Ecological Biogeography of Southern Ocean Islands: The Importance of Considering Spatial Issues

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abstract: Understanding patterns of among-island variation in species richness has long been an important question in ecology and biogeography. However, despite the clear spatial nature of the data used for such investigations, the spatial distribution of the different sampled locations is rarely explicitly considered, which may be critical for statistical and biological reasons. In a recent study, Chown et al. (1998) investigated the relationships between species richness of different indigenous and introduced taxonomic groups and a variety of variables characterizing Southern Ocean islands, and here, we use these data to address spatial issues. As predicted, we found spatial autocorrelation in species richness for terrestrial taxa with high dispersal ability or for terrestrial taxa that had time to disperse locally (introduced land birds and indigenous taxa) but not for taxa that had low opportunity to disperse to nearby islands (introduced plants, insects, and mammals), which suggests that colonization from nearby islands has played an important role in shaping present-day patterns of among-island variation in species richness. Interestingly, in several cases, the estimated effect of variables changed when spatial covariance was incorporated. Moreover, the absence of autocorrelation of some variables allowed us to confirm some important results of Chown et al. (1998), notably those involving the potential impact of human presence on the biodiversity of these islands. Overall, our results illustrate the importance of considering spatial structures in ecological studies. This is notably the case when dispersal processes can be expected to explain some of the observed patterns.

Keywords: geographic scale, island biogeography, local richness, regional richness, spatial autocorrelation, dispersal.

Studying the ecological biogeography of oceanic islands that have suffered only limited influence from human activities may be of considerable biological and conservation relevance (MacArthur and Wilson 1967; Rosenzweig 1995). The examination of large-scale patterns may reveal underlying processes, such as colonization from nearby locations and local extinction, that are responsible for determining the composition of local communities. Previous studies have shown that the Southern Ocean islands represent a particularly suitable system for identifying factors affecting local species richness. In a recent article, Chown et al. (1998) reexamined the relationship between physical variables, human occupancy, and species richness of different taxa on 25 Southern Ocean islands. They claim that previous qualitative and empirical analyses relating physical variables to species richness of Southern Ocean islands were encumbered by different flaws that may have explained the "anomalous" patterns reported in the literature, namely, that area had less influence on species richness on these islands than past glacial extent, isolation, and low temperature (Chown et al. 1998). In their article, Chown et al. (1998) report results of regressions between biogeographical variables and species richness of islands in which they specifically distinguished introduced and indigenous species in their newly compiled species lists for vascular plants, insects, birds, and mammals and in which the variable describing island size excluded area covered by glaciers.

Since the Southern Ocean islands are distributed over a very large geographic area, one can expect large-scale processes to have played an important role in determining species number and composition of local communities. Indeed, it is increasingly recognized that ecological communities are organized by a variety of processes operating at different spatial scales (Ricklefs and Schluter 1993; Cornell and Karlson 1996; Griffiths 1997). For instance, island properties such as physical characteristics should be thought of as proximate factors that contribute to determine species richness and composition of local communities that can be considered as samples from a colonizer pool available in the region. The size and composition of this colonizer pool are themselves determined by history and the effects of large-scale factors. One way to tackle

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these issues (and that illustrates the importance of considering the hierarchical nature of ecological factors and processes that determine species richness of local communities) is to investigate spatial autocorrelation in the considered variables. The statistical significance of spatial autocorrelation is also of much importance and it has been proposed that checking for the presence of spatial autocorrelation in data should be a preliminary step in ecological studies dealing with large-scale patterns (Legendre 1993).

Spatial autocorrelation may be loosely defined as the property of random variables that take values, at pairs of sites a given distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of observations (Legendre and Legendre 1998). An important consequence of autocorrelation is the potential statistical problem it brings with it: the value of a variable at one point in space is not independent of those at other points in space, and thus, an important assumption of standard statistical tests is violated, namely, that values of studied variables are independent among data points (Cliff and Ord 1981; Legendre 1993). The presence of spatial autocorrelation in the data indicates that a part of the variance of the studied variables is explained by the effect of spatial variability. Spatially independent models do not take this factor into account, which may affect the statistical results, and may consequently lead to erroneous interpretations and conclusions. The alternative is to incorporate space in the analyses by considering the relative geographical position of the locations in which the associated variables were measured. This may give more reliable information on the relationships between the considered explanatory and dependent variables by accounting for the effects of spatial covariance. Statistical approaches and procedures specifically designed to incorporate the spatial structure in the analyses are available and should be used rather than spatially independent procedures when the considered variables, or the residuals of the analyses, are found to be spatially autocorrelated. A possible approach is, for instance, to use spatial covariance models, rather than the nonspatial one, in the regression analyses, especially as suitable statistical procedures are now available (e.g., Littell et al. 1996).

In this article, we use data from Southern Ocean islands published in Chown et al. (1998) to test different predictions about the potential role of spatial attributes in island biogeography. We first investigate spatial autocorrelation in the values of species richness of different taxa and of physical and human variables expected to affect species richness. Second, we carry out regression analyses between species number of some taxa and the explanatory variables by using standard regression models and then models accounting for spatial covariance. We compare the results obtained with the two procedures and discuss how the significance of the relationships between species richness and the explanatory variables can be affected when spatial structuring is taken into account. Finally, we discuss the importance of considering explicitly the spatial structure of systems of islands in attempts to understand the ecological processes and factors determining species richness and composition of local communities.

