Macroecology: The Division of Food and Space Among Species on Continents

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Analyses of statistical distributions of body mass, population density, and size and shape of geographic range offer insights into the empirical patterns and causal mechanisms that characterize the allocation of food and space among the diverse species in continental biotas. These analyses also provide evidence of the processes that couple ecological phenomena that occur on disparate spatial and temporal scales—from the activities of individual organisms within local populations to the dynamics of continent-wide speciation, colonization, and extinction events.

I N THE LAST THREE DECADES, ECOLOGISTS HAVE CONFRONTED the enormous diversity and complexity of the natural world—with varying success. On the one hand, attempts to quantify biological diversity and ecological phenomena have revealed incredible variety. The total number of plant, animal, and microbial species inhabiting the earth is estimated to be between 10 million and 50 million (1). Each of these species has different requirements for existence and characteristic variations in abundance in space and time. Each place on earth is also distinctive and is inhabited by a particular assemblage of species. On the other hand, quantitative approaches have also revealed tantalizingly general patterns that appear to reflect the operation of natural laws that govern the organization of the ecological world. For example, there are striking regularities in the relative abundance of species within a site (2), in the structure of food webs (3), and in the way that the number of species varies with latitude (4). Most of these patterns have been revealed by large-scale, comparative, nonexperimental studies, and most still lack satisfactory mechanistic explanations, although they have been known for more than 20 years.

Since the early 1970s, ecology has become increasingly microscopic and experimental in its approach. As answers to the big questions remained elusive, many ecologists focused on problems that could be solved. It is possible to characterize the effects of physical conditions or of other organisms on a certain species in a particular place by means of controlled, replicated manipulations. The problem, however, is not so much in interpreting the outcome of any single experiment as in synthesizing the results of the many different studies to draw useful generalizations about the organization of the natural world. Without a complementary emphasis on large-scale phenomena, there is little basis for determining which

results simply reflect the idiosyncracies of individual species and particular sites and which reflect the operation of more universal processes.

In an effort to address this deficiency, we have begun studying the ecological patterns and processes that characterize the assembly of continental biotas, specifically North American mammals and birds. The early results offer new insights into the relation between microscopic and macroscopic phenomena and into the general processes that determine the diversity, abundance, and distribution of organisms.

A Macroecological Approach

Our goal is to understand the assembly of continental biotas in terms of how the physical space and nutritional resources of large areas are divided among diverse species. Our approach can be characterized as follows.

1) Explicitly empirical and operational. We use computer analyses of large data sets available for several kinds of organisms. These data are compiled from sources including field guides, systematic surveys, and standardized censuses (5). So far, we have used mainly data on all species of North American breeding land birds and nonvolant terrestrial mammals.

2) Ecologically relevant data. We have focused on variables, such as body mass, local population density, and area and shape of geographic range, that affect the allocation of space and nutritional resources (6). Body mass is closely correlated with the energetic requirements of individuals, local population density indicates the number of individuals that are supported within a small area, and configuration of geographic range characterizes the species distribution.

3) Multivariate analyses. We propose that the allocation of space and nutrients depends on the interaction of variables we just mentioned, as well as others that we have not yet considered. In this respect we depart from several earlier studies that analyzed univariate frequency distributions of the same variables among species (2, 7–9).

4) Statistical distributions of variables among species. Unlike much traditional ecology, which focuses on the attributes of just one or a few species, we draw inferences from the statistical distributions of variables among many species in a diverse biota. This enables us to characterize the pattern of variation in the entire assemblage and to assess the extent to which particular subsets of species or local areas differ from random samples of the entire biota.

5) Taxonomically defined biotas. We analyze assemblages of species of a single large taxon, such as birds or mammals. This ignores ecological relations that are not closely correlated with taxonomy, such as some trophic and competitive interactions. It has

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the advantage, however, of confining the analyses to organisms within phylogenetic lineages that are subject to similar evolutionary constraints.

This approach enables us to phrase our basic question in an alternative way: can we identify ecological processes that affect the evolutionary diversification of a taxon as it exploits the geographic space and trophic resources of a large land mass?

Ecological consequences of body size. One of the well-documented and intriguing generalities about the biological world is the distribution of body sizes among species within different taxonomic groups. There are strikingly similar frequency distributions for the body masses, plotted on a logarithmic scale, for North American birds and mammals (Fig. 1, A and B). The distributions are skewed to the right, with a strong mode between 50 and 100 g. Qualitatively similar relations have been found for many other diverse taxa inhabiting large geographic areas (8).

