

Mapping More of Terrestrial Biodiversity for Global Conservation Assessment

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Global conservation assessments require information on the distribution of biodiversity across the planet. Yet this information is often mapped at a very coarse spatial resolution relative to the scale of most land-use and management decisions. Furthermore, such mapping tends to focus selectively on better-known elements of biodiversity (e.g., vertebrates). We introduce a new approach to describing and mapping the global distribution of terrestrial biodiversity that may help to alleviate these problems. This approach focuses on estimating spatial pattern in emergent properties of biodiversity (richness and compositional turnover) rather than distributions of individual species, making it well suited to lesser-known, yet highly diverse, biological groups. We have developed a global biodiversity model linking these properties to mapped ecoregions and fine-scale environmental surfaces. The model is being calibrated progressively using extensive biological data sets for a wide variety of taxa. We also describe an analytical approach to applying our model in global conservation assessments, illustrated with a preliminary analysis of the representativeness of the world's protected-area system. Our approach is intended to complement, not compete with, assessments based on individual species of particular conservation concern.

Keywords: biodiversity, global, mapping, protected areas, representativeness

Management action to conserve biodiversity is most appropriately planned and implemented at regional or local scales. However, conservation assessments at a global scale can help to justify and stimulate such local activity by providing a big-picture perspective on the current and projected status of biodiversity on the planet. Such assessments may also be used to guide the allocation of conservation resources globally and to provide a broad context within which to evaluate regional-scale conservation prior-

ities. All global conservation assessments—whether focused on the coverage of protected areas (Rodrigues et al. 2004a), the impacts of habitat loss (Gaston et al. 2003), or the potential effects of climate change (Thomas et al. 2004)—require information on the spatial distribution of elements of biodiversity. This knowledge of biodiversity pattern provides the essential foundation on which to build more sophisticated assessments of ecological, evolutionary, and socioeconomic processes.

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The difficulty of mapping spatial pattern in biodiversity depends on the level of biodiversity of interest (e.g., ecosystems, species, or genes). Distributions of broad ecosystems are now relatively easy to map and monitor, thanks to the advent of satellite-based remote sensing. However, satellite imagery tells little about patterns of species composition within ecosystems. Mapping the distributions of species is far more challenging, because the vast majority of species can be detected only through direct field observation or sampling. Current knowledge of species distributions is therefore grossly incomplete. Only a fraction of the planet's species has been described to date (Heywood 1995), and distributional information sufficient to be of any direct use in conservation assessment is available for only a small proportion of these known species (Ferrier 2002). Conservation assessments therefore need to rely heavily on the use of biodiversity "surrogates"—mapped entities whose distributions are likely to concord with spatial pattern in biodiversity as a whole (Margules and Pressey 2000).

Surrogates employed in recent global assessments of terrestrial biodiversity include mapped ranges of vertebrate species (Rodrigues et al. 2004a, 2004b), major habitat types or biomes (Gaston et al. 2003, Brooks et al. 2004), and biogeographical regions or ecoregions (Olson and Dinerstein 2002). While each of these surrogates has particular strengths, they share a potential weakness in the way they have been employed in global assessments. All three surrogates tend to be mapped at a coarse spatial resolution relative to the scale at which land-use or management decisions are typically made on the ground. This mismatch of scales may limit the extent to which these assessments can detect finer-scale bias in the distribution of habitat loss (e.g., toward more productive parts of a landscape) or in the location of protected areas (Pressey et al. 1996, Armesto et al. 1998), especially if the mapped distribution of each surrogate entity encompasses considerable environmental and biological heterogeneity. Such problems are likely to be particularly acute for nonvertebrate components of biodiversity, including invertebrates and plants, because taxa within these groups often exhibit higher rates of spatial turnover (replacement of species) than do vertebrates (Ferrier et al. 1999, Moritz et al. 2001). For example, protecting a portion of the range of a given vertebrate species, or of an ecoregion, does not necessarily ensure good representation of all elements of biodiversity if this protection is biased environmentally or geographically within the mapped distribution of the surrogate entity concerned.

This mismatch between the scale of global assessments and the scale at which actual land-use and management decisions shape regional landscapes may result in a tendency for such assessments to overestimate the representativeness of the world's protected-area system or, conversely, to underestimate the global consequences of habitat loss. Furthermore, in using global assessments based on coarse-resolution surrogates to direct conservation attention to priority regions or "hotspots," there is a risk that important finer-scale priorities

may be overlooked, and therefore never receive the conservation attention they deserve (Ferrier 2002).

To help alleviate these problems, we introduce a new surrogate approach to estimating and mapping spatial pattern in terrestrial biodiversity for global conservation assessments. This approach arose out of work conducted by an informal consortium in the 6 months leading up to the fifth World Parks Congress (Durban, South Africa, September 2003), aimed at providing "proof of concept" of an alternative strategy for assessing the representativeness of the world's protected-area system (i.e., the extent to which this system includes samples of all elements of biodiversity). The approach is intended to complement, not compete with, other assessments based on vertebrate distributions, biomes, or ecoregions. As in those assessments, we use coarse-scale surrogates to provide a solid biogeographical foundation for our approach. However, we then add value to these surrogates by using higher-resolution mapping of environmental attributes to predict spatial pattern in biodiversity at finer scales. The link between biodiversity pattern and mapped environmental attributes is calibrated through statistical modeling of available biological and environmental data.

