

## Primer

# Measuring biological diversity

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As prehistoric cave paintings illustrate, our species has had an enduring appreciation of the variety and abundance of life on Earth. Today, however, concern is focused on the pressure humanity is placing on the natural world, and on the continued ability of ecosystems to deliver the services on which we all depend. To understand the extent of this 'biodiversity crisis' and develop strategies to ameliorate its impact, it is essential to be able to accurately measure biological diversity (a term often contracted to biodiversity) and make informed predictions about how and why this diversity varies over space and time.

Our perception of what constitutes a natural landscape, and of the types of species that are found there, is directly influenced by our own experience, however. For example, the polymath Mary Sommerville talks in her autobiography of watching great shoals of herring and 'whales spouting in every direction' in the Firth of Forth in Scotland, while she was growing up there in the late 1700s. Scottish children today will have no similar memories. The fishing industry that exploited the herring in the Forth has long since collapsed and the whales that once fed on these fish are now a rare sight. This phenomenon has been dubbed a 'shifting baseline' by Daniel Pauly. It highlights the need for reliable quantitative data to track shifts in biological diversity over space and time and for ecologically meaningful metrics and models with which to analyse these data. This primer begins by exploring the historical roots of biodiversity measurement and then examines the diversity of approaches that are currently employed to quantify biodiversity change over space and time. It concludes by discussing the importance of taking account of the different facets and dimensions of biodiversity in both academic research and in conservation management.

## The origin of biodiversity measurement

Charles Darwin's 1855 survey of plants in Great Pucklands meadow (Figure 1), beside his house at Downe in southern England, was probably the first quantitative biodiversity assessment, where biodiversity is defined as the taxa that co-occur at a given place and time. This objective approach to recording nature was the foundation of his groundbreaking insights into natural selection. What is less well remembered is that Darwin also made fundamental contributions to ecology through his novel ideas on the processes that shape patterns of diversity. For example, in his *Origin of Species*, Darwin notes that even slight changes in climate will favour some taxa at the expense of others and lead to compositional change over time. However, it was not until the 20th century that systematic surveys of biodiversity became commonplace and made the formal evaluation of biodiversity change possible. These datasets, which invariably revealed a few dominant taxa alongside many rare species, required new statistical methods — a challenge taken up in the 1930s and 1940s by Isao Motomura in Japan, Ronald Fisher in England and Frank Preston in the US, and one that remains an active research front today. The goal of these methods is to provide a meaningful statistical overview — known as a species abundance distribution — of the pattern of commonness and rarity that characterises biodiversity datasets. Different models of species abundance, such as Preston's log normal and Fisher's log series, depict different scenarios of the relative abundance of species in relation to the size and structure of an assemblage. In this context, size is the number of species present together with their total abundance, and structure includes the evenness of relative abundance, the fraction of rare taxa and the presence of one or more modes in the distribution (Figure 2). Species abundance distributions thus capture the ways in which species abundances vary between ecological communities, and shed light on the processes that govern these patterns.



**Figure 1. Great Pucklands meadow.**

Darwin surveyed the biodiversity of this meadow beside his home at Down House, Kent, England, in 1855. (Photo: © Historic England Photo Library.)

Broadly speaking, ecological theory distinguishes between biological drivers of these abundance patterns (such as the competition for niche space, and adaptations to the local environment) and neutral theory, which treats species as ecologically equivalent and makes predictions based on the prevalence of stochastic events, such as death, and immigration from a species pool. In practice, both biology and random chance are likely to play a role in influencing the relative abundance of species in an assemblage. In addition, as Bob May noted, an important challenge is to disentangle attributes that reflect ecological mechanisms from the statistical consequences of large numbers. This multipronged view of species abundance distributions is important because it enables researchers to go beyond description and develop null expectations against which predictions can be tested.

