Primer

Biological diversity

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Cave paintings attest to our species' enduring interest in biological diversity. Our early ancestors appear to have enjoyed the aesthetic qualities of nature as well as recognising its importance as a source of food and fuel. Poets and artists throughout history have sought inspiration from the natural world. But the first scientific enquiries about biological diversity emerged when explorers returned with descriptions of sharp contrasts in the variety and number of plants and animals in different parts of the globe. Baron von Humbolt, who travelled in South and Central America between 1799 and 1804, asked why more species are found in tropical regions than in temperate zones. The question he posed continues to be fiercely debated and his answer — climate — remains one of several plausible explanations. A second pervasive pattern, which ecologists also still struggle to fully understand, is the species–area relationship. Early Victorian naturalists first noted that more species are found in larger areas. It turns out that every tenfold increase in area leads, approximately, to a doubling in the number of species harboured.

This two-pronged approach of describing patterns of biological diversity, and then endeavouring to understand the reasons why the composition and variety of the biota varies from place to place, remains popular. But the threat of unprecedented rates of species extinction has added new urgency and led to a surge of interest in the function of biological diversity, particularly in terms of the services provided to humankind, and in its conservation.

Although the concept of biological diversity has a venerable history, the term itself is of surprisingly recent origin and first entered the scientific literature in the 1950s. Its more widely used contraction, biodiversity, came to prominence after being adopted as the title of E.O. Wilson's influential 1988 book. Biological diversity is simply the variety and abundance of organisms at a given place and time. The Convention on Biological Diversity (CBD) definition is often cited: "'Biological diversity' means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems."

Defining biological diversity may be straightforward, but measuring it is not. The different organisational levels embodied in the CBD definition need to be tackled in different ways. Within species diversity, for example, can be measured using molecular methods — DNA microarray technology is one approach that is proving increasingly invaluable here. At the other end of the scale, ecosystems are usually evaluated in terms of the numbers of species, or endemics, they support.

Setting aside the difficulties of delineating ecosystems, and defining species — a non trivial issue for many asexual and prokaryote organisms — surveying large areas can be a Herculean task, particularly where invertebrates are involved. In practice, most of the interest in biodiversity measurement has been directed at the CBD's between-species category. This is the type of biological diversity under investigation when farm trials of genetically modified crops are conducted to evaluate their effects on wildlife, or when the bird faunas of, say, oak wood and pine forest are compared.

It is a universal characteristic of ecological communities that some species are extremely abundant, others only moderately common and the remainder, often the majority, rare. This means that community diversity can be partitioned into two components: species richness (the number of species present), and species evenness (the distribution of species' relative abundances). Biological diversity is obviously linked to species richness. But diversity is also assumed to increase as assemblages become more even (Figure 1). This is a meaningful assumption, as it appears that the ability of an assemblage to resist change or recover from a perturbation is related to its evenness as well as to its richness. It also means that diversity can be described in many different ways. Some investigators opt for estimates of species richness. Although these are intuitively easy to understand, because the number of recorded species is correlated with sampling intensity, as well as with
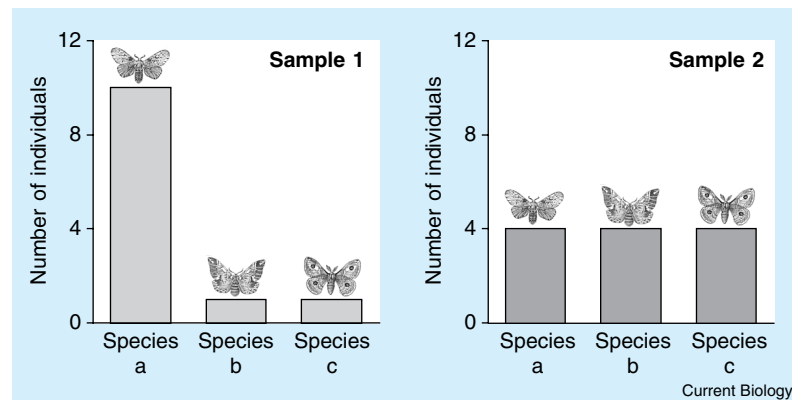