Our modeling takes advantage of revolutionary advances in the availability and quality of two major sources of data: (1) global coverage of digital terrain, climate, soil, and land-cover surfaces, now available at relatively fine spatial resolution (mostly 1-kilometer [km] grids), thanks to recent advances in remote sensing technology, and (2) data sets from biological surveys and specimen collections, containing the locations of observation or collection for large numbers of species across a wide range of higher taxa. The accessibility of such data is improving dramatically as a result of rapid advances in the field of biodiversity informatics, particularly the digitization of museum and herbarium specimen collections (Bisby 2000, Graham et al. 2004).

Here we outline the analytical strategy we are using to develop a global biodiversity model by integrating various sources of biological and environmental data, with a summary of progress made to date in accessing and processing these data sources. We then describe how our biodiversity model can be employed in global conservation assessments, illustrated with a preliminary analysis of the representativeness of the world's protected-area system.

Developing a global model of spatial pattern in biodiversity

To integrate the disparate types of biological and environmental data employed in our approach, we focus our efforts on describing spatial pattern in emergent (or collective) properties of species-level biodiversity (Gaston 2000), rather than attempt to describe distributions of individual species. This means that our approach is well suited to assessing spatial pattern in lesser-known, yet highly diverse, biological groups. The two emergent properties of particular interest here are (1) local richness or "alpha diversity," the number of species occurring at a given location on the planet, and (2) compo-

sitional turnover or “beta diversity,” the difference in species composition between different locations (Whittaker 1972, Ferrier 2002).

The concept of compositional turnover has rarely been addressed explicitly in the conservation biology literature, despite its direct relationship with the more widely studied concept of endemism. The level of endemism exhibited by species occupying a given area is clearly a function of compositional turnover between this area and all other areas. However, as we demonstrate below, there is much to be gained by working directly with turnover itself in conservation assessment, as this approach retains more information on the pattern of complementarity (*sensu* Margules and Pressey 2000) between areas. Several recent ecological papers on the partitioning of regional biodiversity into components of alpha and beta diversity have helped to provide a strong theoretical foundation for the richness–turnover view of biodiversity adopted here (Arita and Rodriguez 2002, Gering et al. 2003).

To develop our global model of spatial pattern in biodiversity, we model richness and turnover as functions of mapped biogeographical units and environmental surfaces with complete global coverage. The model is being calibrated using a wide variety of biological data (figure 1).

Biogeographical and environmental foundations of the model.

Recent mapping of terrestrial ecoregions (867 ecoregions nested within eight biogeographical realms and 14 biomes; Olson et al. 2001) provides a broad biogeographical foundation for our model. Environmental heterogeneity at finer spatial scales is addressed using a range of terrain, climate, soil, and land-cover surfaces with complete global coverage. These include (a) the US Geological Survey’s GTOPO30 digital elevation model (30-second, or approximately 1-km, grid resolution), recently upgraded with data from the National Aeronautics and Space Administration’s Shuttle Radar Topography Mission; (b) various secondary terrain variables (e.g., ruggedness) derived from the GTOPO30 data; (c) 19 bioclimatic variables derived by modeling long-term average temperature and precipitation data from more than 30,000 climate stations worldwide in relation to the GTOPO30 data (Hijmans et al. 2004), using the ANUSPLIN climate modeling software (Hutchinson et al. 1997); (d) seven soil attributes from the International Geosphere–Biosphere Programme Data and Information System (5-minute, or approximately 10-km, grid resolution); and (e) various 1-km resolution land-cover classifications derived from satellite imagery, including the Global Land Cover Characteristics database (from AVHRR, or Advanced Very High Resolution Radiometer, imagery), the MODIS 12 (Moderate Resolution Imaging Spectroradiometer) land-cover products, and the Global