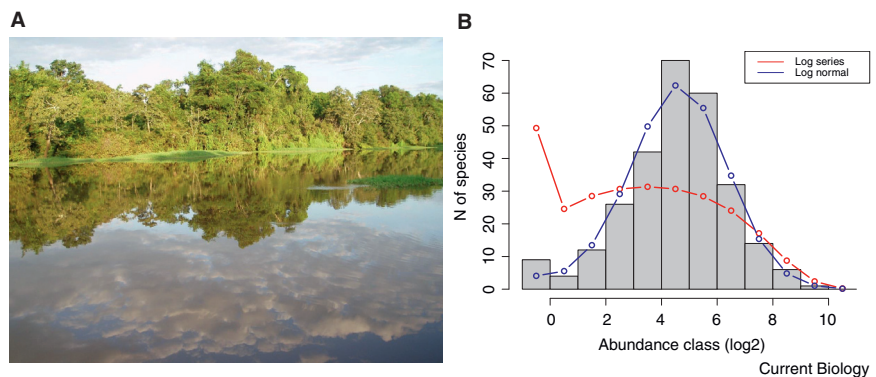
## The biodiversity measurement toolkit

Researchers who investigate trends in biodiversity often rely on synoptic measures that capture features of species abundance distributions.

There is now a large library of such measures drawing on a range of statistical approaches, including some developed by Alan Turing for code-breaking purposes during the Second World War. In essence, these biodiversity metrics ‘turn the dial’ on the weight that relative species abundance has on the resulting measure. For example, an investigator can count the number of species present (usually called species richness), or quantify the fraction of total abundance accounted for by the dominant species, or adopt an intermediate metric that takes both richness and relative abundance into account. In a seminal paper published in 1973, Mark Hill observed that several widely used diversity metrics can be placed in the same statistical framework, which means that measures putting different weight on relative abundance can be expressed in comparable measurement units. This framework is known as ‘Hill numbers’, with Hill (number) 0 being species richness, Hill 1 the exponential form of Shannon diversity, and Hill 2 the reciprocal form of Simpson diversity (itself a form of the probability of interspecific encounter, PIE). Simpson diversity reflects the extent to which an assemblage is dominated by one or a few species; as such it measures a feature of assemblages that is the obverse of assemblage evenness.

### Compositional change

Many investigations quantify shifts in the shape of the species abundance distribution, and/or in one or more of the metrics of diversity that summarise aspects of this distribution, when comparing, for example, exploited and protected woodlands. However, these woodlands might have similar numbers of species and comparable species abundance distributions, yet contain different species assemblages. An analysis that ignored species composition could miss important differences, such as variation in the numbers of native or specialist taxa. Shifts in composition are thus an equally important, but alternative facet of diversity. Measures such as Jaccard (presence/absence data) or Bray Curtis (quantitative data), which make pairwise comparisons



**Figure 2. The species abundance distribution of fish in the flooded forest in Mamirauá Reserve in the Brazilian Amazon.**

(A) The flooded forest. (Photo: Anne Magurran.) (B) Species are assigned to  $\log_2$  abundance classes (representing doubling of abundances). The predicted relative abundances of the log series and log normal models are shown; the latter is clearly the better fit in this assemblage as it predicts fewer low abundance taxa than the log series. (Data taken from Hercos, A.P., Sobansky, M., Queiroz, H.L., and Magurran, A.E. (2013). Local and regional rarity in a diverse tropical fish assemblage. *Proc. R. Soc. B Biol. Sci.* 280, 20122076.)

