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Species loss drives ecosystem function in experiments, but in nature the importance of species loss depends on dominance

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Abstract

Aim: Decades of experimental research have conclusively shown a positive relationship between species richness and ecosystem function. However, authoritative reviews find no consensus on how species loss affects function in natural communities. We analyse experimental and observational data in an identical way and test whether they produce similar results.

Location: North America and Europe (experimental communities); global (natural communities).

Time period: Experimental communities: 1998–2013; natural communities: 1982–2018.

Major taxa studied: Experimental communities: temperate grassland plants; natural communities: temperate grassland plants, tropical forest trees, kelp forest producers and native bees.

Methods: We used an approach inspired by the Price equation to analyse 129 datasets from experimental and natural communities worldwide. We tested how the effects of species loss on ecosystem function varied with dominance and the non-randomness of species loss and, in turn, how these two factors differed between experiments and observations.

Results: Studies carried out in experimental and natural communities reached different conclusions regarding the effects of species loss. First, species loss had greater effects on ecosystem function in experiments than in nature. Second, the importance of species loss was negatively correlated with dominance in nature because as dominance increased, lost species were increasingly those contributing little to ecosystem function. Although experimental and natural communities exhibited similar levels of dominance, an analogous relationship was not possible in experiments because the order of species loss was randomized by design.

Main conclusions: Species loss was sometimes, but not always, the major driver of loss of function in nature. Variation in the importance of species loss was not messy and context dependent; instead, it was predicted by functional dominance. Although results from experimental and natural communities were similar in several key ways, they differed in that species loss was a consistent predictor of ecosystem function in experiments and not in nature.

KEYWORDS

biodiversity, composition, dominance, ecosystem function, experiment, Price equation, species loss, species richness

1 | INTRODUCTION

Global loss of biodiversity doubtless threatens essential ecosystem functions (Cardinale et al., 2012; Hooper et al., 2012; Isbell et al., 2017), but despite decades of experimental and observational research, there is still no predictive understanding of how species loss will impact ecosystem function in nature (Cardinale et al., 2012). Studies in experimental and natural communities often find different results, with experiments pointing to a major role for species richness (e.g., Isbell et al., 2011; Reich et al., 2012; Tilman et al., 2001), whereas studies in natural communities variably find that species richness (Duffy, Goodwin, & Cardinale, 2017; Duffy, Lefcheck, Stuart-Smith, Navarrete, & Edgar, 2016; Grace et al., 2016; Mora et al., 2011), the order of species loss (Larsen, Williams, & Kremen, 2005), dominant species (Genung et al., 2017; Winfree, Fox, Williams, Reilly, & Cariveau, 2015) or aggregate abundance (Smith & Knapp, 2003) drive function. Furthermore, experimental and observational studies define “species loss” differently, consistent with their study designs.

Most experiments have defined species loss as a decrease in species richness (i.e., the number of species) and have isolated the effects of richness by randomizing the species composition of experimental communities at different levels of richness (Schmid et al., 2002). Thus, experiments measure the effect of losing n species, given that those n species were chosen at random. Generally, there is no literal species loss (i.e., species removals, but see e.g., Lyons & Schwartz, 2001; Smith & Knapp, 2003; Wardle & Zackrisson, 2005; Zavaleta & Hulvey, 2004) but instead the comparisons are made among plots that were established with different numbers of species. The results of > 600 biodiversity–ecosystem function experiments have convincingly established that decreasing richness decreases function (Cardinale et al., 2012), with effects of richness being comparable to environmental drivers such as drought, nitrogen fertilization and invasive species (Hooper et al., 2012). Nevertheless, it remains unclear whether the effect of reduced richness, as measured in experiments, mirrors the effect of species loss from natural communities.

Observational studies of the biodiversity–function relationship likewise have rarely studied literal species losses. Instead, they have measured the effects of species loss based on one of two designs: either space-for-time substitutions, in which sites with different levels of anthropogenic effects are compared (Duffy et al., 2016; Grace et al., 2016); or comparisons of sites that do not necessarily differ in levels of anthropogenic change but that do differ in levels of both biodiversity and ecosystem function (Duffy et al., 2017; Genung et al., 2017; Winfree et al., 2015, 2018). The key distinction between species loss in experiments and natural communities is that changes in richness and composition are confounded in natural communities (Larsen et al., 2005; Smith & Knapp, 2003; Suding et al., 2005;

Winfree, Williams, Dushoff, & Kremen, 2014), but not in experiments. Thus, observational studies measure the functional effect of losing the n species that were in fact lost, rather than the expected effect of losing n species at random. This is a limitation in that it is difficult to separate the effects of richness and composition as drivers of function (Fridley, 2002; Mulder, Jumpponen, Högberg, & Huss-Danell, 2002; Tilman & Wardle, 1997). However, it is a strength in that it captures any association between the identity of species most likely to be lost as richness declines and the contribution of these species to function.

