Global climate change is increasingly making migration a necessity for long-term persistence of many species. Increasing temperatures and shifting rainfall regimes are leading to a growing mismatch between species' current distributions and the climates to which they are best suited. This places a premium on plant dispersal into the newly suitable areas and, indeed, threatens extinction for many species if they fail to disperse. In practice, this often requires dispersing over or around large areas of anthropogenically modified landscapes or through narrow corridors crossing such landscapes. The paleorecord shows that past climate shifts have been accompanied by associated shifts in plant species' ranges, although these have often lagged considerably. Historic climate shifts were accompanied by more extinctions on continents in which east–west mountain ranges barred the way. Unfortunately, anthropogenically modified habitats may for many species prove as much a barrier to dispersal as mountain ranges.

Manipulating Dispersal Opportunities to Promote Conservation

Deliberate measures to preserve, enhance, or inhibit plant dispersal opportunities can constitute valuable tools for conservation and management. Restoration and maintenance of natural densities of animal seed dispersers is an integral part of the conservation of any plant population, community, or ecosystem. Construction of corridors that connect habitat remnants can enable dispersal that enhances short-term population persistence and long-term viability in the face of global change. Habitat restoration and reestablishment of native vegetation can often be speeded through the provision of perches for birds that bring in seeds. Deliberate assisted migration of plant propagules to track climate change should be considered, especially where anthropogenic barriers restrict the possibility for unassisted migration. Finally, the introduction and spread of invasive species can be reduced by measures that restrict the transport of propagules by humans.

SEE ALSO THE FOLLOWING ARTICLES

Dispersal, Animal / Dispersal, Evolution of / Integrodifference Equations / Metapopulations / Restoration Ecology / Spatial Ecology

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DIVERSITY MEASURES

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Diversity is a measure of the compositional complexity of an assemblage. One of the fundamental parameters describing ecosystems, it plays a central role in community ecology and conservation biology. Widespread concern about the impact of human activities on ecosystems has made the measurement of diversity an increasingly important topic in recent years.

TRADITIONAL DIVERSITY MEASURES

The simplest and still most popular measure of diversity is just the number of species present in the assemblage. However, this is a very hard number to estimate reliably from small samples, especially in assemblages with many rare species. It also ignores an ecologically important aspect of diversity, the evenness of an assemblage's abundance distribution. If the distribution is dominated by a few species, an organism in the assemblage will seldom interact with the rare species. Therefore, these rare species should not count as much as the dominant species when calculating diversity for ecological comparisons. This observation has led ecologists (and also economists and other scientists studying complex systems of any kind) to develop diversity measures which take species frequencies into account.

There are two approaches to incorporating species frequencies into diversity measures. If the species-abundance distribution is known or can be determined, one or more of the parameters of the distribution function serve as a diversity measure. For example, when a species rank abundances distribution can be described by a log-series distribution, a single parameter, called Fisher's alpha, has often been used as a diversity measure. The parameters of other distributions (particularly the log-normal distribution) have also been used. However, this method gives uninterpretable results when the actual species abundance distribution does not fit the assumed theoretical distribution. This method also does not permit meaningful comparisons of assemblages with different distribution functions (for example, a log-normal assemblage cannot be compared to an assemblage whose abundance distribution follows a geometric series).

A more robust and general nonparametric approach, which makes no assumptions about the mathematical form of the underlying species-abundance distributions, is now the norm in ecology. Ecologists have often borrowed nonparametric measures of compositional complexity (which balance evenness and richness) from other sciences and equated these with biological diversity. The most popular measure of complexity has been the Shannon entropy,

$$H_{Sh} = -\sum_{i=1}^{S} p_i \log p_i, \tag{1}$$

where S is the number of species in the assemblage and the ith species has relative abundance p_i. This gives the uncertainty in the species identity of a randomly chosen individual in the assemblage. Another popular complexity measure is the Gini-Simpson index,

$$H_{GS} = 1 - \sum_{i=1}^{S} p_i^2, \tag{2}$$

which gives the probability that two randomly chosen individuals belong to different species.

However, these two complexity measures do not behave in the same intuitive linear way as species richness. When diversity is high, these measures hardly change their values even after some of the most dramatic ecological events imaginable. They also lead to logical contradictions in conservation biology, because they do not measure a conserved quantity (under a given conservation plan, the proportion of "diversity" lost and the proportion preserved can *both* be 90% or more). Finally, these measures each use different units, so they cannot be compared with each other.

