), supports this mechanism. On the other hand, the area of an island is a core determinant of extinction rates (MacArthur & Wilson 1967) and a crucial variable for colonization (Whittaker & Fernández-Palacios 2007). Both mechanisms are likely to be more important for islands. Furthermore, larger islands have a higher probability to receive diaspores than smaller ones and islands closer to a continent shall receive more diaspores than distant ones. This idea receives support by the significant interaction between area and geographic isolation (Table 2) and the observed differences between continental and oceanic islands (Fig. 2a–c). Additionally, larger islands might provide a comparatively greater potential for *in situ* speciation because larger islands provide geographic features (such as mountain ranges or rivers) that are important for *in situ* speciation (Lomolino 2001). Larger islands may thus compensate their lower species richness due to isolation which in turn could lead to comparably high species numbers as for mainlands. Indeed, we observe that the species richness of islands larger than 10 000 km² is largely indistinguishable from mainlands (Fig. 2b). Interestingly, the species–area relationship of continental islands is more similar to mainlands. Both are characterized by relatively high intercepts (species density per unit area) and relatively shallow slopes compared to islands of oceanic origin (volcanic islands and atolls).

Another challenging aspect of the species–area relationship remains to explain why slopes differ so tremendously between continents and islands. The slope of the global species–area relationship of 0.33 (SAR estimate) obtained for islands falls into the range of previously observed values (MacArthur & Wilson 1967; Rosenzweig 1995) but is much higher than that for mainland regions (0.17; SAR estimate). Our results demonstrate that at a global scale the steeper slope for islands is driven by smaller islands. Whereas larger islands show comparably high species richness like mainlands, smaller islands show lower species

numbers causing a steeper increase of the species–area curve (Fig. 3a). It has been further argued that steeper slopes of islands might be due to isolation, climate or other geographic variables (Rosenzweig 1995; Kalmar & Currie 2006; Whittaker & Fernández-Palacios 2007). Interestingly, we find that after accounting for environmental dissimilarities and geographic isolation within a multi-predictor framework, the difference of slopes between islands and continents remains (Fig. 3b).

The restrictive relationships between most predictor variables and species richness indicate constraining effects of these variables on richness (Fig. 2c–f; compare Kalmar & Currie 2006). This finding also provides support for a theoretical, maximum number of species that can be supported on a given island, an intrinsic ‘carrying capacity’ (Preston 1962; Whittaker *et al.* 2007). Following this line of argument, smaller areas as well as less benign climates constrain the total number of species that can coexist on an island. Alternatively or additionally, harsh climates may constrain the number of potential immigrant species that are able to tolerate the specific conditions and are thus able to successfully colonize an island.

Island geology is revealed as a strong determinant of species numbers. Although strong effects of this factor are observed, island geology is a problematic variable. It is collinear with other variables and combines many putative ecological drivers of island species richness thus limiting biological inference (Supplementary Table S1). However, significant differences remain among islands of different geological origin after statistically accounting for abiotic differences (Fig. 4). This observation strongly points to differences in the origin and in the maintenance of species richness associated with these island types. Atolls, for instance, are known to harbour an impoverished flora consisting of mostly widespread elements of a generalist strand flora (Stoddart 1992). Obviously, the low species numbers of atolls cannot be fully predicted by their remoteness and flat topography alone. Other factors, like the great susceptibility to natural disturbances (e.g. hurricanes, sea level changes and associated submergence during the Pleistocene) might additionally contribute to their low species richness. Continental islands, on the other hand, have a significantly higher diversity than expected from their abiotic conditions. This might be due to the fact that these islands did not have to be newly colonized from mainland source areas which would be also congruent with our observation that geographic isolation is a non-significant determinant for the species richness of this island type. However, as demonstrated by Cody (2006) and others, isolation may have a significant effect on the species richness of continental islands in a regional context. The pattern of spatial autocorrelation that we find in our data points to a strong influence of regional species pools of

either nearby islands or the adjacent mainland. Nearby islands show similar species richness and the SAR lag distance of 1000 km is a reasonable measure of a regional species pool. On remote volcanic archipelagos, the regional similarity might arise from intra-archipelago speciation and dispersal (Price 2004). Continental islands, on the other hand, are more closely tied to the large species pool of adjacent mainland floras.

