Global Patterns of Species Richness: Spatial Models for Conservation Planning Using Bioindicator and Precipitation Data

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Abstract: *We used birds, butterflies, tiger beetles, mean annual precipitation, and spatial statistical models to investigate the applicability of using indicators of species richness for conservation planning on a continental scale. The models were applied to data collected on three grids of squares (each square 275 or 350 km on a side) covering North America, the Indian subcontinent, and Australia. We applied spatial statistical modeling techniques to determine the viability of using a single or multiple indicators to predict spatial patterns of species diversity of ecologically and phylogenetically unrelated taxa. Spatial models are optimal for these analyses because species data typically are not spatially independent, primarily owing to dispersion effects. Furthermore, spatial models can be used to predict species numbers in areas where no observed data are available. We found that the number of tiger beetle species is a useful indicator of the number of butterfly species in North America and of the number of bird species on the Indian subcontinent, but it is not so useful as an indicator of either the number of bird or butterfly species in Australia or of the number of bird species in North America. We also found that the number of butterfly species is a useful indicator of the number of bird species in North America and Australia and that mean annual precipitation is useful for predicting the number of butterfly species in Australia. Although the general model used on all three continental areas is the same, the relative importance of potential indicators in predicting spatial patterns of other taxa changes from continent to continent. We attribute this change largely to differential biogeographical and ecological history, which must be taken into account in the selection and testing of potential indicators.*

Patrones Globales de Riqueza de Especies: Modelos Especiales para la Planificación de la Conservación Usando Datos de Bioindicadores y Precipitación

Resumen: *En este estudio utilizamos aves, mariposas, escarabajos tigre, la precipitación media anual y modelos estadísticos espaciales para investigar la utilidad de los indicadores biológicos de riqueza de especies para la planificación, a escala continental, de la conservación. Los modelos estadísticos se aplicaron a datos obtenidos en cuadrículas (cada cuadrado con 275 o 350 km de lado) que abarcaban Norte América, el Subcontinente de India y Australia. Los modelos estadísticos espaciales permiten determinar la viabilidad del uso de indicadores simples o múltiples para predecir patrones espaciales de riqueza de especies ecológica o filogenéticamente no relacionadas. Los modelos espaciales son óptimos para este tipo de análisis debido a que los datos de las especies no son independientes del espacio donde éstas se encuentran, debido básicamente al efecto de la dispersión. Estos modelos también son utilizados para predecir el número de especies en áreas donde no hay datos disponibles. Los resultados mostraron que el número de especies de escarabajos tigre es un indicador útil de la diversidad de mariposas en Norte América y de aves en el Subcontinente de India, pero no es tan útil como indicador de aves y mariposas en Australia ni de aves en Norte América. El número de especies de mariposas es un indicador útil de las aves en Norte América y Australia. La precipitación es útil para predecir las mariposas en Australia. Aunque el modelo general utilizado en las tres áreas continentales es el mismo, la importancia relativa de los indicadores potenciales para predecir patrones de dis-*

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tribución espacial de otros taxones varía según el continente. Este variación se atribuye principalmente a diferencias en la historia biogeográfica y ecológica. Estas diferencias deben ser consideradas cuando se prueban los indicadores potenciales.

Introduction

Conservation policy decisions must integrate an overwhelming number of biological and socioeconomic factors to prioritize conservation efforts adequately. In addition, economic and political pressures throughout the world dictate that prioritization of these efforts be made quickly and efficiently. Ideally, knowledge of biodiversity, habitat loss, and human impact is needed to make these decisions competently (Sisk et al. 1994).

In focusing on only one of these factors, biodiversity, great logistical barriers exist when we measure even obvious parameters such as species numbers and endemism (Gentry 1992; Colwell & Coddington 1994; Ojeda et al. 1995; Pimm et al. 1995). Methods to study and understand biodiversity must take into account limited resources and a paucity of trained personnel, especially in developing countries. One of the methods proposed to resolve these problems is the use of well known bioindicator taxa that are quickly and easily studied but whose patterns are likely to be representative of many other species (Landres et al. 1988; Noss 1990; Brown 1991; Kremen 1992, 1994; Oliver & Beattie 1993; Pearson 1994).

Because many conservation decisions today are made at a large geographical scale (hundreds or thousands of square kilometers), indicator taxa have become more useful. This large-scale assessment has proven most useful in resolving initial priorities, especially in developing areas where detailed surveys are unavailable (Kuliopulos 1990). An additional advantage is that patterns of biodiversity at large regional scales are generally the product of only a few factors, such as origination and extinction (Cracraft 1992; Rosenzweig 1995), and may be generally represented by one or more indicator taxa. Conversely, at small regional scales, biodiversity patterns are the product of these same factors plus numerous additional factors such as immigration and emigration (Gaston & Blackburn 1996). Thus, the greater number of varying factors makes resultant patterns less likely to be shared by different taxa at small geographical scales. In addition, at small scales, single habitats or ecosystems are often so unique that they are less likely to be broadly represented by a single or a small number of indicator taxa (Currie 1991; Prendergast et al. 1993; Curnutt et al. 1994; Margules & Gaston 1994; Thomas & Abery 1995).

The interests of biogeographers (Fischer 1960; Pianka 1966; Haffer 1969; Wilson 1974; Schall & Pianka 1978; Huston 1979; McCoy & Connor 1980; Letcher & Harvey 1994) and conservation planners (Myers 1990; Ceballos & Brown 1995; Kremen 1994) have melded in studies of the spatial distribution of species numbers and endemics to apply bioindicators as an important technique for the preliminary prioritization of conservation efforts. Earlier, Pearson and Cassola (1992) and Pearson and Ghorpade (1989) proposed that the family of tiger beetles (Cicindelidae) be used as an indicator for quickly and accurately determining areas of high diversity and endemism on a continental scale. Pearson and Cassola (1992) found that tiger beetle species numbers and butterfly and bird species numbers were strongly correlated on large grids of squares, 275 or 350 km per side. But they failed to take into account spatial correlations in the data and, consequently, made assumptions that likely invalidated their inferences and conclusions. Carroll and Pearson (1998) refined the methodology and developed a spatial statistical model for comparing tiger beetles and butterfly species numbers in North America. As expected, latitude and longitude (Pagel et al. 1991) were found to be critical in the prediction of spatial patterns of butterflies. Also, tiger beetles were found to be an effective bioindicator of the numbers of butterfly species. Using the observed spatial dependence and the relationship between the numbers of tiger beetle species and butterfly species, Carroll and Pearson (1998) demonstrated that accurate prediction is possible in regions for which data are unavailable but which are close to areas where data have been collected.

We have expanded on previous research by developing and testing spatial statistical models used to predict areal species distributions on similarly gridded squares across three large continental regions—North America north of Mexico, the Indian subcontinent, and Australia. We used species numbers of tiger beetles and average annual rainfall to predict numbers of species of butterflies. Furthermore, we used species numbers of tiger beetles, species numbers of butterflies, and average annual rainfall to predict numbers of species of birds. Birds and butterflies are two of the few taxa (in addition to tiger beetles) for which relatively accurate global data exist (Brown 1991; Pomeroy 1993; Beccaloni & Gaston 1994; Kremen 1994; Balmford & Long 1995).