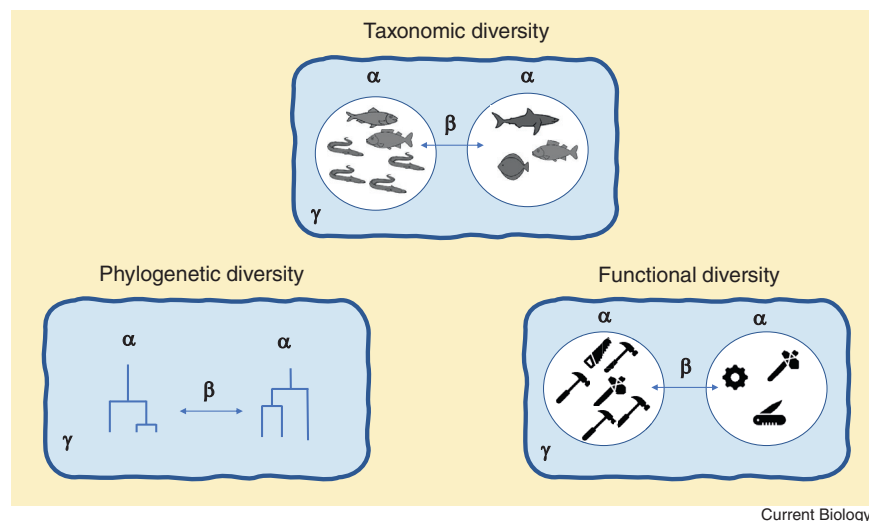
of the (dis)similarity of samples, represent one commonly used approach and can be used to track compositional shifts between sites, as well as along a time series or gradient. Robert Whittaker described these two complementary facets of biodiversity as alpha ( $\alpha$ ) and beta ( $\beta$ ) diversity, with alpha diversity referring to the ‘level’ of diversity (such as species richness, or the value of Simpson diversity) in a focal study site, and beta diversity as compositional differences between these study units of alpha diversity. He further pointed out that gamma ( $\gamma$ ) diversity is the overall diversity of the wider landscape within which alpha and beta diversity are investigated (Figure 3).

### Sampling matters

One of the challenges in biodiversity measurement is that the ‘amount’ of diversity detected tends to increase with sampling effort. Thus, if a site is studied for longer, or a wider area is surveyed, more species are likely to be encountered. This phenomenon has methodological implications for researchers, particularly as most diversity metrics do not scale linearly with area or time — in other words, the chances of two individuals belonging to the same species will be affected by the spatial extent or time window of a study. Fortunately, there is an effective statistical toolkit, developed by Anne Chao and others, that enables researchers to

make fair comparisons in studies in which sampling effort varies. This uses a technique called rarefaction/extrapolation and makes it possible to estimate the value of diversity metrics at a standardised sampling effort.

There are also important differences in how biodiversity change plays out at local, regional and global scales. For example, species extinctions are increasing at a planetary level, leading to a net loss in the Earth’s biodiversity, but local ecological communities may gain species, including non-native ones as well as species responsive to local climatic shifts. This is the sort of reshuffling of species abundances and identities that Darwin predicted. Moreover, rapid changes in temporal beta diversity at a local level can occur alongside homogenisation of composition within a region, as illustrated, for example, by changes in marine fish communities in the northeastern Atlantic. In recent years the same taxa are common throughout the seas to the west of Scotland, whereas a few decades ago assemblages in the northern and southern latitudinal bands were more distinct. Drivers such as warming or habitat transformation can foster this homogenisation, which is sometimes dubbed ‘the shopping mall’ effect because it mirrors the loss of variety in retail outlets in shopping centres around the world in recent years.



**Figure 3.  $\alpha$ ,  $\beta$ ,  $\gamma$  diversity.**

The three dimensions of diversity — taxonomic, phylogenetic and functional diversity — can be viewed in the same  $\alpha$ ,  $\beta$ ,  $\gamma$  framework in which  $\alpha$  diversity is the diversity of a site or other study unit,  $\beta$  diversity the ‘compositional’ difference of these sites, and  $\gamma$  diversity the diversity of all the sites in the entire wider assemblage. Analogous metrics can be used to quantify the facets of these different dimensions of diversity. For example, it is possible to quantify richness (a metric of  $\alpha$  diversity) of taxa, phylogenetic trees, or traits, and to evaluate the difference or divergence between sites ( $\beta$  diversity) in each of the three dimensions of diversity.

### Taxonomy, traits and trees

Historically, most of the emphasis has been on ‘taxonomic’ diversity, that is diversity in the identities of species, classified, for example, by a Linnaean taxonomy that uses a binomial nomenclature for naming taxa. There are other ways of categorising organisms, however, and substantial advances have been made in approaches that quantify biodiversity from the perspective of diversity in the types of trait that organisms exhibit, and/or in respect of their placement, relative to one another, in a phylogenetic tree. Although these approaches focus on different properties of the taxon of interest, they can all be viewed from the perspective of alpha, beta, and gamma diversity (Figure 3) with measures expressed in terms of equivalent concepts such as richness, evenness and turnover. There is a growing toolkit of computational approaches for quantifying trait and phylogenetic diversity. A recent innovation, again led by Anne Chao, has been to build an integrative approach to biodiversity measurement that brings together taxonomic, trait and phylogenetic diversities and expresses them in comparable units

within the context of the Hill number framework.