Dominance, or the tendency of communities to contain many rare and few common species (McGill et al., 2007), is an important feature of ecological communities that differs between experimental and observational studies. Experiments investigating the biodiversity–function relationship tend to equalize the initial abundances of species (but see e.g., Lamb, Kennedy, & Siciliano, 2011; Wilsey & Potvin, 2000; Wittebolle et al., 2009) to isolate the effects of species richness (Schmid et al., 2002). However, it is unclear how species abundances and contributions to function change over time in experiments. Do they, either quickly or over many years, start to mimic the higher functional dominance (an analogue of numerical dominance, in which contributions to function replace abundance) seen in natural communities (Schleuning, Fründ, & García, 2015)? This question is important, because systematic differences in functional dominance between experimental and natural communities could lead to predictable differences in the biodiversity–function relationship. The basic prediction is that high functional dominance makes species richness less important to function, because a few common species could provide most of the function (Dangles & Malmqvist, 2004; Grime, 1998; Smith & Knapp, 2003; Winfree et al., 2015). In contrast, when communities are even, it is more likely that species richness will be important. This broad prediction is not system specific and provides some reason to expect that dominance could mediate the effects of species loss in a similar way across ecosystem functions.

In sum, to advance research on biodiversity–ecosystem functioning in real-world communities we need to know, first, whether experimental and natural communities differ in functional dominance, and second, whether functional dominance mediates the consequences of species loss for ecosystem function. We analysed 129 datasets from across the globe, of which 36% came from biodiversity–function experiments and 64% from natural communities, and answered the following questions. First, does species loss, as measured through changes in species richness and species composition, have similar effects on ecosystem function in experimental and natural communities? Second, do experimental and natural communities have similar levels of functional dominance, and how does functional dominance mediate the effect of species loss on function?

Third, are species lost at random in experimental and natural communities, and how does non-randomness in the order of species loss affect function?

2 | METHODS

2.1 | Price equation partition

The Price equation was first developed to partition the drivers of microevolutionary change in mean phenotype (Price, 1972). The Price equation partition used here reinterprets and builds on the same mathematics to partition the difference in ecosystem function between two sites (a higher-function “baseline” site and a lower-function “comparison” site) into three additive terms: richness, composition and context dependence (Fox, 2006; Fox & Kerr, 2012; for details, see Supporting Information Appendix S1). Hereafter, we refer to our partition as the “ecological Price equation” for simplicity, although we are not claiming that any one definitive “ecological Price equation” exists. The ecological Price equation divides a between-site decline in function into components attributable to different drivers. Thus, the ecological Price equation reverses the question traditionally asked by biodiversity–function experiments, which is, “Given a change in the number of species, how does function change?”, and instead asks, “Given a between-site difference in function, how much can be assigned to changes in the number of species?”. Both questions are interesting, and our use of the ecological Price equation does not advocate for one over the other.

The ecological Price equation compares pairs of sites, and in each case asks why one has higher function than the other. The mathematics of the ecological Price equation shows that three, non-exclusive answers are possible, each corresponding to one ecological Price equation term. First, the higher-function site might simply have many more species. This would be captured by richness (RICH), which is the expected change in function if species loss is random with respect to function. We emphasize that this is richness in a strict, literal sense, that is, the number of species present. It is not inclusive of the identities of those species, nor any positive complementarity resulting from higher richness. Second, the higher-function site might have species that contribute, on average, more function. This would be captured by composition (COMP), which adjusts the expectation set by RICH because species are almost never lost exactly at random with respect to function. For example, if species lost between the higher- and lower-function site had above-average contributions to function, COMP would augment RICH because the effects of species loss were greater than the random expectation. Third, species present at both sites might contribute more to function at the higher-function site. This would be captured by the context dependence effect (CDE), which includes all between-site differences in function not attributable to between-site differences in species richness or composition. The CDE captures any compensatory (or depensatory) responses of the remaining species to species loss, effects of between-site differences in environmental conditions, and any other factors causing

the remaining species to function differently at different sites. In this paper, we use the term “species loss” to refer the sum of the richness and composition effects (Supporting Information Appendix S1). This can be considered the direct or immediate effects of a species no longer being present at a site. Box 1 shows a general framework for interpreting ecological Price equation results, based on the signs and relative magnitudes of species loss and context dependence.

The ecological Price equation approach offers two important advantages. First, it creates a natural contrast between effects directly attributable to changes in the number and identity of species (i.e., species-level effects; RICH and COMP) and those that are not (CDE). Abundance, in particular, is often a confounding factor in observational studies, whereas experiments control the initial abundance (often by seeding species at equal densities, e.g., Reich et al., 2012; Tilman et al., 2001; Weigelt et al., 2010). The ecological Price equation partitions abundance effects into the CDE and can, therefore, be used to make comparisons among studies that did, or did not, control abundance. Second, the ecological Price equation separates the random (RICH) and non-random (COMP) effects of species loss. Thus, it can compare among studies that did, or did not, enforce random species loss by design.