Beyond the logistical advantages of modeling using these three taxa, they represent a breadth of ecological trophic levels, including predators (tiger beetles), herbivore/nectivores (butterflies), gramnivores, insectivores, frugivores, and top carnivores (birds). These three taxa also represent a range of vagility from intercontinental movements (birds) to wide local dispersal (butterflies) and limited dispersal (tiger beetles). Thus, any strong relations of species spatial patterns among such ecologically and behaviorally diverse taxa make the indicators potentially even more reliable and useful (Conroy & Noon 1996). Because some evidence indicates that precipitation patterns can have a strong influence on species richness, perhaps related to a combination of productivity and evapotranspiration rates (Currie 1991; Pimm & Gittleman 1992), we also incorporated into the model the average annual precipitation within each square.

At this relatively large geographical scale, we assumed that most terrestrial taxa are under similar biogeographic influences, and these common factors cause patterns such as spatial distributions of species over latitudinal gradients (Currie 1991; Rohde 1992; Kaufman 1995). At the same time, most taxa within a continental area are influenced by topography, barriers to dispersal (Gaston & Blackburn 1996), centers of evolution (Cracraft 1994), and precipitation patterns (Smith et al. 1994) unique to that continent (Mani 1974; Keast 1981). Our general hypothesis is that, because of these abiotic and biotic patterns, a carefully selected taxon or suite of taxa can be used to repesent reliably the spatial patterns of many phylogenetically related and unrelated species' distributions with general spatial modeling techniques applied to each continental area. In the process of developing and testing the models, we can obtain an indication of the relative importance of the abiotic (longitude, latitude, and precipitation) and biotic (species numbers of bioindicator taxa) predictor variables in predicting species numbers of phylogenetically and ecologically unrelated taxa.

Methods

To determine the effectiveness of using biotic and abiotic indicators of species numbers, we analyzed data collected in North America, the Indian subcontinent, and Australia (see Appendix). Previous studies have shown that squares between 275 and 350 km per side are convenient sizes to organize species numbers data (Pearson & Cassola 1992). For instance, squares of this size were the largest within which two to five collections or observations of tiger beetles will be representative of the entire square (Pearson & Ghorpade 1989). These squares were small enough to minimize the number of different habitats or extreme differences in rainfall without becoming so narrow that the relations of spatial patterns among different taxa were negated (Prendergast et al. 1993). The grid for North America contained 208 squares (Figs. 1 & 2) and for the Indian subcontinent 61 squares (Fig. 3); both grids had squares 275 km on a side. Because the fauna in Australia was less well known, we increased the size of the squares to 350 km per side. For Australia the grid contained 67 squares (Fig. 4). When it was not feasible (primarily in coastal regions) to obtain exact squares, as far as possible squares were established within areas approximately equal to those of the other squares.

For a methodological model to be useful in even the least-studied areas of the world, we used data types that were most likely to be available in these areas. Hence, we used regional publications, taxonomic revisions, and private field notes to determine the total number of tiger beetle species and breeding bird species (nonaquatic and nonmarine) (Pizzey 1980; Ali & Ripley 1987; National Geographic Society 1987), and, for Australia and North America, the number of breeding butterfly species (Common & Waterhouse 1982; Scott 1986) known for each of the squares. Precipitation maps for each geographical area were used to average the annual precipitation within each square.

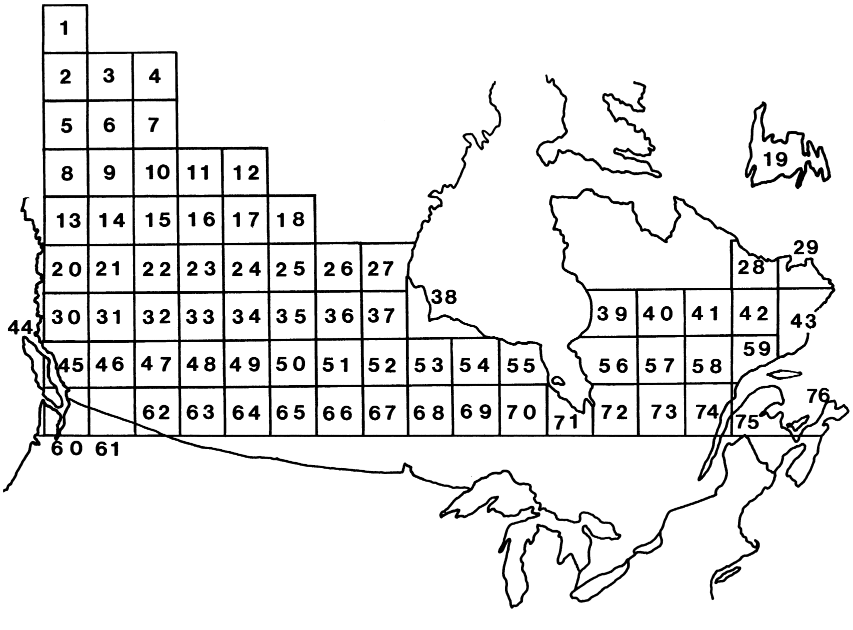

Figure 1. Arrangement and numbers of grid squares across northern North America. Each square 275 km per side.

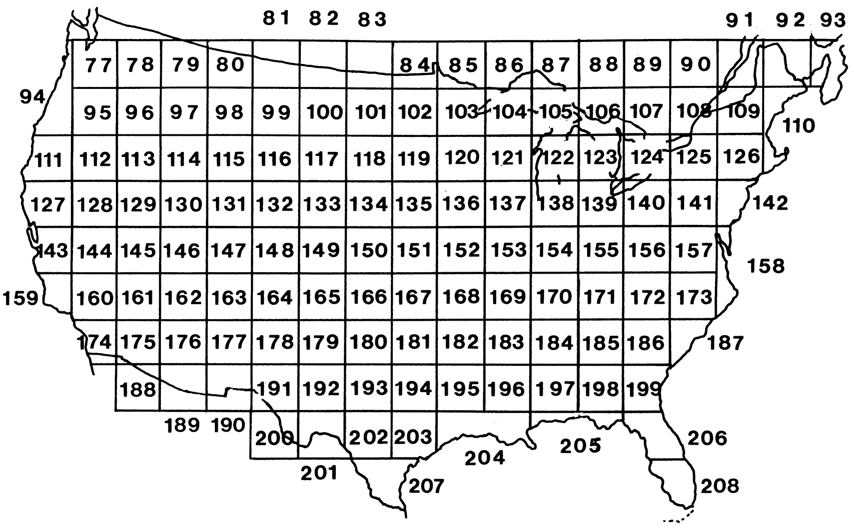

Figure 2. Arrangement and numbers of grid squares across southern North America. Each square 275 km per side.

We built five predictive models. Complete details of the construction of the types of models used in this research are given by Carroll and Pearson (1998). In this section we present the primary considerations associated with parameter estimation, hypothesis testing, and cross-validation. For each of the three data sets, we built a model to predict the number of bird species (the response variable) in each square. For the North American and Australian data, we initially used as predictor variables the number of butterfly species, the number of tiger beetle species, and the average annual rainfall in the corresponding square. Because no butterfly data were available for India, we first treated only the number of tiger beetle species and the average annual rainfall as predictor variables. For North America and Australia, we also developed models to predict the number of butterfly species (the response variable) in a square, initially using as predictor variables the number of tiger beetle species and the average annual rainfall in the corresponding square. After the initial models were fit and model assumptions were validated, we applied hypothesis tests and cross-validation techniques to determine which of the predictor variables were useful for predicting the areal distributions of the number of species of the response variables.