DIVERSITY MEASURES THAT OBEY THE REPLICATION PRINCIPLE

Robert MacArthur solved these problems by converting the complexity measures to "effective number of species" (i.e., the number of equally abundant species that are needed to give the same value of the diversity measure), which use the same units as species richness. Shannon entropy can be converted by taking its exponential, and the Gini–Simpson index can be converted by the formula $1/(1 - H_{GS})$. These converted measures, like species richness itself, have an intuitive property that is implicit in much biological reasoning about diversity. This property, called the replication principle or the doubling property, states that if N equally diverse groups with no species in common are pooled in equal proportions, then the diversity of the pooled groups must be N times the diversity of a single group. Measures that follow the replication principle give logically consistent answers in conservation problems, rather than the self-contradictory answers of the earlier complexity measures. Their linear scale also facilitates interpreting changes in the magnitudes of these measures over time; changes that would seem intuitively large to an ecologist will cause a large change in these measures.

Mark Hill showed that the converted Shannon and Gini–Simpson measures, along with species richness, are members of a continuum of diversity measures called Hill numbers, or effective number of species, defined for $q \neq 1$ as

$${}^{q}D = \left(\sum_{i=1}^{S} p_i^{q}\right)^{1/(1-q)}. \tag{3a}$$

This measure is undefined for $q = 1$, but its limit as q tends to 1 exists and gives

$${}^{1}D = \lim_{q \to 1} {}^{q}D = \exp\left(-\sum_{i=1}^{S} p_i \log p_i\right) = \exp(H_{Sh}). \tag{3b}$$

The parameter q determines how much the measure discounts rare species. When $q = 0$, the species abundances do not count at all, and species richness is obtained. When $q = 1$, Equation 3b is the exponential of Shannon entropy. This measure weighs species in proportion to their frequency and can be interpreted as the number of "typical species" in the assemblage. When $q = 2$, Equation 3a becomes the inverse of the Simpson concentration and rare species are severely discounted.

The measure ${}^2D$ can be interpreted as the number of "relatively abundant species" in the assemblage.

All standard complexity measures can be converted to effective number of species. Since these and all other Hill numbers have the same units as species richness, it is possible to graph them on a single graph as a function of the parameter q. This diversity profile characterizes the species-abundance distribution of an assemblage and provides complete information about its diversity. All Hill numbers obey the replication principle.

Diversity measures that obey the replication principle are directly related to the concept of compositional similarity. If we pool N assemblages in equal proportions, the ratio of the mean single-assemblage diversity to the pooled diversity will vary from unity (indicating complete similarity in composition) to $1/N$ (indicating maximal dissimilarity in composition), as long as the mean single-assemblage diversity is defined properly. This diversity ratio can be normalized onto the unit interval and used as a measure of compositional similarity. Many of the most important similarity measures in ecology, such as the Sørensen, Jaccard, Horn, and Morisita–Horn indices of similarity, and their multiple-assemblage generalizations, are examples of this normalized diversity ratio.

The diversity of an extended region, often called the gamma diversity, can be partitioned into within- and between-assemblage components, usually called alpha and beta diversities, respectively. When all assemblages are assigned equal statistical weights, the beta component of a Hill number is the inverse of the diversity ratio described in the preceding paragraph. Beta diversity is thus directly related to compositional differentiation and gives the effective number of completely distinct assemblages (i.e., assemblage diversity). When the diversity measure is species richness or the exponential of Shannon entropy, this interpretation of beta diversity is valid even when the assemblages are not equally weighted.

The apportionment of regional diversity among assemblages gives clues about the ecological principles determining community composition. In order to test hypotheses about the factors determining community assembly and intercommunity differentiation, biologists need to compare the observed patterns against those that would be produced by purely stochastic effects. The expected values of alpha, beta, and gamma diversities of order 2 (Simpson measures) can be predicted from a purely stochastic "neutral" model of community assembly. This quality makes order 2 measures particularly important in community ecology. Approximate predictions can also be made for order 1 measures.

DIVERSITY MEASURES THAT INCORPORATE SPECIES' DIFFERENCES

Evelyn Pielou was the first to notice that the concept of diversity could be broadened to consider differences among species. All else being equal, an assemblage of phylogenetically or functionally divergent species is more diverse than an assemblage consisting of very similar species. Differences among species can be based on their evolutionary histories (in a form of taxonomy or phylogeny) or by differences in their functional trait values. Diversity measures can be generalized to incorporate these two types of species differences (referred to respectively as phylogenetic diversity and functional diversity).

Evolutionary histories are represented by phylogenetic trees. If the branch lengths are proportional to divergence time, the tree is ultrametric; all branch tips are the same distance from the basal node. If branch lengths are proportional to the number of base changes in a given gene, some branch tips may be farther from the basal node than other branch tips; such trees are non-ultrametric. A Linnaean taxonomic tree can be regarded as a special case of an ultrametric tree.