Data for mammals suggest, however, that these body size distributions vary with spatial scale; that is, with the size of the area sampled. Comparable frequency distributions are shown for North American mammals for two successively smaller scales (Fig. 1, C to F). As our scope of study changes from the entire continent, to biomes (large regions with relatively uniform climate and vegetation), to small patches of very uniform habitat, the distributions change in a regular way. Each smaller scale contains a smaller subset of the species in the larger fauna and proportionately fewer small and medium-sized species. Although the distribution for the entire continent is highly modal, with a peak at approximately 100 g, the distributions for the local habitat patches are virtually flat, with an

Fig. 1. Frequency distributions of body masses (on a logarithmic scale) among species of North American land birds (**A**) and land mammals (**B**) for the entire continent, for land mammals within biomes (**C**, northern deciduous forest; **D**, desert), and for land mammals within small patches of relatively uniform habitat within each of these biomes (**E**, Powdermill Reserve; **F**, Rio Grande Bosque).

approximately equal number of species in each logarithmic size category. This pattern appears to be very general and holds for the mammal faunas of the 21 biomes and for an equal number of local habitat patches that we have analyzed.

We suggest that at least three kinds of mechanisms are necessary to produce this pattern. At present these should be regarded as hypotheses, supported by the following reasoning and data.

First, interspecific competition within local habitats is hypothesized to cause flat, log-uniform distributions (Fig. 1, E to F). Since the pool of species available on the continent or in the regional biome to colonize local habitats has a highly modal distribution of body sizes, some kind of strong negative interaction appears to prevent local coexistence of similar-sized species. The only process that we are aware of that can consistently have this effect is competitive exclusion. Competition strong enough to prevent coexistence should be restricted to species that are similar in their use of food or other resources. We hypothesize that local faunas are made up of several guilds, each of which uses a different food resource (for example, in the case of mammals: flesh, green vegetation, seeds, and fruit) and experiences strong competition among similar-sized species. This hypothesis is consistent with the evidence that local guilds of mammals and at least some other organisms consist of species that are more different in body size than expected from the random assembly of species from regional or continental pools (10).

Second, differential extinction of species of large body size is hypothesized to prevent the occurrence of numerous large species in the continental biota. Large organisms are constrained to have relatively low population densities because each individual requires large quantities of food and other resources. Since probability of extinction increases with decreasing population size (11), large species require large geographic ranges in order to persist for substantial time periods. This is consistent with the low frequency of large species and the much higher frequency of modal-sized species with small geographic ranges in both mammals (Fig. 2) (12) and birds (6). If extinction differentially eliminates large species with small ranges and competition tends to prevent local coexistence of similar-sized species in the same guild, these two processes together should be sufficient to account for the low frequency of large species in the continental biota.

Third, energetic constraints related to body size are hypothesized to cause the greater specialization of smaller organisms that result in the modal-sized species replacing each other with high frequency from habitat to habitat across the landscape. Such a pattern of spatial turnover is a necessary consequence of the systematic flattening of the frequency distributions of body sizes from continent to biome to local habitat patch (Fig. 1). Hutchinson and MacArthur (7), who first called attention to the highly modal distribution of mammalian body sizes for the entire North American continent, suggested that the smaller species were more specialized in their use of some essential resources than their larger relatives.