We excluded the number of bird species as a predictor variable in the models developed to predict the num-

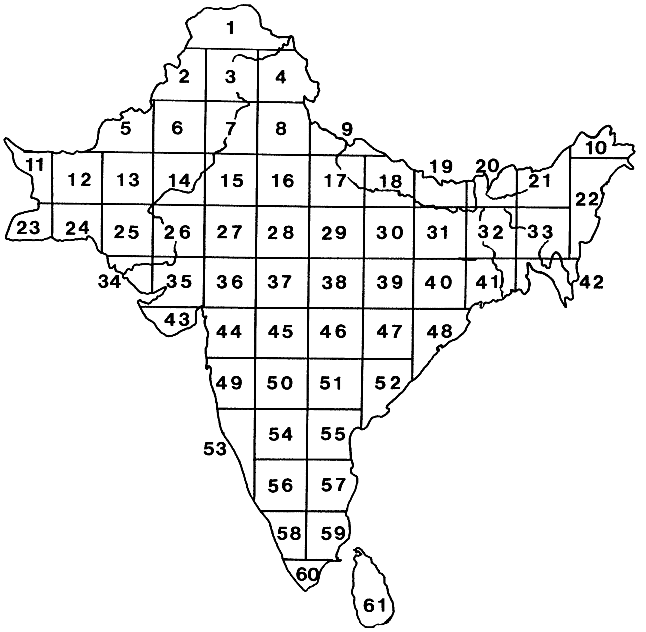

Figure 3. Arrangement and numbers of grid squares across the Indian subcontinent. Each square 275 km per side.

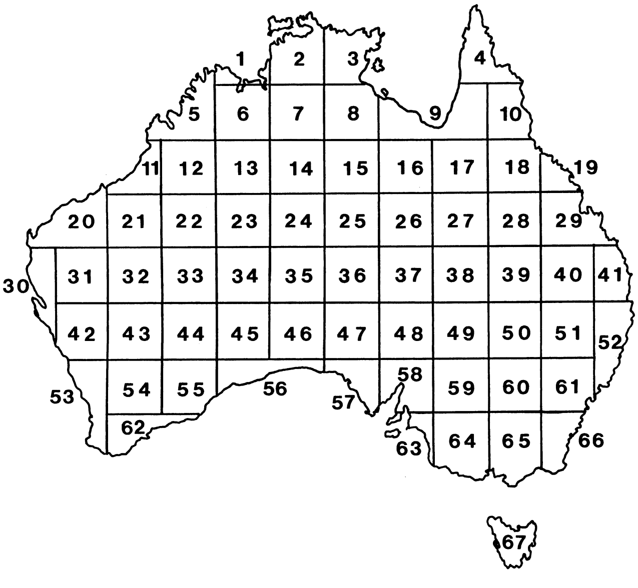

Figure 4. Arrangement and numbers of grid squares across Australia. Each square 350 km per side.

ber of butterfly species because collecting initial data on the number of bird species in many unexplored areas is highly labor intensive (Pearson & Cassola 1992).We anticipated that models of the type we constructed may be used in future conservation management decisions, and in these situations it is unlikely that a taxon for which data are difficult to collect would be used as a bioindicator of a taxon for which data are more easily gathered. Furthermore, for the same reason we did not develop models to predict the number of tiger beetle species in a region using birds and butterflies as bioindicator taxa. Naturally, in areas where bird data are available, for instance, the procedure that we developed can be modified readily.

When building models to predict the number of butterfly species in both North America and Australia, we found, using residual plots from initial models of the untransformed data and robust-resistant exploratory analyses (Cressie & Horton 1987), that a log-transformation of the butterfly data was necessary to stabilize the variance. When the bird data were modeled no transformation was required. In some analyses we Winsorized (Hampel et al. 1986; Cressie 1991) the data to mitigate the possible influences of unusual observations on predictions and inferences. Finally, we found by using cross-validation techniques and bivariate plots that the island effect that influences the data collected on Tasmania in Australia made this observation appear unusual when compared with the remainder of the Australia data. Hence, because of its unique characteristics, this observation was deleted from the data set. For all analyses, we reported the results completed using transformed, edited data when such modifications were required.

To build the models, we identified the latitude and longitude of the approximate center of each of the squares and used these spatial coordinates to represent the location of the square. We let $Z(\boldsymbol{s})$ represent the response variable at site $\boldsymbol{s} = (x,y)'$, where x and y are the latitude and longitude, respectively, expressed in degrees, and the prime indicates the transpose (an operation defined for matrices) of the vector. We assumed that $Z(\boldsymbol{s})$ is the realization of a random process and that $\boldsymbol{s}$ is contained in a fixed domain D and we modeled the response variable at site $\boldsymbol{s}$ as

$$Z(s) = \mu(s) + \delta(s), \quad (1)$$

where

$$\mu(s) = \beta_0 + \beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 y^2 + \beta_5 xy + \beta_6 Q_1(s) + \beta_7 Q_2(s) + \beta_8 Q_3(s) \quad (2)$$

is the mean of the process; $Q_1(\boldsymbol{s})$ is the number of butterfly species at site $\boldsymbol{s}$; $Q_2(\boldsymbol{s})$ is the number of tiger beetle species at site $\boldsymbol{s}$; $Q_3(\boldsymbol{s})$ is the average annual rainfall at site $\boldsymbol{s}$; β_k, $k = 0, \ldots, 8$ are parameters to be estimated; the error vector $\boldsymbol{\delta} = (\delta(\boldsymbol{s}_1), \delta(\boldsymbol{s}_2), \ldots, \delta(\boldsymbol{s}_n))'$ is a realization of a $n \times 1$ vector of second-order stationary random variables with expectation zero and covariance matrix Σ; and n is the number observations in the data set. The mean structure accounts for the large-scale variation in the data. The first six terms in equation 2 model the trend surface (Haining 1990); the final terms, $Q_l(\boldsymbol{s})$, $l = 1,2,3$, are included to model the relationship between the bioindicator taxa, the annual average rainfall, and the number of species of the response variable in a region. Naturally, when we modeled the number of butterfly species in a region as the response variable, Q_1 is omitted from the mean structure. Furthermore, when modeling the Australian bird data, we found the fit and predictive capability of the model improved by including Q_1^2 in the mean structure. We evaluated which of the predictor variables was a useful indicator of the number of species in a square for each model by determining if β_k, $k = 6,7,8$, was significantly different from zero. We used generalized least squares (Searle 1971; Rao 1973) to account for the spatial correlations in the data when parameters were estimated and hypothesis tests were conducted. The error structure, $\delta(\boldsymbol{s})$, accounts for the small-scale spatial variation in the response variable. The spatial correlations in the data are characterized by the off-diagonal elements in Σ. It is important to note that when we refer to large-scale and small-scale spatial variation we are referring to the decomposition of the data based on the model in equation 1. This terminology should not be confused with the similar use of these terms to express the size of grid squares in the region under investigation.