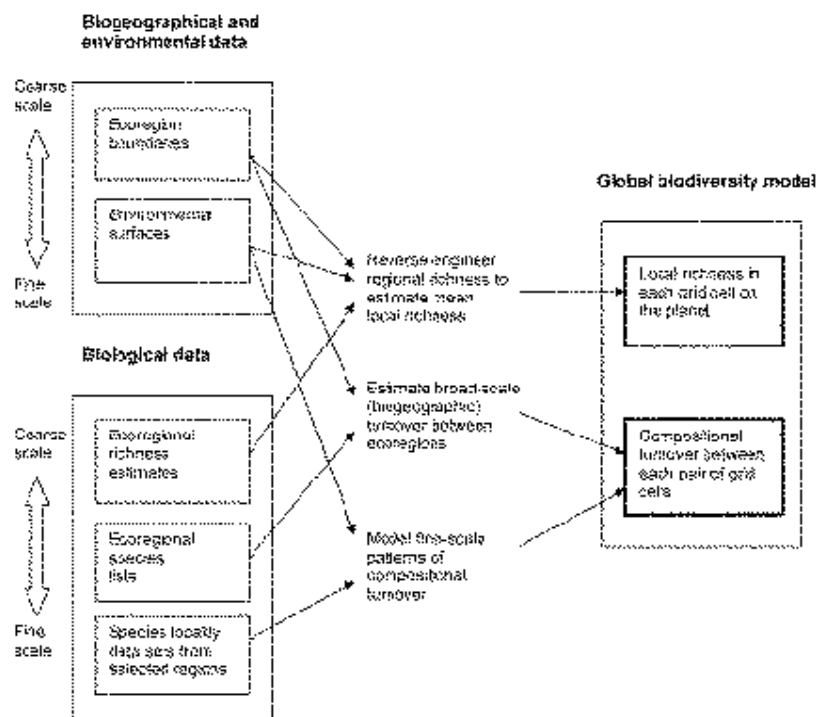


Figure 1. General strategy for developing our global biodiversity model.

Land Cover 2000 data set (from SPOT, or Système pour l’Observation de la Terre, imagery). Examples of a number of these environmental data sets are depicted in figure 2.

We initially converted all of the biogeographical and environmental data sets to a common 30-second (1-km) grid, containing approximately 200 million terrestrial grid cells for the planet (excluding Antarctica). However, in the interests of computational efficiency, most of our analyses to date have been performed using a slightly generalized 2.5-minute (5-km) version of the grid, containing approximately 8 million terrestrial grid cells. Analysis at the finer 1-km resolution will probably become more practicable in the near future as a result of ongoing improvements in computer processing speed.

To develop our model describing spatial pattern in biodiversity, the richness (r_i) of grid cell i is modeled as a function of the ecoregion (e_i) in which the cell occurs and the vector (X_i) of environmental values for the cell (one value for each of the mapped terrain, climate, and soil variables outlined above):

$$r_i = f(e_i, X_i).$$

The focus here is on estimating potential richness, or the number of species expected to occur in a grid cell if that cell were still in a natural state. However, our approach can readily accommodate relative indices of potential richness in place of estimates of the absolute number of species.

The model addresses turnover (or beta diversity) by modeling the dissimilarity (d_{ij}) in species composition between any pair of grid cells i and j as a function of the ecoregions in which

the two cells occur and the environmental values for the cells:

$$d_{ij} = (e_p X_p e_p X_j).$$

Dissimilarity is defined here as the mean proportion of species occurring in one cell that are not expected to occur in the other cell (Wilson and Shmida 1984, Faith et al. 1987), again estimated as if both of these cells were still in a natural state. The

vectors X_i and X_j can also include the latitude and longitude of each site, thereby allowing the dissimilarity of sites to be shaped by geographical separation in addition to environmental difference.

Calibrating the model using available biological data. If our global biodiversity model is to contribute usefully to conservation assessment, it must make predictions that match real patterns of biological richness and turnover as closely as possible. To achieve this, we use various sources of biological data to define and calibrate the functions in our model that link richness and turnover to mapped ecoregions and environmental surfaces. We view this calibration as an incremental process. Although we have already accessed and analyzed a large number of biological data sets since commencing this work in early 2003, we suspect that these data sets represent only the tip of the iceberg in relation to the total pool of biological data that could be used to calibrate our model. The model therefore has considerable potential for ongoing refinement.

To date, we have directed more effort to calibrating the turnover component of our model than to calibrating the richness component. Given our initial interest in assessing the representativeness of the world's protected-area system, we felt that turnover (beta diversity) would be likely to play a much more significant role in determining representativeness than would variation in local richness. To calibrate the turnover component of our model, we are using biological data recorded at two very different spatial scales. Broad biogeographic turnover between ecoregions is addressed by analyzing compiled lists of species occurring in each ecoregion. At present, such lists are available across all ecoregions only for vertebrates, in an extensive data set compiled by one of us (J. F. L.). This data set records the presence or absence of more than 26,000 mammal, bird, reptile, and amphibian species in each of the world's 867 ecoregions. These data allow ready estimation of the broad level of compositional dissimilarity between all possible pairs of ecoregions. Rapidly improving access to digitized specimen-locality data sets should allow the estimation of turnover between ecoregions to be extended to plants and invertebrates within the next few years.