2.2 | Datasets used

We searched for datasets using the following four criteria. First, the dataset had to include a measurement of ecosystem function expressible as a sum of species contributions. Second, the dataset had to include replicate sites (or plots, in the case of experiments) at which species composition and function were measured. These are basic requirements for using the ecological Price equation. Third, the dataset had to include a second level of sampling, either temporal (e.g., sampling the same collection of sites in a subsequent year) or spatial (e.g., measurements of function replicated with the same design in different regions of the world). This was to generate a range of functional dominance values for each ecosystem function. Fourth, to make our results more comparable with experiments, we focused on datasets in which ecosystem function providers belonged to the same trophic level. Fifth, we specifically searched for datasets that would represent a diversity of functions: aquatic and terrestrial, delivered by plants and animals, and spanning multiple continents.

2.3 | Data from experimental communities

We analysed 46 datasets from three long-running biodiversity–ecosystem function experiments, all of which measured aboveground biomass of grassland plant species: Biodiversity II, BioCON and the Jena experiment ($n = 46$ datasets from experiments in total). Biodiversity II manipulated plant species richness in one-, two-, four-, eight- and 16-species plots. BioCON manipulated species richness in one-, four-, nine- and 16-species plots. BioCON also included a two-by-two factorial manipulation of CO₂ (ambient and elevated) and nitrogen (unfertilized and

BOX 1 Simplified interpretations of Price equation terms

In broad terms, ecological Price equation results can be placed in four categories (the top four rows above; the fifth row is included only for completeness). These categories are based on the sign, and in some cases the relative magnitudes, of the species loss and context dependence terms. The first and second rows correspond to results from natural and experimental communities, respectively. Interpretations and example communities provide a likely explanation for each result. “Shared” means shared between the higher- and lower-function sites, that is, species that are present at both sites. “Smaller” and “larger” describe the relative magnitude of terms within rows. In the right columns, shapes are different species, sizes represent contributions to function, and open shapes with dotted borders indicate the absence of species (i.e., a species loss).

Sign of Species Loss	Sign of Context Dependence	Likely Interpretation	Higher-function Site	Lower-function Site
Negative (Smaller)	Negative (Larger)	Higher-function sites tend to have more species, but most species that turn over between sites have low function. Shared species have highly variable contributions to function across sites.		
Negative (Larger)	Negative (Smaller)	Higher-function sites tend to have more species, and species turnover includes species with substantial contributions to function. Shared species have slightly variable contributions to function across sites.		
Negative	Positive	Higher-function sites tend to have more species. After species loss, persisting species increase contributions to function, but cannot completely offset the effects of species loss. This could be because declines in species richness reduce complementarity.		
Positive	Negative	Higher-function sites tend to have fewer species. This requires that shared species contribute more function when richness is lower. Perhaps, in high-richness sites, competition from low-functioning species limits the performance of functionally-dominant community members.		
Positive	Positive	This result is not mathematically possible.		

fertilized), yielding four global change treatments (e.g., ambient CO₂ and nitrogen fertilization). We analysed each global change treatment separately and found the same patterns across all four treatments. The Jena experiment is known for high maximum richness (it contains one-, two-, four-, eight-, 16- and 60-species plots) and large plot size (20 m × 20 m). For all three biodiversity-ecosystem function experiments, species were seeded at equal densities when establishing plots. For all experimental data, we excluded the one-species plots to make experiments more comparable with natural communities. Each year of each experiment was a dataset [$n = 12$ for Biodiversity II, $n = 28$ (7 years × 4 treatments) for BioCON, and $n = 6$ for Jena], and the ecological Price equation partitioned variation in function among plots.

2.4 | Data from natural communities

There were 83 datasets from natural communities, spread across four ecosystem functions. Our first ecosystem function was crop

pollination by wild bees (Winfree et al., 2018). We analysed pollination provided to blueberry ($n = 3$ years of data), watermelon ($n = 5$ years) and cranberry ($n = 2$ years) crops by wild bee species. Each crop-year combination was a dataset, and replicate farms within crop-years were sites ($n = 10$ datasets in total across three crops). Our second ecosystem function, collected by the Santa Barbara Coast LTER (Long-Term Ecological Research) group, was producer biomass in kelp forests at nine sites off the California coast. Each year of kelp forest surveys was a dataset ($n = 19$ datasets in total). Our third ecosystem function was aboveground carbon storage in tropical forests. We used tree abundance data from four different continents, collected by the Tropical Ecology Assessment and Monitoring (TEAM) Network. Datasets were TEAM Network locations in different parts of the world (e.g., Manaus in Brazil; $n = 8$ datasets in total), and sites were 1-ha forest plots within each location. We used allometric equations from (Chave et al., 2005) and wood density estimates (Zanne et al., 2009) to translate abundances to carbon storage. Our fourth ecosystem function was aboveground

