Global meta-analysis reveals no net change in local-scale plant biodiversity over time

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Global biodiversity is in decline. This is of concern for aesthetic and ethical reasons, but possibly also for practical reasons, as suggested by experimental studies, mostly with plants, showing that biodiversity reductions in small study plots can lead to compromised ecosystem function. However, inferring that ecosystem functions will decline due to biodiversity loss in the real world rests on the untested assumption that such loss is actually occurring at these small scales in nature. Using a global database of 168 published studies and >16,000 nonexperimental, local-scale vegetation plots, we show that mean temporal change in species diversity over periods of 5–261 y is not different from zero, with increases at least as likely as declines over time. Sites influenced primarily by plant species' invasions showed a tendency for declines in species richness, whereas sites undergoing postdisturbance succession showed increases in richness over time. Other distinctions among studies had little influence on temporal richness trends. Although maximizing diversity is likely important for maintaining ecosystem function in intensely managed systems such as restored grasslands or tree plantations, the clear lack of any general tendency for plant biodiversity to decline at small scales in nature directly contradicts the key assumption linking experimental results to ecosystem function as a motivation for biodiversity conservation in nature. How often real world changes in the diversity and composition of plant communities at the local scale cause ecosystem function to deteriorate, or actually to improve, remains unknown and is in critical need of further study.

spatial scale | permanent plots | ecosystem services

A huge number of experiments has investigated the effects of species diversity (typically the number of species) on ecosystem function in small study plots (≤400 m^2), with a general consensus emerging that processes such as primary productivity and nutrient uptake increase as a function of the number of species in a community (1–6). These experiments thus appear to provide a powerful motivation for biodiversity conservation, given that ecosystem functions underpin many ecosystem services from which people benefit, such as forage production and carbon sequestration (1). However, the link between diversity-function experiments and the widespread argument that ecosystem function should motivate biodiversity conservation (7–11) hinges on the untested assumption that global biodiversity declines apply to the small scale (2). Experimental studies typically focus on small spatial scales not only for practical reasons, but also because organisms, plants in particular, typically interact over short distances (12), and so it is at the small scale that biodiversity is most likely to have an important impact on the functioning of ecosystems (13–15).

Habitat loss, invasive species, and overexploitation, among other factors, have accelerated global species' extinction well beyond the background rate (16–18), and it is tempting to assume that a global decline in biodiversity is necessarily accompanied by declines at smaller spatial scales. However, this is not a logical inevitability because, unlike other key variables involved in global environmental change, biodiversity at large scales (often termed gamma diversity) is not an additive function of biodiversity at smaller scales (alpha diversity). If global temperature or atmospheric CO_2 concentrations, for example, are increasing at the global scale, the net change over time within local areas must, on average, be positive. However, because local species losses may be accompanied by immigration of species from elsewhere, decreases in biodiversity at the global scale do not necessarily result in any biodiversity change at smaller scales (16, 19, 20). Here we present a global synthesis testing for directional changes in local-scale biodiversity of terrestrial plants, which have been the focus of most well-replicated biodiversity-ecosystem function (BDEF) experiments. We focus on the most commonly studied component of biodiversity—species diversity—estimated by metrics that reflect the number of species (richness) and/or the equitability of their abundances (indices of diversity or evenness).

Results and Discussion

We conducted a systematic global meta-analysis of plant species diversity change over time in >16,000 plots (median plot area = 44 m^2) from all major vegetation types (Fig. 1), including areas under profound and direct human influence (e.g., urban areas or pastures) and more pristine areas. Effect sizes were calculated as the log ratio of species diversity [e.g., species richness (*SR*)] in the year of the final survey (*Y2*) and the initial survey (*Y1*) divided by

Significance

A major advance of the last 20 y at the interface of biological, environmental, and conservation sciences has been the demonstration that plant biodiversity positively influences ecosystem function. Linking these results to applied conservation efforts hinges on the assumption that biodiversity is actually declining at the local scale at which diversity–function relationships are strongest. Our compilation and analysis of a global database of >16,000 repeat survey vegetation plots from habitats across the globe directly contradict this assumption. We find no general tendency for local-scale plant species diversity to decline over the last century, calling into question the widespread use of ecosystem function experiments to argue for the importance of biodiversity conservation in nature.

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Data deposition: Our database is provided as Dataset S1.

See Commentary on page 19187.