Predictions

As spatial autocorrelation of physical variables of islands may be the result of large-scale patchiness or gradients of different physical properties, we expected at least two physical variables to be positively autocorrelated: distance and sea-surface temperature variables. The distance variable measured the distance of each island to the nearest continent. We expected this variable to be autocorrelated for small distance classes since several Southern Ocean islands are situated at tens of kilometers from each other but thousands of kilometers from the nearest continent. Similarly, we expected the variable sea-surface temperature to be positively autocorrelated because of the gradient of temperature from temperate islands to colder subantarctic ones.

Positive spatial autocorrelation in species richness for small distance classes could suggest that the number of species in a given island may be at least partly predicted by those of neighboring islands. This could suggest that local communities from islands close to each other are linked by dispersal, and this is consistent with colonization events from nearby islands as an important factor in shaping local communities. Conversely, no spatial autocorrelation in species richness could suggest that colonization events from nearby islands did not play an important role in determining the composition of local communities. Independent of dispersal, communities may also be similar due to similar characteristics of the islands. The importance of colonization events from nearby islands could be expected to vary depending on the taxa considered (we can expect different taxa to be associated with different dispersal and colonization abilities) and also on the period of time species had to colonize other islands. We thus predicted that spatial autocorrelation in species richness would exist for indigenous vascular plants, insects, and land birds; that spatial autocorrelation may not exist for introduced species with low expected-dispersal abilities, that is, vascular plants, insects, and land mammals, because of short colonization time; and that it would exist for the group of introduced species with higher expected-dispersal abilities, that is, land birds.

The existence of spatial autocorrelation in the data likely brings with it a problem of statistical nonindependence among data points and can affect the outcome of the analyses of the relationships between the response variable (species richness of a given taxonomic group in our case) and the considered explanatory variables. We expected this problem to be more present when the former variable exhibits some autocorrelation (see also Lennon 2000). Indeed, the absence of spatial autocorrelation in species richness would indicate that all species were available to all islands whatever their location and that among-island variation in species richness could be simply related to differences in islands characteristics. In such a case, no difference is expected to be introduced in the estimates of the association between species richness and the explanatory variables when investigated at the scale of the entire island system, and we predicted that the models accounting for the relative location of islands will not fit the data better than the nonspatial model. Conversely, spatial autocorrelation in species richness may be the consequence of some environmental variable varying at a regional scale or of the sharing of a common colonizer pool among islands situated nearby. In both cases, this may be independent of the island characteristics considered in the model and may explain part of the pattern. In such a case, we predicted that the spatial covariance models would fit the data better than the nonspatial model does and that these models would produce nonspatially autocorrelated residuals and would give different estimates of the investigated relationship.

Methods

Data

Data analyzed in this work come from tables 1 and 2 of Chown et al. (1998). The study sample is composed of 25 islands in which eight variables were measured: ice-free area (IFA; variable in square kilometers), maximum altitude (altitude variable in meters), minimum age of surface rocks (age variable in million years), distance to the closest continent excluding Antarctica (distance variable in kilometers), sea surface temperature (°C), rank of extent of glaciers at the Neogene maxima of each island (glaciation variable), date of first modern human occupation (date variable), and number of human occupants per year (occupants variable). Moreover, eight taxonomic assemblages were considered in the study with a distinction between indigenous and introduced species: indigenous vascular plants, introduced vascular plants, indigenous insects, introduced insects, indigenous seabirds, indigenous land birds, introduced land birds, and introduced mammals. Species richness for these groups ranged from 0 to 188 for indigenous plants, from 6 to 237 for indigenous insects, and from 0 to 38 for indigenous land birds. Species richness of introduced organisms was lower, although it ranged from 0 to 101 for introduced plants.

Spatial Autocorrelation Analyses

Spatial autocorrelation in the explanatory and dependent variables was investigated by drawing correlograms (Cliff and Ord 1981; Legendre 1993) in which Moran's I (1950) spatial autocorrelation coefficients were plotted on the ordinate against equidistant classes among the 25 islands on the abscissa. Moran's I spatial autocorrelation coefficient behaves in a manner similar to Pearson's correlation coefficient (see Legendre and Fortin 1989) and measures the similarity between observations from pairs of locations for each distance class. Tests of significance for each individual autocorrelation coefficient plotted on the correlogram (Sokal and Oden 1978; Cliff and Ord 1981; Legendre and Legendre 1984) and Bonferroni corrections for multiple testing (see Oden 1984) were carried out to determine whether there was significant spatial structure in the different variables. The shape of the correlogram was used to indicate the type of spatial structure present (Legendre 1993). Of particular significance is the value of the Moran's I for small distance classes, which can show evidence of positive spatial autocorrelation between nearby locations. Analyses were carried out using software "R" (Legendre and Vaudor 1991), which can convert pairs of latitudinal and longitudinal coordinates into distances between the different islands and produce spatial correlograms.

Relationships between Species Richness and Island Characteristics

Analyses of the relationships between the explanatory variables and species richness of the different groups were performed using the MIXED procedure of the SAS statistical package (Littell et al. 1996). The MIXED procedure uses the coordinates of the locations in which the explanatory and the dependent variables were measured and allowed us to use a nonspatial model and to incorporate a model that accounts for spatial covariance (spherical, gaussian, or exponential covariance models) in the regression analysis. In the latter case, initial values of the spatial covariance parameters (sill, range, and nugget in geostatistics notation) were given to the program in order to improve convergence and the likelihood of obtaining reasonable estimates. These initial values were first obtained by plotting semivariograms of the residuals of nonspatial simple regressions between species richness of each taxonomic group and each explanatory variable (Littell et al. 1996). In our work, we used the VARIOWIN program (Pannatier 1996) to plot semivariograms.