Geostatistical techniques were used to model the spatial relationships in the response variables (for details see Journel & Huijbregts [1978] or Cressie [1991]). The spatial relationship between the number of species of the response variable at two sites separated by the distance vector $\boldsymbol{h}$ is characterized by the variogram (Matheron 1963). The spatial covariance was then obtained from the variogram. In practice, the real variogram is seldom if ever known and, as in this study, must be estimated. But because in model 1 both the mean and the small-scale variation depend on the spatial coordinates at the sites, estimation of the variogram was complicated (Cressie 1991; Gotway & Hartford 1996). Consequently, for variogram estimation we first obtained surrogate residuals by forming a grid based on latitude and longitude, separating the data into the appropriate grid square, and then applying either median polish (Tukey 1977; Cressie 1986) or, in one case, regression analysis to obtain residuals that were then used to obtain the empirical variogram.

Because the empirical variogram is not necessarily negative definite, we fit a negative definite semivariogram model to the empirical semivariogram estimated from the residuals. In building the five models for this research, we tried many different variogram models and in each case selected the best-fitting model.

After we fit the semivariogram, we estimated the elements of Σ and used generalized least squares to estimate and make inferences about the parameters in model 1. (See Gotway & Cressie [1990] and Gotway & Hartford [1996] for discussions concerning the properties of the parameter estimates when Σ is estimated.) Consequently, we were then able to evaluate the viability of using bioindicators and average annual rainfall to indicate species richness patterns. To determine if one or both of the indicator species and average annual rainfall were useful to indicate the number of species in the response variable, we tested the hypotheses

$$H_0 : \beta_k = 0 \text{ and } H_a : \beta_k \neq 0 \quad (3)$$

for $k = 7,8,9$. We used generalized least squares to estimate the parameters and computed the sums of square errors associated with each model. We conducted hypothesis testing using standard hypothesis tests (Rao 1973). Because the predictor variables may be collinear, for each data set many models were fit and tested to determine which model was to be further evaluated by cross-validation techniques. To determine the validity of distributional assumptions, we examined residual plots and normal probability plots.

In equation 2 we included the terms involving latitude and longitude (x, y, x^2, y^2, and xy) to account for large-scale spatial variability. These effects (e.g., the latitude gradient) may influence both the response variable and one or both of the bioindicators. By including these terms in the model, we accounted for any large-scale variation in the trend surface of the response variable. Hence, we were confident that should a significant relationship between one or both of the bioindicators and the response variable be found, the significant result is not the consequence of unmodeled large-scale variation that simultaneously influences the numbers of both species.

The development and implementation of successful regional conservation strategies depends heavily on the direct knowledge or reliable prediction of continental-scale spatial biodiversity (Curnutt et al. 1994; Kaufman 1995). To illustrate the improvement in prediction accuracy that can be attributed to using bioindicators or average annual rainfall as predictors of species patterns, we used cross-validation techniques. Universal kriging, a spatial prediction methodology, was used to obtain predictions of the number of species in a particular square, and cross-validation was used to demonstrate the degree of improvement in the predictive accuracy of the number of species in a square attributable to the use of the bioindicator variables or average annual rainfall (for details see Carroll & Pearson 1998).

Equation 1 is a specific example of the more general model associated with universal kriging and a zero-mean, second-order stationary random process, $\delta(\cdot)$ (Cressie 1991; Gotway & Hartford 1996; Haas 1996). The more general model is

$$Z(s) = \sum_{j=1}^{p+1} x_{j-1}(s)\beta_{j-1} + \delta(s),\ s \in D, \quad (4)$$

where $\beta_{j-1}, j = 1, \ldots, p + 1$, are unknown parameters; $x_{j-1}(\boldsymbol{s}), j = 1, \ldots, p + 1$, are predictor variables associated with the datum at location $\boldsymbol{s}$ in D; and $\delta(\cdot)$ is as it was defined above. In all of our applications we included all six of the trend surface terms in the predictive model. To determine the effect on the predictive accuracy of the added predictor variables, Q_1, Q_2, and Q_3, we applied universal kriging two times when predicting each of the response variables. The first set of predictions was obtained using universal kriging and only the six trend surface terms as predictors. The second set of predictions was obtained again using universal kriging and the six trend surface terms, but this time we also added one or more of the terms Q_1, Q_2, and Q_3, depending on which ones were found to be significant when the hypotheses in equation 3 were tested. The two sets of predictions were then compared by means of the cross-validation statistic presented below.

When obtaining the universal kriging prediction, we let $\boldsymbol{s}_0$ represent a site with no observed datum for the response variable. The universal kriging estimator of $Z(\boldsymbol{s}_0)$ is

$$\hat{Z}(s_0) = \sum_{i=1}^{n} \tau_i Z(s_i). \quad (5)$$

If the data are from a Gaussian process, the predictor in equation 5 is unbiased and has minimum mean squared prediction error. (See Cressie [1991:154] for the expression used to obtain the coefficients $\{\tau_i\}$, $i = 1, \ldots, n$, and the mean squared prediction error, $\sigma^2(\boldsymbol{s}_0)$, associated with $\hat{Z}(\boldsymbol{s}_0)$.)

The degree of improvement in predictive accuracy obtained by using one or more of Q_1, Q_2, and Q_3 as predictors of the response variable may be evaluated by cross-validation techniques (Stone 1974; Cressie 1991). Cross-validation techniques compare the closeness of the true number of species of the response variable (either birds or butterflies) in a square to the predicted number. The cross-validation statistic used in this research was

$$CR = \left[(1/n) \sum_{j=1}^{n} \left(Y(\boldsymbol{s}_j) - \hat{Y}_{-j}(\boldsymbol{s}_j) \right)^2 \right]^{1/2}, \quad (6)$$

where $Y(\boldsymbol{s}_j)$ is the true number of species of the response variable at site $\boldsymbol{s}_j$ (in untransformed units), n is the number of observations in the data set that are used for cross-validation, and $\hat{Y}_{-j}(\boldsymbol{s}_j), j = 1, \ldots, n$, is the prediction of the untransformed number of species of the response variable at site $\boldsymbol{s}_j$. For the three applications for which we were predicting the number of bird species in a square (in North America, India, and Australia), no transformation of the response variable was required. Hence, in these models the data $Z(\cdot)$ were in the original units, and we computed $\hat{Y}_{-j}(\mathbf{s}_j) = \hat{Z}_{-j}(\mathbf{s}_j)$ by leaving $Z(\mathbf{s}_j)$ out of the data set and using the remaining observations to predict $Z(\mathbf{s}_j)$. When we were predicting the number of butterfly species in a square (in North America and Australia), a log transformation of the data was required to stabilize the variance. Consequently, in these two cases the data $Z(\cdot)$ were the logarithms of the original species counts, and we computed $\hat{Y}_{-j}(\mathbf{s}_j)$, an unbiased predictor of $Y(\mathbf{s}_j)$, using a function of $\hat{Z}_{-j}(\mathbf{s}_j)$ (Cressie 1991: 135), where $\hat{Z}_{-j}(\mathbf{s}_j)$ was obtained by leaving $Z(\mathbf{s}_j)$ out of the data set and using the remaining observations to predict $Z(\mathbf{s}_j)$.