Figure 1. Evenness and diversity.
These two samples of moths have the same number of species (three) and individuals (twelve), but the greater evenness in species abundances in sample 2 means that it would be considered more diverse.

the size of the area investigated and the duration, in time, of the survey, such measures can be subject to considerable bias. Sampled species richness may underestimate true species richness by a large margin. Fortunately, there are statistical tools to help overcome these problems.

Alternatively, it is possible to fit a species abundance distribution and use one of its parameters to describe community diversity. Ronald Fisher, an early champion of this approach, introduced the log series model in 1943. The log series describes a situation where there is a preponderance of rare species; its parameter α is a robust and meaningful diversity statistic. Other models offer different insights into community structure. The log normal model, for instance, typically provides a good fit to large and heterogenous assemblages, particularly of their core (non-vagrant) species.

One reason why no single model fits all communities is simply that ecologists have different working definitions of assemblages. Some researchers focus on tightly defined taxonomic and trophic groupings, such as the ant fauna in a grassland, whereas others are interested in broader collections, such as Amazonian fishes. Ecological processes, however, could also account for observed variations in species abundance. Robert MacArthur's innovative broken-stick model represented one of the first attempts to predict the likely distribution of abundances should resources be divided amongst species in certain ways. Stephen Hubbell's 'unified neutral model' is a recent, if controversial, attempt to understand the mechanistic basis of biodiversity. It assumes that all species have the same demographic properties and that species abundances in local communities reflect, to an extent that depends on migration rate, the structure of the regional assemblage. There is still considerable scope for the development of biological process models.

The final approach, an index combining elements of richness and evenness, is the most popular method of diversity measurement. These so-called 'heterogeneity measures' have found particular application in environmental management and in monitoring the consequences of anthropogenic change. A large number of such measures exist. As diversity measures vary in the relative weight they place on richness and evenness, inconsistent rankings of diversity may result. A practical implication of this is that users need to be careful to ensure that diversity is being measured in comparable ways. Diversity indexes, such as the popular Shannon and Simpson measures shown in Box 1, are sometimes described as non-parametric, in the sense that they are not parameters of fitted models. However, the underlying distribution of species abundances will influence the value of a diversity measure, and its ability to discriminate between sites.

It is human nature to value some organisms more highly than others. Birds and mammals have wide appeal, insects and nematodes fewer advocates. The conservation literature reflects this bias with 69% of papers devoted to vertebrates — a group that accounts for a mere 3% of species in nature. We also attach greater significance to unusual or emblematic animals and plants than we do to the commonplace ones. Conventional diversity statistics make no distinction between species, other than to take heed of their relative abundances, but there is growing interest in techniques that capture some of these valued attributes. For example, measures of phylogenetic diversity can be used to identify species of special conservation interest or to measure the pattern of relatedness in a sample. In the latter case, a sample with six species belonging to a single genus would be deemed less diverse than one with six species all from different families — a pattern that accords with human perceptions of diversity. A similar approach can be used to estimate the functional diversity of an assemblage. Here, variety of traits, rather than taxonomic status, is assessed.

It is crucial to be able to measure biodiversity, both because of its significance to human life on earth, and because species are being lost at accelerating rates. Biological diversity underpins human civilisation in multiple ways. Not only do we receive direct benefits in the form of fuel, pharmaceuticals, pollination, crops and wild harvests, but we also depend on its contribution to nutrient cycles, climate regulation and soil formation. Economists have estimated the financial value of ecosystem goods and services to be on a par with the total gross national product of the world. Ecosystem function is related to biodiversity in numerous and sometimes complex ways; indeed, this topic is currently the target of intense research activity. Like so much else in ecology and evolution, these ideas can be

traced back to Charles Darwin. *The Origin of Species* describes an early 19th century experiment showing that grasslands composed of several species are more productive than monocultures. Other benefits of biodiversity are less easy to quantify but also irreplaceable. Many people gain a great deal of pleasure from what Charles Elton termed 'wild beauty'. The case can also be made that biodiversity has intrinsic value and warrants preservation for its inherent worth alone.

