

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 ($\leq 400 \text{ m}^2$), 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 (Y_2) and the initial survey (Y_1) divided by the time interval in decades (Fig. 2). Overall, the distribution of

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](#).

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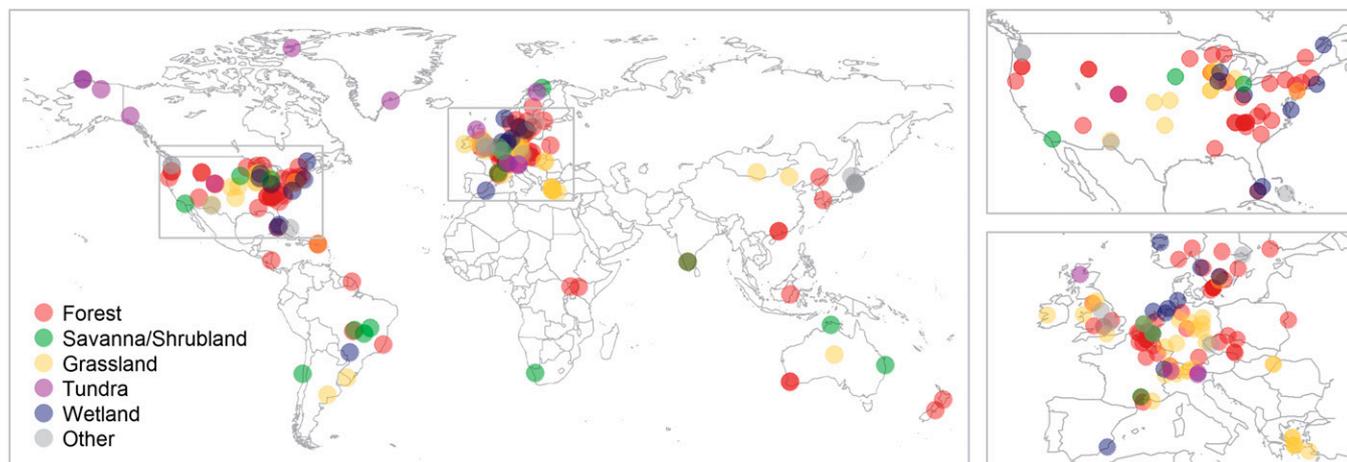


Fig. 1. Global distribution of the repeated vegetation surveys in this study. *Insets* show detail for North America and Europe. The “Other” category includes urban vegetation, primary successions (on volcanic rock), desert, or multiple vegetation types. Dots are semitransparent, such that darker colors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

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. 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 ($< 20\%$), either positive or negative. In grasslands, where the most and the

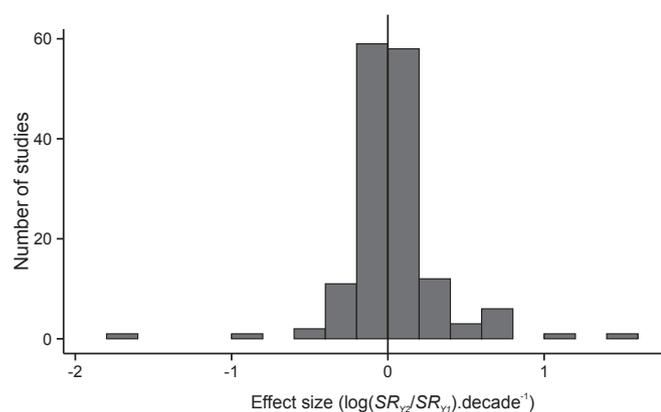


Fig. 2. Temporal change in plant species richness. Histogram for all studies of the change in species richness (SR) between time points 1 and 2, expressed as a log ratio per decade. A histogram of raw species richness changes (i.e., not reexpressed per decade), also centered on zero, is shown on the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