Finer-scale turnover within regions is being explored through statistical analysis of selected biological survey and collection data sets. These data are subjected to generalized dissimilarity modeling (GDM), a new nonlinear technique for analyzing turnover in species composition between pairs of survey or collection localities in relation to environmental differences between, and geographical separation of, these localities (Faith and Ferrier 2002, Ferrier 2002, Ferrier et al. 2002). Once such a model

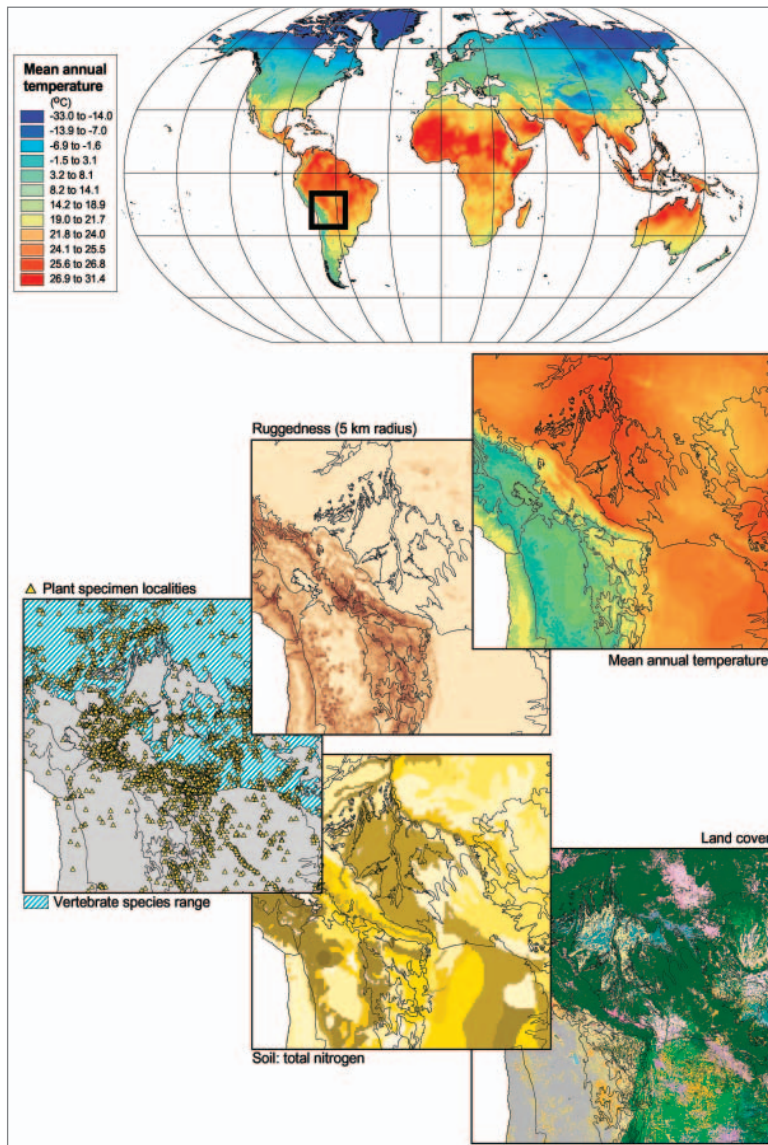


Figure 2. Examples of the data used to develop the global biodiversity model. Black lines in the detailed maps are ecoregion boundaries. The temperature surface is derived from WorldClim (Hijmans et al. 2004). Plant specimen localities are from the Missouri Botanical Garden's TROPICOS database. The vertebrate species range is based on the lists of species occurring within each ecoregion compiled by one of us (J. F. L.). The land-cover map is based on the Global Land Cover 2000 data set. The ruggedness surface is derived from the GTOPO30 digital elevation model. The soil data are from the International Geosphere-Biosphere Programme Data and Information System.

has been derived with GDM, it can be used to predict the level of compositional dissimilarity expected between any pair of localities (in this case, 5-km grid cells) within a region, based purely on environmental and geographical attributes.

To date we have focused our analysis of finer-scale turnover on plants and invertebrates, partly to complement an existing vertebrate-based global assessment (Rodrigues et al. 2004a, 2004b), but also because plants and invertebrates exhibit more rapid spatial turnover in species composition than do vertebrates. However, there is considerable scope for extending the approach to include vertebrates in the future. Ideally, we would hope to acquire biological data to analyze turnover patterns within every individual ecoregion. In reality, however, this is made difficult by the sheer number of ecoregions and by the absence or unavailability of suitable data for many of these. At this stage, we are working with a relatively sparse sample of biological data sets from across the planet. To date, our statistical modeling of finer-scale turnover patterns has employed more than 1.1 million locality records for more than 98,000 species of plants and invertebrates (mostly arthropods and, to a lesser extent, mollusks). This data set has been collated from a large number of sources and includes at least some data for every combination of biogeographical realm and major biome. In general, however, our study has addressed the tropical moist forest biome more rigorously than the other biomes, as this was a particular focus of our initial data acquisition efforts.

To cope with gaps in the geographical coverage of our turnover analyses, we take the predictive capability of GDM one step further and use models of turnover derived from selected regions to extrapolate patterns across similar regions (e.g., in the same realm and biome). To do this, we assume that rates of turnover—that is, the amounts of compositional turnover expected per unit change in each environmental variable and per unit geographical separation—are reasonably consistent between these regions. Any problems arising from violations of this assumption (e.g., marked discontinuities in patterns of turnover) should diminish as we improve the geographical coverage of our analyses by incorporating additional biological data sets. To gain a better understanding of the magnitude of such problems, some of us are working on a related research project using biological data from a number of moist tropical forest regions to evaluate how effectively models fitted to data from any one region perform in predicting turnover patterns in the other regions.

