Mass ratio effect underlie ecosystem responses to environmental change. Change in dominance drives ecosystem response to global environmental change

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Abstract:

1. Random species loss has been shown experimentally to reduce ecosystem function, sometimes more than other anthropogenic environmental changes. Yet, controversy surrounds the importance of this finding for natural systems where species loss is non-random.
2. We compiled data from 16 multi-year experiments located at a single native tallgrass prairie site. These experiments included responses to 11 anthropogenic environmental changes, as well as non-random biodiversity loss either the removal of uncommon/rare plant species or the most common (dominant) species.
3. As predicted by the mass ratio hypothesis, loss of a dominant species had large impacts on productivity that were comparable to other anthropogenic drivers. In contrast, the loss of uncommon/rare species had small effects on productivity despite having the largest effects on species richness.
4. The anthropogenic drivers that had the largest effects on productivity nitrogen, irrigation, and fire experienced not only loss of species but also significant changes in the abundance and identity of dominant species.
5. *Synthesis*. These results suggest that mass ratio effects, rather than species loss per se, are an important determinant of ecosystem function with environmental change.

Article:

1 INTRODUCTION

Humans are dramatically altering Earth's terrestrial ecosystems through burning of fossil fuels, climate changes such as warming and the magnification of droughts and deluges, nutrient eutrophication, and the suppression or intensification of disturbance regimes (Smith, Knapp, & Collins, 2009; Steffen et al., 2015). In recognition that species are being lost at rates far exceeding those historically observed due to these and other anthropogenic changes (Pimm et al., 2014), numerous experiments have examined the impacts of simulated biodiversity loss on ecosystem functioning. The widely accepted consensus from these biodiversity-ecosystem functioning (BEF) experiments is that loss of biodiversity leads to declines in ecosystem functions, such as productivity (Cardinale et al., 2011, 2012; Hector et al., 1999; Hooper et al., 2012; Tilman et al., 2001), with these effects equivalent to or exceeding those caused by other human-driven environmental changes (Hautier et al., 2015; Hooper et al., 2012; Tilman, Reich, & Isbell, 2012). Yet, a vigorous debate continues to surround the interpretation of results from BEF experiments (Pillai & Gouhier, 2019) and their relevance for 'real-world' ecosystems (van der Plas, 2019; Wardle, 2016).

By varying richness through random draws of species from a constrained species pool, a majority of BEF studies make the faulty assumption that species are lost randomly from communities as a result of anthropogenic change (Lepš, 2004; Wardle, Bardgett, Callaway, & Putten, 2011). Instead, non-random loss of species is likely the norm (Gaston, 2010; Wardle, 2016). Fundamentally, non-random species loss arises from a pattern that characterizes a broad range of communities: species vary in their abundances, with often only a few highly abundant species and many uncommon or rare species. All else being equal, uncommon and rare species are more susceptible to loss by virtue of having low abundances (Fischer & Stocklin, 1997; Leach & Givnish, 1996; Thomas, 1994; Wilsey & Polley, 2004), whereas common species are least likely to be lost due to their high abundances (Duncan & Young, 2000). The traits that confer abundance also are thought to determine the impacts of species loss on ecosystem functioning (Grime, 1998). Rare species typically have weak effects on ecosystem processes (except in the case of keystone species; Power et al., 1996). Common species have large effects on ecosystem processes if they are dominant in the community (Avolio et al., 2019), as predicted by the mass ratio hypothesis (Grime, 1998). Consequently, non-random loss of rare versus. common species should have dramatically different effects on ecosystem functioning (Sala, Lauenroth, McNaughton, Rusch, & Zhang, 1996).

Given that non-random loss typifies 'real-world' communities, it is crucial to understand the nature of non-random species loss because such scenarios of loss likely vary dependent on the type of anthropogenic change. For example, loss of rare species can occur with extreme drought (Hoover, Knapp, & Smith, 2014; Tilman & Haddi, 1992) and altered disturbance regimes (Koerner et al., 2014), whereas loss of common species has been found with chronic nutrient deposition (Avolio et al., 2014; Isbell et al., 2013) and selective harvesting (Gaston, 2010). In addition, duration and magnitude of anthropogenic perturbations are likely important. The hierarchical response framework predicts that chronic resource alterations resulting from anthropogenic change will result in the largest impacts on ecosystem function when turnover

(loss or change in identity) of dominant species occurs (Smith et al., 2009). Similarly, large magnitude pulse perturbations, such as climate extremes, are also expected to invoke large changes in ecosystem function if dominant species are impacted (Smith, 2011).

When compared to the numerous BEF experiments manipulating richness randomly (e.g. Cardinale et al., 2011), far fewer studies have imposed scenarios of non-random loss of species (Isbell, Losure, Yurkonis, & Wilsey, 2008; Losure, Wilsey, & Moloney, 2007; Smith & Knapp, 2003; Smith, Wilcox, Kelly, & Knapp, 2004; Zavaleta & Hulvey, 2004; Zobel, Zobel, & Rosén, 1994). In the few cases where non-random loss has been considered experimentally, richness effects on ecosystem functioning can be smaller (e.g. Smith & Knapp, 2003) or larger (e.g., Zavaleta & Hulvey, 2004) than observed in random loss experiments. Observational studies in natural systems mirror these results; richness has effects on ecosystem function that are not consistent (Adler et al., 2011; Grace et al., 2007), opposite (Grace et al., 2016) or smaller than (van der Plas, 2019) those observed in random loss experiments (Cardinale et al., 2011; De Laender et al., 2016). These conflicting views of the importance of biodiversity in driving ecosystem functioning point to the need to consider 'real-world' (non-random) patterns of species loss versus those simulated in the majority of BEF experiments (Wardle, 2016; Wardle et al., 2011). Resolving these conflicting perspectives is key to both understanding and forecasting future ecosystem functioning and stability.

