
III.1

Biodiversity: Concepts, Patterns, and Measurement

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OUTLINE

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Life on Earth is diverse at many levels, beginning with genes and extending to the wealth and complexity of species, life forms, and functional roles, organized in spatial patterns from biological communities to ecosystems, regions, and beyond. The study of biodiversity encompasses the discovery, description, and analysis of the elements that underlie these patterns as well as the patterns themselves. The challenge of quantifying patterns of diversity at the species level, even when the organisms are known to science, is complicated by the problem of detecting rare species and the underlying complexity of the environmental template.

GLOSSARY

- α , β , and γ diversity.** The species diversity (or richness) of a local community or habitat (α), the difference in diversity associated with differences in habitat or spatial scale (β), and the total diversity of a region or other spatial unit (γ)
- biodiversity.** The variety of life, at all levels of organization, classified both by evolutionary (phylogenetic) and ecological (functional) criteria
- diversity index.** A mathematical expression that combines species richness and evenness as a measure of diversity

evenness. A measure of the homogeneity of abundances in a sample or a community

functional diversity. The variety and number of species that fulfill different functional roles in a community or ecosystem

rarefaction curve. The statistical expectation of the number of species in a survey or collection as a function of the accumulated number of individuals or samples, based on resampling from an observed sample set

relative abundance. The quantitative pattern of rarity and commonness among species in a sample or a community

richness estimator. A statistical estimate of the true species richness of a community or larger sampling universe, including unobserved species, based on sample data

species accumulation curve. The observed number of species in a survey or collection as a function of the accumulated number of individuals or samples

species–area relation. The generally decelerating but ever-increasing number of species as sampling area increases

species richness. The number of species in a community, in a landscape or marinescape, or in a region

1. WHAT IS BIODIVERSITY?

Although E. O. Wilson first used the term *biodiversity* in the literature in 1988, the concept of biological diversity from which it arose had been developing since the nineteenth century and continues to be widely used. Biodiversity encompasses the variety of life, at all levels of organization, classified both by evolutionary (phylogenetic) and ecological (functional) criteria. At the level of biological populations, genetic variation among individual organisms and among lineages contributes

to biodiversity as both the signature of evolutionary and ecological history and the basis of future adaptive evolution. Species that lack substantial genetic variation are thought to be more vulnerable to extinction from natural or human-caused changes in their environment.

It is at the species level that the term *biodiversity* is most often applied by ecologists and conservation biologists, although higher levels of classification (genera, families, orders) or patterns of evolutionary diversification are sometimes also considered, especially in paleontology. Species richness is the number of species of a particular taxon (e.g., birds or grasses) or life form (e.g., trees or plankton) that characterize a particular biological community, habitat, or ecosystem type. When data are not available at the community, habitat, or ecosystem level, political units (counties, states or provinces, countries) are often used as the basis of statements about species richness.

Within biological communities and ecosystems, functional diversity refers to the variety and number of species that fulfill different functional roles. A *food web* and some measure of its complexity and connectivity is one way to depict the functional diversity of a community. Another is the classification and enumeration of species representing different *functional groups*, such as primary producers, herbivores, and carnivores. Within forest communities, for example, plant functional groups that are often distinguished include fast-growing pioneer species that quickly colonize disturbed habitats, slower-growing species that characterize mature forests, and plants that fill special functional roles, such as those that fix atmospheric nitrogen. A marine biologist working on soft-bottom communities might categorize benthic organisms by the physical effect they have on the substrate as well

as by source of nutrients. In microbial communities, microbial taxa that depend on and transform different chemical substrates represent distinct functional groups.

At the level of landscapes, marinescapes, or ecosystems, biodiversity is conceived on a landscape or larger scale, often in terms of the number, relative frequency, and spatial arrangement of distinguishable ecosystem types, or *ecoregions*.

2. RELATIVE ABUNDANCE: COMMON SPECIES AND RARE ONES

The species that characterize any natural community differ in relative abundance, usually with a few species quite common and most species much less so. Another way of looking at it is that most individuals belong to the few common species in a typical community. For example, in a study of the soil “seed bank” in a Costa Rican rainforest, by B. J. Butler and R. L. Chazdon, the 952 seedlings that germinated from 121 soil samples included 34 species. The most common single species was represented by 209 seedlings, and the next most common had 109. In contrast, the least common 15 species each had 10 or fewer seedlings.