As anticipated by MacArthur & Wilson (1967) and various others from regional-scale studies (e.g. Cody 2006), area and geographic isolation, indeed emerge as the strongest drivers of island species richness also at a global scale (69% is explained by area and distance alone). However, water and energy-related variables and topography show strong additive effects when simultaneously controlling for differences in area and isolation. The *ad hoc* model thus combines aspects of MacArthur and Wilson's Equilibrium Theory (variables area and isolation) with climate-based (Wright 1983; Hawkins *et al.* 2003; Currie *et al.* 2004) and heterogeneity-based diversity approaches (Shmida & Wilson 1985; Guégan *et al.* 1998). The model provides a first global, quantitative baseline of insular plant diversity that is in accordance with many previous observations and anticipated patterns (Whittaker & Fernández-Palacios 2007). As demonstrated previously for mainland regions (Kreft & Jetz 2007), our model illustrates the interplay of different core drivers on species richness and may provide a quantitative baseline for predicting species numbers of less studied island floras. It may be further used to derive quantitative predictions of changes in species richness as a result of climate change or non-native species. The latter leads to a strong increase in net species richness on islands (Sax *et al.* 2002). The intended or unintended introduction of non-native species caused by humans might be interpreted as an abolishment of the geographic isolation that formerly maintained the biogeographic integrity of the respective flora. Although regional-scale studies suggest that species–area–distance relationships might be different for native and non-native species (Rejmánek *et al.* 1991), replacing the distance to the mainland of an island by zero should give at least an idea about the expected magnitude of species richness changes. The global biogeographic consequences of island introductions certainly merit further research.

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REFERENCES

- Arrhenius, O. (1921). Species and area. *J. Ecol.*, 9, 95–99.
- Barthlott, W., Mutke, J., Rafiqpoor, M.D., Kier, G. & Kreft, H. (2005). Global centres of vascular plant diversity. *Nova Acta Leopold.*, 92, 61–83.
- Bivand, R. (2006). *Spdep: Spatial Dependence: Weighting Schemes, Statistics and Models*. R Package Version 0.3-17. <http://cran.r-project.org/src/contrib/descriptions/spdep.html>. Last accessed on 14 June 2005.
- Brown, J.H. (1971). Mammals on mountaintops: nonequilibrium insular biogeography. *Am. Nat.*, 105, 467–478.
- Buckley, L.B. & Jetz, W. (2007). Insularity and the determinants of lizard population density. *Ecol. Lett.*, 10, 481–489.
- Cody, M.L. (2006). *Plants on Islands – Diversity and Dynamics on a Continental Archipelago*. University of California Press, Berkeley.
- Connor, E.F. & McCoy, E.D. (1979). The statistics and biology of the species–area relationship. *Am. Nat.*, 113, 791–833.
- Connor, E.F. & Simberloff, D. (1978). Species number and compositional similarity of the Galápagos flora and avifauna. *Ecol. Monogr.*, 48, 219–248.
- Currie, D.J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.*, 137, 27–49.
- Currie, D.J., Mittelbach, G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A. *et al.* (2004). Predictions and tests of climate-based hypotheses of broad-scale variations in taxonomic richness. *Ecol. Lett.*, 7, 1121–1134.
- Dormann, C.F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Glob. Ecol. Biogeogr.*, 16, 129–138.
- Fortin, M.-J. & Dale, M.R.T. (2005). *Spatial Analysis: a Guide for Ecologists*. Cambridge University Press, Cambridge.
- Guégan, J.-F., Lek, S. & Oberdorff, T. (1998). Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, 391, 382–384.
- Harris, L.D. (1984). *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press, Chicago.
- Hawkins, B.A. & Diniz-Filho, J.A.F. (2004). 'Latitude' and geographic patterns in species richness. *Ecography*, 27, 268–272.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M. *et al.* (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2006). *The WorldClim Interpolated Global Terrestrial Climate Surfaces*, version 1.4. Available at: <http://biogeography.berkeley.edu/>. Last accessed on 26 November 2006.
- Hobohm, C. (2000). Plant species diversity and endemism on islands and archipelagos, with special reference to the Macaronesian islands. *Flora*, 195, 9–24.
- Jetz, W. & Rahbek, C. (2002). Geographic range size and determinants of avian species richness. *Science*, 297, 1548–1551.
- Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.*, 19, 101–108.

