

Terrestrial Ecoregions of the World: A New Map of Life on Earth

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The tapestry of life on Earth is unraveling as humans increasingly dominate and transform natural ecosystems. Scarce resources and dwindling time force conservationists to target their actions to stem the loss of biodiversity—a pragmatic approach, given the highly uneven distribution of species and threats (Soulé and Kohm 1989, Olson and Dinerstein 1998, Mace et al. 2000, Myers et al. 2000). Unfortunately, the ability to focus strategically is hindered by the absence of a global biodiversity map with sufficient biogeographic resolution to accurately reflect the complex distribution of the Earth's natural communities. Without such a map, many distinctive biotas remain unrecognized. In this article, we address the disparity in resolution between maps currently available for global conservation planning and the reality of the Earth's intricate patterns of life. We have developed a detailed map of the terrestrial ecoregions of the world that is better suited to identify areas of outstanding biodiversity and representative communities (Noss 1992). We define ecoregions as relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use change.

Our ecoregion map offers features that enhance its utility for conservation planning at global and regional scales: comprehensive coverage, a classification framework that builds on existing biogeographic knowledge, and a detailed level of biogeographic resolution. Ecoregions reflect the distributions of a broad range of fauna and flora across the entire planet, from the vast Sahara Desert to the diminutive Clipperton Island (eastern Pacific Ocean). They are classified within a system familiar to all biologists—biogeographic realms and biomes. Ecoregions, representing distinct biotas (Dasmann 1973, 1974, Udvardy 1975), are nested within the biomes and realms and, together, these provide a framework for comparisons among units and the identification of representative habitats and species assemblages.

A NEW GLOBAL MAP OF TERRESTRIAL ECOREGIONS PROVIDES AN INNOVATIVE TOOL FOR CONSERVING BIODIVERSITY

Although our ecoregions are intended primarily as units for conservation action, they are built on the foundations of classical biogeography and reflect extensive collaboration with over 1000 biogeographers, taxonomists, conservation biologists, and ecologists from around the world. Consequently, ecoregions are likely to reflect the distribution of species and communities more accurately than do units based on global and regional models derived from gross biophysical features, such as rainfall and temperature (Holdridge 1967, Walter and Box 1976, Schulz 1995, Bailey 1998), vegetation structure (UNESCO 1969, deLaubenfels 1975, Schmidtbüsen 1976), or

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spectral signatures from remote-sensing data (Defries et al. 1995, Loveland and Belward 1997). None of these other approaches emphasizes the importance of endemic genera and families (higher taxa), distinct assemblages of species, or the imprint of geological history, such as the strong influence of past glaciations or Pleistocene land bridges, on the distribution of plants and animals.

Existing maps of global biodiversity have been ineffective planning tools because they divide the Earth into extremely coarse biodiversity units. These units are typically well beyond the size of landscapes tractable for designing networks of conservation areas, the largest of protected areas, or the 50,000 km² threshold for restricted-range species (Stattersfield et al. 1998) that are of particular concern (Stuart Pimm [Center for Environmental Research and Conservation, Columbia University, NY], personal communication, 2000). The average size of our ecoregions is roughly 150,000 km² (median 56,300 km²), whereas the biotic provinces of Udvardy (1975) have an approximate mean of 740,000 km² (median 306,000 km²) and the biodiversity hotspots of Myers et al. (2000), which represent threatened regions with high concentrations of endemic species, have an approximate mean of 787,760 km² (median 324,000 km²).

We subdivided the terrestrial world into 14 biomes and eight biogeographic realms (Figure 1). Nested within these are 867 ecoregions (Figure 2). This is roughly a fourfold increase in resolution over that of the 198 biotic provinces of Dasmann (1974) and the 193 units of Udvardy (1975). The increased resolution is most apparent in the tropics (between the Tropics of Cancer and Capricorn) where Dasmann (1974) and Udvardy (1975) identify 115 and 117 units, respectively, compared

with 463 found in the ecoregion map. Biodiversity assessments that employ large biotic provinces or hotspots often fail to discern smaller but highly distinctive areas, which may result in these areas receiving insufficient conservation attention. The island of New Guinea is illustrative. Dasmann and Udvardy treat the island as a single unit, whereas the new terrestrial map distinguishes 12 ecoregions: four lowland and four montane broadleaf forests, one alpine scrub ecoregion along the central cordillera, a mangrove forest, a freshwater swamp forest, and a savanna–grassland, all with distinct biotas and ecological conditions.