Our current approach to calibrating the local-richness component of our model relies heavily on estimates, generated by the Nees Institute for Biodiversity of Plants at the University of Bonn, of the total number of vascular plant species occurring in each of the world's 867 terrestrial ecoregions. The total richness of a given ecoregion is likely to be a function of both the average local richness and the level of compositional turnover between locations within that region. To remove the contribution of turnover, we use generalized additive modeling (Lehmann et al. 2002) to fit a regression model relating the estimates of ecoregional richness to the area of

each ecoregion, and to the mean and standard deviation of each of the fine-scale environmental variables within the ecoregion. This model is then used to reverse-engineer the ecoregional richness values to estimate the average richness expected in a 5-km grid cell (in a natural state) within each ecoregion (by setting the area variable to 25 km² and each of the standard deviation variables to zero). All cells in a given ecoregion are therefore assumed to have the same potential local richness, but this richness is allowed to vary between ecoregions. In the future, we hope to remove the need for this assumption of constant potential richness within an ecoregion by pursuing more rigorous approaches to estimating finer-scale spatial variation in richness, including statistical analysis of local richness estimates (derived from biological survey or collection data) in relation to mapped environmental surfaces (Leathwick et al. 1998).

Applying the model to global conservation assessment

Our global model of spatial pattern in biodiversity could benefit greatly from further refinement, and from further evaluation of predictions against expert knowledge. However, we are confident that, once implemented more fully, the model will add considerable value to existing global conservation assessments. We have already developed and tested an analytical approach to using predictions from our model to assess the representativeness of protected-area systems.

Our approach is founded on well-established principles of the species–area relationship (Rosenzweig 1995), which describes the relationship between number of species (S) and area (A) as a power-law function:

$$S = cA^z,$$

where c and z are constants. This relationship is often used to predict the proportion of species that will be retained in a region if the habitat in that region is reduced to a specified proportion of the original area:

$$S_{\text{retained}} / S_{\text{original}} = (A_{\text{retained}} / A_{\text{original}})^z.$$

While this approach is most often used to estimate the effects of habitat loss, it also has direct applicability to assessing the representativeness of protected-area systems (Zurlini et al. 2002). This involves treating the habitat in protected areas as if it were the only habitat retained in a region, and estimating the proportion of species retained or represented accordingly. This hypothetical scenario is invoked purely as a means of assessing the representativeness of protected areas, not as a means of assessing retention of biodiversity in the landscape as a whole (for which the benefits to biodiversity of other types of land use would need to be properly considered).

The species–area approach is usually applied to relatively large areas: to whole biogeographical regions, for example, or to the global distribution of whole biomes (Malcolm and

Markham 2000, Brooks et al. 2002, Thomas et al. 2004). This assumes that reduction in habitat is distributed randomly across the region or biome of interest (Ferrier 2002). However, as demonstrated by Seabloom and colleagues (2002), violations of this assumption—resulting, for example, from bias in habitat reduction toward certain parts of a region or biome—may lead to overestimation of the proportion of species retained. Unfortunately, such bias in the distribution of habitat reduction (or, conversely, protection) is likely to be the rule rather than the exception in most parts of the world (Pressey et al. 1996, Armesto et al. 1998). Here we address this problem head-on by adapting the traditional species–area approach to work with our continuous model of spatial pattern in the distribution of biodiversity. To do this, we draw on principles of the “environmental diversity” approach proposed originally by Faith and Walker (1996) as a means of assessing the representativeness of protected areas within a continuous environmental or biological space.

Assuming that for all n grid cells in a study area (e.g., the whole planet) we have estimated the relative richness of each cell (if it were still in a natural state, i.e., r_i) and the compositional dissimilarity between each pair of cells (d_{ij}), and that we know the state (s_j) of habitat in each cell (in this case, 1 = protected and 0 = unprotected), then we can predict the proportion of species represented (p) as

$$p = \left\{ \frac{\sum_{i=1}^n \left[\frac{\sum_{j=1}^n (1-d_{ij})s_j}{\sum_{j=1}^n (1-d_{ij})} \right]^z r_i}{\sum_{i=1}^n \frac{r_i}{\sum_{j=1}^n (1-d_{ij})}} \right\}^{\frac{1}{z}}$$

where z is the exponent of the species–area relationship, which for all of the analyses described here was set at 0.25, a widely accepted value for this type of assessment (Brooks et al. 2002, Zurlini et al. 2002, Thomas et al. 2004). The quantity within the square brackets, to which this exponent is applied, is an estimate of the proportion of habitat protected, equivalent to $A_{\text{retained}} / A_{\text{original}}$. However, in our case, we view grid cells as sitting within a continuum of spatial turnover in biodiversity, not within discrete classes or regions. We therefore estimate the proportion of total habitat protected for those species that once occurred in a given focal cell i as a weighted average of the state of all related cells within this continuum. The weight given to related cell j in this calculation is based on the expected proportion of species shared with the focal cell ($1 - d_{ij}$). The contribution that related cells make to the estimated proportion of habitat protected for a given focal cell therefore declines with increasing dissimilarity between these cells, leveling off at zero once cells are predicted to share no species.