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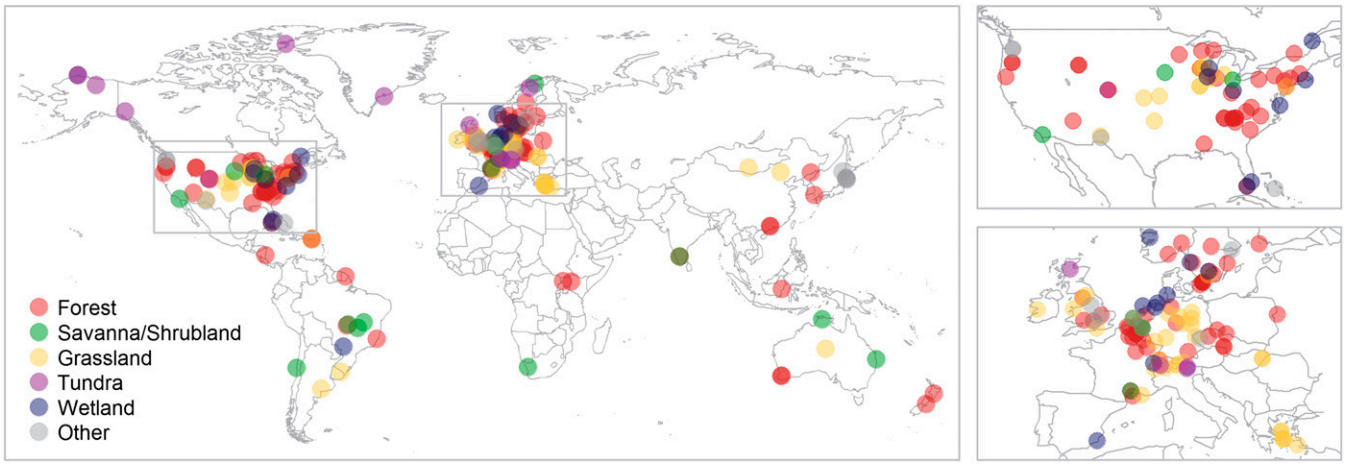

Fig. 1. Global distribution of the repeated vegetation surveys in this study. *Insets* show detail for North America and Europe. The "Other" category includes urban vegetation, primary successions (on volcanic rock), desert, or multiple vegetation types. Dots are semitransparent, such that darker colors indicate overlap of multiple studies.

the time interval in decades (Fig. 2). Overall, the distribution of temporal changes in plant species richness was centered on zero (Fig. 2 and Tables S1 and S2), with qualitatively similar results for the subset of studies in which diversity or evenness indices were reported (Fig. S1 and Table S2) and regardless of whether diversity changes were expressed per decade or as raw log ratios (Fig. S2; i.e., there is no assumption of linear changes over time).

We used the interpretations of the authors of the original papers to classify papers according to possible drivers of vegetation change. Recognizing the considerable uncertainty in such interpretations using observational data, we use these categories to explore the possibility of explaining some of the variation among studies, rather than to conduct strong tests of particular hypotheses. Consistent with intuition, marked increases in species richness over time were found in studies in which authors attributed vegetation change to succession following major disturbances such as fire, severe storms, or logging (Postfire and Postdisturbance in Fig. 3), and to a lesser extent, to the cessation of grazing. A tendency for temporal declines in species richness were found when authors attributed vegetation change to plant species' invasions and to a lesser extent climate change; in both of these cases, the 95% credible intervals overlapped zero

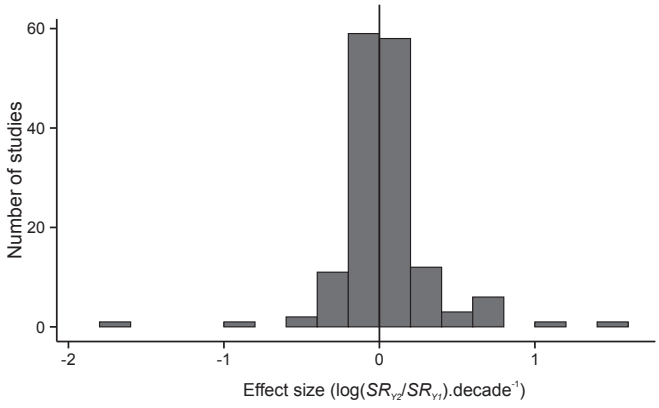

Fig. 2. Temporal change in plant species richness. Histogram for all studies of the change in species richness (*SR*) between time points 1 and 2, expressed as a log ratio per decade. A histogram of raw species richness changes (i.e., not reexpressed per decade), also centered on zero, is shown on the right edge of Fig. S2.