One important energetic consequence of body size seems sufficient to explain the pattern: requirements of individuals for energy and at least some nutrients scale as a fractional exponent (approximately 0.67 power), rather than linearly (1.0 power), with body mass (13). The physiological reasons for this are still poorly understood, but the ecological implications are profound. Because most of the variables that affect the capacity to collect and process food scale linearly with mass (14, 15), large animals can cover a larger area, ingest more food relative to their requirements, retain the material in the gut for a longer period, and extract a greater fraction of the energy and nutrients than small animals. This enables large species to feed on lower quality foods and to include a much wider array of items in the diet. We hypothesize that small species have smaller geographic ranges and replace each other more fre-
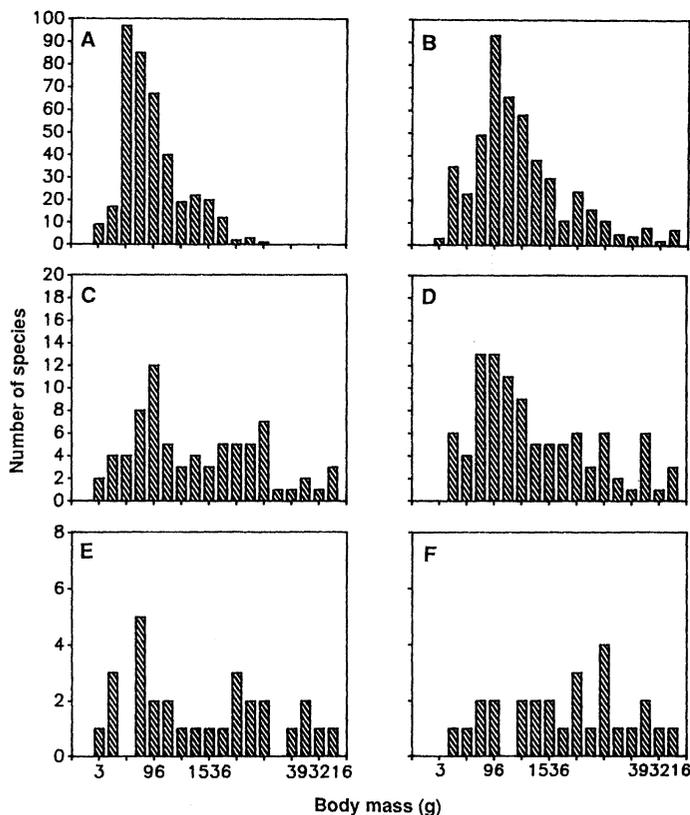
quently across the landscape than their larger relatives because they confine themselves to habitats where foods of sufficiently high quality (to meet their more stringent energy and nutrient requirements) are in adequate supply.

The hypothesis that energetic constraints related to body size are important in the organization of these biotas is supported by other patterns in the organization of North American mammal and bird assemblages. One example is the low frequency in the continental bird and mammal faunas of the very smallest species, those with masses less than the modal size of approximately 100 g (Fig. 1, A and B). Insight into this pattern is offered by the relation between body mass and average population density (Fig. 3). Although there is much scatter in these data, all the points fall within well-defined bounds, which we hypothesize to reflect basic constraints. Some of these, such as the decrease in maximum population density with increasing body size, are quite straightforward. But the maximum population density also decreases with decreasing body size for birds weighing less than about 100 g. Mammals and beetles show a qualitatively similar pattern (16). Even the most abundant of the smallest species in the fauna are not as numerous as some of their larger relatives.

We hypothesize the following explanations for this constraint on maximum population density of the smallest species with a taxon. As mentioned earlier, daily energy requirements (E) of individuals are closely correlated with their body mass (M), such that $E = kM^{0.67}$, where k is a taxon-specific scaling constant (13). Over a wide range of body sizes, the area of the territory or home range used by an individual (A) is also closely correlated with size, varying as $A = cM^{1.0}$, where c is also a constant (14). The difference in the slopes (exponents) of these allometric equations means that the energy requirement of an individual per unit area of its territory increases with decreasing body size, $E/A = aM^{-0.33}$.

We suggest that down to some threshold body size, species are able to compensate for these increasing food requirements per unit area of territory and still maintain high local population densities. This is accomplished, at least in part, by specializing on habitats where individuals can forage efficiently. Below this threshold body size, however, individuals would no longer be able to meet their energy requirements if territory size were to continue to decrease. They can obtain adequate food only by restricting their foraging to rich, widely spaced patches of resources. These patches will also tend to be ephemeral, in part because rich patches will be depleted by the foraging of the individuals that discover them. This argument has three logical consequences. First, because the proportion of patches that are sufficiently productive to support food requirements should decrease with decreasing body size below 100 g, this will account for the apparent constraint on maximum population densities of birds and mammal species with body masses less than 100 g (Fig. 3). Second, this same reasoning will also account for the declining number of species in these smallest size classes (Fig. 1, A to B). Third, if the richest patches tend to be both widely dispersed and ephemeral, then individuals that exploit them should have to move large distances over their lifetimes.

