Biodiversity

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Introduction

Biodiversity can be referred to as the sum total of all of the plants, animals, fungi, and microorganisms on Earth; their genetic and phenotypic variation; and the communities and ecosystems of which they are a part. This definition implies that biodiversity encompasses three traditionally recognized levels of organization: intraspecific, interspecific, and ecosystem diversity. The intraspecific or genetic diversity level refers to the genetic diversity residing within a given species, including the genetic variation within and among populations of the same species. For example, the genes that determine the variation in flower color among plants within a population and the genes responsible for the variation in plant stature among populations located at different elevations represent such intraspecific diversity. The interspecific diversity or species diversity level is most commonly known as species richness (typically within a given group of organisms, such as plants, birds, etc.) in a community. The diversity of ecosystems level refers to the variety of ecosystems present in a given region, such as the presence of mangroves, savannas, tropical forests, and temperate forests found along an elevation gradient within a mountainous typical tropical region.

This standard definition of biodiversity implies a logical functional link between the three levels it comprises and could be articulated, qualitatively, as follows: the organisms that make up a population of a given species behave and respond to their environment as they do as a result of the features determined by their genetic constitution; the contingent of such individuals in a population or group of populations constitutes a species, and the collection of species in a given region are constituents of communities that, together with their physical environment, form the ecosystems, landscapes, and, ultimately, the biomes of the Earth.

Beyond the intraspecific, interspecific, and ecosystem diversity levels, the biodiversity of a given region can be manifested by these additional facets: (1) morphofunctional diversity, represented by the variety of life forms

among plants or, its rough zoological equivalent, the diversity of functional groups among animals; (2) the concentration of endemic organisms, that is the cooccurrence of taxa (species, genera, families) with a restricted geographic distribution; and (3) the agrobiodiversity, best reflected by the variety of domesticated and cultivated plants and animals and their wild relatives. Next, we briefly review each of these biodiversity facets.

Morphofunctional diversity is seldom recognized as an important facet of biodiversity, although its relevance is ecologically and evolutionarily crucial, for it represents the amazing variety of responses organisms have evolved to deal with the environmental pressures of their habitats. The examples of Figures 1 and 2 highlight this facet of biodiversity. The panel of plants (Figure 1) includes a diversity of life forms depicting a selected variety of ways in which plants from desert ecosystems deal with the crucial limiting factor, water. Thus the panel includes (clockwise arrangement): cacti of several types (e.g., a sahuaro and an opuntia), shrubs with tiny or absent leaves (e.g., ocotillo and creosote bush), succulent rosette-like shrubs and treelets (e.g., agaves), arborescent palm-like plants (e.g., yuccas), and ephemeral annual plants (e.g., dahlia). Such life-form diversity can be astonishing. For example, a description of the floristic diversity of Mexican desert ecosystems included 32 readily distinguishable life forms. The animal example of Figure 2 shows the diversity of morphofunctional groups among one single group of mammals, bats, depicting the variety of evolutionary routes these animals have developed to solve the challenge of finding and using their food resources, clockwise in the diagram, including, fruit-feeding (e.g., Artibeus), nectar-feeding (e.g., Choeroniscus), blood-feeding Desmodus), insect-feeding (e.g., and (e.g., Lonchorrhina) bats. The diversity of adaptations to such variety of feeding habits is dramatically displayed in Figure 2 by the variations in the animals' heads.

The concentration of taxa in a given geographical region, evolved and found nowhere else on the planet, that is, the concentration of endemisms, is an important facet of biodiversity, not only from the biogeographical (the geographic distribution of taxa) and evolutionary

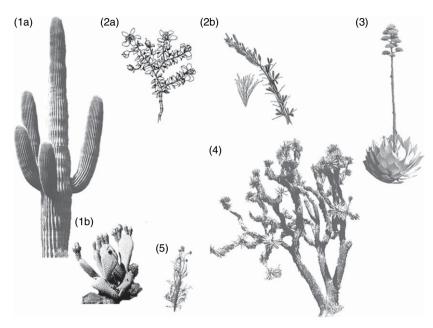


Figure 1 Biodiversity expressed as the variety of plant life forms that can be found in a desert. Life forms include: (1a) columnar and (1b) prickly pear cacti; (2a) creosote bush and (2b) ocotillo shrub; (3) succulent rosette-like agave (with reproductive structure); (4) palm-like yucca (Joshua tree); and (5) annual herb (dahlia).

