Perspective

Biological Diversity: Where Is It?

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TO PRESERVE BIOLOGICAL DIVERSITY, WEALTHY NATIONS usually save the large and cuddly species that excite the public's imagination (*1*). This is not necessarily a bad strategy. The relatively large size of these species means that their population densities are low. Consequently, the minimal numbers required for persistence inhabit large areas and many other less charismatic species are protected under their umbrella. Furthermore, large species are often top predators and thus play crucial, so-called keystone roles in the community's dynamics. Yet such a species-biased approach is not necessarily appropriate for the great majority of animal species that are not furred and feathered, or for plants, or, indeed, for all organisms in species-rich tropical nations deciding on how to allocate land for national parks. The obvious strategy protects areas of greatest diversity. Two recent papers on mammals by Mares in this issue and Pagel *et al.* (*2*) illustrate the complex biological issues involved in predicting what diversity might remain after future planners have taken a cookie cutter to their wilderness.

At the outset, estimating the total number of species on the planet is not trivial. Counting one, two, three . . . would be difficult enough, even if all the species were described—and probably the majority are not. Small species escape our notice. The number must be estimated from what we know about general features of ecological communities and their food webs (*3*). Understanding how species are distributed across the planet is even more daunting. One tactic documents the patterns in diversity among the furred and feathered, understands their causes, and applies the principles to other groups.

Diversity is described by two parameters: point or α-diversity, (practically, the number of species in a specified area) and β-diversity, the turnover of species across space. Empirical patterns of diversity have a long history (*4*). Continent-wide maps of α-diversity based on individual species' ranges, cross-continental comparisons, and their interpretation are not new either (*5*). Theory predicts α-diversity to increase with the total number of individuals encompassed (*6*), and so to increase with both the area sampled (the well-documented species-area relation) and the productivity per unit area. Empirically, we also know that α-diversity is less on remote islands and increases as we move toward the equator. (Total tropical diversity also owes much to the large area of the tropics, a fact easily overlooked on maps with Mercator projection). There are surprises, however. The α-diversity typically peaks along gradients of productivity, declining in the most productive systems (*7*); some taxa are more diverse further north (*8*), and some deserts host unusually diverse plant communities (*9*). The longitudinal, westward increase in vertebrate diversity in North America is also large (*2, 5*).

We know less about β-diversity. As a first step, we must understand how large are species' ranges, for there are two extreme scenarios. If ranges are large, then α-diversity is almost independent of the area sampled and the national park cookie cutter can be placed anywhere. Alternatively, total diversity may be high, while α-diversity is low with species' ranges being small and adjoining rather than overlapping. Many parks would be needed to protect diversity. The 523 species of North American mammals are geographically very restricted. The median range is only 1.2% of the area of the continent but range size increases greatly with latitude. Our north temperate experience of many local, but very few global species extinctions following extensive and long-term changes to our environment sends the wrong message to managers of tropical diversity. The gray wolf and grizzly bear have been extirpated from much of Europe and eastern North America but survive locally across ranges that once covered most of three continents. Moreover, even historically, eastern North America supported relatively few species. Tropical species range much less widely and are that much more vulnerable, and there are many more species to lose.

Species ranges tend to follow the major habitat divisions (rain forests, deserts, and so on) for these divisions are themselves defined by their constituent species. In North America, areas with more of the 23 habitats defined by Pagel *et al.* have more species of mammal. Species most commonly occupy only one or two of these habitats. Mares identifies six major habitats in South America. The two of greatest areal extent are drylands and the Amazon lowlands. Theory (*6*) predicts the diversity of an area to scale as the $(\text{area})^{0.25}$. The drylands are about twice the size of lowlands, ought to contain 18% more species and have 19% more mammals. But what about endemic species, those found only in one habitat? The drylands house 53% more endemic mammalian species and 440% more endemic genera than the lowlands. The concentration of diversity is in the western montane forest. It has 11% of the area, yet 76% as many mammalian species as the lowlands, 63% as many endemics.

The drylands' reputation for being areas of low diversity is false, at least for mammals. Nor do they merely contain a subset of species found in the rain forests. Mares shows that 68% of the mammalian species (and 95% of the genera) in the Amazon lowlands are found in other habitats. Much as we might be appalled by the rates of tropical deforestation, we cannot ignore the drier areas.

Useful as cautionary tales, these results also point to serious gaps in our knowledge. We do not always understand the causes of α-diversity: there are many theories but little consensus. Unless we understand the principles, we have no chance of predicting patterns among other species groups and in other areas where the rate of environmental change may preclude even our describing the species, let alone mapping their ranges. We know far too little about β-diversity to predict its current patterns, or its future, when remnant natural areas are surrounded by highly modified habitats. Part of the problem is familiar: larger remnants increase α-diversity, more remnants increase β-diversity. The optimal allocation of remnants involves knowing both diversities. Even less clear is whether species will survive outside these protected remnants other than human commensals that, like the starling, have followed us worldwide. And to what extent will these commensals penetrate the natural areas? We clearly know too little about where the diversity is, why it is there, and what it will become.

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