Assemble Time Series Reveal Biodiversity Change but Not Systematic Loss

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The extent to which biodiversity change in local assemblages contributes to global biodiversity loss is poorly understood. We analyzed 100 time series from biomes across Earth to ask how diversity within assemblages is changing through time. We quantified patterns of temporal α diversity, measured as change in local diversity, and temporal β diversity, measured as change in community composition. Contrary to our expectations, we did not detect systematic loss of a diversity. However, community composition changed systematically through time, in excess of predictions from null models. Heterogeneous rates of environmental change, species range shifts associated with climate change, and biotic homogenization may explain the different patterns of temporal α and β diversity. Monitoring and understanding change in species composition should be a conservation priority.

Habitat destruction, pollution, and overharvesting, as well as climate change and invasive species, have led to conspicuous reductions in biological diversity (1). Globally, increasing numbers of species are under threat (2), populations of vulnerable taxa are declining (3), and ecosystem function is changing as a result (4). Although these large-scale patterns emerge from processes that are based on local community structure, as yet there is no comprehensive analysis of how temporal change in ecological assemblages contributes to this global picture. Because the implementation of conservation and management decisions is typically at the scale of local to regional ecosystems (5, 6), knowledge of biodiversity change within assemblages is essential to inform policy. A comparative analysis of change across taxa, biomes, and geographic regions also provides insights into the mechanisms involved. Here, we use a definition of biodiversity that includes components of species richness, composition, and relative abundance of species. We use standardized biodiversity monitoring of assemblages over years and decades to assess global patterns of temporal change in species diversity.

We quantified change in biodiversity through time by two measures: temporal trends in α diversity and temporal β diversity (7). Temporal α diversity is a measure of diversity within a sample. It can be measured as species richness or with related diversity metrics that take species abundances into account. To measure temporal change in α diversity, we calculated, for each time series, the slope of the long-term relationship between diversity and time. Typically, β diversity is used to compare the composition of different communities in space, but it can also be used to compare the composition of a single community through time. Temporal β diversity (temporal turnover) quantifies differences in species composition between two (or more) samples separated in time. Temporal turnover can be measured with metrics of similarity to track changes in species identities (and sometimes their abundances) through time, either by comparing adjacent sampling periods or with reference to a single baseline sample or time period. Because turnover metrics incorporate shifts in species composition, they potentially provide a more sensitive indicator of community change (8) than does α diversity.

Given widespread evidence of habitat change (9), abnormally high extinction rates (10), and documented declines of many species (2, 3), we predicted that most assemblages would exhibit a decrease in α diversity through time, although the pattern and extent of change may differ among taxonomic groups, climatic regions, and marine or terrestrial realms and with spatial scale (11). For example, there is no evidence of consistent loss of biodiversity among terrestrial plants (12). Similarly, as a consequence of long-term changes in species composition, we expected increases in temporal β diversity measured relative to an early baseline sample.

To quantify biodiversity change, we gathered all data sets we could find that met a priori quality criteria (13) for standardization, long-term quantitative sampling. This collection includes more than 6.1 million species occurrence records from 100 individual time series. There are 35,613 species represented, encompassing mammals, birds, fish, invertebrates, and plants. The geographical distribution of study locations is global, and includes marine, freshwater, and terrestrial biomes, extending from the polar regions to the tropics in

References and Notes
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Supplementary Materials
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both hemispheres (Fig. 1). The collective time interval represented by these data is from 1874 to the present, although most data series are concentrated in the past 40 years (Fig. 2). (See table S1 for a full description of the data sets used in the analysis and their sources.) We measured temporal $\alpha$ diversity with 10 metrics, including species richness, and temporal $\beta$ diversity with four metrics, including the Jaccard similarity index. A strength of our analysis is that we calculate all metrics from the original data, rather than relying on published summary statistics, and thus are able to standardize sampling effort within each time series. Details of statistical standardization of data sets, choice of $\alpha$ diversity metrics, and null distributions for $\beta$ diversity metrics based on Markov chain Monte Carlo (MCMC) methods and neutral model analyses are described in (13).

Surprisingly, we did not detect a consistent negative trend in species richness (Fig. 2A) or in any of the other metrics of $\alpha$ diversity (fig. S1). The overall slope (estimated by allowing each study to have a different intercept, but constraining all studies to have the same slope) is statistically indistinguishable from zero (Fig. 2). However, not all data sets have constant species richness. In a mixed model in which both the

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**Fig. 1. Distribution of the survey sites included in our analysis.** Data sets are color-coded to reflect their climatic region: pink, global; royal blue, polar; turquoise, polar-temperate; green, temperate; gold, temperate-tropical; red, tropical. See table S1 for details and sources of the data sets.