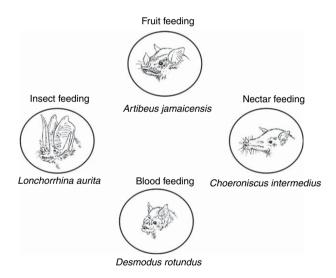


Figure 2 Diversity of bat feeding habits. Head characteristics reflect functional attributes required to exploit specific feeding sources. For example, the very large ears and nose-leaf of Lonchorrhina aurita are associated to sensorial capacity needed to prey on flying insects. In Choeroniscus intermedius, the long snout and a long tongue allow reaching nectar at the base of flower tubes.

(the fact that they frequently represent evolutionary novelties) points of view, but also because regions of high levels of endemism become a priority in biodiversity conservation. This is because the alteration or destruction of regions with high concentrations of endemism (the so-called hot spots), would bring about the irreplaceable loss of unique products of evolution. Endemism can be expressed at different levels: species, genera, families,

orders, or even phyla can be endemic to a given region. In Figure 3, we show the restricted distribution of a pair of pine species (Pinus spp.) endemic to Mexico. These species, restricted to temperate forests of that region, evolved in situ and have not been found in other temperate forests of the globe, apart from those shown in the map. Furthermore, both species contrast in its range of distribution within the country. Populations of Pinus

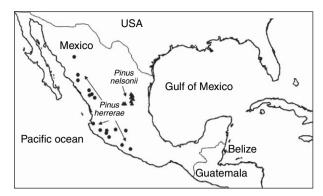


Figure 3 Two contrasting levels of endemism illustrated by species in the genus Pinus within the territory of Mexico. While P. herrerae is distributed on the mountains of the western Sierra Madre and the Trans-Mexican Volcanic Belt, but cannot be found in any other country, P. nelsonii is restricted to an area of a few square kilometers in the arid lands of northwestern Mexico.

herrerae can be found along the mountains of western Sierra Madre and the Trans-Mexican Volcanic Belt, while P. nelsonii is restricted to a small arid area in northeast Mexico.

Agro-biodiversity is represented by the cultivated and domesticated plants and animals present in a given region; this facet includes as well the wild relatives from which traditional indigenous cultures have selected the forms

adapted to the environments in which they are cultivated or propagated to satisfy diverse human needs. Although this facet of biodiversity represents a minor fraction of the global contingent of species of plants and animals, its importance is crucial, as it represents the vast majority of the food we consume. Agro-biodiversity emerges from the combination of two factors: availability of biodiversity in terms of the wild relatives, and the application of traditional management and knowledge leading to domestication. (Thus this facet of biodiversity includes also cultural diversity and traditional knowledge.) In the case of plants, this has determined the existence of a few regions of the world, popularly known as the Vavilovian domestication centers, or agro-biodiversity centers (Figure 4). This handful of centers of origin and domestication of plant crops has contributed significantly to human development and well being and, in addition, such centers are areas of great concern from the biodiversity conservation perspective. Among the roughly 2500 crop species, just 103 supply over 90% of the calories humans consume, directly or indirectly, and just three grasses (cereals), rice, wheat, and maize, supply about 60% of the total. In addition, some 15 plants are cultivated as sources of fiber, and thousands more are used as ornamentals or sources of medicines. Agrobiodiversity also illustrates intraspecific or genetic diversity. We do know that most crops are genetically diverse,

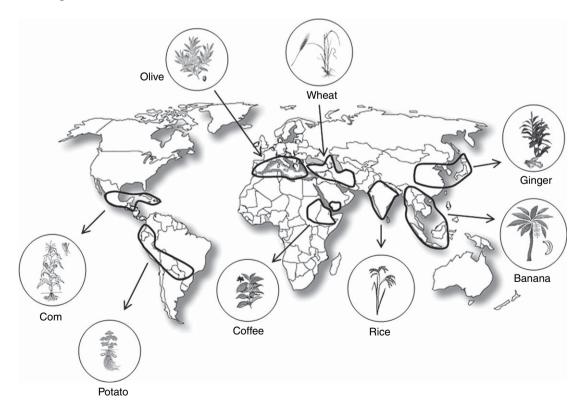


Figure 4 The Vavilovian centers where traditional knowledge and human intervention on wild plants led to the origin of some of the most important crops.

