Biodiversity may wax or wane depending on metrics or taxa

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Biodiversity changes have proven surprisingly complex to estimate and understand. While there are negative trends at a global scale such as the substantial losses of vertebrate species (1), changes at local scales may show large variation, with no clear overall trend (2, 3). Because assessing and improving the status of biodiversity are at the core of international agreements such as the Convention on Biological Diversity and the associated Aichi Biodiversity Targets for 2020 (4), we need to know when trends in biodiversity may differ and the causes of such differences. In PNAS, Magurran et al. (5) report that different components of biodiversity do not have the same trends over time in tropical freshwater ecosystems, and that these trends differ among taxonomic groups (fishes, invertebrates, and diatoms).

Magurran et al. (5) quantify biodiversity changes at 16 river sites in Trinidad over 19 time points covering the dry and wet seasons of 5 y. They collected over 670,000 individuals, which were identified at different resolutions in fishes (species), invertebrates (family), and diatoms (morphospecies) because taxonomy is still poorly known for many groups in the tropics. They focus on two aspects of biodiversity changes: temporal α diversity, measured using the number of species and functions of their relative abundance, and temporal β diversity, which represents change in assemblage composition over time and is measured as turnover in species identities and relative abundance (Fig. 1). Different diversity measures emphasize different characteristics of assemblages (6). Magurran et al. (5) use 11 metrics, ranging from the number of observed or estimated species at a site and metrics emphasizing evenness or dominance to a range of (dis)similarity measures to evaluate compositional differences between assemblages. These are based on either presence/absence or abundance data and emphasize turnover in species identities (species replacement) and nestedness [associated with richness change (7)]. In this tropical ecosystem, Magurran et al. (5) regard situations where α diversity declines or where compositional dissimilarity increases (change in temporal β diversity) as unfavorable. Most time series did not show evidence for a systematic change in α diversity, whereas trends in temporal β diversity were more variable and differed among taxonomic groups. The numbers of sites exhibiting statistically significant change in α diversity were two, one, and zero, respectively, for fish, invertebrates, and diatoms, whereas for β diversity, the numbers were two, two, and five sites, respectively.

The study by Magurran et al. (5) highlights that while species turnover may be high and change, the number of species or the relative species dominance within an assemblage may not show significant changes. Temporal variability of α diversity may be represented as bounded fluctuations around some equilibrium value, as when one defines population regulation as fluctuations in numbers of individuals around so-called "carrying capacity." Evidence for such regulation of one diversity dimension exists for a wide set of plant and animal assemblages, given, of course, that major disturbances such as land use transformation are excluded (8). As for population regulation, this implies a negative covariation among species fates (considering species extinction and colonization as analogous to individual death and fecundity). Studies of single species or single groups may therefore lead to biased understanding or prediction of diversity changes, since other species or groups may show opposite responses. Take some of the models predicting biodiversity changes, which are based on single-species distributions and use climate covariates as predictors. Species distribution models can be stacked; that is, species are modeled independently and predictions added to provide predictions for diversity. However, if diversity is indeed regulated, one should try to constrain such models by including species dependencies, and how to achieve this is an active research topic (9). Studies like that of Magurran et al. (5), by quantifying how much local diversity fluctuations are bounded, are important contributions to this debate.

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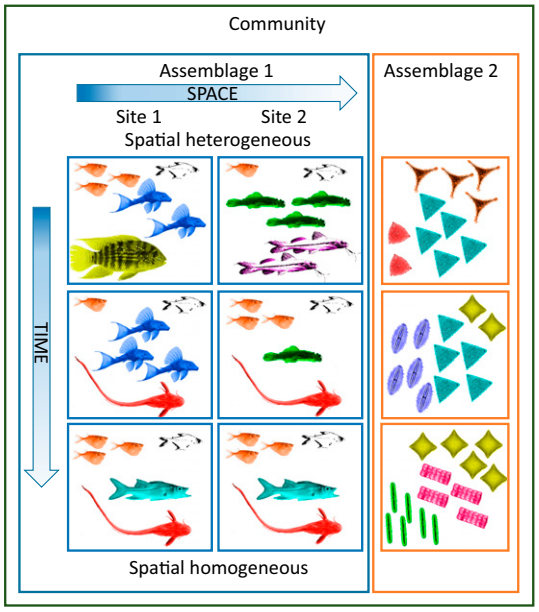

Fig. 1. Dimensions of diversity changes. That temporal variation in α diversity, the number or relative dominance of species, is bounded does not mean that change in temporal β diversity is also small: assemblage turnover can lead to final assemblages that are very different from the initial ones. Such temporal processes may also be associated with spatial β diversity changes, with dissimilar assemblages leading to similar assemblages (homogenization). Some species might not be detected (shown in gray), which may influence our estimates of diversity changes. Magurran et al. (5) show that for fishes, invertebrates, and diatoms in tropical streams, change in different diversity dimensions is not consistent for a given assemblage and when comparing assemblages for the same dimension; here, diatom assemblages show higher turnover than fish assemblages. Fish images adapted from ref. 24.

