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Plant Diversity in Forests

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Measurement of Diversity

Diversity can be measured either as species richness, the number of species per unit of land surface area or per unit number of individuals in a sample, or as a derived index that attempts to reflect the variation in relative abundance within a community as well as its richness. Commonly used indices of diversity are the Simpson's index (D) and the Shannon index (H), which are defined as follows:

$$\text{Simpson's index } D = \frac{1}{\sum_{i=1}^{S} P_i^2}$$

and

$$\text{Shannon index } H = -\sum_{i=1}^{S} P_i \ln P_i$$

where S is the total number of species in the community and P_i is the proportion of individuals represented by the ith species. These indices have the useful property that their values increase with greater evenness in the relative abundance of species for a given species richness.

Distribution of Diversity at Large Scales

At a global scale, the diversity of plants in forests, as in all plant communities, varies with climate and soil conditions, although there is also a pervasive imprint of history that disrupts large-scale relationships between plant diversity and biophysical conditions under some circumstances. The relationship between climate and plant distribution was promoted by the systematic collation of climate data by the German ecologist Heinrich Walter that allowed him to conduct a comparative analysis of the distribution of diversity at large spatial scales. By representing climates using a standardized format (referred to as a 'klimadiagram'), Walter proposed a hierarchical classification of world vegetation in which vegetation 'types' are nested within vegetation 'zones.' Four of Walter's vegetation zones possess vegetation types that can be described as forests: the tropical-cum-subtropical, warm temperate, cool temperate and cold temperate vegetation zones (the fifth, the Arctic vegetation zone, does not possess forests although dwarf trees are present in Arctic vegetation). Walter determined that the distinction between vegetation zones was determined on the basis of temperature, and that the series of vegetation types within each vegetation zone were differentiated on the basis of rainfall-related criteria.

Temperature

Classifying vegetation was the first step to obtaining a mechanistic understanding of the distribution of world vegetation. Subsequent work has refined our knowledge of the distribution of diversity, and robust generalizations are now possible. First, it is evident that forests lying closer to the equator possess a higher plant species richness and diversity than forests at higher and lower latitudes. This statement assumes that the comparison being made is of forests at the same altitude, subjected to equivalent rainfall regimes and excludes forests growing on soils that are deficient in their availability of plant nutrients, such as N, P, or K, or supply an extreme of potentially toxic elements such as Ni or Al. Thus a hypothetical transect starting on the equator in wet evergreen tropical lowland rainforest in Southeast Asia and running north through the warm temperate evergreen and cool temperate deciduous forests of eastern Asia and thence into the cold temperate (boreal) forest of eastern Siberia would encounter forests of decreasing plant diversity with increasing latitude. This gradient in plant diversity is expressed among the trees that form the forest canopy, but is also observed among other life-forms such as shrubs and herbs. Some life-forms (such lianas and epiphytes) are rare or absent outside the tropics. Similar transects running north from equatorial forests in Africa and South America would not encounter such a well-ordered sequence of vegetation zones. The southern hemisphere lacks cool temperate deciduous forests at low altitudes and lacks boreal forest entirely because the continental land-masses do not extend sufficiently far south. Diversity of plants in forests also declines with increasing altitude on mountains at all latitudes, although the

precise nature of these changes varies as a function of local site conditions.

Rainfall

The second most important factor influencing the distribution of plant diversity at large spatial scales is the amount and seasonal distribution of rainfall. Walter recognized series of vegetation types related to such changes in moisture regimes within each of the five vegetation zones, and in climates that are capable of supporting forests, vegetation types are synonymous with forest types. Within the tropical-cum-subtropical vegetation zone, which lies at the lowest latitudes in South and Central America, Africa and Madagascar, South and Southeast Asia, and the Pacific, plant diversity in forests decreases along the series of vegetation types represented by tropical lowland evergreen rain forest, tropical semievergreen rainforest, tropical deciduous forest and Savanna. At these latitudes, plant diversity is lowest in semidesert and perennial plants are absent from true deserts, but these are not forests. Along this series, mean annual rainfall declines from approximately 1800–5000 mm in climates supporting evergreen tropical forest to approximately 250–700 mm in climates supporting Savanna vegetation, while the number of dry months per year (defined as months that receive <100 mm on average) increases from 0–4 to 7–11 for the same comparison. Both total annual rainfall and the seasonal distribution of rainfall have important influences on plant distribution and diversity in the tropics. At the wetter end of the gradient, the transition between vegetation types is driven by the number of dry months rather than the total annual rainfall, but the converse is true at the drier end of the main climatic gradient.