One way to plot such species abundance data (an approach originated by R. H. Whittaker) is a *rank-abundance curve*, in which each species is represented by a vertical bar proportional to its abundance. Figure 1 shows such a plot for the seed bank data. Notice the long “tail” of rarer species. A community with such striking disparities in abundance among species is said to have low evenness. A rank-abundance plot for a hypothetical community with perfect evenness would be flat instead of declining, indicating that every species had the same abundance.

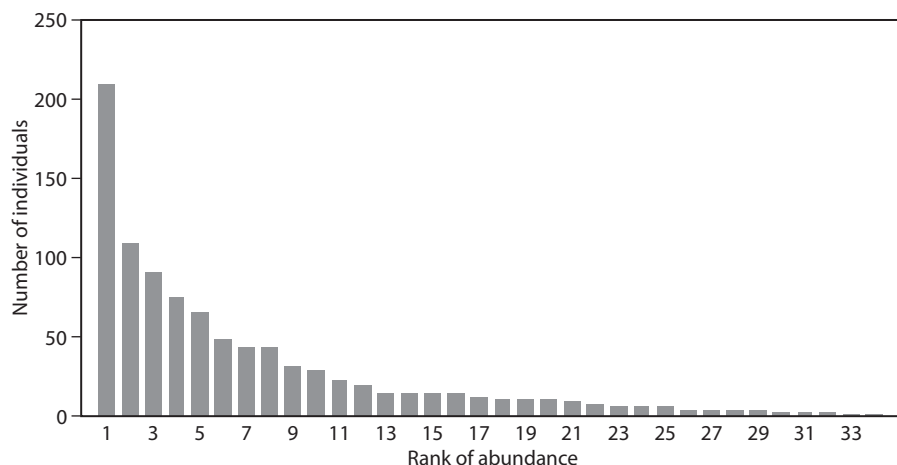


Figure 1. A rank-abundance curve.

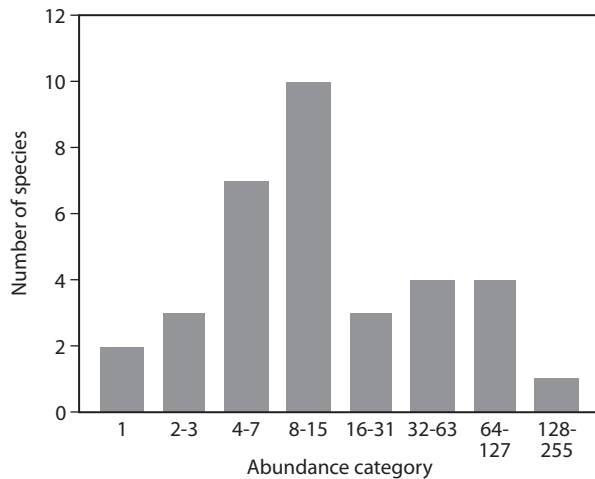


Figure 2. A log abundance plot.

Another way to plot the same species abundance data is to count up the number of species in each abundance category, starting with the rarest species, and plot these frequencies against abundance categories, as in figure 2. It is customary to use abundance categories in powers of two, which gives a *log abundance plot* (originated by F. W. Preston). When relative abundance distributions approximate a *normal* (bell-shaped) curve in a log abundance plot (the seed bank data in figure 2 come close), the statistical distribution is called *lognormal*. Lognormal distributions of relative abundance are common for large, well-inventoried natural communities. Many other statistical distributions have been used to describe relative abundance distributions, including the *log-series* distribution, which is described later in the context of diversity indices.

Conservation biologists are concerned with relative abundance because rare species are more vulnerable to extinction. Some species that are rare in one community are common in another (e.g., gulls are rare in many inland areas, but common along coasts), but some species are scarce everywhere they occur (e.g., most large raptors). In a classic paper, D. Rabinowitz classified species by three factors: (1) size of geographic range (not localized versus localized); (2) habitat specificity (not habitat specific versus habitat specific); and (3) local population density (not sparse versus sparse). She pointed out that there are seven ways to be rare, by this classification, but only one way to be common: not localized, not habitat specific, not sparse. Species that are rare by all three criteria (localized, habitat specific, and sparse), such as the ivory-billed woodpecker in the United States, are the most vulnerable to extinction.