Components of diversity may also play an important role in understanding how ecosystem functions are impacted by biodiversity changes. For example, Spaak et al. (10) showed using both a theoretical model and empirical data on plankton and periphyton that despite constancy in species richness, essential ecosystem function such as primary production could change by an order of magnitude. In other words, an absence of change in α diversity does not mean that important ecosystem function will stay the same: Species turnover without change in the number of species may lead to functional changes. Indeed, as Magurran et al. (5) point out, when and why temporal β diversity impacts ecosystem functioning is an open question. One way to make progress is to focus on species traits related to ecosystem functions instead of species lists (i.e., to study functional diversity). This adds another dimension to biodiversity studies. For example, Frainer et al. (11) found that functional trait distribution changed rapidly with increasing sea temperature in the Barents Sea. Investigating stability and turnover of functional diversity, and how they are related to ecosystem stability and functions, is an intriguing extension of the work by Magurran et al. (5).

That patterns observed in raw biodiversity changes may not reflect the true underlying patterns was suggested for one of the first studies claiming that α diversity fluctuated around a narrow equilibrium (12 and commentary by Nichols et al. 13). Even with intensive sampling and standardized field methods, assumptions of high and constant detectability may not be warranted (14). Magurran et al. (5) account for this by using two diversity measures that correct for the number of unseen species, and patterns appear to be robust. However, given that detectability most likely varies among taxonomic groups and between seasons, using complementary approaches such as in the study by Chao et al. (15) may add to our understanding of the sources of variation in diversity trends, so as to disentangle measurement from process variability. Magurran et al. (5) also assess how taxonomic resolution may affect patterns of diversity changes by repeating the same analyses at the species and family levels for fishes, again finding that patterns were robust.

Most biodiversity analyses, including that by Magurran et al. (5), are framed in a hypothesis testing framework. The comparison of trends in α and β diversity used the number of significant vs. nonsignificant trends (or the corresponding value of the test statistics) compared with a null model of no temporal change. Such indirect comparison with a baseline has long been criticized (16), but a direct comparison is made difficult by the lack of a common scale for changes in different dimensions of diversity. In other words, when can we say that a given change in one dimension of diversity is larger than a change in another dimension of diversity? For example, how can we compare the loss of a single species out of 10 (a change in α diversity) with a change in β diversity such as measured by the Jaccard dissimilarity, which uses the proportion of species that are unique to two assemblages, and is therefore constrained to be in [0,1]. Scaling diversity dimensions would help in framing analyses of biodiversity changes in an estimation, and not a hypothesis testing framework (17), and would link the effects of drivers of biodiversity changes to the ecosystem consequences.

In addition to temporal variation in biodiversity, spatial variation is another dimension (Fig. 1). Combining these dimensions led McGill et al. (18) to identify 15 types of biodiversity trends. Although not a major focus in the study by Magurran et al. (5), changes in spatial β diversity show a trend toward homogenization (declining spatial dissimilarity) in fish and invertebrates and a trend toward larger spatial heterogeneity in diatoms (figure S12 of ref. 5). Recently, Magurran et al. (19) analyzed marine fish assemblages over three decades and found elevated temporal species turnover, leading to an increase in spatial homogenization. They argued that the community shifts were associated with climate change (i.e., a spatial pattern of unevenly rising ocean temperatures). In another long-term, large-scale marine study, Ellingsen et al. (20) showed that fish assemblages became less homogeneous (spatial β diversity increased) when a dominant apex predator (Atlantic cod) declined due to overfishing. These two studies show that even for the same taxonomic group (northern Atlantic marine fishes), different drivers may be important in different contexts. Although the study by Magurran et al. (5) is not designed to identify drivers of change within the short time frame, it opens perspectives on identifying drivers of the different components of biodiversity within ecosystems.

While the empirical basis for assessing some of the biodiversity trends is relatively adequate for specific biomes and groups (e.g., plant species richness in temperate areas), we usually have very poor coverage for most measures of diversity. This is particularly true for tropical or high sea environments (21), and for noniconic groups such as invertebrates or unicellular organisms such as diatoms. Indeed, very few monitoring programs have the resources needed to measure accurately in time and space the changes in biodiversity components (22). The study by Magurran et al. (5) is

an important reminder that without an increasing effort, we may often wrongly extrapolate diversity changes based on single measures, regions, or emblematic taxonomic groups. Alexander von Humboldt, who inspired Charles Darwin and initiated much of our current understanding on species distributions, climate, and human-driven changes by his explorations of biological diversity in the tropics, from the rainforest to the high mountains (23), would not disagree.

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