One context in which these approaches are increasingly being applied is in the investigation of microbial systems. Fuelled by advances in molecular technology it is now evident that microorganisms are highly diverse and play critical roles in supporting the Earth’s ecosystems. In our own species, a diverse microbiome is viewed as an essential component of good health. Like fish in the Amazon’s flooded forest, the diversity of these taxa is quantified in the framework of alpha, beta and gamma diversity, and techniques such as rarefaction are adopted here as well to ensure that sampling effects do not lead to misleading results.

Richard Southwood first remarked on the diversity of diversity metrics in his classic *Ecological Methods* textbook. Increased computational power, new methodological approaches, and the era of ‘big data’ have extended the scope of earlier understanding of variation in biodiversity over space and time, while reinforcing the importance of the alpha/beta/gamma perspective when interpreting these patterns. For instance, analyses of biodiversity

change in local assemblages across the globe have reported no net shift in species richness but marked change in species composition, which has the potential to begin to alter ecosystem functioning and may be an important early warning signal of widespread ecosystem restructuring.

### Challenges in measurement and reporting

At the same time, these insights are nuanced and can be complex to interpret, and as such raise substantial challenges for managers and policymakers. There is broad consensus that the world’s biodiversity is imperilled, yet in contrast to the debate on climate change, where the focus is on a single target, biodiversity is quantified using a range of approaches, the relevance of each being the context in which it is used. It is a little like measuring an elephant, and having to decide whether trunk length, or skin colour, or weight, or mitochondrial DNA, or its microbiome, or social status should be used to provide the best summary metric.

Although many of the concerns about the biodiversity crisis have been voiced in terms of biodiversity loss, ‘loss’ needs to be qualified by the spatial and temporal scale of the assessment and by the composition of the taxa involved. Measures that track alpha diversity tell only part of the story. Compositional change — temporal beta diversity — appears to precede change in alpha diversity, yet is harder to explain to non-specialist audiences given the limited availability of accessible synoptic measures. In both cases there are choices to be made about baselines. Should current trends be interpreted in relation to patterns from a few decades ago, or from Darwin’s or Somerville’s time? In practice, because quantitative biodiversity data are generally only available for periods of decades rather than centuries, analyses tend to focus on recent change, although historical records, reconstructed assemblages, and examination of palaeoecological communities can provide informative benchmarks. The popular narrative of biodiversity change also places a lot of weight



on 'regime shift' or step change in assemblage structure and function, but is it the case that gradual reorganisation of systems is a much more widespread phenomenon than abrupt change? There are still many unresolved issues in the quantification and interpretation of biodiversity change.

It is not just temporal data that are patchy. A further difficulty is that assessments of biodiversity change are thwarted by data gaps, with rich tropical areas and invertebrate assemblages being particularly underrepresented in biodiversity databases. New technological innovations, including sampling of environmental DNA (eDNA), remote sensing, networks of camera traps and sensors, and acoustic surveys have the potential to fill these gaps and automate sampling and analyses. A non-trivial challenge will be to provide continuity with existing biodiversity time series collected using traditional methods and to interpret change in the alpha/beta/gamma framework that underpins all biodiversity measurement. It is also important to report uncertainty in assessments of biodiversity change. The IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, [www.ipbes.net](http://www.ipbes.net)) does this by stating whether trends are 'well-established', 'established but incomplete', or 'inconclusive'.