3. MEASURING AND ESTIMATING SPECIES RICHNESS

On first consideration, measuring species diversity might seem an easy matter: just count the number of species present in a habitat or study area. In practice, however, complications soon arise. With the exception of very well-known groups in very well-known places (for which we already have good estimates of total richness anyway), species richness must generally be estimated based on samples. First of all, even for groups as well known as birds or flowering plants, not all species that are actually present are equally easy to detect. Although size, coloration, and—for animals—behavior can affect the detectability of individuals, relative abundance is the most important influence on the effort required to record a species. As every beginning stamp or coin collector soon discovers, the common kinds of coins or stamps are usually the first to be found. As the collection grows, the rate of discovery of kinds new to the collection declines steadily, as rarer and rarer kinds remain to be found.

For species richness, this process can be depicted as a *species accumulation curve*, sometimes called a *collector's curve*. The jagged line in figure 3 shows a species accumulation curve for the seed bank data of figure 1, as the 121 soil samples were added one at a time to the total. Because the order in which the soil samples were added to the collection was arbitrary, a smoothed version of such a curve, called a rarefaction curve, makes more sense. Conceptually, a rarefaction curve can be produced by drawing 1, 2, 3, . . . N samples (or individuals) at a time (without replacement) from the full set of samples, then plotting the means of many such draws. Fortunately, this is not necessary, as the mathematics of combinations allows rarefaction curves to be computed directly, along with 95% confidence intervals (the dashed lines in figure 3), based on work by C. X. Mao and colleagues. Rarefaction curves are especially useful for comparing species richness among communities that have not been fully inventoried or have been inventoried with unequal effort.

Richness estimation offers an alternative to rarefaction for comparing richness among incompletely inventoried communities. Instead of interpolating “backward” to smaller samples as in rarefaction, richness estimators extrapolate beyond what has been recorded to estimate the unknown asymptote of a species accumulation curve. Simple (regression-based) or sophisticated (mixture model) curve-fitting methods of extrapolation can be used, or nonparametric richness estimators can be computed. The latter depend on the frequencies of the rarest classes of observed species to

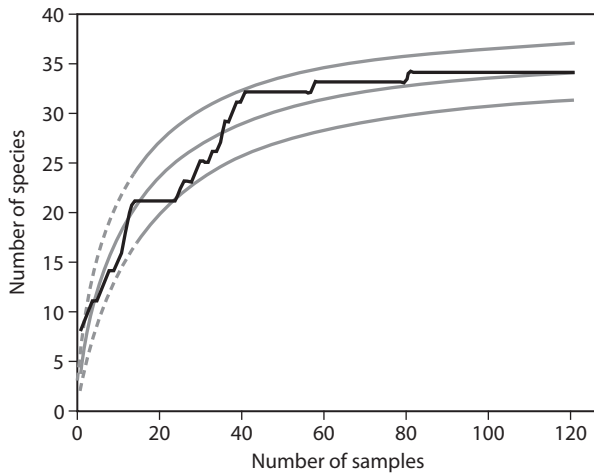


Figure 3. Species accumulation and rarefaction curves.

estimate the number of species present but not detected by the samples. The simplest nonparametric estimator, *Chao1*, augments the number of species observed (S_{obs}) by a term that depends only on the observed number of *singletons* (a , species each represented by only a single individual) and *doubletons* (b , species each represented by exactly two individuals):

$$S_{\text{est}} = S_{\text{obs}} + \frac{a^2}{2b}.$$

For the seed bank example of figures 1 and 2, when all samples are considered, 34 species were observed. Of these species, two were singletons, and two were doubletons, so that the estimated true richness is 35 species, confirming the visual evidence from the rarefaction curve that the inventory was virtually complete. The real utility of estimators, however, lies in their potential to approximate asymptotic species richness from much smaller samples. Figure 4 shows the same rarefaction curve (solid line) as in figure 3, with the estimated (asymptotic) species richness (shown by the dashed line) for the *Chao1* estimator, which begins to approximate true richness with as few as 20 samples. (The estimator curve shows the mean of 100 random draws for each number of samples.) It should be noted that richness estimators are not a panacea for problems of undersampling. Hyperdiverse communities with large numbers of very rare species, such as tropical arthropods, have so far resisted efforts to provide reliable nonparametric richness estimators.