The last of these leads to the testable prediction that lifetime territory size and movements should vary inversely with body size for birds and mammals weighing less than about 100 g. This prediction is not only counterintuitive, it also contradicts equations for the allometric scaling of territory size and movements based on birds and mammals over a wide range of body sizes (14). We tested our prediction with data on desert rodents (Fig. 4) (17). There is a great deal of scatter in the average population densities of these species as a function of their body mass, but, as in birds, species of intermediate size are most abundant (Fig. 4A). More importantly, as predicted, as body mass decreases below the threshold of approxi-
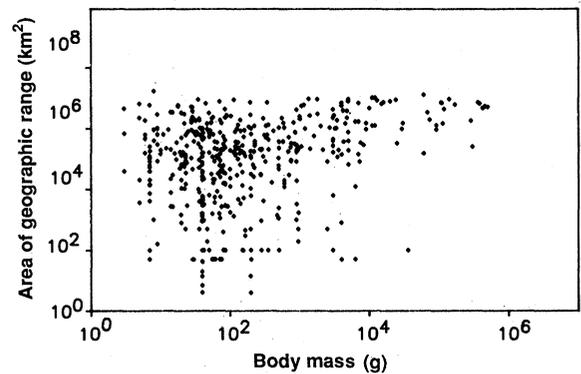
Fig. 2. Relation between area of geographic range and body mass (plotted on logarithmic axes) for the species of North American land mammals. Species of large body size tend to have large geographic ranges.
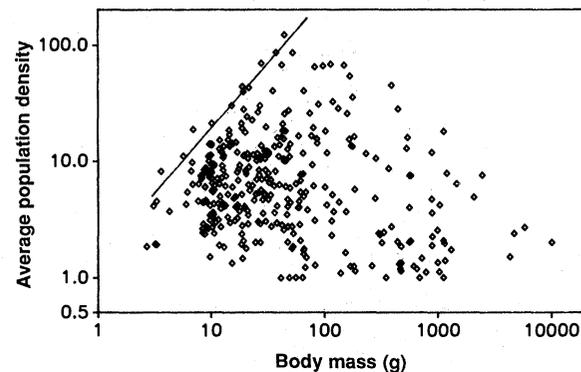

Fig. 3. Relation between average population density and body mass (plotted on logarithmic axes) for the species of North American land birds (6). Diagonal line, the decrease in maximum population densities of the species weighing less than approximately 100 g.

mately 100 g, individuals move longer distances over their lifetimes (Fig. 4B).

So far we have discussed how energetic constraints related to body size are important in the division of space among species. Now let us consider the allocation of energy more explicitly. Which body sizes use the most energetic and nutritional resources? Is the greater population density per species and the greater number of species of modal-sized birds and mammals compared to their larger relatives sufficient to compensate for their lower food use per individual? The prevailing wisdom has been that small organisms did indeed dominate the flow of energy and nutrients through ecosystems (18).

We address this question on two levels. First, on a per species basis, how is food consumption related to body size? We know from the allometric equation $E = kM^{0.67}$ approximately how energy use per individual scales with body mass. Because all organisms are made of essentially the same chemical compounds, we assume that requirements for other nutrients scale similarly. Multiplying E by population density gives a good estimate of energy use per species per unit area. We made such calculations for two spatial scales, within local habitats (19) and for the continent as a whole (Fig. 5a) (20), and both give similar results. Although there is much variation among species of similar body size, large organisms consistently obtain most of the energy and nutrient resources. Second, if we sum the values for the species within a logarithmic body size class, how is total food consumption by individuals of all species related to body size? The results for birds on a continent are shown (Fig. 5B). Despite the smaller number of species and of individuals per species, large organisms consume at least as much energy and nutrients as their smaller relatives. Within local habitats the dominance of large

organisms is even more pronounced, because there are more nearly equal numbers of species in all size classes (Fig. 1, E to F).

Together these data suggest a consistent view of the importance of body size–dependent energetic constraints in the ecology of mammals and birds. As body size decreases, individuals are faced with increasing energy and nutrient requirements per unit area of their territory and they become increasingly specialized to meet these demands. Initially, maximum population density increases with decreasing size, as increasing numbers of species divide up space and habitats according to their special requirements. Eventually a threshold body size is reached at which most areas are not sufficiently productive to support individuals, and then both maximum abundance per species and number of species decrease. Another consequence of these relationships is that energy and nutrient consumption, especially within local habitats, is dominated by the larger species. These energetic constraints of body size, together with intense competition between species of similar size within habitats and differential extinction of large species with small geographic ranges, seem necessary and perhaps sufficient to account for the systematic variation in body size distributions with spatial scale (Fig. 1).

