Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2006) **15**, 72–81

RESEARCH PAPER

A global model of island biogeography

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ABSTRACT

Aim The goal of our study was to build a global model of island biogeography explaining bird species richness that combines MacArthur and Wilson's area–isolation theory with the species–energy theory.

Location Global.

Methods We assembled a global data set of 346 marine islands representing all types of climate, topography and degree of isolation on our planet, ranging in size from 10 ha to 800,000 km^2. We built a multiple regression model with the number of non-marine breeding bird species as the dependent variable.

Results We found that about 85–90% of the global variance in insular bird species richness can be explained by simple, contemporary abiotic factors. On a global scale, the three major predictors — area, average annual temperature and the distance separating the islands from the nearest continent — all have constraining (i.e. triangular rather than linear) relationships with insular bird species richness. We found that the slope of the species–area curve depends on both average annual temperature and total annual precipitation, but not on isolation. Insular isolation depends not only on the distance of an island from the continent, but also on the presence or absence of other neighbouring islands. Range in elevation — a surrogate for diversity of habitats — showed a positive correlation with bird diversity in warmer regions of the world, while its effect was negative in colder regions. We also propose a global statistical model to quantify the isolation-reducing effect of neighbouring islands.

Main conclusions The variation in avian richness among islands worldwide can be statistically explained by contemporary environmental variables. The equilibrium theory of island biogeography of MacArthur and Wilson and the species–energy theory are both only partly correct. Global variation in richness depends about equally upon area, climate (temperature and precipitation) and isolation. The slope of the species richness–area curve depends upon climate, but not on isolation, in contrast to MacArthur and Wilson's theory.

Keywords

Birds, climate, diversity, island biogeography, isolation, richness–energy, species–area, species–energy, species richness.

INTRODUCTION

Variation in species richness among islands gave rise to one of the most fruitful areas of ecology. The simple hypotheses proposed in MacArthur and Wilson's (1967) *The theory of island biogeography* spawned an enormous literature with both theoretical and conservation implications (Gilbert, 1980; Rosenzweig, 1995; Whittaker, 1998) that are discussed in most contemporary ecological textbooks; yet the literature that addresses the factors that determine species richness on islands contains a very curious gap.

MacArthur and Wilson (1963, 1967) proposed that species richness on islands is the result of immigration (sometimes reinforced by speciation) and extinction. They hypothesized that

DOI: 10.1111/j.1466-822x.2006.00205.x

Table 1 Dependent and independent variables used in our regression models explaining non-marine bird species richness, $n = 346$

Variable	Minimum	Maximum	Median
No. of species	0	547	28.5
Island area (km^2)	0.085	820033	625.0
Highest elevation (m)	3	5030	710.5
Mean annual temperature (°C)	−26	30	20.3
Total annual precipitation (mm)	25	5470	1077.5
Distance to continent (km)	0.23	6178	364.0
Neighbour index*	2.7e-07	1823	0.012

*No units (based on eqn 2).

larger islands have lower extinction rates than smaller ones, and that islands further from the mainland have lower immigration rates than coastal islands. Their hypothesis predicts that species richness should covary positively with island area in a set of similarly isolated islands. Further, richness should covary negatively with distance from the source of colonists in a set of islands of similar size. The classic tests of the mechanisms involved in the equilibrium model of island biogeography examined these predictions mainly at local to regional scales. Thus, the data implicitly excluded the effects of factors that vary over larger spatial scales (e.g. climate or evolutionary history).

In contrast, many other studies of biodiversity gradients have focused on habitat variables that might somehow limit diversity. Hutchinson (1959), for example, hypothesized that species richness is limited by the partitioning of available energy among the species present in any locality (Hutchinson, 1959; Brown, 1981). Gradients of richness would thus arise where energy availability differs among regions. Similarly, areas with more diverse habitats may have more species (Kerr & Packer, 1997; Ricklefs & Lovette, 1999). Latham and Ricklefs (1993) suggest that regional differences in evolutionary history largely determine spatial variation in species richness. Tests of these ideas have typically examined species richness over very large spatial extents (e.g. Adams & Woodward, 1989; Francis & Currie, 2003).

Wright (1983) attempted to refine MacArthur and Wilson's theory using the species–energy hypothesis (Hutchinson, 1959; Brown, 1981). He proposed that islands are essentially energy collectors. The amount of energy collected by an island varies with primary productivity per unit area, and it increases in proportion to island area. Islands that are warm and wet (i.e. high actual evapotranspiration: AET) are more productive, and therefore more speciose than islands with low AET. To test this idea, Wright (1983) related land and freshwater bird species richness on 28 islands around the world to the product of island area and per-unit-area net primary productivity. Wright's regression model explained statistically nearly 80% of non-marine bird species richness by total net primary productivity per island. However, Wright did not address the question of isolation, which figures prominently in works deriving from MacArthur and Wilson. The high percentage of explained variance in Wright's results seems to suggest that isolation has a negligible influence on insular diversity. However, almost all the islands in Wright's data were on continental shelves. Therefore, just as MacArthur and Wilson excluded the effects of variables such as climate by focusing on individual archipelagos so, too, Wright excluded the effects of isolation by considering islands located at relatively small distances from the nearest continent (median = 171.5 km, $n = 36$; cf. Table 1).