including many land races that exist in the major cereals and crops such as bananas, cassava, potatoes, and tomatoes. Likewise, cabbage, cauliflowers, broccoli, kohlrabi, brussels sprouts, calabrese, and kale are all selected variants of Brassica oleracea. In the case of animals, from the approximately 50 000 described vertebrate species, 30-40 species of birds and mammals have been domesticated; a few of them have a global distribution (except for the Antarctic) and are extremely abundant: cattle (1300 million), sheep (1200 million), pigs (850 million), and chickens (10 billion). Again, the degree of intraspecific variation in animals is impressive, including about 800 distinct breeds each of cattle and sheep.

In sum, biodiversity is a very inclusive concept, involving several facets and levels of organization. Nevertheless, the level of species is the one that has received the greatest attention. Yet, as we describe in the next sections, even at this level our global knowledge is still limited.

Metrics of Biodiversity

The most commonly used method to describe the biodiversity occurring in a particular locality is based on the enumeration of the species present therein. This metric is known as species richness (S). The enumeration of the total number of species present in most habitats is a formidable task. For example, it has been suggested by a team of British ecologists that recording the total number of species in a single hectare of tropical forest would require employing up to 20% of the 7000 systematists active worldwide. Even when aimed at more specific groups (e.g., plants or insects), quantification of species richness might still be problematic if the group under inspection is particularly speciose, its taxonomy is poorly known, or is hard to survey in the field. Therefore, most of the characterizations of S are based on sampling protocols and the inferences that can be drawn from them. Here we provide an example of sampling to assess S.

An increasingly popular analytical procedure is that of species accumulation curves. These curves depict how species richness accumulate with increased sampling effort, as shown in Figure 5, based on plant species recorded in ten $50 \text{ m} \times 2 \text{ m}$ transects established in the understory of a rain forest site in southeast Mexico. The survey included only woody plants of <1.5 m height, to assess the forest's regeneration potential, and was performed in homogeneous habitat (i.e., not including microtopographic variations such as ravines, river beds, or flooded areas; this would likely bring about different sets of species). Species richness associated with any given number of transects (sampling effort: two, three, up to ten)

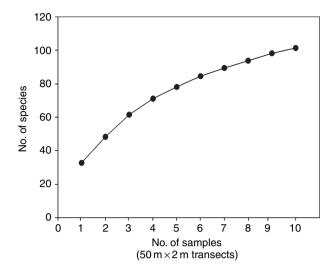


Figure 5 Species accumulation curve derived from plant species sampled in ten independent transects established in rainforest understory in southeast Mexico. Each point is an estimate of the number of species expected for a given sampling effort (i.e., number of transects). As sampling effort increases, the slope of the curve becomes shallower, indicating that species inventory is approaching completeness (i.e., lesser new species are being added).

is represented as a mean value that was calculated using, in a random sequence, the entire set of the ten transects. Thus a sampling effort of two transects shows the mean of all possible combinations of two transects, and so on, up to a predetermined limit of 100 combinations. In this example, S was calculated applying an estimator that takes into account the relative representation of rare species, that is those represented by a single individual ('singletons'), and those represented by at least two individuals ('doubletons'). The ratio of singletons and doubletons will determine to what extent the observed number of species needs to be increased to estimate S. When such a ratio is zero, the number of observed species can be considered to represent a complete inventory of species. The graph shows that at this site the estimated number of plant species in the understory habitat of the rainforest, based on the sampling effort of ten transects, is close to 110 and the rate of accumulation of additional species, as sampling effort increases, is very low. This approach, in addition to providing a trend of species accumulation (S), gives an idea of the completeness of the species inventory, whereby the shallower the slope of the curve at its right extreme, the lower the number of new species expected to be added with additional sampling. In this particular case, the known number of species in the understory microhabitat in this forest is close to the estimated value.