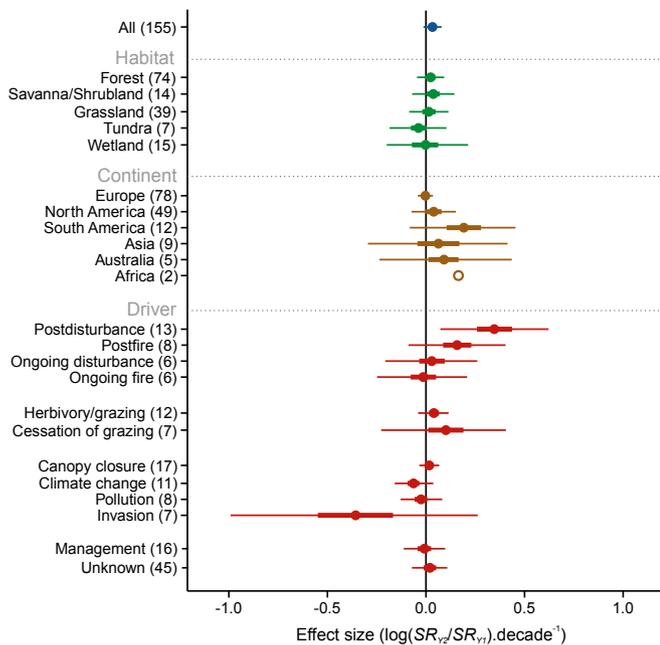


Fig. 3. Temporal change in plant species richness in subsets of studies in different habitats, on different continents, or with different drivers of vegetation change. Mean $\pm 50\%$ (thick lines) or 95% (thin lines) credible intervals are shown for all subsets represented by at least five studies;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

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 \times 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-m² 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 Kingdom 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 $\leq 1,000$ m²); 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 (Y_2) and first (Y_1) 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 Y_1 and Y_2 : $ES = t^{-1} \log(SR_{Y_2}/SR_{Y_1})$. 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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Supporting Information

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SI Methods

Papers, Studies, and Data Sets. Data meeting our criteria were found in 148 papers. Six papers reported data separately for two to three distinctly different habitat types, which we considered as separate studies, for a total of 168 studies. Individual studies often reported data separately for multiple sites within a single habitat type, which we considered separate data sets, for a total of 346 data sets. All authors contributed to an initial round of data extraction, after which each line of data were rechecked by two authors (M.V. and L.B.), working together closely to resolve any discrepancies or ambiguities and to ensure a standardized protocol across all papers.

Candidate Drivers of Vegetation Change. In cases for which the authors of a paper identified a primary driver of temporal vegetation change (262/346 data sets), we classified drivers as follows: ongoing disturbance, postdisturbance succession (disturbances include severe storms, volcanos, logging, drought, disease, and fire, with fire analyzed separately as the only subcategory with $n \geq 5$), ongoing or increased grazing/herbivory, reduced grazing/herbivory, climate change, pollution (mostly atmospheric nutrient deposition), plant invasion, increased canopy density (i.e., reduced light), altered hydrology, or management (this category includes altered regimes of multiple factors simultaneously, such as fertilization, mowing, grazing, or coppicing, when no one such activity was identified as the primary driver). Ongoing disturbances are those that occurred (often repeatedly) during the study period, whereas postdisturbance succession indicates studies for which the first vegetation survey was conducted after the last disturbance event. Three individual studies had unique drivers (urbanization, fragmentation, and seabird colonization) and were not included in this analysis.

Statistical Analysis. We first used a multilevel approach including Markov chain Monte Carlo (MCMC) simulations in R version 2.15.2 and OpenBUGS via the R2OpenBUGS package (1, 2). With multiple data sets in many studies, data sets were not independent of one another, and we incorporated this dependency into a multilevel model. For data set i in study j , the log ratio can be rewritten as $t_i^{-1} \log(SR_{Y2,i}/SR_{Y1,i}) = ES_{j(i)} + \varepsilon_i$. The ES_j are the study-level effect sizes that come from a common distribution $ES_j \sim N(\mu_{ES}, \tau^2)$, in which μ_{ES} is the grand mean, or population-average trend in diversity over time. The ε_i term expresses the data set level error. Thus, the analysis is a random-effect meta-analysis, not assuming a single effect size value that is common to all studies (3). The posterior distribution of μ_{ES} , with credible intervals expressing the uncertainty about μ_{ES} , indicates whether on average diversity is increasing or decreasing over time. The superpopulation SD , τ , represents variation among the modeled distribution of effect sizes from which our studies were selected, rather than only variation within the set of studies included in our meta-analysis.