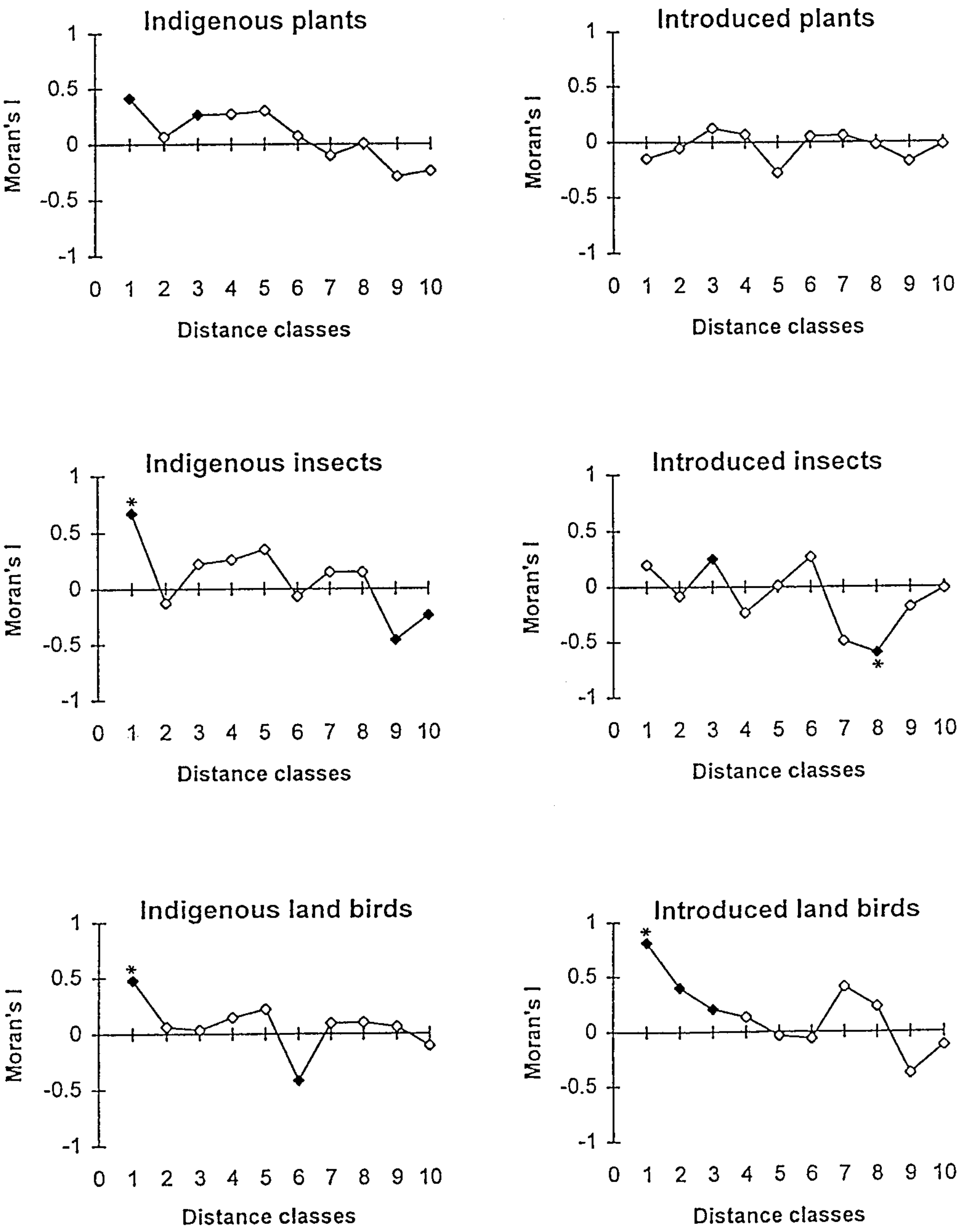

Figure 1: Spatial autocorrelograms of species richness for plants, insects, and land birds of Southern Ocean islands. Data used are from tables 1 and 2 of Chown et al. (1998). Black dots correspond to Moran's I significant at $P < .05$ level. Asterisk = Moran's I that is significant at $P < .0033$, which corresponds to the corrected Bonferroni level. Distance classes are of 700 km.

Among the models we tried (nonspatial model and spherical, gaussian, and exponential covariance models), the most parsimonious model was selected based on the Akaike's Information Criterion (AIC) and was used to give the estimates of the relationship between the pair of variables considered. Model selection based on AIC allowed us to compare models based on both their fit to the data and their number of parameters (Burnham and Anderson 1998). With the MIXED procedure of SAS, AIC is calculated as log likelihood − k (k being the number of model parameters); the greater the value of AIC, the more parsimonious the model is among those tested (see Littell et al. 1996). The use of the two other criteria provided by the software would have led to the same results.