The delineation of ecoregions

We began by accepting the biogeographic realms of Pielou (1979) and Udvardy (1975) and modifying the biome systems of Dinerstein et al. (1995) and Ricketts et al. (1999) (Figure 1). We then consulted existing global maps of floristic or zoogeographic provinces (e.g., Rübel 1930, Gleason and Cronquist 1964, Good 1964), global and regional maps of units based on the distribution of selected groups of plants and animals (e.g., Hagmeier 1966), the world's biotic province maps (Dasmann 1973, 1974, Udvardy 1975), and global maps of broad vegetation types (e.g., UNESCO 1969, deLaubenfels 1975, Schmidthüsen 1976). These were useful for evaluating the extent of realms and biomes, the first two tiers in our hierarchical classification. We then identified published regional classification systems to be used as a baseline for ecoregion boundaries. Data and consultations from regional experts were also important for final ecoregion delineations.

The use of widely recognized biogeographic maps as a basis for ecoregions enhances the utility of the map as a planning tool in different regions. For example, White's (1983) phytogeographic regions serve as the basis for the ecoregions of the Afrotropics. The Australian ecoregions are derived from Thackway and Cresswell's (1995) biogeographic regionalization. Nearctic ecoregions are adapted from the ecoregion systems of Omernik (1995), Gallant et al. (1995), Wiken et al. (1989), and Rzedowski (1978). A more diverse set of sources was used for the Neotropics, including habitat classifications for Brazil from the Instituto Brasileiro de Geografia Estatística (IBGE 1993), the vegetation maps of Huber and Alarcon (1988) and Huber et al. (1995) for Venezuela and Guyana, and Holdridge's (1977) life zones for Central America. The western Palearctic

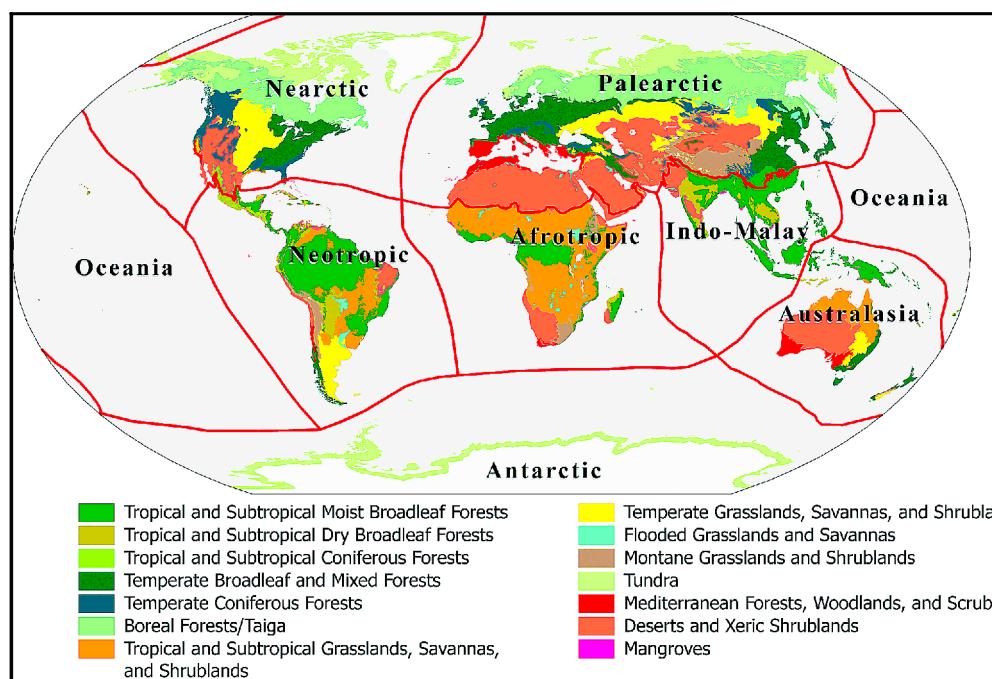


Figure 1. The ecoregions are categorized within 14 biomes and eight biogeographic realms to facilitate representation analyses.