When information on species relative abundance is also available, more revealing descriptions of diversity can be undertaken by considering the distribution of individuals among species. One example of a common

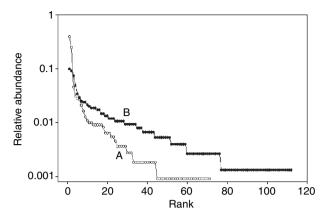


Figure 6 Dominance–diversity curve comparing species richness and abundance of plant species sampled in two rainforest sites in southeast Mexico. Each species (represented by one circle) is ranked according to its abundance from more abundant (left) to less abundant (right) along the *x*-axis. Site B presents a more diverse species assemblage than Site A both in term of richness and in terms of the equitability in which individuals are distributed among species.

approach is the use of rank-abundance plots, also known as dominance-diversity curves (Figure 6). In this type of plot, species are plotted in an increasing ranking sequence, from left to right on the x-axis, according to their abundance (far left the most abundant, far right the rarest). Proportional abundance is displayed on the y-axis using log₁₀ scale, so that the resulting curve reflects the hierarchical distribution of abundances across species. Therefore, dominance/abundance plots readily display species equitability and comparisons among species assemblages with different species richness and equitabilities are easily accomplished. Figure 6 shows the dominance/diversity curves for two tropical rainforest understory sites, A with 71 species, and B with 112 species (each species represented by open and closed circles, respectively). The plot highlights that while in Site A only a few species are clearly abundant, monopolizing a considerable proportion of the dominance (biologically interpreted as monopolization of the available resources), in Site B species are more evenly distributed. The contrast between Sites A and B shows that, in addition to the difference in the number of species, those of Site A are less equitably distributed than in Site B. Ecologists embrace the notion of equitability and use a metric to define it, evenness, with the implication that, complementary to species richness, the greater the evenness of a site, the greater its ecological diversity. The underlying idea is that if one (or few) species dominate the species assemblage, the community is not very diverse ('too much of the same'), whereas if no species dominate, the community is probably more diverse. Imagine these species represent prey of a predator looking for diversity of food resources in these two

communities. Clearly the latter would appear as more diverse than the former to the predator.

The interest of having a synthetic measure of diversity based on the combination of two of its most distinctive attributes, species richness and species relative abundance, has favored the development of a wide variety of so-called diversity indices. These indices are sensitive to the number of species recorded but also to how contrasting their abundances are. Different indices are more or less sensitive to the characteristics of the data used for their calculation. For example, some indices are sensitive to variations in sample size while others are not. In addition, some diversity indices give greater weight to species richness (e.g., the Shannon-Wiener index) and others to the dominance of the commonest species (e.g., the Simpson index). Simpson's index assesses the probability that any two individuals taken at random from a community will belong to different species. It is easy to imagine how such probability would be high in a tropical forest in which tree species diversity is very high, compared to a low probability in a boreal forest where most trees belong to the same species.

In order to illustrate the importance of evenness, Box 1 shows the procedure to calculate the Simpson index (1/D) to compare the diversity of two hypothetical bird communities. The first step is to multiply the number of individuals in each species (n_i) by its frequency minus one $(n_i - 1)$. The resulting products $(n_i^*(n_i - 1))$ are then divided by the product of the total number of individuals recorded (N) by N-1. Finally, the resulting ratios ($n_i^*(n_i 1)/N^*(N-1)$) are added up over all the species to calculate D. The Simpson index is expressed as the inverse of D (i.e., 1/D), in order to obtain increasing values of the index with increasing diversity. In the example presented in **Box 1**, Site 1 is about 2 times more diverse than Site 2, despite the fact that both sites have the same species richness (S = 8). Differences in the relative abundance of species can be further examined by calculating the associated evenness index $(E_{1/D})$ that results from dividing the observed index by the maximum diversity, that is, when all species are represented by the same number of individuals. The $E_{1/D}$ values show that the bird assemblage of Site 1 is considerably more 'even' that that of Site 2. This is consistent with the fact that the most abundant species of Site 2 accounts for 59% of all individuals in the assemblage (high dominance), while the most abundant species of Site 1 only represents 20% of the total.

The development of new methods to analyze and characterize diversity is a very active field of research. Recent approaches try to combine taxonomic and functional species traits with traditional information on species richness and abundance to generate more comprehensive descriptions of diversity. This may allow distinguishing between localities, even when they have the same number of species and similar

A hypothetical example showing how the distribution of individuals among species changes the diversity of bird assemblages occurring in two sites. Although the two sites have the same number of species, the more even distribution of individuals among species at Site 1 leads to a higher Simpson diversity index and evenness than at Site 2 (see text for details).