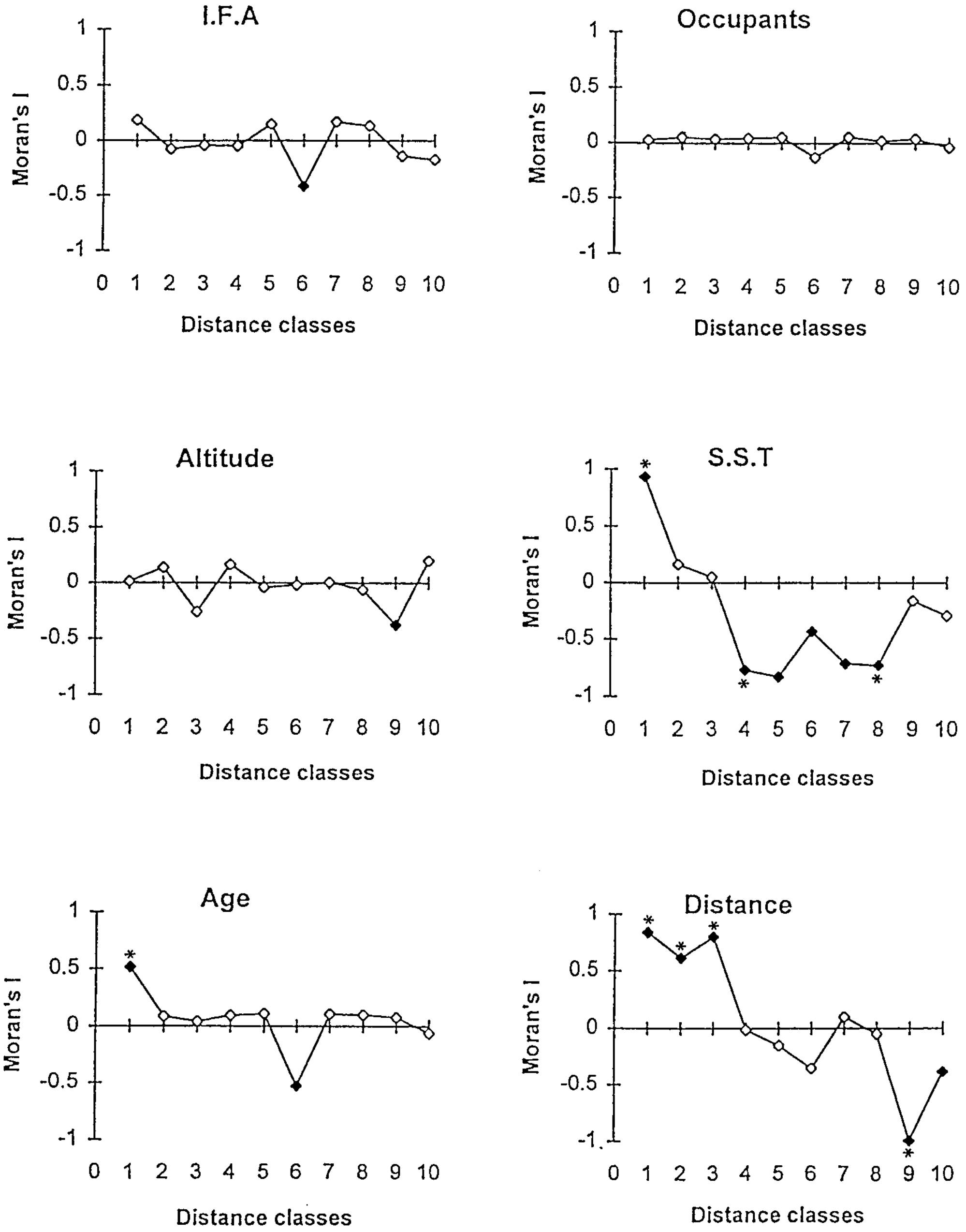

Figure 2: Spatial autocorrelograms of physical variables of Southern Ocean islands. Data used are from table 1 of Chown et al. (1998). Black dots correspond to Moran's I significant at $P < .05$ level. Asterisk = Moran's I that is significant at $P < .0033$, which corresponds to the corrected Bonferroni level. Distance classes are of 700 km. *I.F.A.* = ice-free area; *S.S.T.* = sea-surface temperature.

Since we have been faced with a relatively high number of intercorrelated explanatory variables (see tables 1 and 3 in Chown et al. 1998), while the number of species was very low in the case of some taxa (see table 2 in Chown et al. 1998) and there were only 25 islands, we avoided multivariate analyses and followed the advice of James and McCulloch (1990) by considering variables separately in bivariate analyses with the use of Bonferroni corrections for assessing the significance of the relationships. Thus, when interpreting the significance of the *F* value of the relationship between species richness of a given taxonomic group and one explanatory variable, we considered the corresponding *P* value divided by the total number of tests conducted for that taxonomic group.

Results

Spatial Autocorrelation in Species Richness and Explanatory Variables

As we predicted, a significant spatial autocorrelation was found in species richness of indigenous taxa (vascular plants, insects, and land birds) and introduced taxa with high dispersal abilities (land birds) but not in introduced taxa with low dispersal abilities (vascular plants, insects, and mammals; fig. 1; the autocorrelogram for species richness of introduced mammals did not show any significant values for the 10 first distance classes either). These results suggest that colonization events from nearby islands may have played an important role in determining the richness of these island communities. This also suggests that time lags since human-mediated introduction of species to islands may not have been long enough for species with low dispersal abilities to colonize nearby islands.

Among the explanatory variables considered, sea surface temperature and distance to the nearest continent were found to exhibit significant spatial autocorrelation (fig. 2), which is consistent with our predictions. Interestingly, the variable describing island age was also found to be autocorrelated, whereas the amount of ice-free area and the number of human occupants, two variables expected to explain significant proportions of variation in species richness of different taxa, did not show any evidence of positive spatial autocorrelation (fig. 2). Similarly, the variables glaciation and date from first modern occupation were not found to exhibit significant spatial autocorrelation.