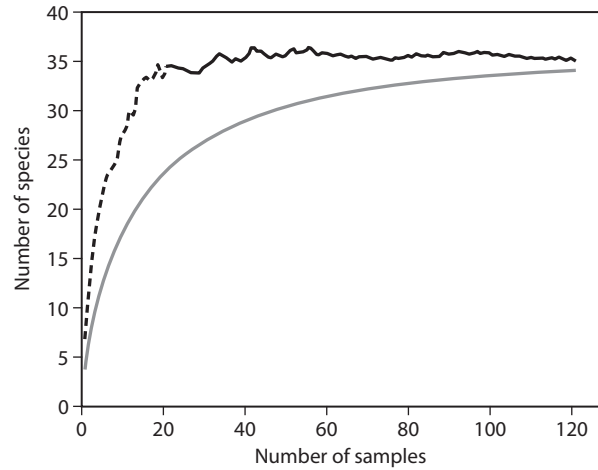


Figure 4. Estimated species richness and rarefaction curves.

4. SPECIES DIVERSITY INDICES

The concept of diversity, including biodiversity itself as well as the narrower concept of species diversity, is a human construct without any unique mathematical meaning. The simplest measure of species diversity is species richness, but a good case can be made for giving some weight to evenness as well. For example, the subjective sense of tree species richness is likely to be greater for a naturalist walking through a forest composed of 10 species of trees, each equally represented, than a forest of 10 species in which one species contributes 91% of the individuals and the others each 1%.

Diversity indices are mathematical functions that combine richness and evenness in a single measure, although usually not explicitly. Although there are many others, the most commonly used diversity indices in ecology are *Shannon diversity*, *Simpson diversity*, and *Fisher's α* . If species i comprises proportion p_i of the total individuals in a community of S species, the Shannon diversity is

$$H = -\sum_{i=1}^S p_i \ln p_i \text{ or, preferably, } e^H$$

and Simpson diversity is

$$D = 1 - \sum_{i=1}^S p_i^2 \text{ or, preferably, } D' = \left(\sum_{i=1}^S p_i^2 \right)^{-1}.$$

Both Shannon and Simpson diversities increase as richness increases, for a given pattern of evenness, and increase as evenness increases, for a given richness, but

they do not always rank communities in the same order. Simpson diversity is less sensitive to richness and more sensitive to evenness than Shannon diversity, which, in turn, is more sensitive to evenness than is a simple count of species (richness, S). At the other extreme, a third index in this group, the *Berger-Parker index*, depends exclusively on evenness; it is simply the inverse of the proportion of individuals in the community that belong to the single most common species, $1/p_i(\max)$. Because rare species tend to be missing from smaller samples, the sensitivity of these indices to sampling effort depends strongly on their sensitivity to richness. In practice, which measure of diversity to use depends on what one wishes to focus on (pure richness or a combination of richness and evenness), the relative abundance pattern of the data, comparability to previous studies, and the interpretability of the results. These four diversity measures (richness, the exponential form of Shannon diversity, the reciprocal form of Simpson diversity, and the Berger-Parker index) can be shown to be specific points on a diversity continuum defined by a single equation based on the classical mathematics of Rényi entropy, as first shown in the ecology literature by M. O. Hill in 1972 and periodically rediscovered since then. L. Jost, in 2005, reviewed these relationships and provided compelling arguments for preferring the exponential version of Shannon index and the reciprocal (D') version of the Simpson index.

Fisher's α is mathematically unrelated to the Rényi family of indices. It is derived from the log-series distribution, proposed by R. A. Fisher as a general model for relative abundance:

$$\alpha x, \alpha x^2/2, \alpha x^3/3, \alpha x^4/4, \dots, \alpha x^n/n,$$

where successive terms represent the number of species with 1, 2, 3, ..., n individuals, and α is treated as an index of species diversity. Estimating α from an empirical relative abundance distribution, however, depends only on S (the total number of species) and N (the total number individuals) but nevertheless requires substantial computation because iterative methods must be used. Fisher's α is relatively insensitive to rare species, and the relative abundance distribution need not be distributed as a log-series.