(Fig. 3). It is important to note that species recognized as invasive represent only a small subset of nonnative (i.e., exotic) species, the introduction of which often increases regional or local richness (20).

Temporal change in species richness was also independent of plot area, temporal duration, and the latitude and longitude of a given study (Table S3 and Fig. S2). The insensitivity of temporal richness change to study duration suggests that our results likely reflect the range of local-scale richness changes one might expect over both the short and long term (our database includes ≥10 studies in each 10-y range of temporal durations up to 60 y, median duration = 18 y; Fig. S2). That is, factors such as spatial constraints and stabilizing species interactions (21) likely buffer against prolonged local-scale diversity change in either direction.

It is important to note that our results do not pertain to species losses caused by human activities at the global scale, for which there is broad scientific consensus and which have justifiably prompted conservation actions based on the ethical, cultural, and instrumental values that people place on different species (16–18, 22). Our results also do not in any way undermine conservation efforts aimed at enhancing or maintaining large-scale ecosystem services, such as flood protection or soil stabilization. It is clear that the conservation or restoration of intact ecosystems, for example, along coastlines or steep slopes, is crucial to the delivery of such services (1, 18, 23). However, our results have fundamentally important implications for assessing the argument that biodiversity conservation can be justified because biodiversity loss compromises ecosystem function. The term biodiversity loss is ubiquitous in highly influential BDEF studies (1–5, 13, 24), and the argument that biodiversity loss is as important a driver of ecosystem processes as factors such as global warming or UV radiation rests on the explicit assumption that broad-scale species losses (intermediate estimates falling between 21% and 40%) apply to, or even underestimate, negative trends at the local scale (2). Our global meta-analysis, specifically designed to match the spatial scale of BDEF experiments, directly contradicts this assumption. Declines in species richness of <20% have negligible effects on ecosystem function (2), and although a few of our data sets show richness declines of 50% or more, declines of >20% were found in only 8% of data sets. Thus, small-scale biodiversity loss is certainly occurring in some locations, although rarely to a sufficient degree that we would expect important effects on ecosystem function. Interestingly, an even greater number of studies show diversity increases of >20% (15%), and most studies show low amounts of change (<20%),

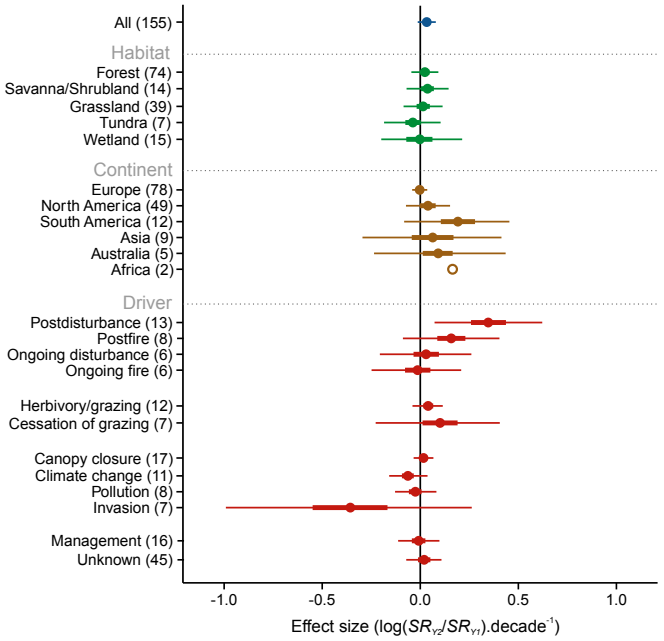

Fig. 3. Temporal change in plant species richness in subsets of studies in different habitats, on different continents, or with different drivers of vegetation change. Mean ±50% (thick lines) or 95% (thin lines) credible intervals are shown for all subsets represented by at least five studies; for sake of completeness, the raw mean is shown for the two studies in Africa for which species richness data were reported.

either positive or negative. In grasslands, where the most and the largest BDEF experiments have been conducted, there is no tendency for diversity declines across the >3,000 plots and 39 studies in our database (Fig. 3).