Assessing the Significance of the Associations between Species Richness and the Explanatory Variables Using Spatial Covariance Models

As predicted, we found that in the case of introduced plants, insects, and mammals, for which there was no evidence of spatial autocorrelation in species richness, the spatial covariance models did not fit the data better than the nonspatial model in the regression analyses. For instance, the results of the nonspatial model, as well as those of the spatial one, show that the number of mammal species was significantly related to the number of occupants (nonspatial model: $\mathrm{AIC} = -24.516$, $\mathrm{intercept} = 0.3967 \pm 0.1455$, $\mathrm{slope} = 0.2703$, Type III $F = 33.29$, $P = .0001$; spatial model: $\mathrm{AIC} = -26.516$, with same values for intercept, slope, Type III F, and P). The AIC of the second model is lower than the AIC of the first model because it includes two more parameters (see Littell et al. 1996). This result suggests that human presence has affected the biodiversity of these islands, which confirms an important conservation conclusion derived from the study of Chown et al. (1998).

However, when species richness showed evidence of spatial autocorrelation (indigenous plants, insects, and land birds and introduced land birds), comparison of AIC values of the nonspatial model with those of the spatial covariance models showed that the latter fit the data better in almost 100% of the cases (table 1). The *F* values as well as the levels of significance of the relationships between species richness and the different explanatory variables given by the spatial models were very different from those given by the nonspatial model. It is notable that, depending on the analyses, the point estimates (e.g., slope) and also the uncertainty estimates (e.g., SE of the slope) were affected (table 1). This suggests that the presence of spatial autocorrelation in species richness affected the estimates of the relationships between species richness of these taxonomic assemblages and the explanatory variables. Of particular significance was the relationship between area and indigenous-insect species richness (which became highly significant when a model accounting for spatial covariance was used) and the relationships between age and indigenous–land bird species richness and between distance to the nearest continent and introduced–land bird species richness (which became nonsignificant). With regard to the relationship between distance to the nearest continent and indigenous-insect species richness, AIC values of both models were not sufficiently different to determine which model fit the data best.

For indigenous vascular plants, it appears that spatial autocorrelation did not significantly affect the relationship between the different explanatory variables and species richness. Indeed, the nonspatial model as well as the selected spatial model show that only island area was significantly relevant for species richness of this group. Nonetheless, the *F* value of the relationship between area and species richness is slightly stronger when the effect of spatial covariance was accounted for. Similarly, the *F* value of the relationship between the altitude variable and species richness became over twice as large and thus was significant at the .01 level after Bonferroni correction.

Unlike what the results of the nonspatial regression model suggested, island area was found to be significantly relevant for species richness of indigenous insects at the .01 level after Bonferroni correction, while the effect of the altitude variable was at the limit of significance. In the case of the relationship between distance to the nearest continent and indigenous-insect species richness, the *F* value given by the spatial model was twice as low as that given by the nonspatial model. However, one could not determine which model fit the data best since AIC values of both models were not sufficiently different. Indigenous–vascular plant species richness was also found to be significantly relevant for species richness of indigenous insects even when the effect of spatial covariance was

Table 1: Results of simple regressions of $\log(n+1)$ species richness of four taxonomic groups on the different physical, human occupancy, and biological variables considered by Chown et al. (1998)