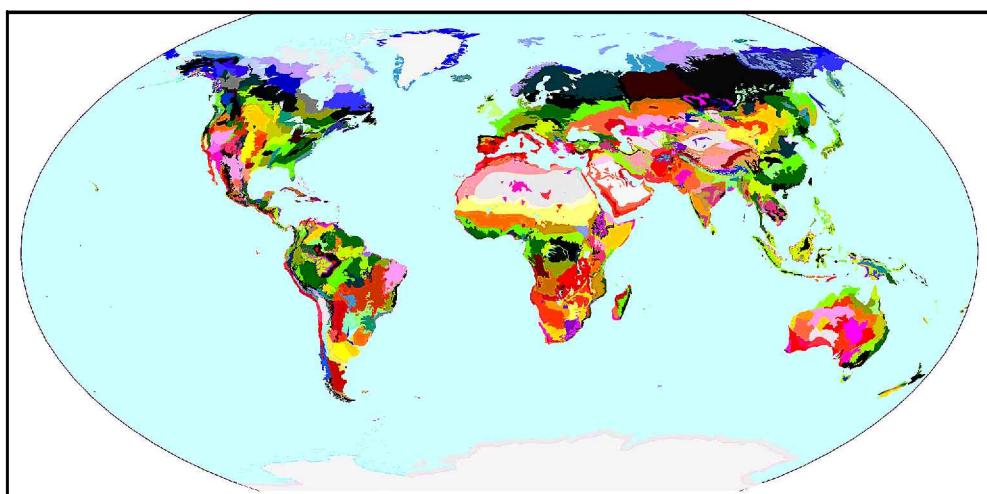


Figure 2. The map of terrestrial ecoregions of the world recognizes 867 distinct units, roughly a fourfold increase in biogeographic discrimination over that of the 193 units of Udvardy (1975). Maps of freshwater and marine ecoregions are similarly needed for conservation planning.

tic ecoregions (except Africa) were developed in concert with the DMEER (2000) project. The ecoregions of Russia are adapted from Kurnaev (1990) and Isachenko and colleagues (1988), Japan from Miyawaki (1975), China from the systems developed by the Chinese Vegetation Map Compilation Committee (1979) and the Changchun Institute of Geography and Chinese Academy of Sciences (1990), and Southwest Asia from Zohary (1973). The major divisions for Indo-Malayan ecoregions are based on the MacKinnon (1997) units that build upon Dasmann's and Udvardy's biotic provinces. A key to the terrestrial ecoregions of the world map (Figure 2), the sources for ecoregions, technical descriptions, and digital data are available at the Web site www.worldwildlife.org/science

Most existing systems required that units be aggregated or divided, or that boundaries be modified, to achieve three goals: (1) match recognized biogeographic divisions inadequately reflected in that system, (2) achieve a similar level of biogeographic resolution of units, and (3) match units and boundaries in adjacent systems, when necessary. Where widely accepted biogeographic maps were unavailable, we relied first on landforms and second on vegetation to inform the biotic divisions. For example, montane and lowland habitats support distinct biotic communities and dynamics. These were separated where they occurred over extensive areas. Detailed vegetation maps were then consulted. Vegetation is an important proxy for both plants and invertebrates, which together constitute the vast majority of species. Most invertebrates, and to some extent vertebrates, are associated with different plant communities, particularly where ecoclimatic differences are strong (e.g., tropical wet forest versus tropical dry forest).

The appropriate delineation of ecoregions was obvious in many cases. The sand pine scrubs of central Florida, for example, support many endemic species and higher taxa, and one can confidently discern the distinctiveness of its biota as well as its geographic extent. Other ecoregions required closer

scrutiny to discern the influence of historic events on present-day distributions. For example, the effects of changes in sea level and land bridges in the Philippines archipelago during the Pleistocene have resulted in several island ecoregions in close proximity harboring many unique taxa (Heaney 1986, 1991). Delination of ecoregions varied slightly in boreal and polar habitats, where species assemblages are relatively homogeneous across large regions. Thus, dynamics and processes were emphasized, such as major variations in climate, fire disturbance regimes, and large vertebrate migrations (Ricketts et al. 1999).

Three caveats are appropriate for all biogeographic mapping approaches. First, no single biogeographic framework is optimal for all taxa. Ecoregions reflect the best compromise for as many taxa as possible. Second, ecoregion boundaries rarely form abrupt edges; rather, ecotones and mosaic habitats bound them. Third, most ecoregions contain habitats that differ from their assigned biome. For example, rainforest ecoregions in Amazonia often contain small edaphic savannas. More detailed biogeographic analyses should map the less dominant habitat types that occur within the larger ecoregions, and ecoregion conservation strategies should address their requirements.