Most measures incorporating species differences are generalizations of the three classic species-neutral measures: species richness, Shannon entropy, and the Gini–Simpson index. Vane-Wright and colleagues generalized species richness to take into account cladistic diversity (CD), based on the total nodes in a taxonomic tree (which is also equal to the total length in the tree if each branch length is assigned to unit length). Faith defined the phylogenetic diversity (PD) as the sum of the branch lengths of a phylogeny connecting all species in the target community. These two measures can be regarded as a generalization of species richness (see Table 1).

Rao's quadratic entropy is a generalization of the Gini–Simpson index that takes phylogenetic or other differences among species into account:

$$Q = \sum_{i,j} d_{ij} p_i p_j, \tag{4}$$

where d_{ij} denotes the phylogenetic distance between species i and j, and p_i and p_j denote the relative abundance of species i and j. It gives the mean phylogenetic distance between individuals in the assemblage.

TABLE 1

A summary of diversity measures and their interpretations based on Hill numbers (all satisfy the replication principle)

Diversity order	Traditional diversity measures	Taxonomic diversity measures (L levels)	Phylogenetic diversity measures over T years (Ultrametric)	Phylogenetic diversity measures over $\overline{T}$ mean base changes (Non-ultrametric)	Functional diversity measures over R trait-based distances
$q = 0$	Species richness	CD/L	PD/T	$PD/\overline{T}$	FD/R
$q = 1$	$\exp(H_{Sh})$	$\exp(H_p/L)$	$\exp(H_p/T)$	$\exp(H_p/\overline{T})$	$\exp(H_p/R)$
$q = 2$	$1/[1-(H_{GS})]$	$1/[1-(Q/L)]$	$1/[1-(Q/T)]$	$1/[1-(Q/\overline{T})]$	$1/[1-(Q/R)]$
Diversity or mean diversity of general order q	${}^qD$: Hill numbers (effective number of species)	${}^q\overline{D}(L)$: Mean effective number of cladistic nodes per level	${}^q\overline{D}(T)$: Mean effective number of lineages (or species) over T years	${}^q\overline{D}(\overline{T})$: Mean effective number of lineages (or species) over $\overline{T}$ mean base changes	${}^q\overline{D}(R)$: Mean effective number of functional groups up to R trait-based distances
Related measure		${}^q\overline{D}(L) \times L$: effective number of total cladistic nodes for L levels	${}^q\overline{D}(T) \times T$: effective number of lineage-lengths over T years	${}^q\overline{D}(\overline{T}) \times \overline{T}$: effective number of base changes over $\overline{T}$ mean base changes	${}^q\overline{D}(R) \times R$: effective number of functional distances up to R trait-based distances

H_{Sh}: Shannon entropy; H_{GS}: Gini–Simpson index; CD: cladistic diversity (total number of nodes) by Vane-Wright et al.; PD: phylogenetic diversity (sum of branch lengths) by Faith; FD: functional diversity (sum of trait-based distances) by Petchey and Gaston; Q: quadratic entropy by Rao; H_p: phylogenetic entropy by Allen et al. and Pavoine et al.; $\overline{T}$: mean base change per species for nonultrametric trees; ${}^qD$: Hill numbers (see Eq. 3a); ${}^q\overline{D}(L)$, ${}^q\overline{D}(T)$, ${}^q\overline{D}(\overline{T})$, and ${}^q\overline{D}(R)$: phylogenetic diversity by Chao et al. (see Eq. 6).

Shannon's entropy has also been generalized to take phylogenetic distance into account, yielding the phylogenetic entropy H_p:

$$H_P = -\sum_i L_i a_i \log a_i, \tag{5}$$

where the summation is over all branches, L_i is the length of branch i, and a_i denotes the abundance descending from branch i.

Since Shannon entropy and the Gini–Simpson index do not obey the replication principle, neither do their phylogenetic generalizations. These measures of phylogenetic diversity will therefore have the same interpretational problems as their parent measures. These problems can be avoided by generalizing the Hill numbers, which obey the replication principle. The generalization requires that we specify a parameter T, which is the distance (in units of time or base changes) from the branch tips to a cross section of interest in the tree. The generalization is

$${}^q\overline{D}(T) = \left\{ \sum_{i \in \boldsymbol{B}_T} \frac{L_i}{T} a_i^q \right\}^{1/(1-q)}, \tag{6}$$

where $\boldsymbol{B}_T$ denotes the set of all branches in this time interval $[-T, 0]$, L_i is the length (duration) of branch i in the set $\boldsymbol{B}_T$, and a_i is the total abundance descended from branch i. This ${}^q\overline{D}(T)$ gives the mean effective number of maximally distinct lineages (or species) through T years ago, or the mean diversity of order q over T years.