5. THE SPATIAL ORGANIZATION OF BIODIVERSITY

Imagine walking through a forest into a grassland or snorkeling across a coral reef beyond the reef edge toward the open sea. The testimony of our own eyes confirms that the biosphere is not organized as a set of smooth continua in space but rather as a complex

“biotic mosaic” of variably discontinuous assemblages of species. On land, the discontinuities are driven in the shorter term by topography, soils, hydrology, recent disturbance history, dispersal limitation, species interactions, and human land use patterns, and in the longer term and at greater spatial scales by climate and Earth history. The same or analogous factors structure biodiversity in the sea.

If you were to keep track of the plant or bird species encountered, in the form of a species accumulation curve, during a long walk in a forest followed by a long walk in an adjacent grassland, the curve would first rise quickly, as the common forest species were recorded, leveling off (if the walk is long enough) as the rarest forest species are finally included. The number of species accumulated at that point (or a species diversity index computed for the accumulated data) is called the α diversity (or local diversity) for a habitat or community, a concept originated by R. H. Whittaker. (Note that α diversity has nothing to do with Fisher's α , in terms of the names, although the latter may be used as one measure of the former.) As you leave the forest and enter the grassland, the curve will rise steeply again, as common grassland species are added to the list. Once rarer grassland species are finally included, the curve begins to level off at a new plateau. The increment in total species (or the change in a diversity index) caused by the change in habitat is one measure of β diversity, in Whittaker's terminology (sometimes called *differentiation diversity*), although there are many ways to quantify β diversity and little agreement about which is best. The total richness or diversity for both habitats combined (the second plateau in the species accumulation curve) is the γ diversity (regional diversity) for this hypothetical forest-grassland landscape.

The forest-to-grassland example presents a classic illustration of β diversity, as originally conceived by Whittaker, but the concept has been generalized to include spatial differentiation of biotas within large expanses of continuous, environmentally undifferentiated habitat as well as between isolated patches of similar habitat. Within expanses of homogeneous habitat, β diversity is usually considered to be the result of *dispersal limitation*—the failure of propagules (fruits, seeds, juveniles, dispersive larval stages, migrants, etc.) to mix homogeneously over the habitat—but in practice, it is often hard to rule out subtle differences in environment as a cause of biotic differentiation.

6. ESTIMATING β AND γ DIVERSITY FROM SAMPLES

Estimating β or γ diversity for a region or landscape, from samples, is a daunting prospect for any but the

best-known groups of organisms. Over larger spatial or climatic scales, the “patches” of the mosaic can be better viewed as ordered along gradients, in either physical or multivariate environmental space. Unfortunately, the geometry of the biotic mosaic is remarkably idiosyncratic (although it may be properly *fractal* for some organisms at some scales), which means that designing a scheme for estimating richness at large spatial scales is likely to require many ad hoc decisions—it is more like designing trousers for an elephant than finding yourself a hat that fits.

A common approach to coping with idiosyncratic biotic patterns is to take advantage of biotic discontinuities to define “patch types” in the mosaic for sampling purposes. For example, the vegetation of treefalls in a forest might be distinguished from the riparian (streamside) vegetation and from the mature forest matrix. Or the fish fauna of isolated patch reefs might be distinguished from the fish fauna of fringing reefs. An alternative is to select sampling sites along explicit gradients, such as elevational transects on land or depth and substrate gradients in the sea. Both strategies represent forms of stratified sampling in which the strata are the patch types or gradient sites, and multiple samples within them are treated as approximate replicates, meaning, in practice, that samples within patch types or gradient sites are expected to be more similar than samples from different types or sites.

Any particular definition of patch types and the scale that underlies them is inevitably somewhat arbitrary. A seemingly less arbitrary alternative would be spatially random sampling over the entire region of interest, analyzed using a multivariate approach to assess the relationship of richness and species composition to underlying environmental and historical factors. But, given limited resources (are they ever otherwise?), random sampling over heterogeneous domains is often highly inefficient because of the uneven relative abundance of patch types: the biota of common patch types are oversampled compared to the biota of rarer patch types, which may even be missed entirely. If one accepts a within- and between-patch-type design framework, the definition of patch types (or sample spacing on gradients) is best made at the design phase based on expert advice and whatever prior data exist, with the possibility of later iterative adjustment.