More generally, research in the past three decades on island species richness has concentrated on the study of particular archipelagos, which represent very limited subsets of the set of islands that exist globally. These studies often examined different sets of independent variables. Consequently, the predictor variables related most strongly to species richness often differed not only among taxa but also among archipelagos. One interpretation of these results is that the factors that determine richness on islands are local and idiosyncratic (e.g. Slud, 1976). Another possible explanation is that regional differences in evolutionary history have strongly affected diversity (e.g. Ricklefs, 2004). In addition, the importance of predictor variables in various studies depends strongly on scale (i.e. the range of variation in area, isolation, elevation, etc.) and on the mobility of the taxa studied (Martin, 1981; Rosenzweig, 1995; Whittaker, 1998, 2000). In the present paper we show that it is possible to construct a global area–isolation–climate model, encompassing virtually the full scale of variability in all the predictor variables used (Table 1).

Acknowledging that many factors *can* be related to patterns of richness under particular circumstances, we propose to test simultaneously the disparate set of hypotheses discussed above by examining bird species richness on islands covering a full range of area, elevation, isolation and climate. In particular, we inquire how much of the global variation in species richness is related to climate (temperature and precipitation), island area, isolation, topography (e.g. Ricklefs & Lovette, 1999) and biogeographical region.

METHODS

We examined the relationship between bird species richness and island characteristics based on published records from islands worldwide. We collected data describing 346 islands ranging in area from less than 0.1 km^2 to more than 800,000 km^2, located in all major geographical and climatic regions on Earth (Fig. 1). The data include the full range of island types, from isolated tropical atolls to Antarctic islands embedded in permanent ice. Although most of our data were included nonsystematically (i.e. we included data as we encountered them), we did seek actively to maximize the range of variability in predictor variables and to minimize collinearity by finding islands with particular characteristics (e.g. large islands with low elevation, small coastal islands, small satellite islands, etc.).

Islands in this study are nearly always single landmasses. About two dozen are atolls (these may have separate islets within their lagoon) and half a dozen are fragmented islands (highly compact groups forming a single ensemble, e.g. Andros in the Bahamas or Aru near New Guinea). We did not include recently formed volcanic islands, tidal islands, islands located in freshwater

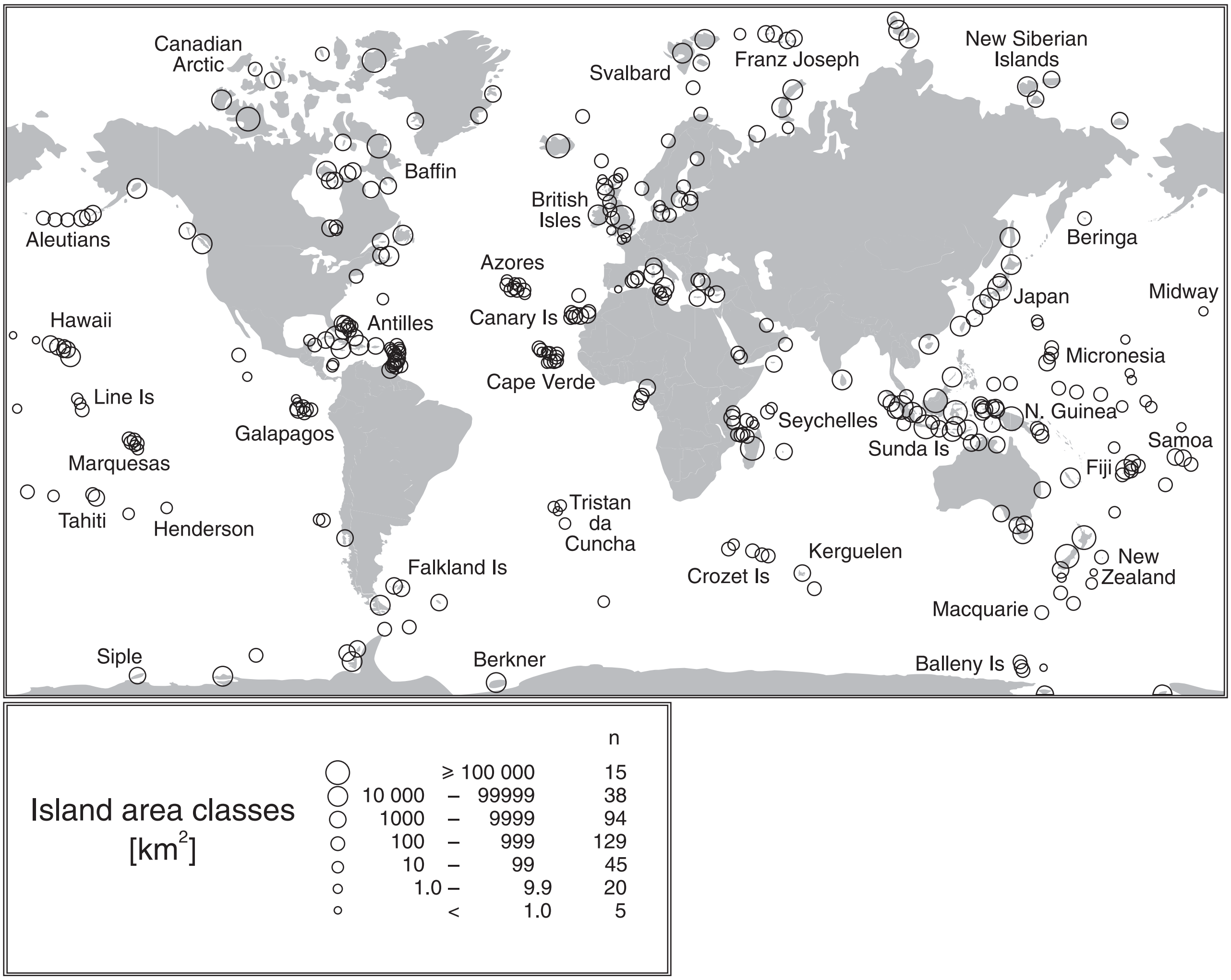

Figure 1 Spatial distribution of the 346 islands included in this study.

bodies or data pooled over groups of islands (e.g. the Philippines as a single unit: Wright, 1983).