Meta-analyses often use variance estimates to weight different observations. However, variances around mean species richness values were only reported in 30% of the studies in our data set, and none reported the covariance between the nonindependent mean $SR_{Y1,i}$ and $SR_{Y2,i}$ values, which is needed to calculate the variance of the log ratio (4). Thus, we took an unweighted approach in the multilevel analysis, assuming the data-level errors to follow a common distribution $\varepsilon_i \sim N(0, \sigma^2)$ (5). Minimal prior information was introduced by using vague priors for the parameters τ and σ : both $\sim U(0, 100)$ and $\mu_{ES} \sim N(0, 10,000)$ (5).

Three independent Markov chains were run for 100,000 iterations, discarding the first 5,000 (burn-in), and retaining one out of each hundred iterations (thinning) (6). This analysis was complemented by a more conventional bootstrapped fixed-effects meta-analysis.

A subset of studies reported diversity and/or evenness metrics; these data were analyzed using the same multilevel approach as for the species richness data (effect sizes). We recognize that absolute or proportional changes in these metrics are not as easily interpreted as changes in species richness, so these analyses focused on testing for directional trends rather than attempting to relate any such changes to biodiversity-ecosystem function (BDEF) experiments. In 35 of 38 studies, Shannon diversity was reported [$H = -\sum p_i \ln(p_i)$, in which p_i is the relative abundance of species i]. For analysis, we calculated $\exp(H)$, the “numbers equivalent” transformation of H , which is more quantitatively comparable among studies (7). In 18 studies, the Pielou evenness metric was presented [$E = \exp(H)/S$, in which S is the number of species in the plot]. We characterized the distribution of effect sizes for each of these metrics.

Justification for Excluding Experimental Studies. Our primary goal was to characterize temporal diversity change plant communities that represent the real world, defined as any place that was not manipulated experimentally for the purposes of studying vegetation change. As such, we deliberately did not consider experimental studies, such as those that manipulate temperature, soil nutrients, CO_2 , etc. Although such experiments can provide important clues as to which species might increase or decrease in abundance due to environmental changes under more natural conditions, the rate of environmental change (e.g., an instant doubling of atmospheric CO_2 concentration) far exceeds the rate of change experienced by natural communities. There is also likely insufficient time for species that might benefit from the modified conditions to colonize. As such, we restricted our analysis to studies reporting temporal diversity changes under the conditions experienced in the real world, which includes locations across the globe experiencing a wide variety of environmental and anthropogenic drivers of vegetation change. This database is not a biased set of studies focusing only on pristine vegetation (*SI Text*).

One type of experiment that does, in fact, mimic the real (i.e., nonexperimental) rate of environmental change is habitat fragmentation. The largest such study is the Biological Dynamics of Forest Fragments project in Brazil, where, surprisingly, no differences were found between intact forest and fragments of 1–100 ha in terms of plant species richness or diversity (Fisher's α) over 22 y (8). Large trees in small fragments experienced greatly elevated mortality, with a consequent alteration of tree size structure (8) and a reduction in carbon storage (9), but species losses were offset by gains in species better adapted to disturbed conditions. These results support both the absence of directional species diversity trends found in our meta-analysis, and also our contention that other effects of environmental changes on ecosystem function (in this case effects of mortality and species turnover on carbon storage) likely render any effects of species diversity per se negligible. A somewhat less realistic fragmentation experiment, in which patches of grassland (Kansas) of between 32 and 5,000 m² were created, found similar results: larger patches contained more species, but in equivalent small areas (1-m² plots) there was no such difference (10), although there were compositional differences (11). These studies reveal two

important lessons for our study. First, the inclusion of such experiments should not alter our conclusion of no net diversity change over time. Second, the conventional wisdom that plant

biodiversity generally declines in response to certain drivers of change, such as habitat fragmentation, may not apply to small spatial scales.