The cross-validation statistic, CR, is a measure of goodness of prediction similar to the PRESS statistic often used in regression analysis (Draper & Smith 1981). Small values of CR indicate that, in general, the estimated values are close to the true values. In the next section we present the result of the hypothesis tests and the cross-validation studies for each of the five predictive models.

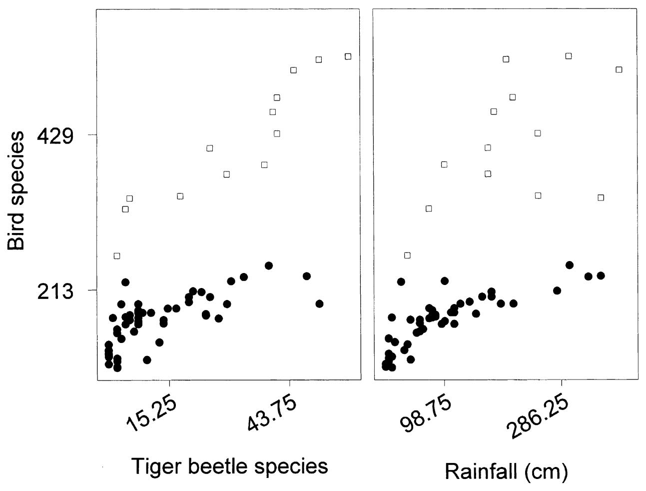

Figure 6. Species numbers and average annual rainfall in India. The numbers on the axis lines indicate either species numbers or average annual rainfall. Observations obtained in northern mountainous regions are designated by squares.

Results

We found a strong relationship between the number of bird species and the number of butterfly species in both North America and Australia (Figs. 5–7). The plots of the number of bird species versus the number of tiger beetle species showed that these taxa tended to be related, but not as strongly as were birds and butterflies. The plots of the number of butterfly species versus the number of tiger beetle species indicated a fairly strong relationship in North America and a weaker relationship in Australia. Average annual rainfall was not closely related to the number of either bird species or butterfly species in North America and India. In Australia, however, the average annual rainfall was more closely related to these taxa, particularly to the number of butterfly species.

Based on the results of hypothesis tests (all conducted at the $\alpha = 0.01$ level) and cross-validation statistics, we determined if one or more of the predictor variables—the bioindicator taxa and average annual rainfall—were useful for predicting species richness patterns. Looking first at the data collected on the number of bird species across North America, we found that the number of butterfly species and the number of tiger beetle species were significantly related to the number of bird species in a square. That is, we rejected both hypotheses H_0 :

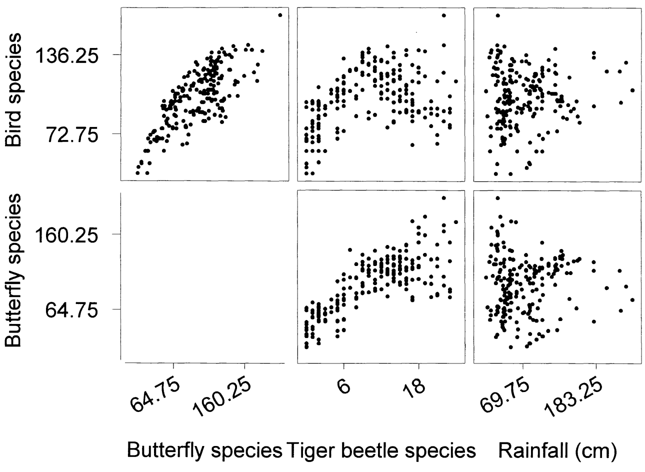

Figure 5. Species numbers and average annual rainfall in North America. The numbers on the axis lines indicate either species numbers or average annual rainfall.

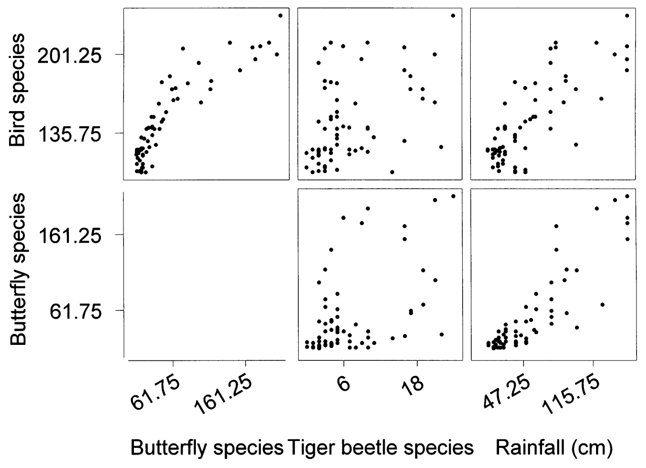

Figure 7. Species numbers and average annual rainfall in Australia. The numbers on the axis lines indicate either species numbers or average annual rainfall.

$\beta_7 = 0$ and $H_0 : \beta_8 = 0$. (See Table 1 for the associated *p* values of these and other hypothesis tests.) We were unable to reject the hypothesis ($H_0 : \beta_9 = 0$) that average annual rainfall was significantly related to the number of bird species. The value of CR computed when the six trend surface terms, Q_1, and Q_2 were included in the mean structure was 6.198. When computed a second time with only the six trend surface terms in the mean, the value of CR was 8.714, an increase of over 40%. This increase suggested that there is a substantial decrease in predictive accuracy when the bioindicator taxa were omitted from the model. Further investigation using cross-validation statistics revealed that nearly all of the increase in the predictive accuracy attributed to using butterflies and tiger beetles as predictors was due to the butterfly predictor variable. This result was also suggested by the relative sizes of the test statistics when the hypothesis tests were conducted. Hence, we concluded that, for predicting the number of bird species in North America, the number of butterfly species was the more useful indicator.

Turning to the butterfly data gathered in North America, we found that the number of tiger beetle species was a useful predictor of the number of butterfly species in a square and that the average annual rainfall was not significant. We computed CR twice: once with and once without tiger beetles in the mean structure. The respective values were 11.508 and 12.908. (Recall that the trend surface terms were included in the mean structure of all models.) Although the increase, about 12%, was not as striking as in the first analysis, it should not be ignored and suggests that tiger beetles can contribute to the prediction of other taxa.

To determine if these results could be generalized to other parts of the world, we investigated data collected in India and Australia. No butterfly data were available for India. When the number of tiger beetle species and average annual rainfall were used as predictor variables of the number of bird species, we found that tiger beetles were a useful bioindicator and that the average annual rainfall was not a useful predictor. The values of CR computed first with and then without the number of tiger beetle species in the mean structure were 58.759 and 96.939, respectively. The nearly 65% decrease in predictive accuracy when tiger beetles were omitted provided strong evidence of their usefulness as a bioindicator.

Finally, we look at the data collected in Australia. When the number of bird species was modeled, we found that the number of butterfly species was a useful bioindicator but that the number of tiger beetle species and the average annual rainfall were not significant predictors. The bivariate plot of birds versus butterflies (Fig. 7) suggested that the relationship between the number of bird species in a square and the corresponding number of butterfly species may be nonlinear. Consequently, in addition to Q_1 we added Q_1^2 to account for the nonlinearity. Two subsequent hypothesis tests, one to determine if both of these terms can simultaneously be eliminated from the model and a second to determine if the quadratic term alone can be eliminated from the model, were found to be significant, both *p* values ≤ 0.0001. Hence, both Q_1 and Q_1^2 were retained in the model. The value of CR computed with both the linear and quadratic butterfly terms in the model was 11.532. When these two terms were omitted, CR increased over 54% to 17.797. These results supported those observed in the North America data set that indicated the importance of butterflies as a bioindicator of birds.