The number of breeding bird species on each island was determined from annotated checklists and distribution tables in international field guides and ornithological journals (see Appendix S1). We also used range descriptions and range maps in cases where this could be undertaken unambiguously (i.e. not in cases where a species could be absent from an island even though its geographical range overlaps the island). For New Caledonia and three islands in the Lesser Sundas (Flores, Sumba and Timor) we used the number of breeding land and freshwater bird species indicated in Wright's study (1983).

We included only species described as breeding, or probably breeding, on a given island. Thus, migratory birds were counted only in their breeding range. We did not try to include all recorded species from each island because 'complete' checklists tend to include varying numbers of vagrant species, depending on sampling intensity. There were rarely sufficient data to distinguish among non-breeding winter visitors, migrants, regular vagrants, irregular vagrants, etc.

In addition to extant and recently extinct species, we included species extirpated within the past 400 years, using information from Walters (1980), Fuller (1987), Ripley (1977) and Greenway (1958). We also included species that are likely to have independently — i.e. without direct human intervention — colonized islands. By including both recent natural colonists and extirpated species, we may have overestimated instantaneous species richness. We did this because it was rarely possible to pinpoint times of extinction or colonization. However, because cases of observed natural colonization are rare (an order of magnitude less frequent than extinctions), their effect on our analyses is probably minimal. Fossil species, introduced species and established populations of domesticated birds were excluded from our analysis.

We also excluded marine species from our study because their distribution patterns are likely governed by factors other than those affecting terrestrial birds. These are the Spheniscidae (penguins), Procellariiformes (albatrosses, shearwaters, storm petrels, etc.), Phaethontidae (tropic birds), Sulidae (boobies and gannets), Fregatidae (frigate birds), Stercorariidae (skuas) and Alcidae (auks). Marine species or local marine populations of species in the following taxa were also excluded: Pelecanidae (pelicans), Phalacrocoracidae (cormorants), Anatidae (ducks and geese), Laridae (gulls and terns) and Rynchopidae (skimmers).

We used average annual temperature and total annual precipitation — the two readily obtainable components of actual evapotranspiration — as our descriptors of climate. For islands having weather stations, we calculated the island's mean temperature and precipitation from local weather station records (Walter & Lieth, 1967; Wernstedt, 1972). For islands without any weather station, temperature and precipitation were inferred from measurements at the nearest weather stations and from maps showing temperature and precipitation gradients (see Appendix S1). We would have liked to examine relationships between richness and potential evapotranspiration (Currie, 1991) and/or net primary production (Adams & Woodward, 1989). However, these data proved to be unavailable for many small islands.

To examine isolation effects we considered three factors: (1) distance from each island to the nearest continent, (2) distances to other neighbouring islands and (3) the area of these neighbours. We hypothesized that the effect of neighbouring islands on the richness of a target island is additive, and that richness could, in principle, depend on all islands closer than the continent. We postulated that the importance of a neighbour as a potential source of colonization is proportional to its area (A, km^2), and inversely proportional to the distance (D, km) that separates it from the target island. A general formula for the neighbour effect (η) can therefore be written as:

$$\eta = \sum \frac{A^{a}}{(D+1)^{b}} \qquad \text{eqn 1}$$

where the exponents a and b are empirical constants, estimated iteratively by modifying them to maximize the correlation with species richness. Theoretically the summation includes all islands closer than the continent but, for practicality, we omitted neighbours that would contribute only negligibly to the summation because they are too small and/or too distant. Thus, the 346 islands of our data set each have, on average, 8.5 neighbours (SD = 7.9). For 19 islands we found no sizeable neighbour closer than the continent. So that these would not be missing cases in the analyses, we assigned a hypothetical neighbour half the size of the smallest neighbour in our data set, located at half the distance to the continent (the midpoint of the possible range). This is analogous to adding a value of 0.5 to data before log transformation so that values of 0 do not become undefined. Distance to the neighbour (km) was increased by 1 in eqn 1 to prevent very close neighbours from having inordinate influence on η.

Isolation was measured as the linear distance over open sea. For island chains, the distances between islands were summed, excluding the distances over the land areas of the 'stepping stones'. Neighbouring islands having no land birds at all were excluded from our neighbour index. (It would be biologically meaningless, for example, to consider a large Antarctic island as a potential source of colonization for a smaller island nearby, if the larger island does not support land bird species at all. For the same reason, Antarctica was not considered as a continent or a neighbour.)