By applying an appropriate z -value, the proportion of habitat protected for the species that once occurred in each cell is used to estimate the proportion of these species repre-

sented within protected areas anywhere in their range. The remainder of the formula then combines these individual cell-based estimates into an overall estimate of the proportion of species represented in the entire study area. In performing this aggregation, the formula makes appropriate adjustments for the relative richness of cells and the expected level of overlap in composition between cells.

Representativeness of the world's protected-area system

Brooks and colleagues (2004) pose two fundamental questions of interest to global assessments of protected-area coverage, or global gap analyses: (1) How much of biodiversity is currently protected? (2) Where should new protected areas be established to move toward complete coverage? To demonstrate the applicability of our approach to addressing the first of these questions, we conducted a preliminary analysis of the representativeness of the world's entire system of protected areas. We assessed protected-area coverage using version 5 of the World Database of Protected Areas, or WDPA, compiled by the United Nations Environment Programme's World Conservation Monitoring Centre. The specific data set we employed incorporated the filters applied by Rodrigues and colleagues (2004a), including the elimination of records with no locational information and the conversion of point records with associated areal information (but no shape information) into circular shapes of the same area. We ignored points without any areal information. All types of protected areas (i.e., all management categories recognized by the World Conservation Union) were included in our analysis.

To estimate the representativeness of the protected-area system using our approach, all grid cells intersecting protected areas were assigned a state (s_j in the formula above) of 1 and the remaining cells a state of 0. Our analysis therefore estimated the proportion of species that would be represented in protected areas if all other unprotected habitat were removed. As noted earlier, this analysis was aimed purely at estimating the representativeness of protected areas, not at assessing the retention of biodiversity across entire landscapes. Furthermore, in this initial analysis, we assumed that all protected areas afford an equally high level of protection of the elements of biodiversity they contain. In other words, we did not incorporate any information on the varying levels of management effectiveness and security of protected areas.

Running this analysis with the current version of our biodiversity model yielded a global estimate of 0.572. In other words, the analysis predicted that approximately 57% of the world's terrestrial species would be represented in existing protected areas, while 43% would not. The latter estimate is substantially higher than similar estimates made recently for vertebrates alone (approximately 12% of species not represented in protected areas; Rodrigues et al. 2004a). This difference suggests that the current case for expanding the world's protected-area network, and for complementing this network through sympathetic management of lands outside protected areas, might be made even stronger by considering

finer-scale patterns of turnover and richness for nonvertebrate components of biodiversity. The difference warrants closer investigation, particularly in relation to earlier published predictions that taxa such as plants and insects with higher rates of spatial turnover, and therefore higher levels of endemism, require a larger total area of protection to achieve comparable levels of representation (Rodrigues and Gaston 2001, Rodrigues et al. 2004a).

To assess variation in levels of representativeness across different parts of the world, we broke down our results by biogeographical realm and biome (figure 3). This analysis suggests that for most combinations of realm and biome, existing protected areas provide representation for only moderate proportions of the biodiversity occurring within these divisions (figure 3a). However, when the estimated number of unrepresented species within each division is expressed as a proportion of the estimated total number of unrepresented species worldwide, it appears that most such species are likely to be concentrated in particular combinations of realm and biome, with a marked bias toward tropical environments (figure 3b).

These estimates of representativeness (figure 3) must not be interpreted as indicating the relative priority of areas for additional protection. Conservation priority should be assessed and mapped at a finer spatial resolution than whole realms, biomes, or ecoregions, to avoid the problems of scale mismatch discussed earlier. Note, however, that the analysis from which we derived these summary results was performed across the entire planet at the 5-km grid resolution of our biodiversity model (with the potential for such analysis to be performed at 1-km resolution in the near future). As a by-product, the analysis therefore generates various indices of representativeness mapped across the landscape at this relatively fine resolution (figure 4). While such mapping could make a valuable contribution to assessing conservation priorities, this information would first need to be combined with rigorous consideration of other important factors, such as intactness (condition) and threat, and of ecological, evolutionary, and socioeconomic processes (Margules and Pressey 2000).