Despite these diverse benefits, the total number of species that share the planet with us is unknown to within an order of magnitude. Mammals and birds, and to a lesser extent fish, reptiles, amphibians and flowering plants, are generally well catalogued. Even so, new species regularly turn up in well-studied taxa. Over 10 monkey species have been described in Brazil since 1990, and a similar number of lemur species have been found in Madagascar over the same period. About 10,000 new species across all taxa are recorded per year. In total, records exist for about 1.5 million species, though this number is uncertain, because details are distributed across many databases and in some cases the same species is tallied under two or more separate names or synonyms.

What is certain is that the number of documented species underestimates the actual number by a considerable margin, and that most of the species unknown to science are invertebrates. A variety of approaches have been used to deduce the total. Detailed surveys of hitherto unexplored habitats are one approach; inferences based on the ratios between well-documented and poorly studied taxa another. Estimates range from 5 to 100 million species. However, there is reason to believe that the true number is in the region of 10 million. This is because figures at the higher end of the range depend on extrapolations utilising data on tropical forest beetles and marine nematodes, and hinge on assumptions about the specificity of the fauna. Although individual tropical tree species support a diverse range of beetles, a large proportion of these beetles probably also occur on other species. Similarly, although there is high nematode richness in small areas of the sea bed, many of these species are cosmopolitan and have large ranges.

It is often said that we are in the midst of the 6th mass extinction the earth has experienced. Unlike its five predecessors, including the dinosaur extermination in the late Cretaceous, the present situation is attributable to a single species — ourselves. Introductions of exotic species, loss of habitat, overexploitation and reinforcing interactions between these processes — Jared Diamond's 'evil quartet' — are responsible for this unfortunate situation. Uncertainty about global species richness makes it difficult to estimate, with any degree of confidence, exactly how many species will go extinct.

The rate at which species are being lost can, however, be deduced by several independent methods that provide a consistent, if depressing, picture. For example the species area 'rule', mentioned in the introductory paragraph, can be used to estimate the rate of species loss due to habitat destruction. Estimates of tropical deforestation are typically in the region of 1–2% per annum. This means that between 0.25% and 0.5% of the species that depend on these habitats will be committed to extinction each year.

Alternatively, the International Union for the Conservation of Nature and Natural Resources (IUCN) 'red lists' of species at risk can be used to infer the proportions of extant species expected to go extinct within the foreseeable future. Its most recent census (November 2004) revealed 15,589 species to be in a perilous position. Around 15–20% of species in a range of vertebrate taxa appear likely to become extinct within the next century. The assumption must be that the less charismatic and well-studied groups share this fate. To this end the World Summit on Sustainable Development, which met in Johannesburg in 2002, agreed to aim for a reduction in the current rate of loss of biological diversity by 2010. More effective sampling strategies and a deeper understanding of the role that biological diversity plays in the functioning of ecosystems will play a crucial part in achieving that goal.

There is growing interest in the search for planets in the 'habitable zone' of stars, that is, planets with the potential to support life. One question that arises is how life began; the Huygens mission to Saturn's moon Titan, which is thought to resemble the Earth as it was about 4.5 billion years ago, may shed light on that. But if life is ever detected in other solar systems, attention will probably switch to ecological issues. It would be fascinating to discover whether the pattern of relative abundance, the species–area relationships and latitudinal gradients in diversity we are familiar with here on Earth are replicated elsewhere in the Universe.

Further reading
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  http://viceroy.eeb.uconn.edu/esti-mates (Software for biodiversity estimation).
  http://www.nature.com/nature/insights/6783.html (Nature 'insight' into biodiversity).

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