Species richness (S) values were transformed as $S' = (S + 0.5)^{0.2}$ in order to stabilize residual variance in statistical analyses. In practice, this transformation is close to the logarithmic transformation that has been used more commonly in earlier literature. The fifth root transformation yields residuals that conform more closely to a normal distribution in the present data set. The results presented below are qualitatively identical when the logarithmic transformation is used.

Independent variables in our analyses were transformed before analysis such that their distributions would be approximately symmetric. Thus, we related species richness to the following environmental variables: (1) logarithm of the total land area of an island in km^2; (2) range in elevation on the island, i.e. the difference in metres between sea level and the highest point, raised to the power of 0.4; (3) mean annual temperature in °C, untransformed; (4) total annual precipitation in mm, raised to the power of 0.4; (5) distance to the continent measured as the shortest distance over open sea to the nearest continental coast in km, raised to the power of 0.2; (6) logarithm of the neighbour index (defined by equation 3); and (7) we also included faunal region in our analyses: a categorical variable with seven levels: Palearctic, Oriental, Ethiopian, Australasian, Nearctic, Neotropical and Antarctic/sub-Antarctic (Sclater, 1858). The Oriental–Australasian boundary follows Weber's line (Weber, 1902).

RESULTS

Collinearity among predictor variables in our data set is reasonably low (Table 2). Three cases deserve special attention. Mean annual temperature and precipitation are collinear, reflecting the low absolute humidity of cold air. In general, islands in polar regions cannot have as much annual precipitation as tropical islands. Further, as a consequence of convection and Hadley cell circulation, there are few dry islands in temperate regions.

Table 2 Pearson correlation matrix of predictor variables used in our multiple regression models to explain variation in insular bird species richness. For $n = 346$, correlations at $|r| \geq 0.105$ are significant at $P = 0.05$, and at $|r| \geq 0.175$ they are significant at $P = 0.001$

	Log (area)	Elevation$^{0.4}$	Temperature	Precipitation$^{0.4}$	(Distance to cont.)$^{0.2}$
Log(area)	1.000				
Elevation$^{0.4}$	0.580	1.000			
Temperature	–0.272	–0.046	1.000		
Precipitation$^{0.4}$	–0.049	0.130	0.564	1.000	
(Distance to continent)$^{0.2}$	–0.373	0.053	0.164	0.231	1.000
Log(neighbour index)	0.441	0.231	–0.085	0.029	–0.261

Secondly, maximum elevation is related to island size: very small islands cannot be as high as large islands. Thirdly, as distance from the continental shore increases, the abundance of large islands decreases, thus island area is negatively correlated with the distance to the continent. Note that the strongest of these three collinearities is $r = 0.58$.

Islands tend to have a clustered distribution over the globe (Fig. 1). To estimate the extent of autocorrelation in our data, we selected randomly 2000 pairs of islands, and we generated a semi-variogram (i.e. the squared difference in number of species as a function of the distance between the pairs of islands, both fifth-root transformed). The correlation between semivariance and distance in our data set was very weak ($r^2 = 0.035$). We concluded that spatial autocorrelation is not pronounced, and it is unlikely to influence significance tests to any great degree in the models presented below. Nonetheless, to remain conservative we interpret only relationships stronger than $P < 0.001$ (except where noted).

On the global scale, relationships between richness and most environmental variables we examined are restrictive (triangular), rather than simple functions (e.g. Fig. 2). It appears that area, temperature, precipitation and distance to the nearest continent can all potentially set an upper limit to richness, but richness falls below this maximum on many islands due to one or more of the other potential limiting factors. Consequently, in data that include islands globally, richness is significantly related to area, isolation and climate, but no individual correlation dominates (Table 3).

Richness is often related more strongly to interactions among environmental variables than to individual variables (Table 3). Consider, for example, the richness–area relationship (the 'species–area curve'). As a function of temperature, the slope of the richness–area relationship (Fig. 3a) increases progressively from 0.04 at −20 °C to 0.41 at +30 °C (the slope of log–log species–area relationships increase from −0.005 to 0.44). Area, temperature and their interaction can statistically account for 64% of the global variation in insular bird species richness (Table 4, model 1).

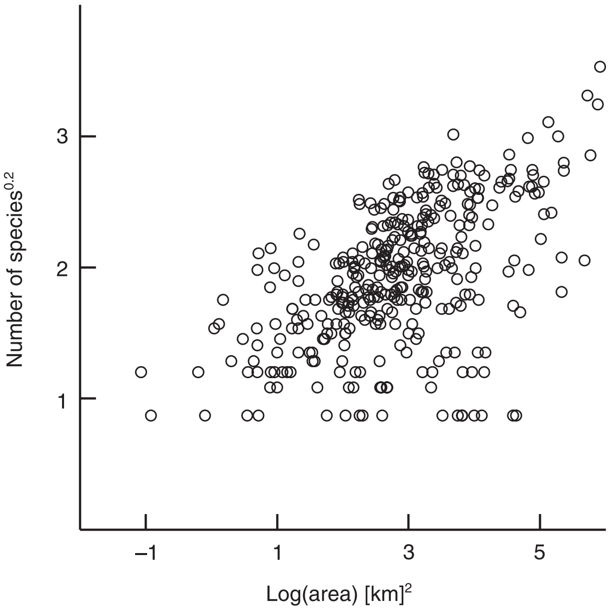

Figure 2 Relationship between the logarithm of bird species richness (plus 0.5) and island area. Similar restrictive (i.e. triangular) relationships are observed when the predictor variable is temperature or precipitation; $n = 346$.