The results of the analysis of the Australian butterfly data revealed that one observation (in square number 4) was highly influential when the parameter estimates in equation 2 were obtained. That is, when this observation was omitted, the parameter estimates changed substantially. Consequently, this observation was particularly poorly predicted when cross-validation statistics were computed. Further investigation showed that the influence of this observation was due to the general tendency of trend surfaces to fit more imperfectly at the edges than in the center (Ripley 1981) and the fact that this square was located on the coast and two degrees north of all of the other observations. Consequently, to mitigate its influence, we deleted this observation in subsequent analyses. The results of the hypothesis tests indicated that neither the number of tiger beetle species nor average annual rainfall was a useful predictor of the number of butterfly species. But because the northern, eastern, and southern coastal areas of Australia tend to

Table 1. Results of the hypotheses tests (*p* values) used to determine if one or both indicator groups and average rainfall indicate the number of species in the response variable.*

	Hypothesis		
Response variable	$H_0: \beta_7 = 0$ *(butterfly)*	$H_0: \beta_8 = 0$ *(tiger beetle)*	$H_0: \beta_9 = 0$ *(rainfall)*
Birds (North America)	≤0.0001	0.0005	0.5925
Butterflies (North America)	—	≤0.0001	0.9883
Birds (India)	—	≤0.0001	0.5976
Birds (Australia)	≤0.0001	0.2779	0.8708
Butterflies (Australia)	—	0.1060	0.1198

*H_0, $\beta_k = 0$ *and* H_a, $\beta_k = 0$ *for* k = *7, 8, 9.*

have both high average annual rainfall and high numbers of butterfly species, we examined the data further to determine why we did not find rainfall to be significant. When average annual rainfall alone was included in the mean structure and the trend surface terms were omitted, we found a significant relationship between the number of butterfly species and average annual rainfall. This finding indicated that, perhaps due to the orientation of the high rainfall areas, the trend surface terms captured the effects of heavy rainfall in the coastal areas, and, thus, adding average annual rainfall to a model that already contained the trend surface terms did not improve the model fit. When we computed cross-validation statistics, we found that the value of this statistic decreased only slightly (from 26.812 to 26.423) when average annual rainfall was added to the model that contained only the trend surface terms.

To further explore the effects of average annual rainfall, we fitted one additional model. In this model we included the trend surface terms and a dummy variable that was set equal to one for observations that fall in squares with average annual rainfall in the upper quartile and set equal to zero otherwise. Hence, the dummy variable simply indicated squares with high average annual rainfall. We found the dummy variable to be a significant predictor ($p = 0.0026$) and that the value of the cross-validation statistic computed using this model was 22.002. The increase of nearly 22% in the cross-validation statistic when the dummy variable was omitted suggested that modeling areas with high average annual rainfall differently from other areas substantially improved predictive accuracy.

Although the primary focus of this research was to investigate the benefits of using biotic and abiotic predictors of areal species richness, we explored how predictive accuracy could be further improved by modifying model 1. Such modifications may be suggested by the researcher's biological knowledge of a particular region or by skillful data analysis. For example, when developing the model for predicting the number of bird species in India, we found that predictive accuracy was substantially improved by including a dummy variable that accounted for the great disparity in the numbers of bird species between the northern mountainous region and the southern plain of the Indian subcontinent. Moreover, not only is there a considerable difference in the average levels between these two regions, but the relationship between the number of tiger beetle species and the number of bird species differs depending on the region (Fig. 6). When these effects were accounted for in the model, the cross-validation statistic decreased by more than half from 58.759 to 25.939. Habitat diversity is a possible biological explanation for the disparities in species numbers between the mountains and the plain and differences in the relationship between the number of tiger beetle species and the number of bird species. In mountainous regions with considerable altitudinal relief, habitat tends to be more diverse, and, consequently, we found greater numbers of bird species. Hence, the differences that we observed between the mountains and the plain may be due to differences in the degrees of habitat diversity between these areas, a factor we will explore in future research.

Discussion

The results of this study indicate that carefully chosen taxa, together with mean annual precipitation, can be used to predict areal patterns of species numbers of other taxa, often regardless of trophic level and vagility differences. But the most useful biotic and abiotic indicators for predicting other taxa differ somewhat, depending on which continental area is investigated. Therefore, applying untested indicators, which have been found to be beneficial in one area, more broadly to other regions may prove to be both misleading and costly. Conversely, biological expertise and careful data analysis may suggest additional useful indicators not previously considered.

Although positive relationships in species numbers among different taxa are more likely to exist at a continental scale, other confounding influences arise at this scale that may alter the capacity of a particular taxon to predict another in several different continental areas. For instance, the data from Australia provide the most obvious departure from generalizations found in North America and the Indian subcontinent. This anomaly emphasizes that, at continental scales of investigation, historical and biogeographical factors (e.g., dispersion, plate tectonics, and centers of speciation) must also be considered when taxa and abiotic factors are selected as candidates for indicators. Long-term isolation (Pianka 1986), short-term cyclic isolation (Haffer 1969), and invasion opportunities (Pearson & Ghorpade 1989), together with differences in altitudinal relief, have had unique effects on each continental area, resulting in divergent spatial patterns. For instance, just as we found in the present study, previous comparisons of species numbers among Australian taxa also have shown stronger relations to climate than similar comparisons in Eurasia (Letcher & Harvey 1994) and North America (Schall & Pianka 1978; Smith et al. 1994). Not only does Australia have a more precipitous gradient in mean annual rainfall from the coast inland, but the variance is so extreme that interior parts of Australia may receive little or no rainfall for years at a time and then be deluged. With such extremes in rainfall, precipitation may have become an overwhelming factor not apparent in comparable habitat types of other continental areas (Schall & Pianka 1978; Smith et al. 1994).

The extreme spatial and temporal variance in precipitation in Australia may in turn make differential vagility among various taxa an important factor. Many Australian birds show a remarkable ability to quickly locate and utilize even the most isolated pockets of rainfall in inland Australia (Keast 1981). Butterflies, to a much lesser extent, show some of these capabilities (Common & Waterhouse 1982). Australian tiger beetles, however, have evolved no such adaptations. Instead, they await rare precipitation events as aestivating larvae or pupae, perhaps for years (W. D. Sumlin III, personal communication). Thus, our assumption of the common influence of climate on all taxa within a continental area is negated for Australia.

The choice of bioindicators for predicting congruent spatial patterns of species richness also must take into account biogeographical differences in ecological factors (Ricklefs & Schluter 1993). In Australia, especially the arid central part of the continent, lizards have apparently taken over some of the niches occupied by birds in similar habitats on other continents (Schall & Pianka 1978). Thus, because of an often ambiguous negative relation in species numbers of lizards and birds, possibly because of competitive exclusion, lizards would be a poor taxon to choose as a bioindicator for spatial patterns of bird species numbers. In lowland tropical rain forests, primates, either as competitors or as nest robbers, appear occasionally to have a negative influence on birds (Pearson 1982), and these two taxa would also not be appropriate as predictors of each other's spatial patterns of species distributions.