Although comparisons of α diversity among patch types by rarefaction are interesting in their own right, they fail to provide the information needed to estimate γ diversity because some species are likely to be shared among patch types and some species may be missed by the sampling in all patch types. If we had full knowledge of the biota (complete species lists) for all patch

types within a region, it would be simple to determine the total biota for two, three, . . . all types combined, computing some measure of (average or pair-specific) β richness (species turnover) along the way. For sampling data, the problem is much more difficult. Undetected species within patch types are not only undetected, they are unidentified, so that that we do not know whether the same or different species remain undetected in different patch types.

Nonetheless, it is possible in principle to estimate lower and upper bounds for γ (regional) richness. The union of detected species lists for all patch types, pooled, provides a lower-bound estimate of total domain richness, on the assumption that every species undetected in one patch type is detected in at least one other patch type. The sum of total richness estimates over all patch types (including undetected species from each patch type, using nonparametric estimators or extrapolation techniques), adjusted for the number of observed shared species, is an approximate upper-bound estimate of total regional richness, assuming that undetected species included in the estimates are entirely different for each patch type and were detected in none.

The truth inevitably lies between these bounds, for data from nature. To estimate the true regional richness, we need information about the true pattern of shared species among patch types. Statistical tools for estimating the true number of species shared by two sample sets, including species undetected in one or both sets, are scarce, and this is an area in which much more work is needed. Many studies have attempted to address the problem of estimating β diversity, or pooling samples (between patch types or random samples) by using similarity indices, such as the Sørensen or Jaccard indices. Unfortunately, the number of observed, shared species is almost always an underestimate of the true number of shared species because of the undersampling of rare species. This means that species lists based on samples generally appear proportionally more distinct than they ought to be, similarity indices are routinely biased downward, and slope estimates for the decline in similarity with distance (“distance decay of similarity”) are likely to be overestimated. Recently, A. Chao and others have developed estimation-based similarity indices that greatly reduce undersampling bias and promise to help correct this longstanding dilemma. These indices are based on the probability that two randomly chosen individuals, one from each of two samples, both belong to species shared by both samples (but not necessarily to the same shared species). The estimators for these indices take into account the contribution to the true value of this probability made by species actually present at both sites but not detected in one or both samples.

7. SPECIES-AREA RELATIONS

Ecologists and biogeographers have long documented a striking regularity in the pattern of increase in the species count as larger and larger geographic areas are considered. When the number of species or its logarithm (depending on the case) is plotted against the logarithm of area, an approximately linear relationship is revealed. With either plot (a log-log power curve or a semilog exponential curve), the pattern on arithmetic axes is a decelerating but ever-increasing number of species as area increases. This pattern, known as the species-area relation (SAR), has been called one of the few universal patterns in ecology, but its causes are not simple.

There are many variants on SARs, but the primary dichotomy separates plots based on nested sampling schemes from plots in which the areas of increasing size are distinct places, such as islands in lakes or seas, habitat islands on land, or simply political units (states, countries) of different areas. There are two important causes for the increase in species count with increasing area. The first cause is undersampling. Especially in the case of nested sampling schemes, in which smaller areas lie within larger ones, the smaller units may be too small or too poorly sampled to reveal all species characteristic of the habitat(s) they represent. In this case, the supposed SAR for the smaller areas is better described as a species accumulation curve or rarefaction curve. B. D. Coleman and colleagues pointed out that, even for a completely homogeneous species pool, larger areas will have more species because they contain more individuals; the model they proposed is virtually indistinguishable from a rarefaction curve.

The second cause of increasing species count with area is β diversity, in all its varieties. (1) Within large expanses of homogeneous habitat, species composition may vary spatially simply because of dispersal limita-

tion, so that larger areas contain more species. (2) Larger areas are more likely to include a greater number of habitat types or ecoregions, each with its own distinct or partially distinct biota. (3) For very large areas, on continental scales, ecologically similar biotas may have very different evolutionary histories. For example, the lizard fauna of coastal Chile and coastal California share many ecological similarities but have no species (or even genera) in common. Such cases could be viewed as an extreme form of dispersal limitation, as we discover to our dismay when alien species from similar biomes on other continents become local invasives (e.g., California poppy, *Eschscholzia californica*, in Chile, and the Chilean ice plant, *Carpobrotus chilensis*, in California).

FURTHER READING

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