Table 3 Correlations between avian richness (fifth root-transformed) and various environmental variables and two-way interaction terms on bird species richness, $n = 346$

Term	r^2	P
Log(area)	0.29	$< 10^{-15}$
Temperature	0.12	$< 10^{-10}$
Precipitation$^{0.4}$	0.08	$< 10^{-7}$
Log(area) × temperature	0.37	$< 10^{-15}$
Log(area) × precipitation$^{0.4}$	0.45	$< 10^{-15}$
Distance to continent$^{0.2}$	0.39	$< 10^{-15}$
Log(neighbour index)	0.18	$< 10^{-15}$
Distance to continent$^{0.2}$ × log(neighbour index)	0.41	$< 10^{-15}$
Elevation$^{0.4}$	0.07	$< 10^{-5}$
Elevation$^{0.4}$ × temperature	0.09	$< 10^{-8}$

Richness depends similarly upon an interaction between area and precipitation (Fig. 3b). Among dry islands, richness is nearly independent of island area, but the richness–area slope increases progressively with precipitation (Fig. 3b). Note that the area–precipitation interaction term alone explains more variance in richness than area and temperature or area and precipitation additively (Table 3).

In our worldwide data, richness is correlated only weakly with elevation range (Table 3), a variable thought to be a surrogate for habitat diversity (e.g. Ricklefs & Lovette, 1999). The simple richness-elevation correlation is so strongly collinear with area (Pearson, $r = 0.58$) that, when both variables are included in a model, elevation range becomes nonsignificant (Table 4, model 4). However, the effect of elevation range has an important interaction with temperature (Fig. 3c). When elevation range and an elevation range–temperature interaction are included together in a multiple regression, they are both significant (Table 5). Cumulatively, temperature, elevation range and their interaction can explain 29% of insular bird diversity (cf. Table 4, model 1).

Richness also relates to an interaction between temperature and precipitation (Fig. 3d). Among very cold islands, richness is either unrelated to precipitation or weakly negatively related. In temperate regions, richness is a moderately peaked function of precipitation, and the peak increases with temperature. In hot regions, richness increases with precipitation. From another perspective, richness is a plateauing function of temperature on dry islands, but on wet islands, richness continues to increase with increasing temperature. The residual variation explained by the temperature–precipitation interaction in multiple regression models is small (Table 5) because it is strongly collinear with other climate descriptors. The simple correlation between richness and this interaction is $r^2 = 0.18$.

Several statistically indistinguishable multiple regression models (e.g. Table 4, model 3) can be constructed that include area, quadratic functions of temperature and precipitation, and

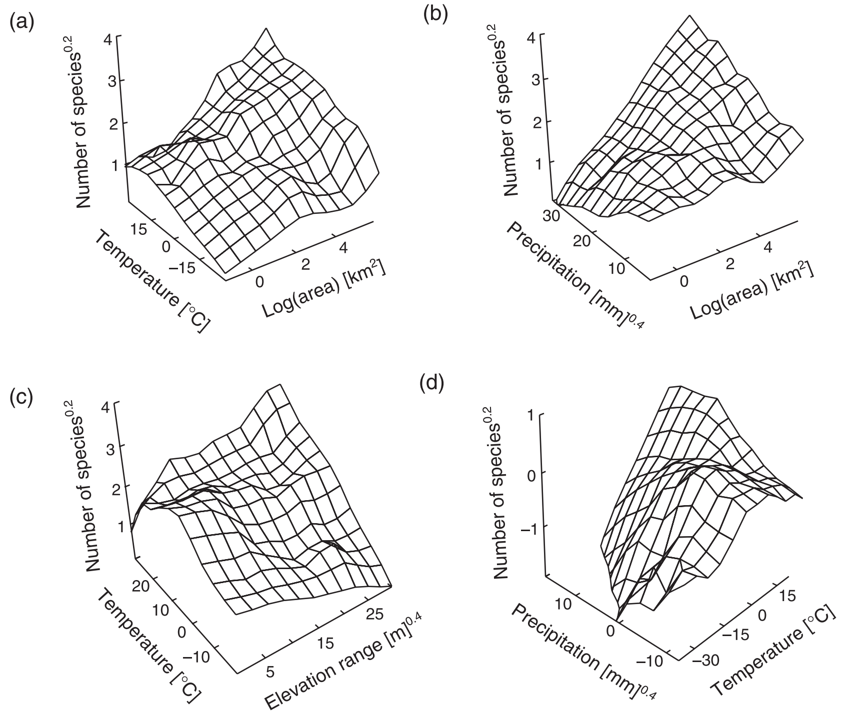

Figure 3 Dependence of bird species richness on interactions between island area, mean annual temperature, total annual precipitation and elevation range on islands. Smoother method: distance weighted least square (DWLS), tension 0.7, $n = 346$. Panel (d) shows residuals after controlling for area.