Series of vegetation types related to variation in moisture regimes can also be recognized in the warm, cool and cold temperate vegetation zones and in the (nonforested) arctic vegetation zone, and plant diversity in forests declines in successively drier climates at these cooler latitudes, as it does in the tropics. The warm temperate series possesses just two vegetation types that can be described as forests: warm temperate rainforests in wetter environments and Mediterranean-type forest (or Savanna or scrub) in sites that experience a winter maximum of rainfall and a distinct cool season. Warm temperate rain forests tend to occur on the eastern fringes of continental land-masses (for example in Japan, south-eastern Australia, and New Zealand) and are intermediate in species richness between evergreen tropical rainforests and temperate deciduous forests. Both the cool and cold temperate vegetation zones also contain two vegetation types that can be described as forests. Cool temperate rainforests occur in areas with a maritime climate that receive winter rains and no summer drought in both the northern hemisphere (in a coastal strip from northern California to Canada) and the southern hemisphere (coastal areas of southern Chile). The characteristics of these two blocks of cool temperate rainforest differ considerably: in the northern hemisphere the characteristic tree species are gymnosperms and include, for example, the redwood (*Sequoia sempervirens*), while the southern hemisphere equivalent is dominated by species of southern beech (*Nothofagus* spp.). In less distinctly maritime temperate climates the dominant forest trees are deciduous and these conditions give rise to the cool temperate deciduous forests of eastern North America and western Europe. There is no southern hemisphere equivalent of these cool temperate deciduous forests. At higher latitudes in the northern hemisphere there is a transition to forests in which gymnosperm trees become dominant across the landscape and in which plant diversity is markedly lower than in the cool temperate forest types just described. These are the cold temperate or boreal forests that circle the northern polar regions. In Europe these forests are referred to as 'taiga' and are dominated by just two species (*Pinus sylvestris* and *Picea abies*), while the North American and East Asian boreal forests are more species-rich. In the most continental climates (i.e., those that experience the lowest winter temperatures and the lowest annual rainfall) of the boreal forest region in eastern Siberia, the evergreen forest gives way to a species-poor forest of deciduous conifers such as larch (*Larix dahurica*). Larch forests clothe 2.5 million km^2 of eastern Siberia, but there is no equivalent climate or forest type in North America.

Soil Conditions

The third factor in the hierarchy of determinants of the distribution of plant diversity in forests is soil conditions. This term by itself obscures a variety of different factors that contribute to plant diversity, and global generalizations are unlikely to be satisfactory. Theoretical models of plant competition can be interpreted to predict either an increase or a decrease in plant diversity along a gradient of soil fertility, and empirical tests of these ideas are few in number. Part of the difficulty with testing these ideas is that changes in soil conditions rarely occur in isolation of changes in climate, in part because climatic conditions themselves influence physical and chemical processes in soils. However, two examples from tropical forests can be used to infer an influence of soil nutrient availability on forest plant diversity.

First, lowland forests in relatively aseasonal environments in the western part of the Amazon basin possess a higher diversity and richness of forest trees than forests in equivalent climates in the eastern Amazon. One potential cause of this difference is the greater nutrient availability in the relatively young volcanic soils in the western Amazon, although it may also be relevant that forests of the western Amazon are exposed to a higher frequency of disturbance by meandering rivers. Disturbance may influence plant diversity in a variety of ways as described below. The second example is less equivocal. Among the tropical lowland forests of both South America and Southeast Asia are patches of forest on highly nutrient-starved podzolic soils characterized by a thick organic layer and a bleached sand-rich mineral horizon. These forests are referred to as 'kerangas' in Southeast Asia and by a variety of labels, including 'caatinga,' in South America, and in both cases they are examples of heathland ecosystems. They are all characterized by a low richness of plant species, including trees, when compared to adjacent forests on richer soils. The mechanisms that determine the relatively low species diversity of tropical heath forests are unknown, but it is possible that the physiological and morphological trade-offs required to tolerate low nutrient conditions have evolved relatively infrequently in tropical lowland tree floras. Similarly, forests growing on soils that supply an excess of plant nutrients that are also potentially toxic at high concentrations (such as Ni in ultramaphic vegetation) are species-poor compared to adjacent forests growing on less extreme soils. Mangrove forests are also species-poor relative to dry-land forests in similar climates, presumably because the physiological adaptations required to tolerate high internal Na concentrations have evolved only rarely.