	Indigenous vascular plants		Indigenous insects		Indigenous land birds		Introduced land birds	
Regression	NSM	SM	NSM	SM	NSM	SM	NSM	SM
Log area:								
AIC	−35.982	−32.780	**−33.655**	**−25.458**	−33.941	−29.752	−33.076	−23.172
Intercept	2.1817 ± .3672	2.7504 ± .3319	**2.9062 ± .3319**	**2.7282 ± .3345**	.4195 ± .3361	1.0603 ± .3360	.1891 ± .3236	.4662 ± .3381
Slope	.2862 ± .0770	.1624 ± .0424	**.1488 ± .0696**	**.1561 ± .0362**	.1945 ± .0704	.0268 ± .0417	.1125 ± .0678	.0586 ± .0314
Type III *F*	13.82	14.66	**4.57**	**18.61**	7.62	.41	2.75	3.47
P	.0011	.0009	**.0433**	**.0003**	.0111	.5263	.1109	.0751
Log altitude:								
AIC	−38.432	−34.456	−34.671	−26.746	−36.117	−29.053	−33.196	−21.839
Intercept	−.0254 ± 1.677	.5806 ± .9505	3.2921 ± 1.4242	1.4160 ± .6769	.6962 ± 1.5166	1.3078 ± .7205	1.3082 ± 1.3358	−.3053 ± .5854
Slope	.5252 ± .2580	.4401 ± .1375	.0352 ± .2191	.3081 ± .0918	.0813 ± .2333	−.0194 ± .1016	−.1017 ± .2055	.1597 ± .0720
Type III *F*	4.14	10.25	.03	11.26	.12	.04	.25	4.92
P	.0535	.004	.8738	.0027	.7305	.8504	.6252	.0367
Log age:								
AIC	−40.663	−38.058	−33.055	−31.063	**−31.490**	**−28.258**	−33.010	−23.653
Intercept	3.1372 ± .2829	3.5555 ± .3648	3.2124 ± .2032	3.4460 ± .3077	**.7755 ± .1899**	**1.2083 ± .2933**	.4370 ± .2028	.8839 ± .3668
Slope	.1116 ± .0851	−.0282 ± .0655	.1534 ± .0611	.0147 ± .0540	**.2228 ± .0571**	**.0055 ± .0133**	.1078 ± .0610	−.0541 ± .0341
Type III *F*	1.72	.19	6.30	.07	**15.23**	**.17**	3.12	2.52
P	.2026	.6705	.0195	.7881	**.0007**	**.6806**	.0905	.1261
Log glaciation:								
AIC	−39.939	−36.145	−34.621	−29.301	−35.838	−28.575	−33.044	−23.456
Intercept	3.2041 ± .2882	3.2910 ± .3478	3.4718 ± .2288	3.3179 ± .3151	1.1009 ± .2412	1.1276 ± .3051	.5574 ± .2136	.7151 ± .3231
Slope	.2495 ± .2764	.2736 ± .2075	.0753 ± .2194	.1935 ± .1627	.1911 ± .2313	.0663 ± .1504	.1516 ± .2048	.0303 ± .1235
Type III *F*	.82	1.74	.12	1.41	.68	.19	.55	.06
P	.3760	.2003	.7347	.2466	.4172	.6637	.4668	.8084
SST:								
AIC	−41.513	−37.914	−35.791	−30.871	−37.837	−25.554	−34.577	−24.217
Intercept	2.9502 ± .4674	3.2880 ± .6882	3.1772 ± .3644	3.2944 ± .5518	1.2765 ± .3983	1.3004 ± .5473	.3759 ± .3457	.6167 ± .5486
Slope	.0518 ± .0515	.0260 ± .0781	.0432 ± .0401	.0241 ± .0621	−.0071 ± .0439	−.0108 ± .0567	.0349 ± .0381	.0158 ± .0573
Type III *F*	1.01	.11	1.16	.15	.03	.04	.84	.08
P	.3243	.7418	.2930	.7017	.8735	.8505	.3683	.7852

Distance:								
AIC	−45.790	−42.884	−34.774	−33.734	−40.830	−30.513	**−33.121**	**−28.438**
Intercept	4.1112 ± .4288	4.0986 ± .5410	4.5505 ± .2656	4.5199 ± .3568	1.9558 ± .3456	1.7172 ± .5451	**1.6380 ± .2472**	**1.5417 ± .3688**
Slope	−.0003 ± .0002	−.0003 ± .0002	−.0005 ± .0001	−.0005 ± .0001	−.0003 ± .0001	−.0002 ± .0002	**−.0004 ± .0001**	**−.0004 ± .0001**
Type III *F*	4.11	1.89	20.22	9.92	6.06	1.22	**21.31**	**6.37**
P	.0544	.1827	.0002	.0045	.0217	.2810	**.0001**	**.0189**
Date:								
AIC	−41.861	−38.974	−35.597	−31.856	−37.362	−30.582	−35.034	−25.426
Intercept	21.4317 ± 7.4267	23.5361 ± 11.056	19.0059 ± 5.6561	17.9570 ± 7.1543	17.1295 ± 6.1074	16.2521 ± 7.7393	13.5277 ± 5.5193	12.5183 ± 6.2798
Slope	−.0095 ± .0039	−.0105 ± .0058	−.0081 ± .0030	−.0076 ± .0037	−.0083 ± .0032	−.0079 ± .0041	−.0068 ± .0029	−.0062 ± .0033
Type III *F*	5.93	3.29	7.50	4.09	6.79	3.79	5.45	3.53
P	.0231	.0828	.0117	.0548	.0158	.064	.0287	.0732
Log occupants:								
AIC	−38.816	−36.516	−35.169	30.460	−36.247	−29.134	−33.690	−22.27
Intercept	2.9482 ± .2709	3.2739 ± .3067	3.3607 ± .2311	3.3707 ± .2969	1.0005 ± .2422	1.2863 ± .3427	.4895 ± .2168	.5541 ± .3173
Slope	.2096 ± .0872	.1090 ± .0504	.0805 ± .0744	.0585 ± .0431	.1119 ± .0786	−.0486 ± .0358	.0828 ± .0698	.0693 ± .0284
Type III *F*	5.77	4.68	1.17	1.84	2.06	1.84	1.41	5.97
P	.0247	.0411	.2908	.877	.1648	.1880	.2477	.0226
Log INDVP:								
AIC	…	…	−24.011	−19.814	−29.314	−24.445	−27.663	−12.395
Intercept	…	…	1.4584 ± .3587	1.8849 ± .3231	−.6885 ± .4517	−.1406 ± .4020	−.9217 ± .4204	−.3265 ± .6489
Slope	…	…	.6132 ± .1012	.4693 ± .0770	.5681 ± .1275	.3867 ± .0921	.4684 ± .1186	.3965 ± .0531
Type III *F*	…	…	36.70	37.12	19.86	17.61	15.59	55.82
P	…	…	.0001	.0001	.0002	.0003	.0006	.0001
Log insects:								
AIC	…	…	…	…	−26.963	−21.870	−24.186	−18.309
Intercept	…	…	…	…	−1.5723 ± .5395	−1.4408 ± .5053	−1.8068 ± .4781	−.9008 ± .4209
Slope	…	…	…	…	.7937 ± .1487	.7677 ± .5053	.6988 ± .1318	.4848 ± .1036
Type III *F*	…	…	…	…	28.48	43.04	28.10	21.89
P	…	…	…	…	.0001	.0001	.0001	.0001

Note: NSM = nonspatial model; SM = selected spatial model; AIC = Akaike's Information Criterion; *P* = *P* value for the corresponding explanatory variable; SST = sea-surface temperature; INDVP = indigenous–vascular plant species richness. Intercepts and slopes are given ± their SEs. Results in bold are more specifically discussed in the main text as examples in which there were large differences between the spatial and nonspatial models.

accounted for. However, since area was significant for indigenous-insect species richness and since area and indigenous–vascular plant species richness were interrelated, it is not entirely clear whether the relationship between indigenous–vascular plant species richness and indigenous-insect species richness expresses an effect of vascular-plant species richness per se or indirectly the effect of area.