By using spatial modeling techniques, we are able to identify the most influential indicators of general areal species patterns and to eliminate those that do not contribute to improving prediction accuracy. These techniques enable us to account for spatial dependencies in the data, a critical consideration when inferences and conclusions are drawn about which biotic and abiotic indicators are useful for predicting spatial patterns of species richness in each continental area. If spatial dependencies exist but are not considered, invalid conclusions may be drawn about the viability of certain indicators (Carroll & Pearson 1998). Furthermore, prediction accuracy may substantially increase when spatial correlations are modeled. Hence, when vital conservation strategy is being formulated, it is essential that spatial correlations in the data be considered to obtain the most accurate predictions of areal species richness.

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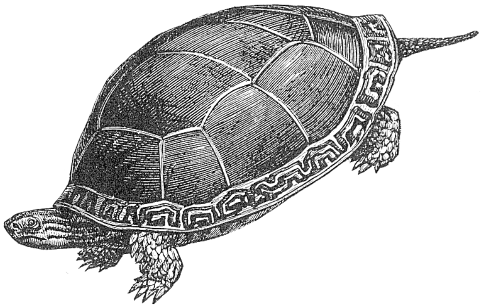


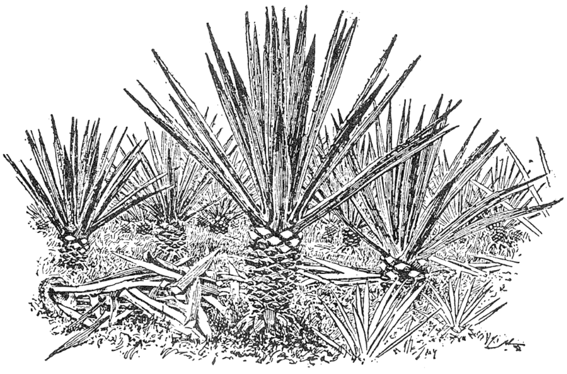
Appendix

Data for each square in the gridded maps (Figs. 1–4).[a]

North America[b]

A	*B*	*C*	*D*	*E*	*F*	*G*
1	64	1	78	20	66	142
2	69	2	77	31	63	139
3	58	2	71	20	65	135
4	52	3	59	19	67	129
5	69	2	81	30	62	136
6	64	2	77	30	64	131
7	56	2	67	40	65	127
8	64	1	97	42	60	132
9	68	2	92	32	61	128
10	57	2	85	40	62	124
11	43	1	70	38	63	118
12	30	1	41	28	64	113
13	61	1	98	79	58	130
14	67	0	94	62	59	126
15	62	1	99	31	60	122
16	59	3	93	28	61	117
17	50	5	77	36	62	111
18	33	0	49	30	63	106
19	39	6	75	123	48	55
20	67	2	99	153	55	128
21	64	2	98	51	57	124
22	77	6	108	42	58	120
23	67	5	104	41	59	114
24	62	4	98	40	59	110
25	56	1	81	39	60	104
26	46	0	69	38	60	100
27	42	0	67	39	60	94
28	22	2	50	80	56	63
29	27	2	59	91	54	58
30	64	0	98	222	53	127
31	72	2	110	85	54	122
32	92	6	113	44	56	118
33	77	6	107	43	57	113
34	74	5	102	42	58	109
35	66	3	88	40	58	103
36	59	2	79	43	58	100
37	50	2	69	42	58	97
38	39	0	68	41	58	91
39	17	0	41	51	56	77
40	18	0	46	76	55	72
41	22	0	49	81	55	68
42	31	0	59	100	53	65
43	31	5	69	101	52	60
44	50	3	95	180	52	127
45	78	4	108	240	51	124
46	103	6	114	53	52	120
47	101	5	116	51	53	117
48	87	9	108	48	54	112
49	86	8	101	49	54	108
50	79	8	103	46	53	105
51	72	5	99	46	55	99
52	64	2	97	49	55	95
53	55	1	83	50	55	90
54	49	0	77	60	54	86
55	40	1	75	62	54	82
56	30	1	59	61	54	78
57	34	1	66	81	53	74
58	34	0	72	81	52	70
59	38	5	74	109	51	66
60	93	7	123	200	48	122
61	117	9	131	56	50	119
62	110	6	133	53	51	115
63	101	14	106	50	51	111
64	92	11	88	44	52	108
65	87	10	90	42	53	104
66	96	9	108	47	53	98
67	83	5	103	50	53	94
68	74	1	99	52	53	91
69	62	2	96	72	52	88
70	61	3	93	70	51	83
71	60	2	95	78	51	79
72	55	1	92	81	51	75
73	52	2	87	86	50	71
74	51	5	93	91	48	68
75	52	6	99	100	47	64
76	53	6	95	128	46	61
77	115	11	123	220	47	122
78	115	12	131	75	47	119
79	122	9	131	68	47	115
80	130	15	119	50	48	111
81	102	16	90	36	49	107
82	91	16	91	39	49	104
83	103	17	98	47	49	101
84	110	14	115	50	49	98
85	86	9	122	60	49	94
86	81	8	112	71	50	90
87	71	6	105	80	50	86
88	68	4	105	81	49	82
89	64	5	107	81	48	78
90	67	5	102	93	48	74
91	77	5	109	96	47	71
92	84	6	119	101	46	68
93	79	6	118	142	45	64
94	95	9	130	230	44	123
95	115	9	134	180	44	121
96	115	10	128	50	45	118
97	135	9	136	75	46	114
98	141	7	124	50	46	111
99	113	12	101	34	46	107
100	104	18	90	30	47	104
101	78	17	83	35	47	101
102	98	16	92	50	47	97
103	119	12	119	65	47	93
104	107	12	117	75	47	90
105	103	11	116	78	47	87
106	99	11	115	86	46	83
107	89	11	111	85	45	79
108	91	12	111	91	45	76
109	97	13	121	100	45	72
110	97	15	128	120	43	70
111	126	9	138	180	41	123
112	116	10	138	35	42	119
113	106	8	125	31	42	117
114	123	8	125	28	43	114
115	140	11	124	53	43	110
116	129	12	117	41	44	107
117	129	20	99	55	44	104
118	81	17	91	45	44	100
119	100	15	90	60	44	97
120	116	13	108	75	45	93
121	126	15	117	75	45	90
122	117	13	119	88	44	87
123	121	12	121	89	44	83
124	115	13	120	90	43	80
125	112	13	121	90	43	77
126	119	18	126	100	42	73
127	130	10	141	120	39	122
128	123	11	126	25	40	119
129	99	9	120	28	40	116
130	129	13	130	28	41	113
131	140	16	136	31	41	109
132	151	18	114	40	42	107
133	120	21	88	41	42	103
134	81	20	79	50	42	100
135	98	20	93	66	42	97
136	105	14	98	81	42	93
137	119	16	111	82	42	90
138	119	17	115	96	42	87
139	115	14	116	95	42	83
140	111	14	124	110	41	80
141	118	15	124	100	41	77
142	121	18	122	120	41	74
143	121	10	129	80	37	121
144	133	14	138	20	37	118
145	108	10	120	23	38	115
146	143	14	134	30	38	112
147	145	13	143	41	38	110
148	178	17	128	52	39	106
149	107	22	83	33	39	103
150	81	23	78	51	39	100
151	91	23	90	68	39	97
152	111	15	108	88	40	95
153	113	13	108	89	40	91
154	118	16	108	98	39	87
155	105	16	105	100	39	84
156	124	12	132	110	38	79
157	115	16	112	120	38	77
158	140	15	103	130	38	74
159	105	8	124	50	35	120
160	124	11	131	35	35	117
161	126	11	134	18	35	115
162	148	16	140	21	36	112
163	165	22	144	30	36	109
164	173	22	122	38	37	106
165	96	22	91	39	37	103
166	88	23	80	60	37	100
167	99	19	93	81	37	95
168	123	12	106	110	37	93
169	121	14	106	110	37	90
170	107	12	105	115	37	87
171	111	14	105	118	37	84
172	123	14	121	122	36	81
173	133	13	101	130	36	78
174	125	13	113	40	33	117
175	106	7	107	13	33	115
176	170	18	140	21	34	111
177	162	18	140	31	34	108

continued



Appendix (continued)