7	Site 1				
	n _i	n _{i-1}	$n_i^*n_{i-1}$	$n_i^* n_{i-1} / N^* (N-1)$	
-	12	11	132	0.037	
	10	9	90	0.025	
×	9	8	72	0.020	
•	8	7	56	0.016	
	7	6	42	0.012	
7	6	5	30	0.008	
	4	3	12	0.003	
- 1	4	3	12	0.003	
	60				
1-	$D=\Sigma(n_i($	26 1/D = 7.937			
77	$E_{1/2} = (1/D)/S = 0.992$				

Site 2						
n _i	n _{i-1}	$n_i^* n_{i-1}$	$n_i^* n_{i-1} / N^* (N-1)$			
20	11	220	0.196			
1	9	9	0.008			
2	8	16	0.014			
3	7	21	0.019			
1	6	6	0.005			
4	5	20	0.018			
2	3	6	0.005			
1	3	3	0.003			
34						
$D=\Sigma(n_i$	68 1/D = 3.728					
$E_{1/2} = (1/D)/S = 0.466$						

species-abundance distributions. For example, if species in one locality belong to a few genera and species in a second locality span over a more ample variety of genera, the latter would be considered as more diverse. A similar situation would occur if species in one locality show a greater variety of functional roles (e.g., animal feeding guilds or plant life forms) than the species in the other locality. In sum, the ample variety of ways biodiversity manifests itself, calls for a diversity of criteria to characterize it.

Spatial Scales of Diversity

An essential aspect of biodiversity is that species contingents vary in their spatial distribution, sometimes abruptly, making it necessary to explicitly consider the spatial scale at which diversity is being analyzed. Figure 7 depicts a simple representation of the different levels of spatial scale at which diversity can be analyzed, portraying a nested scheme of distribution of diversity, scaling up from homogeneous habitats (that we will refer to as localities in this exercise), nested within regions, which in turn are nested within a larger biogeographic region or province. In this scheme, the most basic, local measure of diversity is alpha (α) diversity, which consists of the number of species recorded within a given locality.

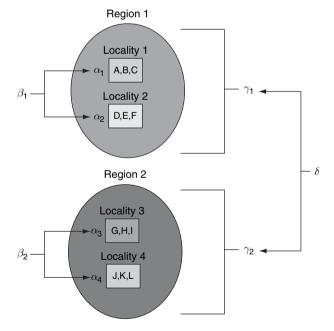


Figure 7 Schematic representation of the different spatial scales at which diversity can be analyzed. The identity of the species found at each locality (α diversity) changes (i.e., species turnover) across localities (β diversity). The combination of α and β diversity makes up the diversity found at the regional level (γ diversity). Similarly, when moving between regions, a turnover in the species identity occurs (δ diversity).

In the four localities depicted in Figure 7, α diversity is the same: each locality contains three different species. However, the identity of each of the species in each of the contingents varies from locality to locality. That is, there is a high turnover of species as we move from one locality to another. Ecologists and conservation biologists use the term beta (β) diversity to refer to species turnover. At the larger spatial scale of the region, we observe that the high turnover of species within each region determines a high level of regional diversity, corresponding to a high gamma (γ) diversity. Finally, given the high species turnover between regions, the overall biogeographic region exhibits a high delta (δ) diversity. It is worth noticing that the specific definitions of locality, region, or biogeographic region are somewhat subjective and vary with the investigator. In any case, the importance of the spatial scales of distribution of diversity for conservation can hardly be overemphasized: if a country, region, or biome is composed of a mosaic of localities of high α diversity with a high species turnover (β diversity), the protection of the country's biodiversity will demand the establishment of many preserves probably of different types, rather than a few or a single one, even of relatively large size.

Time Course of Biodiversity through Geological Time

Our knowledge of the patterns of change of biological diversity through geologic time is mainly based on the information contained in the fossil record. The available fossil evidence suggests that the diversity of families of multicellular marine organisms (**Figure 8**) rose steadily through the Cambrian and Ordovician period, attaining a plateau about 440 million years ago and then was punctuated by a great wave of extinction in the Permian (290–245 million years ago). After this, it steadily increased to the present.