Although we found some predictable variation among studies according to reported drivers of vegetation change, there is a high degree of context dependence in the expected influence of any particular environmental change on diversity. For example, among studies in which vegetation change was attributed to climate warming, species richness increased by 24–119% (log ratio 0.22–0.78, depending on hill aspect) between 1968 and 2000 in the alpine tundra in Yukon, Canada (25), and decreased by 70–75% (log ratio −1.22 to −1.39) between 1950 and 2007 in the Siskiyou mountains in Oregon (26). Similarly, plant community shifts attributed to atmospheric nutrient deposition were associated with a 33% increase in species richness (log ratio 0.29) between 1971 and 1990 in forests of northeastern France (27) and a 35% decline in species richness between 1968 and 2008 (log ratio −0.44) in a grassland in Wales, UK (28). Although one can make general predictions concerning the influence of particular global change drivers on species composition, such as increases in warm-adapted species or decreases in cold-adapted species with climate warming (26), the consequences for local-scale species diversity appear much less predictable, with increases just as likely as decreases in most cases.

Our species richness database represents >8,500 cumulative years of change (318 data sets × 27.4-y average time span), covering much of the globe and most of the 20th and early 21st centuries, a period both preceded and characterized by intense human impacts on the earth. Nonetheless, we clearly have an overrepresentation of studies in Europe and North America. Interestingly, the studies from outside Europe and North America show, if anything, a slight tendency toward increasing local-scale species richness (Fig. 3), such that any geographic bias in our database should not influence our central result that richness is not generally declining over time. As such, we can conclude that in the absence of wholesale habitat conversion (e.g., turning a tropical rainforest into a parking lot or a crop monoculture), local-scale plant diversity has not, on average, declined over the last century (Figs. 2 and 3), nor do the data suggest any reason to predict the future will be fundamentally different from the past.

When sufficiently profound ecosystem transformations occur, such as converting a forest to a suburban garden or replacing a prairie with a cornfield, we assume that any effect of a change in the number of species on ecosystem function will be negligible compared with the effects of other changes: soil perturbation, a wholesale change in the composition of species, the management regime itself, etc. (6). For example, 100-m^2 plots in European forests in our database contain 14–28 plant species (six studies), whereas a typical domestic garden of the same area in the United Kindom contains almost 100 species (29). Likewise, a monoculture of corn contains far fewer plant species than the prairie it replaced. We argue that such increases (forest-to-garden) or decreases (prairie-to-corn) in species richness per se are effectively irrelevant to understanding changes in ecosystem functions, such as productivity or nutrient cycling, brought about by ecosystem transformation. However, species losses or gains from a forest, grassland, or other ecosystem that otherwise remains untransformed may well have an impact on ecosystem function. As such, the approach in many vegetation resurvey studies of not resurveying areas now occupied by human developments (e.g., forests now covered with residential homes and gardens) (30) is entirely consistent with the goals of our study. Following most BDEF studies, we are concerned with situations in which changes in the diversity of species might impact ecosystem function.

If plant biodiversity is not generally declining at local spatial scales, what are the real world implications of small-scale biodiversity manipulation experiments? In some settings, such as forest management or grassland restoration, such experiments closely mimic realistic scenarios (4, 6, 23, 31). Managers have the option of planting few or many species, and it is clear that greater productivity and stability can be expected from more diverse mixtures of species, with the gain in productivity on par with gains expected from other management actions such as fertilization (4). In more natural settings, however, experimental results with plants cannot be used as a motivation or justification for biodiversity conservation in a general way, given that local richness in these ecosystems is just as often increasing as it is decreasing. In addition, although the maintenance of larger-scale regional biodiversity is necessary, over the long term, to maintain local biodiversity via "spatial insurance" (32, 33), we still do not expect global diversity loss to filter down to the local level in the foreseeable future, given the widespread increases in plant diversity at regional scales (hundreds of square kilometers) in recent history due to the spread of nonnative species (19, 20).

Finally, although plant species diversity shows no net directional change at the local scale, individual sites show tremendous variation in the direction and magnitude of biodiversity trends (Figs. 2 and 3), as well as marked changes in the identities, functional characteristics, and abundances of locally co-occurring species (i.e., species composition) (16). These changes are expected to have important consequences for ecosystem function (16, 34), and our results point to a clear need for greater attention to be paid to the consequences of local increases in diversity, which are just as common as decreases, and to changes in species composition independent of diversity changes. How often such real world changes cause ecosystem function to deteriorate, or alternatively to actually improve, remains unknown. Through continued and improved biodiversity monitoring, and experiments that simulate real world changes at the local scale, a more comprehensive understanding of biodiversity change and its consequences can be achieved.