North America[b]

A	*B*	*C*	*D*	*E*	*F*	*G*
178	148	21	115	31	34	105
179	83	21	65	41	35	103
180	85	21	72	51	35	100
181	107	20	89	88	35	96
182	119	17	105	121	35	94
183	117	17	100	123	35	90
184	116	15	99	124	35	87
185	121	15	100	130	34	84
186	133	15	100	128	34	82
187	130	16	99	131	34	78
188	68	8	87	15	31	113
189	208	22	168	31	31	111
190	184	19	139	35	32	108
191	160	19	119	31	32	106
192	77	17	64	36	32	102
193	82	13	78	59	32	99
194	130	21	93	99	32	96
195	131	15	99	128	32	93
196	124	17	96	140	32	91
197	112	14	91	144	32	88
198	112	10	85	138	32	85
199	131	18	91	120	32	82
200	147	16	112	28	30	103
201	105	14	83	41	30	101
202	110	13	101	61	30	99
203	151	23	103	100	30	97
204	127	23	93	149	30	92
205	128	17	87	155	30	86
206	135	19	86	132	30	82
207	177	24	115	59	27	98
208	130	14	82	158	27	82

Indian subcontinent[c]

A	*B*	*C*	*D*	*E*	*F*
1	3	261	40	36	73
2	5	224	30	34	71
3	6	171	45	34	75
4	5	326	75	34	78
5	3	118	10	31	68
6	2	174	15	31	71
7	10	116	45	31	75
8	38	387	100	31	78
9	29	374	170	31	80
10	6	341	350	31	95
11	1	110	5	28	63
12	1	124	10	28	67
13	4	145	10	28	69
14	1	120	15	28	71
15	1	129	35	28	75
16	14	166	60	28	78
17	25	410	170	28	80
18	40	460	180	28	83
19	41	480	210	27	86
20	58	537	300	27	88
21	51	533	200	28	91
22	45	518	380	26	93
23	3	106	5	27	63
24	3	114	10	27	67
25	13	140	20	27	69
26	1	137	40	27	71
27	3	158	65	27	75
28	5	165	95	27	78
29	8	165	115	27	80
30	8	169	100	26	83
31	24	179	150	26	86
32	25	203	175	26	88
33	41	430	250	25	91
34	3	105	15	23	69
35	3	153	55	23	71
36	5	175	85	23	75
37	6	178	85	23	78
38	11	181	110	22	80
39	17	187	115	22	83
40	20	203	160	22	86
41	29	193	190	22	88
42	18	344	250	22	91
43	7	155	60	21	71
44	4	193	210	21	74
45	8	184	80	21	77
46	8	181	115	21	79
47	8	193	125	21	82
48	23	210	175	20	85
49	21	211	280	19	74
50	8	174	80	19	77
51	9	181	110	19	79
52	20	196	140	19	82
53	33	231	330	15	75
54	14	171	60	16	77
55	15	187	75	16	79
56	39	247	300	14	77
57	24	177	80	14	79
58	48	232	350	11	77
59	27	173	75	11	79
60	30	225	100	9	78
61	51	193	125	7	81

continued

Australia[d]

A	*B*	*C*	*D*	*E*	*F*	*G*
1	69	19	164	125	14	127
2	114	19	172	100	14	131
3	101	21	161	88	15	134
4	206	21	201	138	12	144
5	61	17	172	75	17	124
6	63	5	163	60	17	128
7	49	4	147	55	17	131
8	53	5	153	75	17	134
9	58	17	183	90	18	140
10	211	24	234	150	17	147
11	25	14	103	50	19	122
12	19	5	105	50	19	124
13	16	3	104	40	19	128
14	19	1	103	40	20	131
15	21	3	107	40	20	134
16	21	3	123	50	20	138
17	33	5	149	60	20	141
18	195	10	211	120	19	144
19	155	16	188	150	19	148
20	30	22	124	28	22	117
21	21	2	110	23	22	120
22	13	2	104	24	22	123
23	13	2	110	28	22	127
24	17	4	113	28	23	131
25	34	3	108	23	23	134
26	20	0	107	18	23	138
27	26	2	120	30	23	141
28	47	2	145	50	22	145
29	172	16	207	80	22	148
30	26	10	139	23	25	114
31	17	3	122	20	25	117
32	13	7	122	18	25	120
33	12	2	118	18	26	123
34	13	1	122	18	26	127
35	14	2	122	18	27	130
36	16	2	121	13	27	134
37	19	4	122	13	27	137
38	23	5	131	20	27	141
39	37	5	139	30	26	145
40	83	5	177	60	26	148
41	176	9	197	150	25	152
42	34	10	140	30	28	116
43	13	10	120	25	28	119
44	13	8	121	22	29	123
45	14	1	115	18	29	127
46	14	0	119	20	29	130
47	15	4	119	20	29	134
48	19	9	123	25	29	137
49	21	7	118	30	29	141
50	34	5	134	40	29	145
51	66	3	173	50	28	149
52	183	6	208	150	30	152
53	44	3	139	75	33	116
54	19	11	132	40	32	118
55	28	16	129	40	32	123
56	21	2	117	24	32	128
57	29	7	140	45	33	134
58	43	8	160	30	33	137
59	34	6	141	30	33	141
60	36	4	149	58	33	145
61	141	4	211	80	32	149
62	39	5	126	100	34	120
63	47	4	178	40	35	137
64	76	3	206	75	36	141
65	98	2	194	75	36	146
66	115	3	179	90	36	149
67	38	0	75	150	42	147

continued

[a] *Data are from Pearson and Cassola (1992), Pearson and Juliano (1993), Carroll and Pearson (1998), Pearson and Ghorpade (1989), and Pearson and Juliano (1993).*

[b] *A, grid square number; B, number of butterfly species; C, number of tiger beetle species; D, number of bird species; E, average annual rainfall (cm); F, latitude (north); G, longitude (west).*

[c] *A, grid square number; B, number of tiger beetle species; C, number of bird species; D, average annual rainfall (cm); E, latitude (north); F, longitude (east).*

[d] *A, grid square number; B, number of butterfly species; C, number of tiger beetle species; D, number of bird species; E, average annual rainfall (cm); F, latitude (south); G, longitude (east).*