Table 4 Multiple regression models predicting bird species richness (fifth root-transformed) on islands worldwide. Model 1 accounts for the combined effects of area and temperature, and model 2 for area and precipitation. Model 3 is a general species–energy model. Model 4 shows that elevation range has little effect *per se* (cf. Table 3). Model 5 is a climate model without area (cf. model 3). Models 6 and 7 show the effects of our two isolation metrics. $n = 346$

Model	Predictors used in GLMs	*P*	Model r^2
1	Log(area)	0.001	0.64
	Temperature	$< 10^{-7}$	
	Temperature × temperature	$< 10^{-7}$	
	Log(area) × temperature	$< 10^{-4}$	
2	Log(area)	0.035	0.48
	Precipitation$^{0.4}$	0.697	
	precipitation$^{0.4}$ × precipitation$^{0.4}$	0.017	
	Log(area) × precipitation$^{0.4}$	$< 10^{-12}$	
3	Temperature	$< 10^{-15}$	0.70
	Temperature × temperature	$< 10^{-15}$	
	Precipitation$^{0.4}$	$< 10^{-15}$	
	Log(area) × precipitation$^{0.4}$	$< 10^{-15}$	
	Temperature × precipitation$^{0.4}$	$< 10^{-15}$	
4	Log(area)	$< 10^{-4}$	0.29
	Elevation$^{0.4}$	0.150	
5	Temperature	$< 10^{-3}$	0.26
	Temperature × temperature	$< 10^{-3}$	
	Precipitation$^{0.4}$	0.001	
	Precipitation$^{0.4}$ × precipitation$^{0.4}$	0.027	
	Temperature × precipitation$^{0.4}$	0.001	
6	Distance to continent$^{0.2}$	$< 10^{-11}$	0.48
	Distance to continent$^{0.2}$ × log(neighbour index)	$< 10^{-13}$	
7	Distance to continent$^{0.2}$	$< 10^{-10}$	0.54
	Distance to continent$^{0.2}$ × log(Neighbour index)	$< 10^{-9}$	
	Log(area)	$< 10^{-6}$	

interactions among these variables, all with $r^2 = 0.69–0.70$. Their common elements are that all three variables remain in the models, usually involving interaction terms. Area and temperature effects predominate.

Richness on islands is also very clearly related to isolation (Tables 3 and 4, models 6 and 7). The strongest single correlate of richness is the distance to the nearest continent, although the relationship is again triangular (Fig. 4). Richness is also positively

Table 5 A multiple regression model of insular bird species richness (fifth root-transformed) on environmental variables. Variables are listed in order of inclusion by forward selection (beginning with the variables listed in Table 3), with the cumulative proportion of explained variance. The proportion of the variance explained by the variable when added last to the model is also shown, $n = 346$

Term	Cumulative r^2	Increase in r^2, added last
Log(area) × precipitation$^{0.4}$	0.452	0.084
Distance to continent$^{0.2}$	0.728	0.092
Temperature*	0.827	—
Distance to continent$^{0.2}$ × log(neighbour index)	0.847	0.013
Precipitation$^{0.4}$ × precipitation$^{0.4}$	0.858	0.010
Temperature × precipitation$^{0.4}$	0.860	0.003†
Elevation range$^{0.4}$‡	0.877	0.017
Elevation range$^{0.4}$ × temperature‡		

*Temperature, selected by forward selection, becomes non-significant ($P = 0.51$) after the inclusion of elevation range and the elevation range–temperature interaction.

†Not significant in backward elimination.

‡Elevation range and its interaction with temperature are only significant if they are both included in the regression simultaneously.

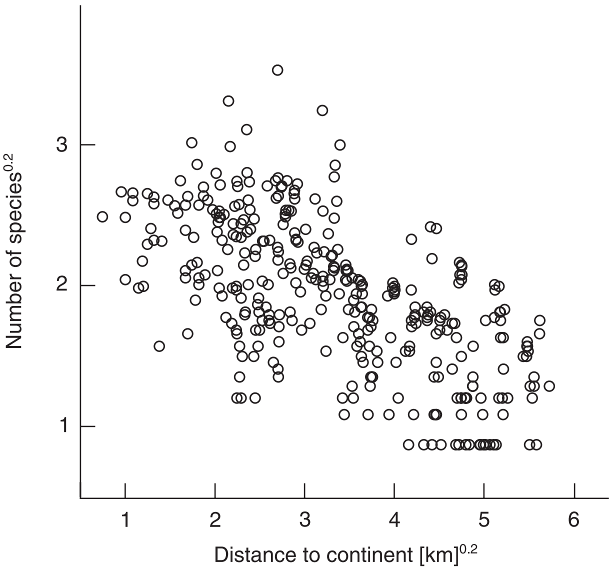

Figure 4 Relationship between species richness and insular isolation (distance to continent = shortest distance over open sea from an island to the nearest continental shore). Note that this relationship is restrictive, approximately triangular (cf. Figure 2); $n = 346$.

related to the presence of neighbouring islands, but much less strongly than to the proximity of a continent (Table 3). By iteratively varying the exponents of neighbour area and distance to neighbour (eqn 1), we found that the correlation between richness and the neighbour index is maximal when the coefficients a and b in eqn 1 are approximately 1 and 2, respectively. In other words, the effect of neighbouring islands is proportional to their area, and inversely proportional to the square of their distance. Thus, equation 1 can be rewritten as:

$$N = \sum \frac{A}{(D+1)^2}. \qquad \text{eqn 2}$$

In multiple regressions, the neighbour index is significant only by its interaction with distance to the continent. This is probably because the effect of neighbours is diminished when the continent is close. Cumulatively, our two isolation metrics can explain statistically 48.5% of the variance in insular bird species richness (Table 4, model 6). The neighbour index is not correlated with distance to the continent (Table 2); its statistical significance indicates that insular isolation is diminished by the presence of neighbouring islands (Table 4, models 6 and 7). Interestingly, we found no significant interaction between area and isolation metrics, suggesting that the slope of the richness–area curve does not depend on isolation.