Other Determinants of Plant Diversity

Taken together, the interpretation presented above could be taken to imply that variation in plant diversity can be explained on the basis of deterministic processes that are driven by the biophysical environment. However, this would be an oversimplification of the origins of variation in forest plant diversity. At least three additional factors must be considered as important in any explanation of diversity: these factors are biogeographic history, the size of the local and regional species pools, and disturbance.

Biogeographic History

The effects of biogeographic history pervade the distribution of diversity, particularly at large spatial scales. Regional differences in diversity have arisen because the distribution of the continents has changed during the evolution of land plants, and because climate itself is not constant in time at any one locality. Thus the effects of tectonic drift and climate change are superimposed on contemporary climate and soil conditions as important determinants of present-day plant diversity. Two examples will be used to illustrate these processes. First, it is well known that the diversity of forest trees in the cold temperate deciduous forests of eastern North America is greater than in the equivalent forests of western Europe, despite the equivalence of the current climate of these regions. This difference has been explained by the difference in the ease of migration of forest trees in North America (where the mountains run north–south) and Europe (where the mountains run east–west) in response to Pleistocene glaciations. As mountains might represent a barrier to plant dispersal, it has been suggested that in Europe plants are prevented by the Alps and the Pyrenees from migrating into relatively warm climates during the onset of glacial conditions in north and west Europe. Similarly, recolonization of formerly glaciated landscapes in northern Europe from refugia in south and eastern Europe is slowed by these montane barriers to dispersal. These barriers to the movement of plants do not exist in eastern North America because the dominant mountain chain (the Appalachians) runs north–south, and dispersal can occur along lowland valley corridors.

The second example illustrating the importance of biogeography derives from the observation that the lowland tropical forests of Africa are less rich in species than forests of tropical South America and Southeast Asia, when sites with a similar contemporary climate are compared. Again, it is possible to interpret this difference as a reflection of changes in climate during the Pleistocene interacting with differences among the continents in the distribution of land at different altitudes. The cumulative frequency distribution of land surface area with increasing altitude rises much faster for Africa than for either of the two other continents, which suggests that average elevation of lowland tropical forest sites is greatest in Africa. Under current climates these differences are not sufficient to fragment lowland forests in Africa, but during drier and cooler phases of the Pleistocene the proportion of the landscape that would have provided climatic conditions suitable for the maintenance of a lowland tropical forest flora would have been much lower in Africa than in South America or Southeast Asia. Thus the African forests would have become more fragmented, and extinctions of forest trees would have been more

prevalent. The differences we observe today are a reflection of these interactions between landscape structure and climate change.

Size of the Species Pool

The second major factor that might disrupt the relationship between biophysical conditions and forest plant diversity is the size of the local and regional species pools. As discussed above, historical explanations can account for some differences in the number of species available to colonize a site, but other factors are also involved. These ideas were brought together in MacArthur and Wilson's theory of island biogeography, which was originally formulated as a theoretical exploration of the effects of island size on species richness, but has now been applied to island-type ecosystems on nonislands. MacArthur and Wilson proposed that the number of species occupying an island could be explained in terms of a dynamic equilibrium between local immigration, emigration, and extinction events. Since the probability of colonization and extinction can be modeled as a function of factors such as island size and remoteness from a source population, it is possible to derive theoretical predictions for island species richness as a function of these factors. The most important of these functions is the species-area relationship, which takes the following form:

$$S = c.A^z$$

where S is species richness, A is island area, and c and z are constants. This function implies that the log of species number is a linear function of log island area.

There are many demonstrations of the effect of increasing area on species richness, including some for forest trees. However, there is also controversy in the ecological literature over whether the increase is driven by a pure 'area effect,' or whether larger areas of island or habitat-island are richer because they contain a greater diversity of habitats. Nonetheless the theory of island biogeography helps explain why remote oceanic islands, such as Hawaii and the Galápagos Islands, possess relatively species-poor floras for their climate and may help to explain why habitat fragmentation reduces forest plant diversity.