Size and configuration of geographic ranges. The number and kinds of species that occur together at any scale are the result of both macroscopic and microscopic processes. On the one hand, the pool of species that are available to colonize a local area depends on the history of speciation and extinction events and on the expansion and contraction of geographic ranges. On the other hand, the origination, spread, and persistence of species in time and space depend on the effect of ecological conditions on the dynamics of local populations and the direction and rate of microevolutionary change. Valuable insights into these reciprocal relations between microscopic and macroscopic processes are offered by patterns in the sizes and configurations of geographic ranges.

The biogeographic barriers that determine the edges of a species range must be ecological limiting factors that prevent the expansion of local populations. Can we make any generalizations about the kinds of ecological variables that limit geographic distributions? We plotted the north-south dimensions of the geographic ranges against the east-west dimensions for North American terrestrial mammal species (Fig. 6A). A species with a circular or square range would fall along the diagonal line, indicating equal dimensions in each direction, and randomly distributed ranges would be dispersed equally around this line. The actual distribution of ranges exhibits a different pattern. The vast majority of the small ranges fall above the line; they are elongate in a north-south direction. In contrast, the majority of the large ranges have their long axis running east-west.

We propose the following explanation for this pattern. Species with small ranges (most of which are of small body size) are limited by habitat types and other variables that are associated with major topographic features, such as mountain ranges, river valleys, and coastlines. In North America these are oriented predominantly north-south. In contrast, species with large ranges are relatively insensitive to these variables and instead are limited by major climatic zones and biome types that are oriented predominantly east-west.

This hypothesis leads to two predictions. First, other taxonomic groups should respond similarly to mammals to the topographic and climatic features of the North American continent. This is supported by the configuration of geographic ranges for land birds in North America, which is qualitatively similar to that for mammals (Fig. 6B). Second, in Europe, where the important topographic features as well as the the major climatic belts run east-west, both the small and large geographic ranges should have their long axis oriented in this direction. This prediction is supported by the configuration of the plots of the geographic ranges of European land birds (Fig. 6C). Although there are fewer European species with very small ranges, even the smallest ones are oriented east-west, in marked contrast to ranges of comparable sizes of North American species.

These patterns show how the configuration of geographic ranges is influenced by ecological conditions that limit local populations of organisms and by continental-scale geography and geology that reflects the tectonic history and climate of the earth. This kind of coupling among disparate scales is emphasized in other studies that try to combine the macroscopic perspectives of biogeography and macroev-

Fig. 4. Relation between (**A**) average population density and body mass and between (**B**) median lifetime dispersal distance of individuals and body mass for 11 species of desert rodents inhabiting a patch of relatively uniform Chihuahuan Desert shrub habitat. Variables are plotted on logarithmic axes from data in (*17*). The distribution of population densities is consistent with the pattern for birds shown in Fig. 3. For species weighing less than approximately 100 g, lifetime movements vary inversely with body size.
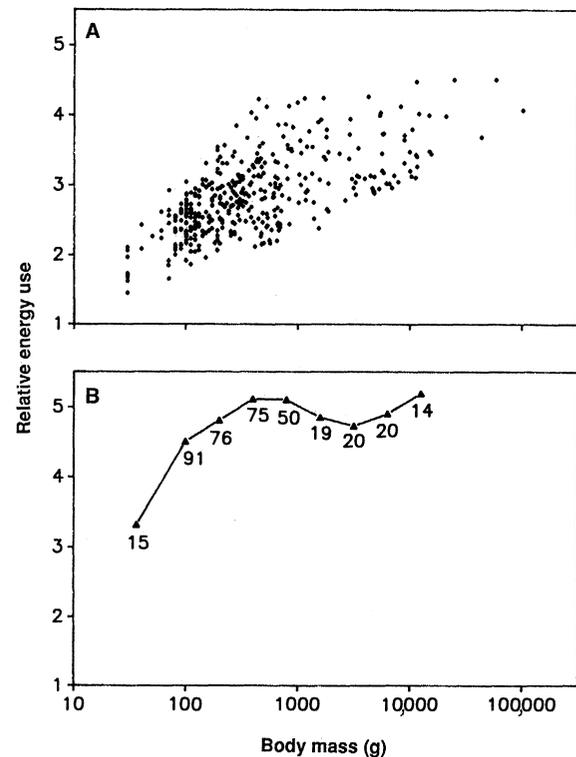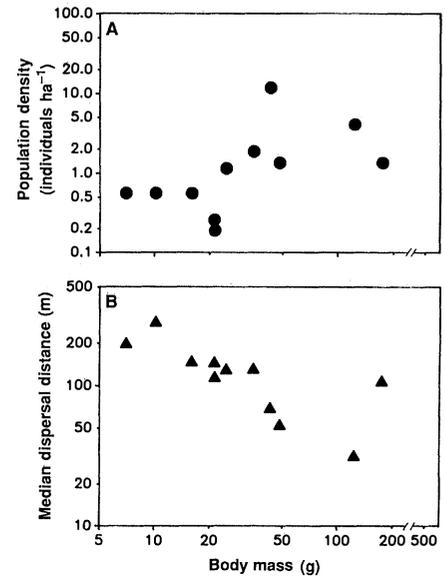