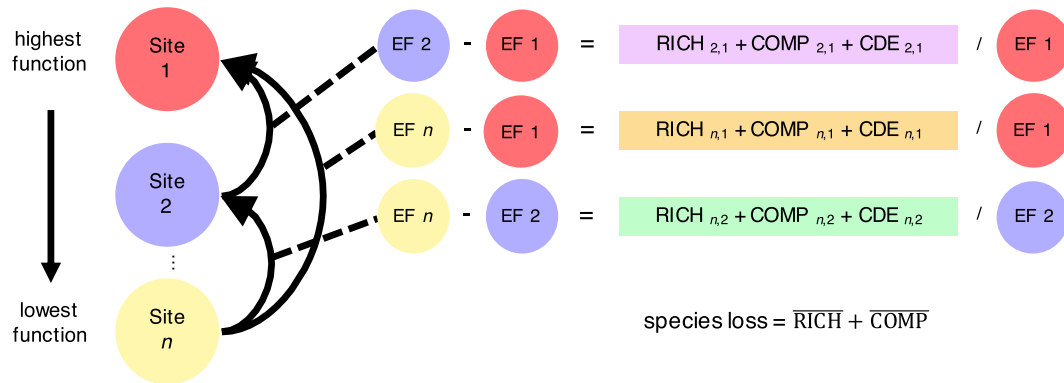


FIGURE 1 The ecological Price equation partitions the difference in ecosystem function (EF) between two sites: a baseline (higher-function) site and a comparison (lower-function) site. The partitions results in three additive terms: richness (RICH), composition (COMP) and context dependence (CDE). Then, for each pair of sites, we divided these terms by baseline function. Thus, all ecological Price equation terms have a range from minus one to one and are unitless, such that comparisons across ecosystem functions are not confounded by different units (e.g., pollen grains versus grams of carbon). Finally, taking the mean values for each ecological Price equation term across all pairwise comparisons yields RICH, COMP and CDE. The sum of RICH and COMP is the effect of species loss [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

biomass of temperate grassland plants in Minnesota, USA, collected by the Cedar Creek LTER group. There were 23 years of data and two habitat types. Each year–habitat type combination was a dataset ($n = 46$ total datasets).

Data sources are listed in the Appendix. See the Supporting Information Appendix S2 for a full descriptions of datasets, functions and how the data were used. Although the experimental and observational communities were sampled at different spatial scales, our results appear to be robust to this difference (Supporting Information Appendix S3).

2.5 | Environmental variation and interpretation of the ecological Price equation

As much as possible, datasets were selected to minimize environmental variation (e.g., habitat type, time of year, precipitation, temperature and elevation) among sites. However, there will doubtless be remaining environmental variation. Although the ecological Price equation does not have a term for environmental variation, the effects of environmental variation are still captured and attributed to the component of community structure through which they act. For example, higher precipitation at a focal site could increase carbon storage by trees indirectly, but it must do so by: (a) increasing focal site species richness; (b) shifting focal site community composition towards higher-function species; or (c) increasing the focal site abundance or per-capita function of species present at both sites.

2.6 | Methods of analysis

For all 129 datasets, we first applied the ecological Price equation to all pairwise comparisons of sites, producing values for RICH, COMP and CDE for each comparison. We then calculated the mean, across pairwise comparisons, of each ecological Price equation term

(Figure 1), yielding: effects of changes in species richness ($\overline{\text{RICH}}$); effects of changes in species composition ($\overline{\text{COMP}}$); or context-dependent changes in the function provided by species that are present at both sites ($\overline{\text{CDE}}$). Overbars indicate that ecological Price equation terms are means (e.g., $\overline{\text{RICH}}$), averaged across all pairwise comparisons of sites within the dataset. To determine whether species loss has similar effects on ecosystem function in experimental and natural communities, we compared the mean ecological Price equation terms (see above) between experimental and natural communities.

Each dataset had one value for functional dominance, which was the mean functional dominance across all sites (or plots) in the dataset. We explored five dominance indices, all in terms of diversity (Hill numbers) of order q , where $0 < q \leq 2$ (Chao & Ricotta, 2019). Results were qualitatively consistent across indices and values of q (Supporting Information Appendix S4); in the Results, we use the third class of indices with $q = 1$. A simplified equation for this form of dominance, specific to $q = 1$, is:

$$1 - \left(\frac{e^H - 1}{S - 1} \right),$$

where H is the Shannon entropy index and S is species richness. To determine whether experimental and natural communities have similar functional dominance, we compared the distributions of functional dominance between experimental and natural communities. Our choice to use functional rather than numerical dominance reflected data limitations, because most datasets reported species-level function, but not abundance. Experiments seeded species at equal densities when establishing plots, but nonetheless the functional dominance could still be high in experimental communities for two reasons: (a) changes in species abundances from their initially equal values; and (b) interspecific variation in per-capita function.

We fitted three models using “lm” in R v.3.5.1 (R Core Team, 2018). We fitted each model to experimental and natural communities

separately. All three included ecosystem function “type” as a categorical predictor and functional dominance as a continuous predictor, fitting separate slopes for dominance within each ecosystem function “type”. Type means a specific ecosystem function (e.g., pollination) for natural communities and experiment name (e.g., Biodiversity II) for experiments. The response variable for the first model was the effect of species loss, $\overline{RICH} + \overline{COMP}$, which was the effect of changes in the number and identity of species. The response variable for the second model was \overline{CDE} , which accounted for changes in the abundance and per-capita function of species present at both sites. The first two models were parallel in that they tested how functional dominance mediated the effect of either species loss or context dependence on function. The third model examined the non-randomness of species loss, using $\overline{COMP/RICH}$ as the measure of non-randomness. This works because \overline{COMP} is zero when species are lost at random with respect to function, and there is no need to adjust \overline{RICH} . As \overline{COMP} moves away from zero, species found at one site but not the other have lower ($\overline{COMP/RICH} < 0$) or higher ($\overline{COMP/RICH} > 0$) than average function.