### Looking ahead

Protecting the world's ecosystems over decades to come is a formidable challenge, but from the perspective of the measurement of biodiversity there are some encouraging developments. Data gaps will increasingly be resolved; the IPBES 2030 Work Programme has as one of its objectives the strengthening of the knowledge base on which its assessments are made, and it will be supported in this venture by emerging technologies. Citizen science will also play a growing role in this endeavour. Ecological theory can still only incompletely predict the consequences for ecosystem structure and function of the current rapid reconfiguration of natural systems, but this is an important research focus with exciting developments on the horizon.

New additions to the biodiversity measurement toolkit will increase the precision and information content of assessments of biodiversity change. Better reporting of these biodiversity metrics to reflect the different facets and scaling properties of biodiversity trends will support conservation efforts. A more nuanced view of how this biodiversity change plays out will also reinforce the message that, while it is right to be gravely concerned about the fate of our planet's ecosystems, we can still act to safeguard Darwin's 'endless forms most beautiful and most wonderful' for generations to come.

### FURTHER READING

- BioTIME database of assemblage time series, <https://biotime.st-andrews.ac.uk>.  
Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., and Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84, 45–67.  
Das Gupta Review (Economics of Biodiversity), [www.gov.uk/government/publications/final-report-the-economics-of-biodiversity-the-dasgupta-review](http://www.gov.uk/government/publications/final-report-the-economics-of-biodiversity-the-dasgupta-review).  
Diaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., et al. (2016). The global spectrum of plant form and function. *Nature* 529, 167–171.  
Dornelas, M., Gotelli, N.J., McGill, B.J., Shimadzu, H., Moyes, F., Sievers, C., and Magurran A.E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299.  
GBIF—the Global Biodiversity Information Facility, [www.gbif.org](http://www.gbif.org).  
Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, <https://www.ipbes.net/>.  
Living Planet Index, [www.livingplanetindex.org](http://www.livingplanetindex.org).  
Magurran, A.E., Dornelas, M., Moyes, F., Gotelli, N.J., and McGill, B. (2015). Rapid biotic homogenization of marine fish communities. *Nat. Commun.* 6, 8405.  
PREDICTS — Projecting Responses of Ecological Diversity In Changing Terrestrial Systems, [www.predicts.org.uk](http://www.predicts.org.uk).  
Sala, E., Mayorga, J., Bradley, D., Cabral, R.B., Atwood, T.B., Auber, A., Cheung, W., Costello, C., Ferretti, F., Friedlander, A.M., et al. (2021). Protecting the global ocean for biodiversity, food and climate. *Nature* 592, 397–402.  
The Convention of Biological Diversity, [www.cbd.int/convention/](http://www.cbd.int/convention/).  
Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A., Grenyer, R., Helmus, M.R., Jin, L.S., Mooers, A.O., et al. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol. Rev.* 92, 698–715.

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## Primer

# Phylogenomics

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The reconstruction of evolutionary relationships among species is fundamental for our understanding of biodiversity. Today, evolutionary relationships are closely related with the depiction of the tree of life, and research on the topic is underpinned by methods in molecular phylogenetics that have grown in popularity since the 1960s. These methods depend on our understanding of how nucleotide or amino acid sequences evolve through time and in different lineages. Armed with this knowledge, researchers can make inferences about the relationships and amount of genomic divergence among species.

The term 'phylogenomics' is primarily used to refer to an extension to phylogenetics that considers not only evolution of nucleotides or amino acids, but also broader processes acting on whole genomes. A dominant simplifying assumption in the field is that genomes are made up of segments that are to some degree independent, including in their evolutionary history. Examining several hundreds or thousands of genomic loci is becoming routine in the biological sciences. However, this has only been possible in the past two decades, with the increasing availability of genome-scale sequencing techniques.

An early insight from phylogenomics that has dominated debate in the field is that genomic regions are very different in terms of the information they contain about evolutionary history. It is common for phylogenomic studies to find that, among thousands of loci, every one has its own individual historical signal. Due to such striking differences in signals across genomic regions, it has become standard to distinguish the evolutionary trees showing the history of individual regions, often called 'gene trees', versus the tree representing the history of all of the genomic regions combined, or 'species tree'.

The data sets used in phylogenomics allow biologists to address questions in a wide variety of fields, such as taxonomy, population genetics, comparative biology and molecular