Fig. 5. Relation between energy use and body mass (on logarithmic axes) for North American land birds (*20*). (**A**) Average values for the species; (**B**) values summed for all of the species in equal-sized logarithmic body size categories. Numerals indicate the number of species in each size class. Large birds use more energy than small ones, on a per species basis and for all species within a size category.

olution with the microscopic approaches of population genetics and physiological, population, and community ecology (21).

Prospects for Synthesis

The patterns and explanations presented here illustrate the kinds of insights that can come from applying the questions posed by ecologists to the spatial and temporal scales normally studied by biogeographers and macroevolutionists. Our analyses suggest that the ecological and evolutionary processes that determine the assembly of continental mammal and bird faunas are reflected in regular patterns of body sizes and geographic range configurations. Comparisons of these patterns across spatial scales suggest mechanistic hypotheses that appear to be supported by available data.

Much remains to be done to assess the generality of the patterns and to test the validity of the explanatory hypotheses. To the extent that we have been able to compile and analyze appropriate data sets, the patterns and processes appear to be similar in birds and mammals, at least within North America. Although the frequency distribution of body sizes appears to be general (Fig. 1, A to B), it remains to be seen whether the other results can be generalized to other kinds of organisms and to other continents. The mechanistic hypotheses that we have proposed do not appear to depend on specific traits (such as endothermy) of birds and mammals or on the geography of North America. Therefore, although we would expect the quantitative details to vary among taxonomic groups and among continents, we predict that the same processes cause qualitatively similar patterns in other organisms and on other large land masses. The general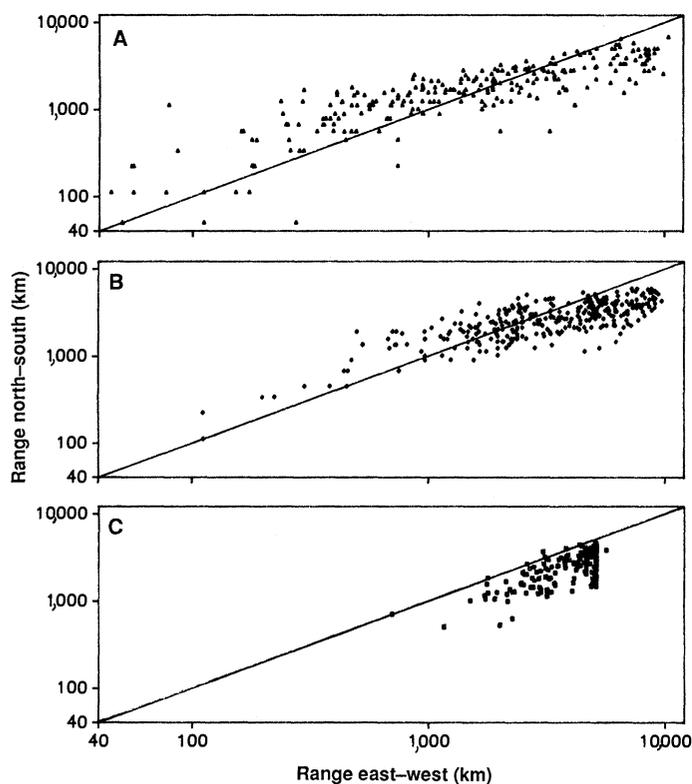ity of patterns can be evaluated by compiling and analyzing similar data for other taxa and regions. The extent to which our mechanistic hypotheses are both necessary and sufficient to account for the patterns can be assessed by further studies designed explicitly to test their assumptions and predictions.