For all three models, a significant effect of dominance nested within “type” would show that the response ($\overline{RICH} + \overline{COMP}$, \overline{CDE} or $\overline{COMP/RICH}$) became more (or less) important to function as function became more concentrated in a few species, as opposed to being spread more evenly among species. Averaging across functions, we expected increasing dominance to decrease the effect of species loss because of a higher proportion of species having small contributions to function. We had no a priori expectation for the effect of dominance on the \overline{CDE} . In the main text, we report p -values and semi-partial correlation coefficients for functional dominance nested within type, rather than for the whole model. This is because we were most interested in the amount of variance specifically described by functional dominance versus any given response variable (effect of species loss, effect of context dependence or the non-randomness of species loss), rather than variance between different “types”. We had no a priori expectation for how mean functional dominance, or any response variable, would vary across “types”. Full model results are available in the Supporting Information Appendix S5.

3 | RESULTS

3.1 | Does species loss, as measured through changes in richness and composition, have similar effects on ecosystem function in experimental and natural communities?

The total change in function between sites ($\overline{RICH} + \overline{COMP} + \overline{CDE}$) did not differ between the experimental and natural communities included in our analysis ($r^2 = .013$, $p = .104$; Figure 2). If species had been lost at random, species loss would have accounted for a slightly greater decline in function in experimental communities than in natural communities. This is shown by a lower (i.e., larger magnitude) value for \overline{RICH} for experimental communities in Figure 2 ($r^2 = .149$,

$p = 3.76 \times 10^{-6}$). Species were lost at random in experiments, as required by design. However, species were not lost at random in natural communities; instead, low-function species were more likely to be lost. This contrast is shown in Figure 2 by a positive \overline{COMP} for natural communities and a significantly lower, near-zero \overline{COMP} for experimental communities ($r^2 = .304$, $p = 7.60 \times 10^{-12}$). Thus, in natural communities, \overline{COMP} partly cancelled \overline{RICH} , because these terms were of opposite signs. As a result, the effect size of species loss on function was greater in experimental communities than in natural communities ($r^2 = .444$, $p = 4.09 \times 10^{-18}$, shown by a more negative $\overline{RICH} + \overline{COMP}$ in Figure 2). If high-function species had been lost, \overline{COMP} would have augmented \overline{RICH} and increased the effects of species loss, but this result was rare in our data. Furthermore, we stress that knowing that low-function species were generally lost does not guarantee a low effect size of species loss as defined by the ecological Price equation, because: (a) species loss incorporates both the number and the identity of lost species (\overline{RICH} and \overline{COMP} , respectively); and (b) for each pairwise comparison, the effects of species loss are scaled by baseline site function (see Methods and Supporting Information Appendix S1). Changes in factors that do not

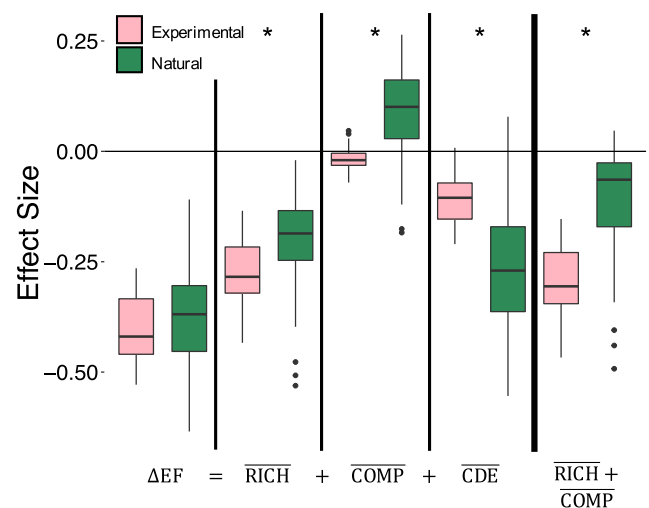


FIGURE 2 The change in ecosystem function between sites (ΔEF) is partitioned into components attributable to changes in richness (\overline{RICH}), changes in composition (\overline{COMP}) and changes in the abundance or per-capita function of species that are present at both sites (\overline{CDE}). Species loss is the total loss of function that occurs as a result of all changes at the species level ($\overline{RICH} + \overline{COMP}$). Effect size is interpretable as follows. The effect size values for ΔEF show that, for two randomly chosen sites, function declines by 35–40% on average between the higher- and lower-function sites. This result was consistent across the experimental and natural communities. For all other terms, effect size is the proportional decline (or, in some cases, increase) in function driven by that term. Asterisks indicate significant differences between experimental and natural communities for a given term, corrected for multiple comparisons with a false-discovery rate of 0.05. Experimental community data are from grassland plant biomass (northern USA and Germany). Natural community data are from temperate grassland biomass (northern USA), kelp forest biomass (near California, USA) tropical forest carbon storage (tropics worldwide) and crop pollination (eastern USA) [Colour figure can be viewed at wileyonlinelibrary.com]