Disturbance

The final factor that must be considered in any consideration of the mechanisms driving forest plant diversity is disturbance. Disturbance is defined and described elsewhere in this volume (*see* **Ecology**: Natural Disturbance in Forest Environments). Forests are subjected to a variety of types and scales of natural disturbance processes, and are also heavily influenced by human activities. By definition, disturbance has short-term negative impacts on diversity at the scale at which the disturbance occurs, for example by removing individuals through tree mortality. However, the relationship between disturbance and diversity at larger and longer spatial scales is complex and not necessarily predictable. One of the most influential theoretical models of the relationship between disturbance and diversity is Connell's intermediate disturbance hypothesis (IDH), which proposes that diversity of plant communities is maximized at the mid-point of plant succession, and in communities that are subjected to intermediate intensities or frequencies of disturbance. According to the IDH, sites very early in succession or those that suffer a high frequency or intensity of disturbance have a low diversity because relatively few species possess the traits associated with colonizing unoccupied or heavily disturbed sites. Diversity initially rises through succession because site conditions are ameliorated by the earliest colonizers, and because species accumulate by random dispersal events, but declines in late succession because a small number of competitively superior species are able to co-opt the available resources and exclude the early colonizing species. However, in most communities the low diversity, late-successional communities rarely arise before a new disturbance event sets back succession to an earlier stage. Thus, diversity is maximized at the mid-point of succession when early-successional, disturbance-dependent species coexist with late-successional competitive dominants.

The IDH is a controversial concept and has rarely been tested adequately for forests. However, in one recent test in a lowland tropical forest in French Guiana it was found that tree species diversity was greater in lightly logged forest than in unlogged forest or forest that had been heavily logged, in support of the IDH. Other attempts to test the IDH in forest communities have either failed to find support for it, or have been flawed in their design or interpretation.

Disturbance to forests by anthropogenic activity can reduce plant diversity, particularly in the tropics. The principal drivers of disturbance are clearance for permanent agriculture and plantation forestry, shifting cultivation, and logging. Fragmentation has independent effects on forest plant diversity because fragmentation increases the amount and importance of edge habitats and brings forest edges close to species that inhabit the forest interior. Small forest fragments also reduce the effective population size of plants and thus increase their probability of

extinction (*see* **Ecology**: Biological Impacts of Deforestation and Fragmentation).

Conclusions

Although patterns in forest plant diversity at large spatial scales are now well described, there are still substantial lacunae in the record that can only be resolved by additional botanical exploration. In some parts of world (for example, areas of the Philippines, Indonesia, and the Atlantic forest of Brazil), it is likely that deforestation and forest fragmentation have already eliminated any further scope for describing natural patterns of forest plant diversity at a more local scale. The mechanisms that determine the large-scale patterns in plant diversity remain poorly understood and are likely to vary substantially between regions and localities. Current theories suggest that the diversity of forest floras reflects a balance between biophysical, historical, and anthropogenic causes, but robust predictions of diversity at a local scale are not yet possible.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation; Natural Disturbance in Forest Environments. **Environment**: Impacts of Elevated CO_2 and Climate Change. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation. **Tree Physiology**: Forests, Tree Physiology and Climate.

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Endangered Species of Trees

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Introduction

Unfortunately the topic of endangered species of trees is a vast one because of the extensive loss of their habitat in most parts of the world and in many cases because of overexploitation. The World Conservation Union's (IUCN) *Red List of Threatened Plants*, published in 1997, lists almost 34000 species of plants that are now threatened with extinction. That is just over 10% of the total number of plant species in the world. These lists include many species of trees. Red data lists exist for many countries and are catalogs of species where future survival in nature is uncertain. Most threatened species of trees are those of the tropical regions and on oceanic islands, in the tropics because of habitat destruction and because of the enormous diversity and often localized distribution of individual species, and on islands because they tend to have many unique endemic species, but also because of habitat destruction and the introduction of alien invasive species that take the place of the native flora. For example, about 85% of the Madagascan flora is endemic to that island nation and only 20% of the original vegetation remains. It is therefore inevitable that some species have gone extinct and others are under threat. A recent red data book for the ten countries of southern Africa cataloged 3900