Terrestrial organisms first appeared about 440 million years ago, with the invasion of the land by the ancestors of plants, fungi, vertebrate animals, and arthropods. In this period, each group increased rapidly in diversity from that time onward. At the species level, terrestrial vascular plants began to diversify markedly around 400 million years ago and declined during the worldwide Permian extinction event that also affected marine organisms profoundly. After this, similar to marine organisms, plants began to diversify around the Mid-Cretaceous Period, some 100 million years ago, with the flowering plants (angiosperms) becoming an extremely diverse and dominant group up to the present.

Thus the fossil records of both marine and terrestrial multicellular eukaryotes indicate maximum diversity at

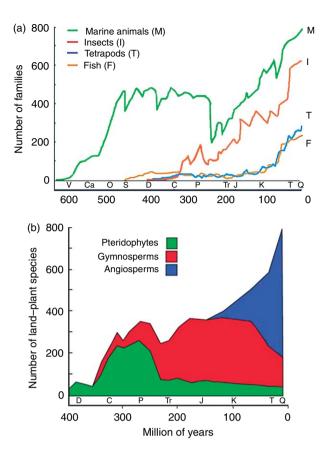


Figure 8 Time course of (a) the number of families of marine animals, insects, tetrapods, and fish through the last 600 million years and (b) the number of land–plant fossil species in three major groups (angiosperms, gymnosperms, and pteridophytes) through the last 400 million years. V, Vendian; Ca, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary; and Q, Quaternary. Reprinted, with permission, from the *Annual Review of Environmental and Resources*, Volume 28 © 2003 by Annual Review.

the present time (**Figure 8**). The present level of marine diversity is estimated to be about twice the average over the past 600 million years, and that of terrestrial diversity is perhaps also about twice its historical average since organisms first invaded the land. The trend has been continually upward despite the five major extinction events that have occurred over the past 570 million years, which essentially covers the history of multicellular organisms (**Figure 8**). An interesting result emerging from the described trends in diversity and our current understanding of extinction levels is that current species diversity, in spite of being the highest in the history of life, represents only *c.* 1–10% of the total diversity that has ever existed on Earth.

Nevertheless, the pattern of temporal increase in biodiversity through the Phanerozoic era we have described must be taken with caution. On the one hand, there is the 'pull-of-the-recent effect' whereby young rocks are more likely than old rocks to be well preserved, and thus the most recent occurrences of species are more likely to be found than the older occurrences. On the other hand, a considerable fraction of the recent marine faunas are known from a few, restricted localities. Although paleontologists have amassed an impressive amount of information and analyzed it with sophisticated statistical methods, the patterns emerging from these analyses, although exciting and compelling, are still in need of further confirmatory work.

Global Magnitude of Biodiversity

Our understanding of the global magnitude of biodiversity, even considering the level for which we have the best information, species, is still very limited. Complete catalogs of the described, valid species exist for only a few groups of organisms, and the total can only be estimated. This figure is estimated to be around 1.5 million and includes exclusively eukaryotic organisms (basically plants, some groups of animals, and some fungi). The number and definition of prokaryotic species and viruses are still very limited. It is not surprising, therefore, that current estimates of the total number of species in the world span over 2 orders of magnitude (10^6-10^8) . Methods employed to estimate global diversity can be classified in three broad categories: (1) ratios of known to unknown groups, (2) extrapolation from samples, and (3) expert opinions by scientists who understand the level of diversity in a particular group of organisms well, or combinations thereof. An example of the first approach is the estimation carried out by ecologists Nigel Stork and Kevin Gaston in 1990. They first noted that the ratio of the number of species of butterflies to all species of insects on the well-known British fauna is 67:22 000. Assuming that such a relationship was robust overall, and based on an estimate of 15 000-20 000 species of butterflies worldwide, they scaled up to a total figure between 4.9 and 6.6 million species of insects. The second approach is illustrated by the study carried out by entomologist Terry Erwin at a rainforest site in Panama. Erwin performed a systematic sampling using a fogging protocol targeted on the beetle fauna living in the canopy of the tree Luehea semannii. Based on the magnitude of the fauna collected and using a series of assumed relationships involving the ratio between beetles and other types of arthropod species, the degree of host specificity of arthropods, and the expected number of tree species to be found in the Tropics, Erwin came up with the astounding estimate of 30 million species of tropical arthropods. Robert May attempted an estimate based on the known relationship between body-size category and number of species of animals. Assuming that such relationship holds for individuals as small as 0.2 mm, May calculated that there might be about 10 million species of animals. All these

estimations are based on a series of assumptions that await confirmation. However, there is some level of agreement that the plausible number of global species falls within a range of 5-15 million and a recent review suggests a best guess of around 7 million species.