involve species loss, that is, the abundance and per-capita function of species present at both sites, accounted for more of the decline in function in natural communities than in experiments ($r^2 = .300$, $p = 1.13 \times 10^{-11}$; shown by a more negative $\overline{\text{CDE}}$ in Figure 2).

3.2 | Do experimental and natural communities have similar levels of functional dominance, and how does functional dominance mediate the effect of species loss on function?

Mean functional dominance was slightly higher in experimental communities than in natural communities, but the distributions were broadly overlapping (Figure 3). However, similarity in the distributions of functional dominance does not mean that the consequences of varying functional dominance were the same in experimental and natural communities.

The effect of species loss ($\overline{\text{RICH}} + \overline{\text{COMP}}$) did not vary with dominance in experiments (semi-partial $r^2 = .080$, $p = .151$; Figure 4a). However, in natural communities, species loss had little effect on ecosystem function at high-dominance sites, whereas it decreased ecosystem function at low-dominance sites (semi-partial $r^2 = .366$, $p = 2.49 \times 10^{-10}$; Figure 4b). Thus, lost species made either major or insignificant contributions to ecosystem function, depending on functional dominance.

Likewise, the effect of context dependence ($\overline{\text{CDE}}$) on function did not change with functional dominance in experiments (semi-partial

$r^2 = .020$, $p = .562$; Figure 4c). However, the effect of context dependence was positively correlated with functional dominance in natural communities (semi-partial $r^2 = .182$, $p = 7.25 \times 10^{-6}$; Figure 4d). Thus, in natural communities, as functional dominance increased and species loss explained less variation in function, context dependence explained more.

3.3 | Are species lost at random in experimental and natural communities, and how does non-randomness in the order of species loss affect function?

Species loss was, by design, random in experiments (semi-partial $r^2 = .076$, $p = .305$; Figure 4e). In natural communities, as functional dominance increased, species lost between sites increasingly made small contributions to function (semi-partial $r^2 = .299$, $p = 1.03 \times 10^{-8}$; Figure 4f). This helps to explain why the importance of species loss decreased with dominance (see section 3.2 above).

4 | DISCUSSION

Understanding the consequences of species loss for ecosystem function is a great challenge in ecology. Species loss consists of two components: the number of lost species and the identity of those species. In other words, species loss includes a decline in richness irrespective of the identity of the species lost (a random component) and any pattern that might exist in the identity of the species lost (a non-random component). Here, we found that the importance of species loss to ecosystem function can be predicted by two factors: (a) whether species loss was random or not; and (b) the extent of functional dominance in the ecological community. In experiments, and in natural communities with low functional dominance, the identity of lost species was random, and the effects of species loss were important. However, in natural communities with high functional dominance, the effect of species loss was weak, because the species that contribute less to function (often, the rare species; Supporting Information Appendix S6) were more likely to be lost. In these natural communities, changes in function were driven by shifts in the abundance and per-capita function of the persistent, functionally dominant species.

Our findings might help to reconcile a discrepancy between the results of biodiversity–ecosystem function experiments, which overwhelmingly find that species richness is a strong driver of ecosystem function (Cardinale et al., 2012), and studies done in natural communities, which have variously implicated species richness (Duffy et al., 2016, 2017; Grace et al., 2016; Mora et al., 2011), the order of species loss (Larsen et al., 2005), dominant species (Genung et al., 2017; Winfree et al., 2015) or aggregate abundance (Smith & Knapp, 2003) as important to function. The contributions of lost species were more important when functional dominance was low, whereas spatial variation in function provided by common species was more important when functional dominance was high. This finding is consistent with

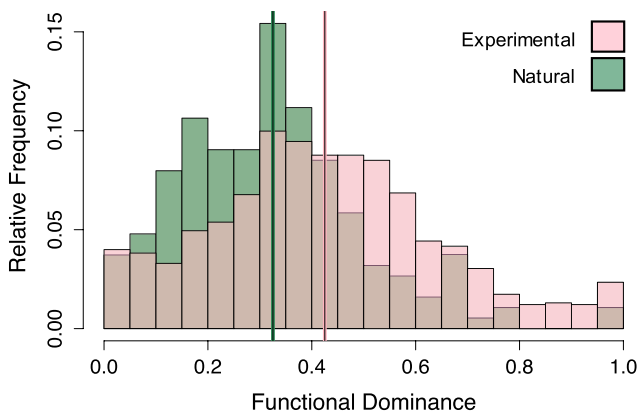


FIGURE 3 The function measured by the experimental community data is grassland plant biomass (northern USA and Germany), and for the natural community data the functions include temperate grassland biomass (northern USA), kelp forest biomass (near California, USA) tropical forest carbon storage (tropics worldwide) and crop pollination (eastern USA). Each ecosystem function (e.g., pollination) or experiment (e.g., Biodiversity II) had a different number of sites or plots. Thus, to give all functions and experiments the same influence on the histogram, we randomly subset each function or experiment to have the same number of sites (natural communities) or plots (experimental communities). The histogram is one representative result from this “random subset” process. Vertical lines are mean values for experimental and natural communities [Colour figure can be viewed at wileyonlinelibrary.com]