- Johnson, M.P. & Simberloff, D.S. (1974). Environmental determinants of island species numbers in the British Isles. *J. Biogeogr.*, 1, 149–154.
- Kalmar, A. & Currie, D.J. (2006). A global model of island biogeography. *Glob. Ecol. Biogeogr.*, 15, 72–81.
- Kerr, J.T. & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, 385, 252–254.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. *et al.* (2005). Global patterns of plant diversity and floristic knowledge. *J. Biogeogr.*, 32, 1107–1116.
- Kissling, D. & Carl, G. (2008). Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.* (DOI: 10.1111/j.1466-8238.2007.00334.x; in press).
- Kreft, H. & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proc. Natl Acad. Sci. U.S.A.*, 104, 5925–5930.
- Kühn, I. (2007). Incorporating spatial autocorrelation may invert observed patterns. *Divers. Distrib.*, 13, 66–69.
- Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74, 1659–1673.
- Lichstein, J.W., Simons, T.R., Shiner, S.A. & Franzreb, K.E. (2002). Spatial autocorrelation and autoregressive models in ecology. *Ecol. Monogr.*, 72, 445–463.
- Lomolino, M.V. (2000). Ecology's most general, yet protean pattern: the species-area relationship. *J. Biogeogr.*, 27, 17–26.
- Lomolino, M.V. (2001). The species-area relationship: new challenges for an old pattern. *Prog. Phys. Geogr.*, 25, 1–21.
- Lomolino, M.V. & Weiser, M.D. (2001). Towards a more general species-area relationship: diversity on all islands, great and small. *J. Biogeogr.*, 28, 431–445.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Mueller-Dombois, D. (2002). Forest vegetation across the tropical Pacific: a biogeographically complex region with many analogous environments. *Plant Ecol.*, 163, 155–176.
- Mutke, J. & Barthlott, W. (2005). Patterns of vascular plant diversity at continental to global scales. *Biol. Skr.*, 55, 521–538.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- Preston, F.W. (1962). The canonical distribution of commonness and rarity. *Ecology*, 43, 185–215.
- Price, J.P. (2004). Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. *J. Biogeogr.*, 31, 487–500.
- Pyšek, P. & Richardson, D.M. (2006). The biogeography of naturalization in alien plants. *J. Biogeogr.*, 33, 2040–2050.
- Rahbek, C. & Graves, G.R. (2001). Multiscale assessment of patterns of avian species richness. *Proc. Natl Acad. Sci. U.S.A.*, 98, 4534–4539.
- Rejmánek, M. (1989). Invasibility of plant communities. In: *Biological Invasions: a Global Perspective* (eds Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. *et al.*). John Wiley and Sons, New York, pp. 369–388.
- Rejmánek, M., Thomson, C.D. & Peters, I.D. (1991). Invasive vascular plants of California. In: *Biogeography of Mediterranean Invasions* (eds Groves, R.H. & Di Castri, F.). Academic Press, Cambridge, pp. 81–101.
- Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Sax, D.F., Gaines, S.D. & Brown, J.H. (2002). Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.*, 160, 766–783.
- Scheiner, S.M. (2003). Six types of species-area curves. *Glob. Ecol. Biogeogr.*, 12, 441–447.
- Shmida, A. & Wilson, M.V. (1985). Biological determinants of species diversity. *J. Biogeogr.*, 12, 1–20.
- Stoddart, D.R. (1992). Biogeography of the tropical Pacific. *Pac. Sci.*, 46, 276–293.
- Tjorve, E. (2003). Shapes and functions of species-area curves: a review of possible models. *J. Biogeogr.*, 30, 827–835.
- Tognelli, M.F. & Kelt, D.A. (2004). Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography*, 27, 427–436.
- UNEP (1998). *Island Directory – Basic Environmental and Geographic Information on the Significant Islands of the World*. Available at: <http://islands.unep.ch/isldir.htm>. Last accessed on 10 July 2005.
- Whittaker, R.J. (2006). Island species-energy theory. *J. Biogeogr.*, 33, 11–12.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007). *Island Biogeography*, 2nd edn Oxford University Press, Oxford.
- Whittaker, R.J., Ladle, R.J., Araújo, M.B., Fernández-Palacios, J.M., Delgado, J.D. & Arévalo, J.R. (2007). The island immaturity – speciation pulse model of island evolution: an alternative to the “diversity begets diversity” model. *Ecography*, 30, 321–327.
- Williams, C.B. (1964). *Patterns in the Balance of Nature*. Academic Press, New York.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2001). The species-area relationship does not have an asymptote. *J. Biogeogr.*, 28, 827–830.
- Wright, D.H. (1983). Species-energy theory: an extension of species area-theory. *Oikos*, 41, 496–506.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Moran's I correlograms for islands (a), mainlands (b), and the combined data sets (c). Shown are patterns of spatial autocorrelation for raw species richness (black) as well as residuals from Generalized Linear (green) and Spatial Linear (red) multi-predictor models (compare Table 2 and Supplementary Table S4).

Figure S2 Geographic patterns of residual variation of island species richness from the multi-predictor generalized linear models (GLMs) and spatial linear models (SLMs). Values represent standard deviations.

Table S1 Matrix of correlation coefficients (Pearson's r) between independent variables for $n = 488$ islands investigated in this study. For the three island types mean values (\pm standard deviations) are given. All variables (except for distance) were log10-transformed. Superior letters indicate

significant differences among islands of different geological origin (Tukey's HSD post hoc test).

Table S2 Single-predictor relationships between vascular plant species numbers on islands, mainland regions and in the combined data set. Results of traditional, non-spatial Generalized Linear Models (GLM). Species richness (response) and all continuous predictor variables (except for distance) were log10 transformed.

Table S3 Two-way interaction effects among all investigated variables and plant species richness on islands. ΔAIC values are shown ($\Delta AIC = AIC_{main} + AIC_{int}$; where AIC_{main} is the Akaike information criterion for the model with only main effects and AIC_{int} including main effects plus interaction terms). High ΔAIC values indicate strong interactive effects. SAR results are shown in the upper right block, GLM result in the lower left block. ΔAIC values > 2 are marked in bold.

Table S4 Multi-predictor models of vascular plant species richness on island and mainland floras and the combined

data set. Results of traditional, non-spatial Generalized Linear Models (GLM).

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