For indigenous land birds, age was not significantly related to species richness when the model accounting for spatial covariance was used (table 1). However, significant relationships between indigenous-plant species richness and indigenous–land bird species richness and between indigenous-insect species richness and indigenous–land bird species richness were found.

In the case of introduced land birds, accounting for spatial covariance affected the significance of the relationship between distance to the nearest continent and species richness, which would suggest that the distance variable was less significantly relevant for species richness for this group when the relative location of islands is considered (table 1). Indigenous–vascular plant species richness and indigenous-insect species richness were, however, found to be significantly associated with species richness of this group even when accounting for spatial covariance. Interestingly, the *F* value of the relationship between indigenous-plant species richness and introduced–land bird species richness became over three times as large, differing greatly from the results of the nonspatial model (table 1).

Discussion

Southern Ocean islands offered a suitable system for investigating the importance of explicitly considering spatial attributes in understanding large-scale patterns of variation in species richness. Analyses of spatial autocorrelation in the physical and human variables characterizing these islands, as well as in species richness of the different terrestrial taxa that Chown et al. (1998) have distinguished, gave interesting biological insight. Significant spatial autocorrelation was found in species richness of indigenous vascular plants, indigenous insects, indigenous land birds, and introduced land birds but not of introduced vascular plants, introduced insects, and introduced mammals. Reexamination of the relationships between species richness of the former taxa with the different nonautocorrelated explanatory variables (area, altitude, glaciation, date, and number of occupants) and with spatially autocorrelated variables (age, distance to the nearest continent, and sea surface temperature) showed that spatial autocorrelation had an effect on the levels of significance of the relationships between species richness of these taxa and the explanatory variables when regression not accounting for spatial covariance was used. In particular, the relationships between area and indigenous-insect species richness, age and indigenous–land bird species richness, and distance to the nearest continent and introduced–land bird species richness were found to be strongly affected by the spatial structure of the data. It is, nevertheless, to be noted that in the case of regression analyses involving nonspatially autocorrelated variables, the results were left unchanged. Of particular importance was the result of the relationship between introduced-mammal species richness and the variable describing the intensity of human presence on these islands (number of occupants), which strongly validates the conclusions of Chown et al. (1998) regarding the impact of human presence on these islands on the conservation of their biotas.

The existence of spatial autocorrelation in species richness of indigenous taxa and introduced taxa with high dispersal ability but not in species richness of introduced taxa with low dispersal ability was predicted. This is consistent with dispersal and colonization from nearby islands as factors explaining part of the patterns of island occupancy of different species and variation in species richness among local communities. This also suggests that time lags since human-mediated introduction of species to islands may not have been long enough for species with low dispersal abilities to colonize nearby islands. In other systems, introduced species have also been reported to have more localized distributions than native species (Griffiths 1997). Therefore, the absence of some species from some islands need not necessarily be related to the effects of island properties that made them unsuitable for these species but may simply be because the species did not reach these islands yet. The occurrence of suitable but empty patches/islands is increasingly recognized (see Hanski 1999) and suggests that dispersal tendency and aptitude of species, as well as historical phenomena (e.g., date of introduction of species in the patch/island system), should be taken into account when examining patterns of occurrence of species and also variation of species richness and composition among islands or habitat patches (Ricklefs and Schluter 1993).

An important ecological issue that patterns of spatial autocorrelation in species richness indicated is that the relative location of islands and the spatial distribution pattern of the island system should be considered when measuring island isolation, rather than the simple distance to the mainland as it was often the case in island-biogeography studies. Indeed, stepwise colonization from nearby islands could balance the effect of distance to the mainland in a system of islands close to each other. In such a case, the size of the potential colonizer pool for islands distant from the mainland will be greater than that for islands situated at equivalent distances to the mainland but within a system of islands organized into different groups geographically distant and isolated from one another, as seems to be the case for some of the Southern Ocean islands. In this context, using Mantel's test (see Manly 1997) to examine the association between a matrix of species similarity among islands with a matrix of interisland distance (e.g., Kadmon and Pulliam 1993) may be one appropriate approach that takes into account the spatial attributes and allows investigation of the effect of island isolation on local communities. Morand (2000) recently reanalyzed data published by Ricklefs and Lovette (1999), using regression on distance variables, and also stressed the importance of considering explicitly the relative spatial location of islands and the degree of vagility of taxa considered in explaining patterns of variation in species richness.