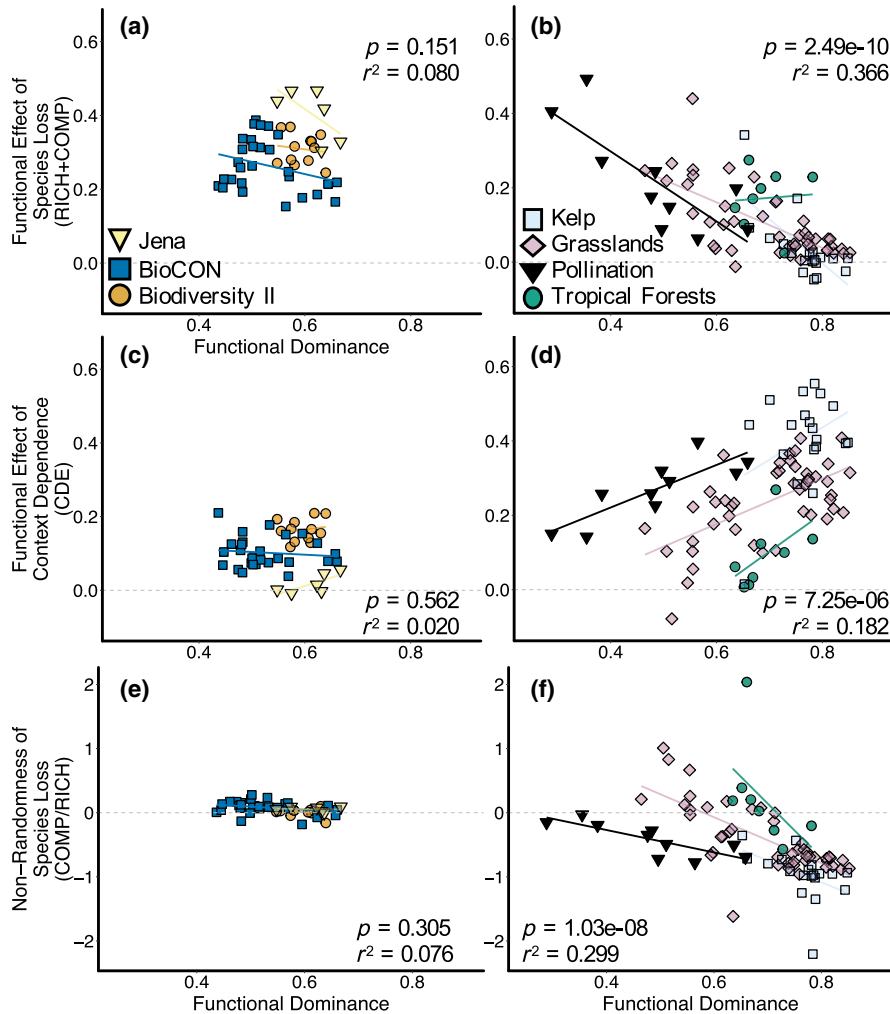


FIGURE 4 (a,c) In experimental communities, functional dominance does not predict how ecosystem function changes as a result of either (a) species loss or (c) context dependence. (b,d) In natural communities, functional dominance (b) decreases the effects of species loss but (d) increases the effects of context dependence, which occurs independent of any changes in richness or composition. (e) In experiments, species are lost at random regardless of dominance. (f) In natural communities, as dominance increases the lost species are increasingly those with low function. The p and semi-partial r^2 values are for the effect of functional dominance nested within different experiments or ecosystem functions. Symbols show experiments (a,c,e; all grassland plant biomass, Minnesota, USA; Germany) or functions (b,d,f; grassland plant biomass, Minnesota, USA; kelp forest biomass, near California, USA; tropical forest carbon storage, tropics worldwide; and crop pollination, eastern USA) [Colour figure can be viewed at wileyonlinelibrary.com]

recent work indicating that species richness and evenness can drive function through distinct mechanisms (Sonkoly et al., 2019).