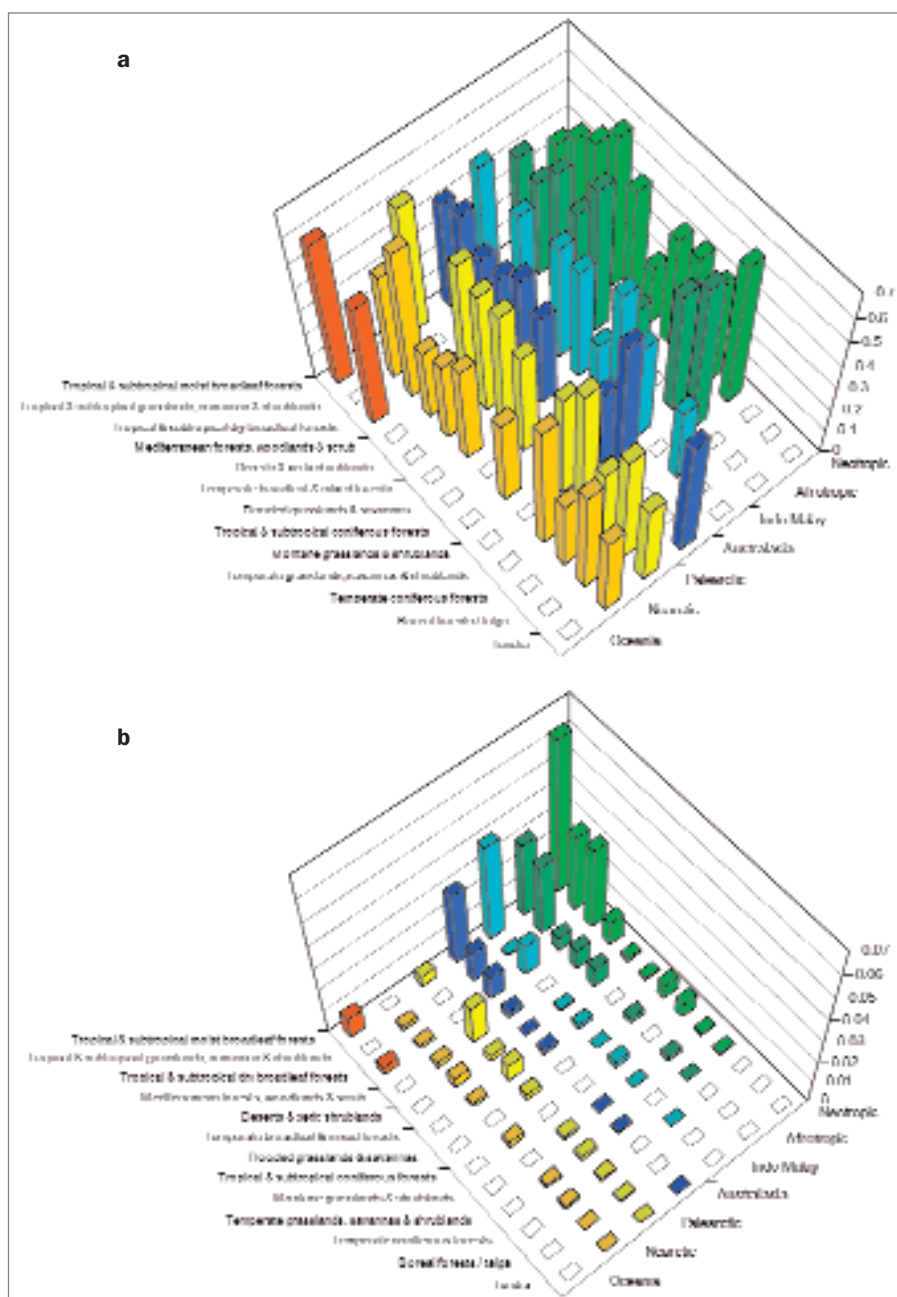


Figure 3. Representativeness of protected areas, broken down by biogeographical realm and biome (as defined by Olson et al. 2001). (a) Predicted proportion of species within each combination of realm and biome that are not represented in existing protected areas. (b) Estimated number of unrepresented species within each combination of realm and biome, expressed as a proportion of the total number of unrepresented species worldwide.

Our approach should also be integrated, wherever possible, with analyses based on individual species. As indicated earlier, our methodology is intended to complement, not compete with, other more traditional approaches to conservation assessment. Where good distributional data and detailed knowledge of protection requirements are available for species of particular conservation concern (including rare or threatened species), this information should always play a key role in as-

assessments of conservation adequacy and priority. Our proposed approach is designed to supplement such species-based assessments by providing information on the extent to which protected areas provide representation of highly diverse biological groups whose distribution and conservation requirements are little known.

Conclusions

The methodology described here offers a powerful and effective means of refining the resolution with which spatial pattern in biodiversity is mapped for global conservation assessments. By integrating disparate sources of biological and environmental data, our approach takes advantage of the complementary strengths of these different types of information. The ecoregional classification provides a sound biogeographical foundation on which we then build considerations of fine-scale pattern in biodiversity relating to fine-scale environmental variation. Calibrating our model using available biological data ensures that its predictions match reality as closely as possible. By focusing on emergent properties of biodiversity (richness and turnover), rather than on individual species, we can more easily accommodate data for lesser-known, yet highly diverse, biological groups.