Tackling spatial issues is not an easy task, and different statistical modeling approaches may be used on the same data (Cressie 1993). An important issue is linked with the spatial scales at which the partitioning of the variance is done. The analyses can, for instance, emphasize having the mean of the dependent variable change with spatial location, which can be done by having a variable describing spatial location by groups of sampling points situated close to each other or by taking different values for the different group of points close to each other (e.g., a variable describing each regional species pool). This may imply choosing groups of points and values for the variable rather arbitrarily. Another possibility is to model the spatial covariance directly in the regression model that can be fitted to the data and compare it with a model not accounting for space. Here, we first explored spatial structure in the different variables using spatial autocorrelation, and then, after detecting clear patterns of spatial autocorrelation in some variables, we carried out regressions that incorporated spatial covariance in order to compare the results with those of analyses not incorporating space. We relied on the MIXED procedure of SAS software for our analyses, and we think that the results illustrate well the potential importance of considering space explicitly in such analyses. We would like to stress that the estimation of the different parameters has to be taken as indicative (Littell et al. 1996), but that clear differences were found that show that more effort should be put into attempting to consider spatial issues in this type of analyses.

The spatial distribution pattern of the islands within the system considered may affect the availability of colonists to local communities and, consequently, may contribute to disparities in regional richness among groups of islands. This seems to be the case for the Southern Ocean islands as analyses of spatial autocorrelation in species richness suggested. Local-regional species richness relationships have been shown to be of much relevance for explaining variation of local richness in recent ecological studies (Hugueny and Paugy 1995; Caley and Schluter 1997; Griffiths 1997, 1999; Oberdoff et al. 1998; Hugueny and Cornell 2000). Indeed, variation in regional species richness represents a large-scale factor affecting local richness and may explain a large part of variation of local richness when local conditions are standardized (e.g., Griffiths 1997). Ignoring this large-scale factor and explaining variation of species richness among islands distributed over large geographic or biogeographic entities simply in term of the effects of variation of island properties may considerably reduce the biological and ecological insight that such studies can provide.

The importance of considering the spatial-distribution pattern of the islands and regional-local species richness relationships stresses how ecological patterns and processes are not independent of the spatial scale at which they are examined (Wiens 1989, 1995). In the case of a system of islands distributed over a large geographic area such as the Southern Ocean islands, the ideal scale to investigate the relationships between island properties and species richness should be that for which propagules of all species are available to all localities (see Cornell and Karlson 1996). For the Southern Ocean islands, investigating these relationships at the scale of the entire island system under an island biogeography approach by using statistical regression models that do not account for spatial covariance brought with it a problem of statistical nonindependence among nearby islands. Accounting for spatial location of the islands allows a better perception of important potential processes.

It is interesting that island area, which is one of the most important conventional island biogeographic variables (MacArthur and Wilson 1967; Rosenzweig 1995), was found to be strongly relevant for species richness of some native taxa (plants and insects) in the present analyses. However, island age was not found to be significantly relevant for species richness of indigenous taxa when accounting for space, contrary to what the results of the nonspatial model have suggested. The "anomalous" character of Southern Ocean islands was more evident for land birds for which area (see also Abbott 1974), age, and distance to the nearest continent were not found to be associated with species richness. They were, however, found to be highly relevant for insect species richness. For indigenous vascular plants, area was found to be the only factor that was significantly associated with species richness in the individual analyses.

As a considerable proportion of the insects in the Southern Ocean islands are herbivores (Gressitt 1970; Chown 1990; Kuschel 1991; Patrick 1994), it was not surprising that species richness of this taxonomic group was strongly related to vascular-plant species richness. Interestingly, when spatial covariance was accounted for, area was also found to be relevant for species richness of indigenous insects, and it could be that the effect of area on habitat heterogeneity (e.g., its effect on plant diversity) may play an important role in determining species richness of indigenous insects. However, because of the strong relationship between area and indigenous–vascular plant species richness, it is not entirely clear which one of them is more significant for species richness of indigenous insects.

As Chown et al. (1998) suggested, it was not surprising that indigenous–land bird species richness was strongly related to vascular-plant species richness and insect species richness, first because vascular plants and insects form the food of the majority of land birds (see also Abbott 1974; Burger 1978) and second because of the strong relationship between species richness of these taxa. However, age of the islands was not found to be relevant for species richness of indigenous land birds when a model accounting for spatial covariance was used, which could suggest that in situ evolution of endemic bird species may not have played an important role in determining patterns of among-island variation in species richness.

With regard to introduced birds, species richness was found to be weakly related to distance to the nearest continent when spatial covariance was accounted for. This may indicate that long-distance dispersal was less important in shaping patterns of occurrence of species and, consequently, on determining patterns of variation in species richness among islands than is colonization from nearby islands through short-distance dispersal. The low dispersal ability of introduced species reported in the literature (e.g., Griffiths 1997) would also support this idea. It should nevertheless be stressed that the analyses of patterns will never reveal for sure what processes led to them.

As factors determining species richness of native taxa are likely to differ from those of introduced taxa, it was important that Chown et al. (1998) drew a clear distinction between these two groups in their work. Interestingly, they also considered the amount of ice-free area rather than the total area of islands to examine the association between island area and species richness, a factor that previous studies (Abbott 1974; Williams 1982; Kuschel 1991) did not take into account. Our work suggests that considering spatial structures, and thus possible regional processes, is also fundamental for understanding patterns of variation in species richness among these islands and for assessing the significance of the effects of different physical, biological, and human factors on local richness. This illustrates once more the complexity of the ecological factors and processes shaping local communities (Wiens 1989; Ricklefs and Schluter 1993). This also means that spatiotemporal processes as well as island characteristics need to be considered when dealing with the conservation of island communities.

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