A multiple regression model (Table 5) incorporating the effects described above can explain statistically 87.7% of the variance in bird species richness among the world's marine islands, yielding a relationship that is no longer triangular (Fig. 5). Note that the main factors are the area–precipitation interaction, distance to the continent and temperature. These three terms can explain 82.7% of the variance in insular bird species richness.

To test if there are significant differences in insular species richness among biogeographical regions we included the categorical variable faunal region in forward- and backward-stepwise models including the variables listed in Table 5. In the forward selection regression, faunal region was the only term

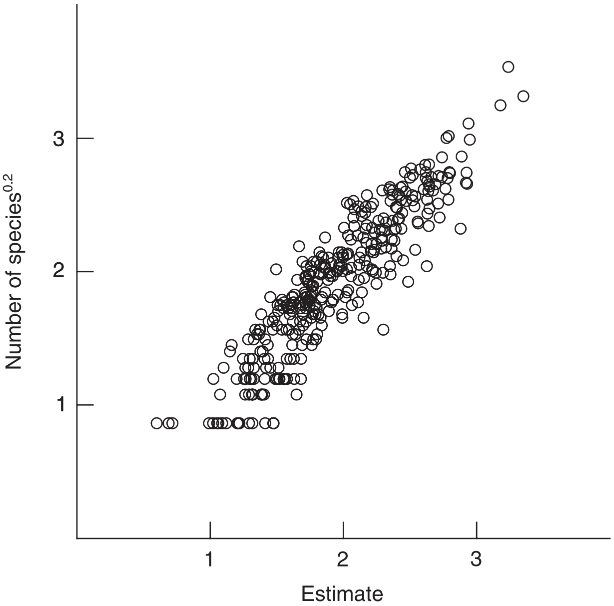

Figure 5 Bird species richness and the estimate of a multiple regression model using three of the predictor variables presented in Table 5: area–precipitation interaction, distance to continent and temperature; $n = 346$.

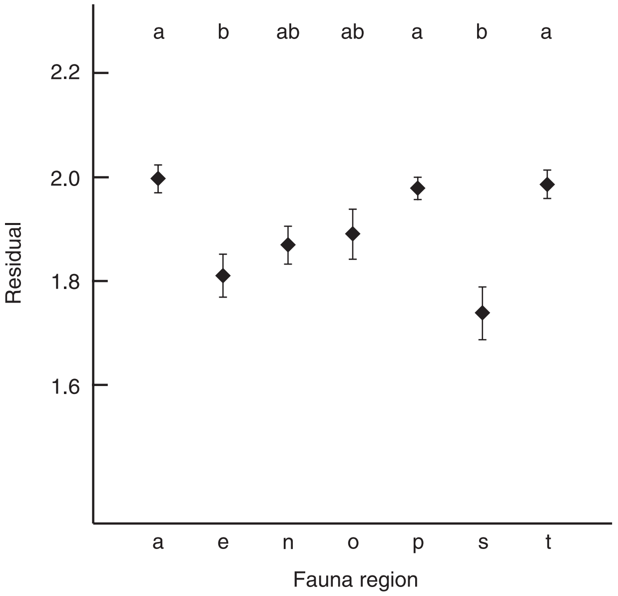

Figure 6 Regional differences of insular bird species richness after accounting for environmental variables describing area, climate and isolation as listed in Table 5 (backward elimination model). Note that results are very similar if we account only for three of these, i.e. area–precipitation, temperature and distance to continent. Abbreviations: a, Australasian, e, Ethiopian, n, Nearctic, o, Oriental, p, Palearctic, s, sub-Antarctic/Antarctic, t, Neotropical; $n = 346$.

eliminated as non-significant. Using backward elimination, faunal region was significant ($P < 10^{-7}$) and the temperature–precipitation interaction is not selected. The effect of faunal region is due mainly to lower than expected diversity in the sub-Antarctic/Antarctic region. *Post hoc* tests showed that there are no significant differences among the Palaearctic, Oriental, Australasian, Nearctic and Neotropical regions (Fig. 6; Tukey's $P \geq 0.2$, with the exception of Palaearctic-Nearctic comparison, where $P = 0.044$).

DISCUSSION

Variation in non-marine bird species richness among oceanic islands worldwide can be related to environmental conditions. Variables describing island size, climate and isolation account for > 87% of the global variation (Table 5). This result is very similar to studies of broad-scale variation in continental species richness (Francis & Currie, 1993; Hawkins *et al.*, 2003). Because this model is applicable to virtually all types of marine islands, there is no evidence to suggest that insular bird diversity is idiosyncratic as has been suggested (cf. Slud, 1976).

As several earlier studies have observed, only very small differences in species richness among faunal regions remain after accounting for contemporary environmental variables (Adams & Woodward, 1989; Francis & Currie, 2003; Hawkins *et al.*, 2003). Although we found diversity to be somewhat lower than expected in the Ethiopian, and especially in the sub-Antarctic/Antarctic regions, we found virtually no differences between faunal regions with outstandingly different history, such as the Australasian, the Palaearctic or the Neotropical regions. The lower than expected diversity in the Ethiopian region may be due to an observer effect (poorer data than elsewhere). In the Antarctic/sub-Antarctic region, diversity may be lower than expected because Antarctica ceased to be a source of potential colonisers long ago.