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SI Text

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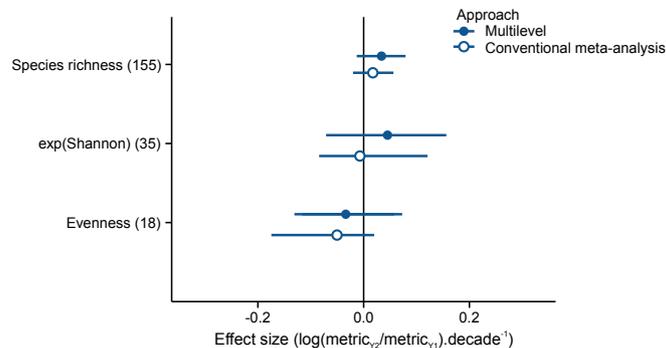


Fig. S1. Comparison of mean effect sizes $\pm 95\%$ credible intervals or 95% bias-corrected CIs in the multilevel analysis and the conventional meta-analysis, respectively. Results are shown for species richness (multilevel analysis shown in the main text), and for the “numbers equivalent” of the Shannon index of diversity [exp(Shannon)] and Pielou’s index of evenness. Bias-corrected CIs are generated via bootstrapping and thus may be asymmetric. See Table S2 and *S1 Methods* for details of analysis.

Table S2. Results of the conventional fixed-effect meta-analyses

Diversity index	<i>N</i>	Weighted mean	95% bias-corrected CI	
Species richness	155	0.017	−0.023	0.053
exp(Shannon)	35	−0.007	−0.084	0.130
Evenness	18	−0.050	−0.175	0.020

In this analysis we estimated the weighted mean of the log ratio (effect size) under the assumption of a single effect size common to all studies (1, 2). As most studies had several data lines in the database, species richness, diversity, and evenness values were pooled at the study level before this analysis by calculating the mean, weighted by sample size. *N* is the number of studies in the analysis. Because calculating the variance of the log ratio requires the covariance between the nonindependent $SR_{Y1,i}$ and $SR_{Y2,i}$ values (3), which was never reported in the original studies, we used the square root of the sample size as a weighting factor for the resampling test (4). The bias corrected 95% CIs were calculated with 2,000 bootstrap resamples (1, 4).

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Table S3. Results of multilevel analysis with covariates

Predictor variable	Mean or no. studies	Median	Range	Model coefficient (γ_1)		
				Mean	95% CI	
Latitude (°)	39.3	46.0	−43.2, 78.9	−0.0016	−0.0036	0.0005
Longitude (°)	−19.2	4.1	−156.7, 172.8	−0.0001	−0.0008	0.0006
Plot area (m ²)	653.5	43.8	0.04, 13,000	0.0004	−0.0019	0.0026
Time interval (y)	25.9	18.0	5, 261	−0.0019	−0.0042	0.0005
Plot permanent (no/yes)	59/96			0.0715	−0.0249	0.1683

Effect sizes across the *j* studies were modeled as $ES_j \sim N(\gamma_0 + \gamma_1 U_j, \tau^2)$, in which U_j is a study-level covariates (1). Iterations were set as for the main analysis and priors of γ_0 and $\gamma_1 \sim N(0, 10,000)$. ES_j was expressed per decade (main text) for all analyses except when using Time interval as a predictor, in which case the raw log ratio was used. Plot area was square root transformed before analysis. The reference level for “Plot permanent” was set as no; the coefficient for this analysis models the increase in effect size in permanent plots. Note that the means here were calculated across studies, such that some means reported across data sets in the main text are slightly different (some studies included multiple data sets).

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Other Supporting Information Files

[Dataset S1 \(XLS\)](#)