Our results suggest that ecological processes often provide the coupling among different levels of biological organization and among different spatial and temporal scales. Variation in the environment ultimately reflects geological, climatic, and oceanographic processes that are themselves coupled over disparate spatial and temporal scales. This environmental variation affects many different levels of biological organization, from the differential birth, death, and movement of individuals within local populations to the differential proliferation, extinction, and dispersal of species in continental and marine biotas.

Other investigators are also providing new insights into macroscopic ecological phenomena by incorporating new information from geology, climatology, and oceanography to develop syntheses between disciplines such as ecology, biogeography, systematics, macroevolution, paleontology, genetics, and microevolution (22). These interdisciplinary efforts promise to contribute importantly to understanding the origin and maintenance of biological diversity. For example, the fossil record studied by paleontologists and macroevolutionists documents periods of wholesale extinctions of species and higher taxa followed by periods of proliferation of new species and lineages (23). The fact that taxa with certain body sizes and geographic range areas differentially survive these catastrophes and speciate afterward suggests that knowledge of ecological processes that affect the assembly of contemporary biotas will contribute to understanding these historical events and vice versa. Also, new techniques are being developed to determine the phylogenetic relationships among species and to reconstruct the biogeographic histories of lineages of related species. When combined with ecological studies, these approaches offer the opportunity to better understand both the constraints of ecological processes on evolutionary events and the effects of evolutionary history on contemporary ecology (24).

Fig. 6. Maximum north-south and east-west dimensions of the geographic ranges of North American (**A**) terrestrial mammals and (**B**) land birds and for (**C**) European land birds. Ranges of equal dimensions would fall on the diagonal line. In North America, small ranges tend to be oriented north-south whereas large ones are elongated east-west. In Europe, ranges of all sizes tend to be aligned east-west.

Conclusions

The data and analyses presented here describe the division of food and space among wild species. As much as possible they represent the situation before the impact of modern humans. Within the last few centuries the exponentially growing population of *Homo sapiens* has changed the rules of resource allocation. Human beings currently use 20 to 40% of the solar energy that is captured in organic material by land plants (25). Never before in the history of the earth has a single species been so widely distributed and monopolized such a large fraction of the energetic resources. An ever-diminishing remainder of these limited resources is now being divided among the millions of other species. The consequences are predictable: contraction of geographic ranges, reduction of population sizes, and increased probability of extinction for most wild species; expansion of ranges and increased populations of the few species that benefit from human activity; and loss of biological diversity at all scales from local to global.

Currently, applied disciplines, such as conservation biology and natural resource management, remain focused primarily on small scales: preservation of individual endangered species, establishment of biological reserves, and management of local natural resources. But the most serious impacts of humans are global in extent and will persist for centuries or even millennia. There is great urgency to expand the spatial and temporal scale of contemporary ecology to address these problems.

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Dendrites, Viscous Fingers, and the Theory of Pattern Formation

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There has emerged recently a new theoretical picture of the way in which patterns are formed in dendritic crystal growth and in the closely analogous phenomenon of viscous fingering in fluids. Some interesting questions that arise in connection with this theory include: How broad is its range of validity? How do we understand dynamic stability in systems of this kind? What is the origin of sidebranches? Can weak noise, or even microscopic thermal fluctuations, play a role in determining the macroscopic features of these systems?

THE THEORY OF PATTERN FORMATION IN NONLINEAR DISSIpative systems has taken some surprising turns in the last several years. One of the most interesting developments has been the discovery that weak capillary forces act as singular perturbations which lead to beautifully delicate and very nearly identical selection mechanisms both in dendritic crystal growth and in the fingering patterns which emerge when a viscous fluid is displaced by a less viscous one. It now appears likely that important progress has been made, but pieces of the puzzle still seem to be missing.

For most of us, dendritic crystal growth brings to mind pictures of snowflakes. Materials scientists may think also about metallurgical microstructures, which provide very practical reasons for research in this field; but it is the snowflake that most quickly captures our imaginations. Kepler's 1611 monograph "On the Six-Cornered Snowflake" (1) is often cited as the first published work in which morphogenesis—the spontaneous emergence of patterns in nature—was treated as a scientific rather than a theological topic. At a time in which the existence of atoms was merely speculation, Kepler mused about hexagonal packings of spheres, but concluded that the

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