Our results show that care must be taken in interpreting the slope of species–area relationships. The species–area relationship is usually described as approximately log-linear (e.g. Arrhenius, 1921; MacArthur & Wilson, 1963, 1967; Schoener, 1976; Triantis *et al.*, 2003). Authors often point out that, for islands, the exponent z of the classic species–area equation (Arrhenius, 1921) is generally $0.15 < z < 0.35$. Differences in z have been attributed to a number of biotic and abiotic factors such as the mobility and range size of species, feeding behaviour (predator vs. prey), range of areas sampled, type of area (islands, habitat islands, mainland), habitat fragmentation, etc. However, z also clearly varies with climate. This was also noted by Malyshev (1975, cited by Venevskaia & Venevsky, 2002). Malyshev's plant study suggests that z varies from 0.07 (deserts and tundra) to 0.36 (tropics). Also, Venevsky and Venevskaia (2003) incorporate an area–climate interaction into their model of plant species richness. These results are compatible with our finding that z varies systematically with both temperature and precipitation (Figs 3a,b and 7).

Although Wright (1983) did not include isolation in his global model of richness on islands, we found that isolation is a very important contributor to the global variation in insular species richness. Our findings on insular isolation can be summarized as follows:

1 Richness depends strongly on the distance between islands and the nearest continental shores (Table 3, Fig. 4), which presumably reflects an effect of isolation.

2 Isolation can be reduced by the presence of neighbouring islands (Table 4, models 6 and 7).

3 The isolation-reducing effect of a neighbouring island is proportional to the size of the neighbour and inversely proportional to the square of the distance which separates it from the target island (eqn 2).

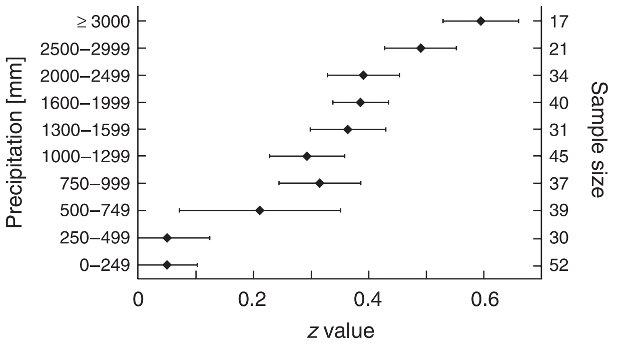

Figure 7 Increase of z slope values of the classic log species–log area relationship with precipitation. Mean z and SE are based on single linear regressions for 10 subsets of the whole dataset, based on ranges of precipitation. The slope of the richness–area relationship also varies continuously with temperature.

4 This neighbour effect is additive and theoretically it depends on all islands that are closer to island A than the nearest continent, although in practice the effect of small and faraway islands is negligible (eqn 2).

5 The importance of neighbours increases with the distance of the target island from the continent.

These relationships are largely consistent with the current understanding of the effect of isolation on species richness (MacArthur & Wilson, 1967; p. 22; Rosenzweig, 1995; p. 236 ff.).

Our results are also consistent with a small effect of habitat diversity on species richness. Our choice to approximate habitat diversity by elevation range rather than a measure of habitat types or vegetation cover was dictated by data availability rather than by theoretical considerations. It is possible that the significance of this term in our regression models underestimates the importance of habitat diversity. Nonetheless, we found that richness is significantly positively related to elevation range in warm areas, and negatively so in polar and sub-polar regions (Fig. 3c). The negative relationship in cold areas is probably because high-elevation zones are too cold to support many species. Note that slope of the richness–elevation relationship varies continuously with temperature; we observe no threshold as suggested by Kerr and Packer (1997).

These results beg the question of what mechanisms produced patterns of richness on islands. Island richness depends upon island area and isolation in a manner that is largely consistent with the mechanisms proposed by MacArthur and Wilson (1963, 1967): colonization, speciation and extinction. In contrast to MacArthur and Wilson, however, we found that the effects of area and isolation are merely additive. Instead of an area–isolation interaction we found strong area–climate interactions (Fig. 3a,b). On the global scale, the species–area relationship is not linear, but restrictive just as are species–climate or species–isolation relationships (Figs 2, 4 and 7).

Richness also depends upon climate in a globally consistent manner, as Francis and Currie (2003) observed for angiosperms. In contrast, our statistical evidence suggests either that regional/historical effects have minor impact on species richness, or that those effects must be very strongly collinear with contemporary climate (cf. Francis & Currie, 2003; Currie & Francis, 2004; Qian & Ricklefs, 2004). The mechanism(s) that underlie the richness–climate correlation are still hotly debated (cf. Hawkins *et al*., 2003; Ricklefs, 2004; Wiens & Donoghue, 2004). This study was not designed to distinguish among them (but see Currie & Francis, 2004).

ACKNOWLEDGEMENTS

This work was supported by a grant from the Natural Sciences and Engineering Research Council of Canada. We thank Robert J. Whittaker and an anonymous reviewer for very constructive criticism of earlier drafts of this work.

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BIOSKETCHES

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Editor: Tim Blackburn

SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 Sources of bird species richness and weather data.