Yet, new species are continuously described sometimes as a consequence of refinements in the taxonomic classifications but commonly as the result of real discoveries from surveys in nature. Current rates of publication of new species are significant, including some 13 000 animal species per year. This makes it evident that the task of describing the total number of species on Earth will not be completed for many decades, even assuming they can all be collected and analyzed by the appropriate experts before they go extinct due to anthropogenic impact. These discoveries are not restricted to smallsized organisms but also include species of large mammals such as monkeys and deer. Even more, exploration of remote areas sometimes results in the discovery of organisms that generate a biodiversity revolution because of their degree of biological novelty. Examples of this are the plant Lacandonia schismatica, found two decades ago in southeast Mexico. This plant was found to belong into an entirely new taxonomic family (Lacandonianceae), due to its spectacular characteristics, including that it presents its reproductive organs with a spatial disposition the other way around from any other known flowering plant: male structures toward the center of the flowers and female structures at the periphery! Equally spectacular as taxonomic novelty is the discovery, a few years ago, of an insect in Africa that combines characteristics of a cricket and a stick insect, so different to any other insect that it required the creation of a new taxonomic order (Mantophasmatodea). All these discoveries underscore the level of uncertainty we have about the magnitude of biodiversity. This uncertainty becomes more striking when we take into consideration that species richness is only one facet of biodiversity, as discussed earlier.

Geographic Distribution of Biodiversity

Among the many trends known about the geographic distributional patterns of biodiversity, the most evident is that of the increase in species diversity with latitude. This trend is consistent across many groups of organisms that have been well analyzed. Among insects this pattern is spectacular. For example, the number of species of ants in local regions increases from about 10 at latitude of 60° N, to some 2000 at latitudes near the equator. Figure 9 highlights the case of plants and a representative group of vertebrates, birds. In both cases, the upper bound limit of species richness shows a dramatic peak at lower latitudes. In the case of plants, different analyses (e.g., local or regional floras, species density comparisons, standardized α



Figure 9 Gradients of latitudinal variation in species richness for birds (left) and plants (right). For both groups, species concentrates toward the Tropics peaking around the equator. The data for plants correspond to the number of species per 0.1 ha in different localities of the Western Hemisphere. The number of bird species is standardized per unit of sampling effort in different localities of the world.

diversity samples, etc.) show a very consistent gradient of decrease in plant species diversity with latitude. In broad geographic terms, species densities range from over 5000 species/10 000 km² in tropical regions, to less than 100 in the highest latitudes. In terms of local (α) species diversity, values range from an average of 270 species per 0.1 ha in Colombia to c. 15 near the USA-Canada border. Breeding birds increase from about 56 species in Greenland, to 105 in New York, to 1010 in Mexico, to 1395 in Colombia.

Another increasingly evident pattern of geographic variation in diversity has to do with intercontinental variation, specifically the patterns comparing the Neotropics (i.e., the tropics of the New World) with the Paleotropics. Data indicate that about 90 000 species of plants, approximately twice as many as in Africa, south of the Sahara, occur in the Neotropics and that the comparable area of Asia is roughly intermediate in this respect. Fogging sampling techniques using standardized protocols to compare data for canopy beetles (e.g., in terms of species per cubic meter) show the same tendency, although the values are even more contrasting than in the case of plants: 1.17 in Panama and 1.15 in Peru > 0.29 in New Guinea > 0.02 in Australia and Sulawesi. Similar trends have been observed in numerous other groups, including butterflies (Neotropics > Southeast Asia > Africa), frogs (Neotropics > Africa/Asia > Papua/ and birds (Neotropics > Africa > Asia/ Australia), Pacific > Australopapuan). In mammals, the number depends on the particular group; specious groups such as bats are considerably more diverse in the Neotropics than in the Old World, while some groups with relatively few species in general, such as primates, show the opposite trend: Old World > New World.