As noted earlier, the biological data we have analyzed to date represent only a small fraction of the total pool of such data that could be used to calibrate, and thereby refine, our model in the future. Emerging collaborative initiatives such as the Global Biodiversity Information Facility, or GBIF, are already revolutionizing the accessibility of data sets containing species locations from across the planet. Rapid advances in remote-sensing technology are also likely to provide ongoing refinement of the environmental surfaces used to analyze and model patterns within the biological data. However, more attention needs to be devoted in the future to understanding and quantifying the effects that error and uncertainty in data inputs (both biological and environmental) have on the reliability of predictions from our model. Finally, there is much potential to extend and refine the potential application of our biodiversity model in global conservation assessment, through better consideration of biodiversity management and retention outside protected areas, and through closer integration with species-based assessments and other environmental, social, and economic data and models. As a first step toward such integration, we are currently extending our approach to assess the likely impacts of habitat loss and climate change on global biodiversity.

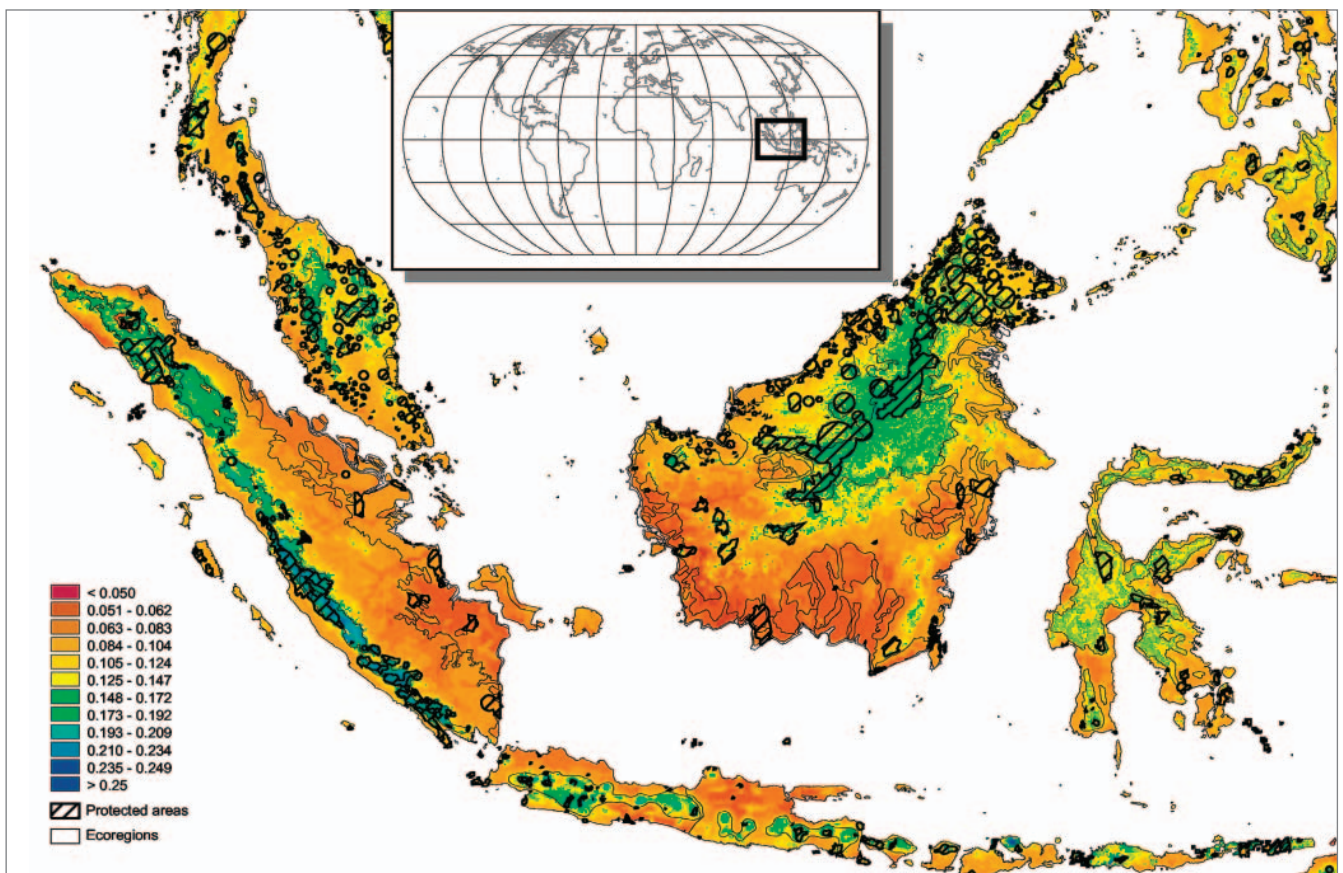


Figure 4. Representativeness of protected areas at the interface between the Indo-Malayan and Australasian realms. This is an example of continuous surfaces of representativeness generated for the entire planet as part of our analysis of the world's protected-area system (see figure 3 for summarized results). The color of each 5-km grid cell indicates the estimated proportion of total habitat protected for those species that once occurred in that cell. The circular protected areas are those for which no boundary information, only a center point and area, was provided in the World Database of Protected Areas.

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