The diversity of a tree with ${}^q\overline{D}(T) = z$ in the time period $[-T, 0]$ is the same as the diversity of a community consisting of z equally abundant and maximally distinct species with branch length T. The product of ${}^q\overline{D}(T)$ and T quantifies "effective number of lineage-lengths or lineage-years." If $q = 0$, and T is the age of the highest node, this product reduces to Faith's PD.

For nonultrametric trees, let $\boldsymbol{B}_{\overline{T}}$ denote the set of branches connecting all focal species with mean base change $\overline{T}$. Here, $\overline{T} = \sum_{i \in \boldsymbol{B}_{\overline{T}}} L_i a_i$ represents the abundance-weighted mean base change per species. The diversity of a nonultrametric tree with mean evolutionary change $\overline{T}$ is the same as that of an ultrametric tree with time parameter $\overline{T}$. Therefore, the diversity formula for a nonultrametric tree is obtained by replacing T in the ${}^q\overline{D}(T)$ by $\overline{T}$ (see Table 1).

Equation 6 can also describe taxonomic diversity, if the phylogenetic tree is a Linnaean tree with L levels, and each branch is assigned unit length. Equation 6 also describes functional diversity, if a dendrogram can be constructed from a trait-based distance matrix using a clustering scheme.

Both Q and H_p can be transformed into members of this family of measures, and they then satisfy the replication principle (see Table 1) and have the intuitive behavior biologists expect of a diversity. The replication principle can be generalized to phylogenetic or functional diversity: when N maximally distinct trees (no shared nodes during the interval $[-T, 0]$) with equal mean diversities are combined, the mean diversity of the combined tree is N times the mean diversity of any individual tree. This property ensures the intuitive behavior of these generalized diversity measures.

ESTIMATING DIVERSITY FROM SMALL SAMPLES

In practice, the true relative abundances of the species in an assemblage are unknown and must be estimated from small samples. If the sample relative abundances are used directly in the formulas for diversity, the maximum-likelihood estimator of the true diversity is obtained. This number generally underestimates the actual diversity of the population, particularly when sample coverage is low. When coverage is low, it is important to use nearly unbiased estimators of diversity instead of the maximum-likelihood estimator. Unbiased estimators of diversities of order 2 are available, and nearly unbiased estimators of Shannon entropy and its exponential have recently been developed by Chao and Shen. Species richness is much more difficult to estimate than higher-order diversities; at best a lower bound can be estimated. A simple but useful lower bound (which is referred to as the Chao1 estimator in literature) for species richness is

$$S_{Chao1} = D + f_1^2/(2f_2),$$

where D denotes the number of observed species in sample, f_1 denotes the number of singletons and f_2 denotes the number of doubletons. Estimation of phylogenetic or functional diversity from small samples should follow similar principles, but merits more research.

SEE ALSO THE FOLLOWING ARTICLES

Conservation Biology / Neutral Community Ecology / Statistics in Ecology

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DYNAMIC PROGRAMMING

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Dynamic programming is a mathematical optimization method that is widely used in theoretical ecology and conservation to identify a sequence of decisions that will best achieve a given objective. When ecosystem dynamics (potentially including social, political, and economic processes) can be described using a model that is discrete in time and state space, dynamic programming can provide an optimal decision schedule. The technique is most commonly applied to explain the behavior of organisms (particularly their life history strategies) and to plan cost-effective management strategies in conservation and natural resource management. Compared with alternative dynamic optimization methods, dynamic programming is both flexible and robust, can readily incorporate stochasticity, is well suited to computer implementation, and is considered to be conceptually intuitive. On the other hand, the optimal results are generated in a form that can be very difficult to interpret or generalize. Furthermore, models of complex ecosystems can be computationally intractable due to nonlinear growth in the size of the state space.

OPTIMIZATION

In mathematics, optimization is the process by which an agent chooses the best decision from a set of feasible alternatives. It plays a central role in a wide range of ecological, evolutionary, and environmental fields. Optimization both provides normative advice to managers in applied ecology (i.e., how to best manage ecosystems) and offers positive insights into the actions of ecological agents (i.e., understanding why organisms behave in particular ways).

Frequently, agents are required to make a sequence of decisions where the outcome will not be realized until all the decisions have been implemented. Such sequential optimization problems are more difficult to solve than optimizations involving single decisions (static optimization), because actions that appear attractive in the short term may not result in the best long-term outcomes. In these situations, agents are required to undertake dynamic optimization. Dynamic optimization requires the