Instead of linking species richness with function without accounting for community composition and abundance, in which case richness is an implicit surrogate for changes in composition and abundance that co-vary with richness, the ecological Price equation assigns effect sizes to all three (Fox, 2006; Fox & Kerr, 2012; shifts in abundance are a component of the context dependence effect). This is an important strength and allowed us to explore how changes in functional dominance affected the relative importance of species loss and context dependence. However, the ecological Price equation also has limitations. For example, it provides less information about the shape of the richness–function relationship, and it is not a tool for identifying the effects of complementarity (Fox, 2006). For two reasons, it is possible that the ecological Price equation could find a weak effect of species loss, whereas a conventional analysis with generalized linear models finds species loss to be correlated with function. First, it is possible that even when dominant species drive changes in function, positive effects of species richness on function are still strong enough to detect statistically. Second, the ecological Price equation defines the effects of “richness” differently from the way in which it is defined in the generalized linear models usually used to analyse biodiversity

experiments (Fox, 2006). The ecological Price equation compares sites with one another in pairwise fashion, allowing it to isolate the effect of species richness per se, defined as the effect of changing species richness independent of any changes in mean function per species. Generalized linear models of biodiversity experiments estimate the often-nonlinear association between species richness and function, averaging over all sites and over the other predictor variables included in the model. There is no straightforward mapping between the terms in the ecological Price equation and the terms estimated by a generalized linear model. Despite these differences, our ecological Price equation analysis is, for experimental communities, in agreement with decades of studies showing that species loss can be a major driver of declines in function (Cardinale et al., 2012). Perhaps the more pressing issue to resolve is the difference between our results and other studies using real-world, observational data that have used sophisticated methods to control for abiotic differences between sites but did not investigate the role of shifts in composition and abundance that occur alongside changes in richness. These studies have found that species richness is an important driver of function (Duffy et al., 2017; Grace et al., 2016). Here, when we separate the effects of composition from richness but cannot account directly for the role of abiotic variation, we find that the importance of species loss is negatively correlated with functional

dominance. Whether richness, composition, abundance or abiotic effects drive ecosystem functioning in nature is a key question for future studies.

Our findings also show that biodiversity–ecosystem function experiments are more similar to natural communities than expected. First, it has been suggested that experiments that equalize the initial abundances of species (Schmid et al., 2002) do not provide an accurate reflection of ecological communities (Kirwan et al., 2007; Lamb et al., 2011; Schwartz et al., 2000), which tend to have a few common and many rare species (McGill et al., 2007). However, we found that the mean functional dominance in experiments was consistent over time (Supporting Information Appendix S7) and slightly higher than functional dominance in natural communities (Figure 3). Thus, it was not differences in functional dominance per se between experimental and natural communities that drove the different effects of species loss. Instead, strong dominance led to the preferential loss of low-functioning species in nature, whereas in experiments strong dominance had no such effect because species identity was randomized. Second, the average decline in function between higher- and lower-function sites, at least for the datasets included in our analysis, was similar in experimental and natural communities (Figure 2). This is a crucial point; the larger effects of species loss in experiments was largely driven by the identity of lost species ($\overline{\text{COMP}}$; Figure 2), not because there was a greater reduction in function between experimental plots relative to between sites in natural ecosystems (see also Supporting Information Appendix S8).

In conclusion, it has often been questioned whether biodiversity–ecosystem function experiments, which are based on random community assembly, provide a good model for the functional effects of species loss in nature, where extinction risk varies among species (Gross & Cardinale, 2005; Loreau et al., 2001; Schlöpfer, Pfisterer, & Schmid, 2005; Srivastava, 2002; Symstad & Tilman, 2001). Here, we used the ecological Price equation to compare the roles in ecosystem function of species loss, in its random and non-random components, with changes in the functional contributions of persistent species, which take place in the absence of species loss. We found that experiments provide a good model system in several important ways. However, the design that allowed experiments elegantly to isolate the effect of richness (i.e., random assignment of species to plots) prevented detection of the non-random loss of low-functioning species, a key factor determining whether species loss matters for ecosystem function in nature.

Continuing to develop an understanding of when, and how often, it is necessary to retain many species to sustain ecosystem function is an ongoing challenge for ecologists and will help to clarify the conditions in which conservation based on ecosystem function extends to the conservation of rare species (Adams, 2014; Kleijn et al., 2015).

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DATA AVAILABILITY STATEMENT

Sources, links and data use licences to publicly available data are given in the Supporting Information Appendix S2. Pollination data is available on Dryad and the appropriate link is given in Appendix S2. Tropical forest data can be accessed by emailing info at wildlifein sights.org.

CODE AVAILABILITY STATEMENT

The R code used to generate the results of this study is available in Figshare at <https://figshare.com/s/981b7ad2ab845ca3ea18>

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BIOSKETCHES

Mark A. Genung studies the community and evolutionary ecology of plant–pollinator interactions.

Jeremy Fox studies population, community and evolutionary ecology and is especially interested in population dynamics.

Rachael Winfree studies the importance of biodiversity for real-world ecosystem functioning. All three authors are interested in the relationship between biodiversity and ecosystem function and especially in the analysis of observational biodiversity–function data.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX: DATA SOURCES

Reich, P. B., Hobbie, S., & Montgomery, R. (2017). BioCON: Biodiversity, Elevated CO₂, and N Enrichment—Experiment 141. Plant aboveground biomass data. Retrieved from <https://www.cedar.creek.umn.edu/research/data/dataset?ple141>

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