Ecoregions as a tool for conservation

How can a map of the world's ecoregions contribute to conserving biodiversity? Our ecoregion map has already been used as a biogeographic framework to highlight those areas of the world that are most distinctive or have high representation value and are therefore worthy of greater attention (Olson and Dinerstein 1998, Ricketts et al. 1999, Wikramanayake et al. 2001). Ecoregions were ranked by the distinctiveness of their biodiversity features—species endemism, the rarity of higher taxa, species richness, unusual ecological or evolutionary phenomena, and global rarity of their habitat type (e.g., Mediterranean-climate woodlands and scrub and temperate rainforests). Ecoregions can also be ranked by threats to biodiversity, the status of their natural habitats and species, and degree of protection (Dinerstein et al. 1995, Olson and Dinerstein 1998, Ricketts et al. 1999, Wikramanayake et al. 2001).

Using this framework, biologists can examine one of the most interesting biological problems: the concordance and mismatches in patterns of richness and endemism for indicator taxa, often birds and mammals, used in conservation priority setting (Stattersfield et al. 1998, Fonseca et al. 2000,

Mace et al. 2000). As an illustration, patterns of richness and endemism by ecoregion for the world's 4,600+ terrestrial mammal species reveal some major differences. The three richest mammal assemblages are in the northern Indochina subtropical forests, the southwestern Amazon moist forests, and the central Zambezian miombo woodlands (Figure 3), whereas the ecoregions with the highest number of endemic mammals are the Central Range montane forests of New Guinea, the Albertine Rift montane forests of Central Africa, and the Sulawesi montane forests (Figure 4). Similar analyses for birds, herpetofauna, and vascular plants are under way, to be incorporated into a database that can be continually improved as new data are acquired. This ecoregion–species database will complement emerging grid-based species datasets by providing insights into the biogeographic relationship among cells (Brooks et al. 2001).

The ecoregion map complements global priority-setting analyses, such as Global 200 (Olson and Dinerstein 1998) and Hotspots (Myers et al. 2000), by providing an even finer level of resolution to assess biodiversity features. For example, the 25 terrestrial hotspots identified by Myers et al. (2000) amalgamate 414 of the 867 ecoregions of the world, and the 23 units of Global 200 contain 402 terrestrial ecoregions. On our map, the Indo–Burma hotspot (Mittermeier et al. 1999, Myers et al. 2000) covers 37 terrestrial ecoregions and Global 200's eastern Himalayan forests (Olson and Dinerstein 1998) encompass four terrestrial ecoregions. The rich mosaic of the map's ecoregions calls attention to the importance of global biodiversity, including those ecoregions that lie outside the species-rich tropics.

New ways of looking at biodiversity loss and global threats—from climate change to oil exploration, mining, road development, and logging—are facilitated by this detailed map of ecoregions. Currently, a consortium of conservation organizations, museums, and

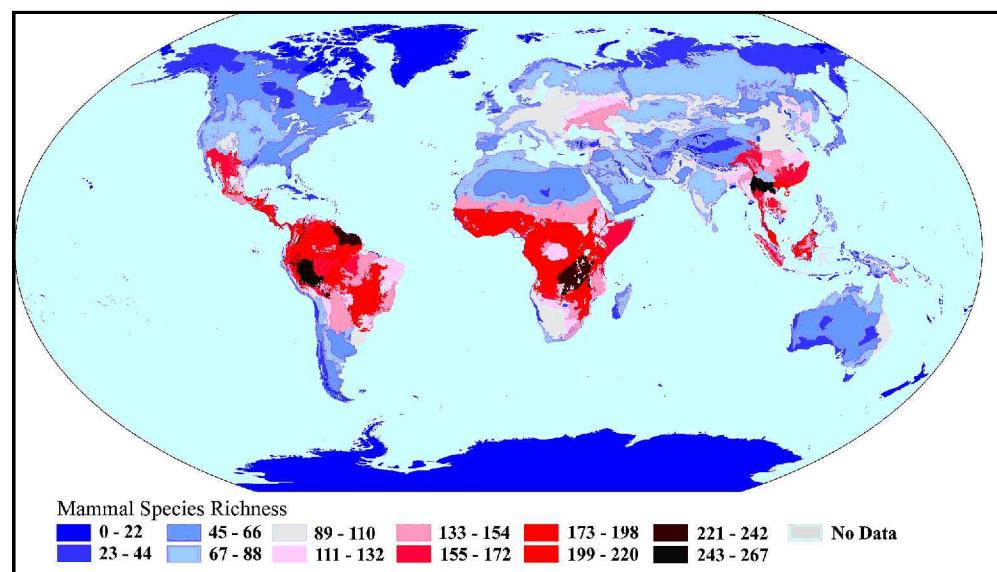


Figure 3. The relative richness of terrestrial mammal species by ecoregion is depicted. Warmer colors denote ecoregions containing richer assemblages.

herbaria are using this base map to frame discussions with logging companies and wood product retailers about reducing the loss of forest biodiversity. It is also being used as a strategic tool to determine conservation investments for the World Bank, the US Agency for International Development, the World Wildlife Fund, the World Resources Institute, The Nature Conservancy, and several foundations (Dinerstein et al. 1995, Roca et al. 1997, Olson and Dinerstein 1998).