Valuation of Biodiversity

The value of biodiversity has been considered from several points of view which can be classified in the following three broad categories: (1) esthetic, (2) ethical, and (3) economic. The esthetic point of view posits the idea that biodiversity includes a wealth of expressions of beauty equivalent to those found in the most esteemed collections of art work. Such an array of beauties ranges from vividly colored beetles and butterflies to whales and ancient forests. Moreover, these expressions of beauty are the result of very long evolutionary processes that exceed by far the age of the most ancient artwork.

The ethical point of view rests on the idea that biodiversity, by itself, has an intrinsic value. This point of view has its roots in philosophical beliefs and considerations that give other forms of life the same rights to exist and meet their needs as humans. This idea is complemented by the notion that *Homo sapiens*, the species currently monopolizing a large share of the energy and resources that support life on Earth, has the ethical responsibility to secure the preservation of other forms of life.

Economics criteria argue that biodiversity provides humanity with monetary revenues directly and indirectly. A classic example of a direct profit coming from biodiversity is illustrated by the variety of chemical compounds obtained from plants, animals, and microorganisms that function as a base for the active ingredients used in a large proportion of the available prescription drugs (e.g., digitalis, morphine, quinine, and antibiotics). In comparison, the notion of indirect profits of biodiversity rests in the realization that several organisms maintain and regulate processes that impact the quality of human life. For example, organisms inhabiting soil (e.g., earthworms and insects) are crucial for maintaining fertility and henceforth allow the growth of crops and forests. Another example is the case of plant pollinators. An important number of crops depend on the 'service' provided by wild pollinators. Efforts have been focused to estimate the economical cost that the loss of such ecological services might involve. In the case of pollination by native insects in the USA, a study estimated that the ecological service they provide is worth \$3.07 billion per

Recent interest in biodiversity valuation has increased in response to the threats it is facing. In this regard, the different criteria we presented have more or less potential to play a role in increasing the awareness about the relevance of conserving biodiversity. Esthetic appreciation of biodiversity has the caveat that it is, in some sense, biased toward the small subset of species that are considered 'charismatic' such as whales or birds. Ethic considerations offer the most comprehensive valuation of biodiversity; however, it seems difficult that this type of philosophy will become internalized by a significant proportion of the humanity in the short term. Finally, the economic arguments are compelling and constitute a more tractable argument within the framework of formal markets. However, there are still a reduced number of cases where it has been possible to document with detail the economical value of the services provided by biodiversity. In the end, it is worth keeping in mind that the level of interrelatedness biological systems usually show, determines that the existence of charismatic, economical, or functionally valuable species depends on the maintenance of an unknown number of associated species and ecological processes.

An appealing approach, related to the three arguments referred to above, is that formulated by the Millennium Ecosystem Assessment (MEA). As a large coalition of international conservation and development organizations, governments, and a significant representation of the scientific international community, the MEA has compiled the most thorough assessment of the state of the planet's ecosystems, emphasizing the goods and services they provide, and the likely effects of potential pathways of human economic development on the provisioning of such goods and services (scenarios) and the interrelations thereof with human well-being. We can summarize the logic of the relationships articulated by the MEA, in brief, as follows: biodiversity, represented by the genes, populations, species communities, and biomes, generates a series of supporting services resulting from ecosystem functioning. Such services, including primary production, nutrient cycling, and soil formation, are the basis for all other ecosystem services. The latter services

belong to three major categories: (1) provisioning services, that is, products obtained from ecosystems, including food, fresh water, fuel wood, fiber, biochemical compounds, and a plethora of other genetic resources; (2) regulating services, those that produce benefits obtained from the regulation of ecosystem processes (e.g., climatic regulation, disease regulation, water regulation, air purification, pollination services, biological control); and (3) cultural services, the nonmaterial benefits obtained from ecosystems. These include the esthetic, inspirational, religious, and spiritual values offered by nature, recreation and tourism, educational services, and cultural heritages. The provisioning of such services impinges on human well-being in terms of affording basic materials for a dignified life, health, security, and good social relations. It is hoped that the framework of and the information summarized in the MEA, together with the formulation of future scenarios depending on different routes of economic development, will be used to guide policy regionally and globally. From a more ecological point of view, another interesting derivation of the MEA is that it can provide the framework to focus on the relevant research addressing the connections between biodiversity conservation and ecosystem services, and the influence of biodiversity on human wellbeing and vice versa.

See also: Applied Ecology.

Further Reading

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