**Fig. 2. Temporal change in $\alpha$ diversity and temporal $\beta$ diversity. (A and B)** Temporal change in species richness (A) and species composition (B) as measured by Jaccard similarity between each sample and the first sample in the time series. Data points are represented by gray circles and models fitted by solid lines. The black line corresponds to a model in which a single slope, but different intercepts, were fitted to all the time series, and is represented here with the mean intercept. The colored lines correspond to a model where each time series had a different slope and intercept. Color coding corresponds to Fig. 1. Figure S10 presents a similar analysis for a different approach to rarefaction.
slopes for species richness differ among assemblages, but do not exhibit systematic deviations. The variation cancels out because there are approximately equal numbers of negative and positive slopes (41 and 59, respectively), and the distribution of slopes is centered around zero, with the majority of slopes being statistically very close to zero (65 of 100 time series; Fig. 3A). This pattern was also observed for short-term changes rather than long-term linear trends: Of 1557 measurements of species richness in two consecutive times, 629 (40%) increased, 624 (40%) decreased, and 304 (20%) did not change (fig. S2). Collectively, these analyses reveal local variation in temporal α diversity but no evidence for a consistent or even an average negative trend.

The variability in slopes of α diversity could be explained by spatial, temporal, and biological attributes of each of the time series. However, for all measures of α diversity, slope is not a significant function of total species richness, extent of the spatial distribution of samples, starting date, or duration of the time series (figs. S3 and S4). Average slopes estimated for the marine and terrestrial time series are not significantly different from zero (fig. S5). Time series for terrestrial plants exhibit, on average, a positive slope for species richness, in contrast to Vellend et al. (12), who found no consistent change. There are no significant patterns for other taxonomic groups. An analysis of slopes by climatic regions reveals that temperate time series have a significantly positive overall slope and different intercept for each time-series baseline (fig. S7). A model with constant overall slope and different intercept for each time series (and with the time axis rescaled relative to each time-series baseline) is also negative. Turnover slopes are therefore almost uniformly negative, which is indicative of systematic change in community composition since the initial census point.

Even in a stochastic time series, some degree of turnover is to be expected because of temporal autocorrelation. However, the patterns of turnover in these time series are more pronounced and negative than what would be expected from simple temporal autocorrelation. Specifically, MCMC simulations of species-specific extinction and colonization produce slopes in turnover of −0.000013 on average, with confidence intervals straddling zero, and an approximately 50-50 distribution of positive and negative slopes (13) (fig. S8). Similarly, neutral model simulations incorporating species abundance show change in similarity two orders of magnitude lower than we observed (13) (fig. S9). The decrease in community similarity observed in our analysis is therefore not a simple consequence of drift and autocorrelation caused by a colonization-extinction Markov model or by a model of neutral dynamics.

These time series collectively exhibit no systematic change in temporal α diversity, although temperate assemblages show, on average, a positive trend in α diversity, whereas at the global scale we detected a negative trend. Moreover, across all climatic regions, realms, and taxonomic groups, temporal β diversity is increasing relative to the baseline (initial) sample. There are several reasons why α diversity may remain constant while temporal β diversity is consistently increasing.

One potential driver is that intensification of trade and transport, combined with the rapid increase in invasions of exotic taxa, is leading to the homogenization of species composition at local scales (14). Although homogenization may lead to a global loss of species, α diversity at local scales may stay constant or even increase as invaders replace residents and β diversity changes through time (11). This was the mechanism that Elton highlighted when he first voiced concerns about global biodiversity loss (15). Additional forces that might contribute to these contrasting patterns of α and β diversity include poleward shifts in geographic ranges as species respond to climate change (16). Moreover, contemporary habitat destruction and species loss is higher in tropical versus temperate regions (9), which is consistent with assessments of change in temporal α diversity in terrestrial plants (12) and population trends of vertebrates (17).