Conservation strategies that consider biogeographic units at the scale of ecoregions are ideal for protecting a full range of representative areas, conserving special elements, and ensuring the persistence of populations and ecological processes,

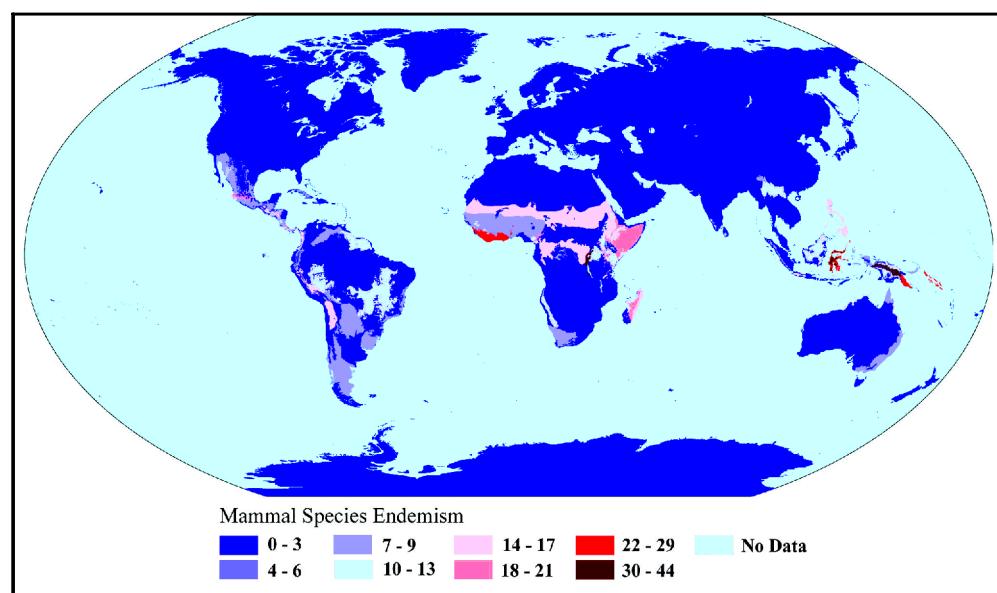


Figure 4. The level of species endemism for terrestrial mammals shows different patterns than that of richness. Warmer colors denote ecoregions containing more endemic species.

particularly those that require the largest areas or are most sensitive to anthropogenic alterations (Noss et al. 1999, Soulé and Terborgh 1999, Groves et al. 2000, Margules and Pressey 2000). Some of the most promising tools for designing networks of conservation areas—gap analysis, equal-area grid analyses, complementarity analyses, and other reserve selection algorithms (Kiester et al. 1996, Margules and Pressey 2000, Williams et al. 1997, 2000)—will be more robust if conducted within the context of biologically defined units such as ecoregions, as the distribution of species and communities rarely coincides with political units. An ecoregion perspective can also help identify whether conservation areas are redundant or complementary across political boundaries.

Ecoregions approximate the dynamic arena within which ecological processes most strongly interact (Orians 1993). This critical component of the ecoregion concept allows us to expand the scope of factors considered in conservation planning to include ecological phenomena as well as distributions of species. Preserving the migrations in East Africa, large predator–prey interactions in the South Asian jungles (Joshi et al. 2001), or sufficient forest cover in the Amazon Basin to maintain rainfall patterns requires conservation efforts across entire ecoregions.

Fortunately, conducting conservation assessments within the framework of larger biogeographic units is an approach that is gaining support in all of the major international conservation organizations and in many government agencies (Groves et al. 2000, Johnson et al. 1999, Mittermeier et al. 1999, Ricketts et al. 1999). Ecoregion-level strategies are receiving increased funding from major conservation donors. This growing interest offers encouragement that ecoregion maps and analyses can heighten awareness about the urgency of biodiversity loss and play an important role in conserving the extraordinary variety of life on Earth.

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