Methods

We searched the literature for papers reporting temporal change in the species richness or diversity of plant communities using the following search criteria in SCOPUS on 11 July 2012: [TITLE-ABS-KEY("plant community" OR "plant communities" OR vegetation OR forest* OR grassland* OR wetland* OR desert* OR savanna* OR tundra* OR steppe* OR shrubland* OR prairie* OR taiga OR rainforest* OR woodland* OR mangrove*) AND TITLE-ABS-KEY (biodiversity OR diversity OR richness OR evenness OR composition) AND ALL (resurvey* OR resample* OR revisit* OR "temporal change")]. This search returned 5,247 papers, the titles of which were scanned to eliminate obviously irrelevant papers, resulting in a list of 627 candidate papers.

Candidate papers were individually examined for data meeting the following criteria: (*i*) species richness, diversity, or change in richness/diversity, were reported for two or more points in time spanning at least 5 y; (*ii*) plots were either permanently marked or semipermanent, the latter indicating that resurveyed plots were located in approximately the same places as originally surveyed plots; (*iii*) plots were ≤5 ha for surveys of trees or ≤1 ha for all other surveys (the vast majority of plots in the analysis were ≤1,000 m^2); and (*iv*) plots were nonexperimental, in that any human influence was not implemented as part of the study itself; for experimental studies (e.g., nutrient addition, burning), data were recorded for control plots only (see further justification in *SI Methods*). We searched the reference lists of the initial 627 papers for additional papers potentially with appropriate data, resulting in a second list of 380 papers, which were examined in the same way. We carefully searched for redundancy (i.e., multiple papers reporting data for the same plots), and in such cases retained the paper with the largest sample size and/or the longest duration. Data meeting our criteria were found in 148 papers, comprising 168 studies and 346 data sets (see *SI Methods* for details and *SI Text* and Dataset S1 for the raw data).

For all data sets, we recorded the number of plots, plot area, plot type (permanent or semipermanent), the first and last years of surveys, country, approximate latitude and longitude, habitat type (forest, grassland, shrubland, savanna/shrubland, wetland, desert, tundra, anthropogenic (e.g., urban), primary succession (postvolcano), many habitats), and the life form(s) surveyed (forb, graminoid, bryophyte, tree, shrub, woody, all). The "all" category for life forms (235/346 data sets) indicated that all plants were recorded, although there was often ambiguity about inclusion of, for example, bryophytes, which might be absent entirely, or tree seedlings in forest understory plots. Mean species richness values were summed across different groups of species in the same plots (e.g., forbs and graminoids, natives and exotics) when such data were presented separately in the original papers. In cases for which the authors of a paper identified a primary driver of temporal vegetation change (262/346 data sets), we used the classification shown in Fig. 3 (*SI Methods*).

Species richness data were available for 155 studies comprising 318 data sets. For each data set, a raw effect size (*ES*) was calculated as the log ratio of mean species richness in the last (*Y2*) and first (*Y1*) years of surveys (most data sets included only two time points). *ES* quantifies proportional change between two groups (35), which is appropriate for quantification of temporal change using the initial state as a control and the end state as a treatment (36). The raw log ratio was standardized to a common decadal time scale (35), by dividing by the time interval (*t*, in decades) between *Y1* and *Y2*: $ES = t^{-1}\log(SR_{Y2}/SR_{Y1})$. The decadal scale effect size was used in all analyses except to test for the relationship between effect size and study duration. Note that the core result in our paper is insensitive to the decade-scale standardization.

ES's were analyzed in two ways: (*i*) presented in the main text, a Bayesian analysis of a multilevel model, in which the nonindependence of multiple data sets within papers is considered explicitly, and in which variation in *ES* can be related to predictor variables (covariates); and (*ii*) in the *SI Methods*, a traditional fixed-effect meta-analysis with each study weighted by the square root of sample size. The same analyses were conducted with *ES* calculated using diversity or evenness indices except for the evaluation of predictor variables, which was omitted due to small sample size. All analyses were conducted in R version 2.15.2 and OpenBUGS via the R2OpenBUGS package. Additional details are provided in *SI Methods*.

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