Our results suggest that local and regional assemblages are experiencing a substitution of their taxa, rather than systematic loss. This outcome may in part reflect the fact that most of the available data are from the past 40 years, which highlights concerns over the problem of a “shifting baseline” in diversity monitoring (18). Nonetheless, we show that at these temporal and spatial scales there is no evidence of consistent or accelerating

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**Fig. 3. Trends in α diversity and temporal β diversity.** (A and B) Slope estimate distributions for species richness (A) and Jaccard similarity (B). Slope estimates (horizontal axis), coefficient of determination $r^2$ (vertical axis), and number of data points in time series (bubble size) are shown for each of the data sets. Bubbles are color-coded as blue (positive slope), red (negative slope), and gray (nonsignificantly different from 0) (13).
loss of α diversity. Most important, changes in species composition usually do not result in a substitution of like with like, and can lead to the development of novel ecosystems (19). For example, disturbed coral reefs can be replaced by assemblages dominated by macroalgae (20) or different coral species (21); these novel marine assemblages may not necessarily deliver the same biodiversity change. We are grateful to all the data providers for making data publicly available and to their funders: Belspo (Belgian Science Policy); NSF; NOAA Marine Fisheries Service (grant NA11NMF4540174); Fisheries and Oceans Canada; Government of Nunavut; Nunavut Wildlife Management Board, Nunavut Tunngavik Inc., and Nunavut Emerging Fisheries Fund; Makivik Corporation; Smithsonian Institution; Atherton Seidell Grant Program; grants BSR-88119102, DEB 9411973, DEB 0008538, DEB 0218039, DEB 0620910, and DEB 0963447 from NSF to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, and to the International Institute of Tropical Forestry, U.S. Forest Service, as part of the Luquillo Long-Term Ecological Research Program; University of Puerto Rico; NSF’s Long-Term Ecological Research program and Fishery Administration Agency: Council of Agriculture, Taiwan; Azores Fisheries Observer Program; and the Center of the Institute of Marine Research (IMAR) of the University of the Azores. In addition, data were provided by the H. J. Andrews Experimental Forest research program, funded by NSF’s Long-Term Ecological Research Program (DEB 08-23380), P. Henderson (Pisces Conservation), U.S. Forest Service Pacific Northwest Research Station, and Oregon State University. Cruise data were collected through the logistical efforts of the Australian Antarctic Division and approved by the Australian Antarctic Research Advisory Committee (projects 2208 and 2953), the Australian Antarctic Data Centre of the Australian Antarctic Division, Tasmania. We are also grateful to the databases that compile these data: OBIS, Ecological Data Wiki, DATRAS, and LITER. Finally, we thank O. Mendivil-Ramos for advice on database design, L. Antúnez, and M. Barbosa and three anonymous referees for comments on earlier versions of the manuscript. The rarefied time series used in our analysis are included as Databases S1 and S2.

Supplementary Materials

www.sciencemag.org/content/344/6183/296/suppl/DC1 Materials and Methods

Figs. S1 to S10

Table S1

Databases S1 and S2

References (23–260)

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Structural Basis for Assembly and Function of a Heterodimeric Plant Immune Receptor

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Cytoplasmic plant immune receptors recognize specific pathogen effector proteins and initiate effector-triggered immunity. In Arabidopsis, the immune receptors RPS4 and RRS1 are both required to activate defense to three different pathogens. We show that RPS4 and RRS1 physically associate. Crystal structures of the N-terminal Toll–interleukin-1 receptor/resistance (TIR) domains of RPS4 and RRS1, individually and as a heterodimeric complex (respectively at 2.05, 1.75, and 2.65 Ångstrom resolution), reveal a conserved TIR/TIR interaction interface. We show that TIR domain heterodimerization is required to form a functional RRS1/RPS4 effector recognition complex. The RPS4 TIR domain activates effector-independent defense, which is inhibited by the RRS1 TIR domain through the heterodimerization interface. Thus, RPS4 and RRS1 function as a receptor complex in which the two components play distinct roles in recognition and signaling.

Plant immune receptors contain nucleotide-binding and leucine-rich repeat domains and resemble mammalian nucleotide-binding oligomerization domain (NOD)–like receptor (NLR) proteins (1). During infection, plant NLR proteins activate effector-triggered immunity upon recognition of corresponding pathogen effectors (2, 3). NLR protein activation of defense mechanisms is adenosine triphosphate dependent, causes defense gene induction, and often culminates in the hypersensitive cell death response (hereafter referred to as cell death) (4–6).

In some cases, plant and animal NLRs function in pairs to mediate immune recognition (7). For instance, both RPS4 (resistance to Pseudomonas syringae 4) and RRS1 (resistance to Ralstonia solanacearum 1) NLRs are required in Arabidopsis to recognize bacterial effectors AvrRps4 from P. syringae pv. pisi and PopP2 from R. solanacearum and also the fungal pathogen Colletotrichum higginsianum (8, 9). Several NLR gene pairs in rice also function cooperatively to provide resistance to the fungus Magnaporthe oryzae (10–14). Similarly,

References and Notes


13. See supplementary materials on Science Online.


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