Here, we compare the effects of anthropogenic environmental changes to the effects of two scenarios of non-random species loss on a key ecosystem function: aboveground net primary productivity (ANPP) and species richness. We use data from 16 experiments which yield 23 treatments (duration from 2 to 28 years, Table 1) that manipulated nutrients (addition of N, P and/or K), water (irrigation to alleviate water limitation or shelters to simulate extreme drought), elevated CO_2, increased temperature, fire (present or absent), grazing by a native large vertebrate (bison present or absent), herbivory by other vertebrates (e.g. deer, rabbits) or invertebrates, or non-random species loss. Our meta-level analysis (sensu Vetter, Rucker, & Storch, 2013) controlled for potentially confounding variables (climate, soils, vegetation type) that complicate findings from meta-analyses that span disparate sites. Instead, we include only experiments conducted at the Konza Prairie Biological Station (Kansas, USA) in native mesic grassland ecosystems with similar soils and initial plant species compositions.

We test the hypothesis that effects of non-random alterations in plant richness are comparable, may exceed or may be far less than the effects of anthropogenic environmental changes on ecosystem function. We specifically contrasted the impacts of two alternative ways in which species loss may occur non-randomly in natural systems with anthropogenic change: (a) rare species are lost first, and thus species loss is inversely related to abundance (Fischer & Stocklin, 1997; Leach & Givnish, 1996; Wilsey & Polley, 2004) or frequency or occurrence in the community (Smith & Knapp, 2003) or (b) where a dominant species is lost (Gaston, 2010). Following Avolio et al. (2019), we define dominant species as a species that has high abundance relative to other species in a community and proportionate effects on ecosystem function. Consistent with the mass ratio hypothesis (Grime, 1998), we predicted that the loss of dominant species would have larger impacts on ecosystem function than changes in richness via the loss of uncommon species. This expectation challenges previous findings that random biodiversity loss (i.e. via changes in richness) drives changes in ecosystem function (Hautier et al., 2015; Hooper

et al., 2012; Tilman et al., 2012). Furthermore, we expected the effects of dominant species loss would have comparable or even larger effects on ecosystem function than other anthropogenic environmental changes.

Table 1. Summary of the 16 experiments comprising 23 treatments utilized in the meta-level analyses

Experimental variable	Treatment levels used in analyses	Study period (no. years)	Source
Nitrogen addition	**0** or 100 kg N · ha^{-1} · year^{-1}	2003–2012 (10 years)	Avolio et al. (2014)
Nitrogen addition	**0** or 100 kg N · ha^{-1} · year^{-1}	2008–2012 (5 years)	La Pierre, Blumenthal, Brown, Klein, and Smith (2016)
Nitrogen addition	**0** or 100 kg N · ha^{-1} · year^{-1}	1986–2012 (26 years)	Collins, Knapp, Briggs, Blair, and Steinauer (1998)
Nitrogen addition	**0** or 100 kg N · ha^{-1} · year^{-1}	1998–1999 (2 years)	Silletti, Knapp, and Blair (2004)
Phosphorous addition	**0** or 100 kg P · ha^{-1} · year^{-1}	2003–2012 (10 years)	Avolio et al. (2014)
Phosphorous addition	**0** or 100 kg P · ha^{-1} · year^{-1}	2008–2012 (5 years)	La Pierre et al. (2016)
Potassium addition	**0** or 100 kg K · ha^{-1} · year^{-1}	2008–2012 (5 years)	La Pierre et al. (2016)
Water addition	**Non-irrigated** or Irrigated	1991–2011 (21 years)	Collins et al. (2012)
Drought	**Ambient rain** or ~66% decrease	2010–2011 (2 years)	Hoover et al., (2014)
CO_2	**Chamber ambient** or 100% enrichment (ANPP only)	1989–1996 (8 years)	Owensby, Ham, Knapp, and Auen (1999)
Warming	**Unheated** or ~+2°C year round	2003–2011 (9 years)	Fay et al. (2011)
Fire	**Unburned** or annual burn (ANPP only)	1984–2011 (28 years)	[a]
Fire	**Unburned** or annual burn (ANPP only)	1989–1997 (7 years)	[a]
Fire	**Unburned** or annual burn	1986–2012 (26 years)	Collins et al. (1998)
Fire	**Unburned** or annual burn (Species comp only)	1983–2000 (18 years)	[a]
Bison grazing	**Unfenced** or bison (large herbivore) exclosure	2007–2008 (2 years)	Knapp et al. (2012); Koerner et al. (2014)
Vertebrate herbivory	**Unfenced** or deer and small herbivore exclosure	2009–2012 (4 years)	La Pierre, Joern, and Smith (2015)
Vertebrate herbivory	**High vertebrate density** or no vertebrates	1985–1986 (2 years)	Gibson, Freeman, and Hulbert (1990)
Invertebrate herbivory	**Untreated** or insecticide aboveground	2009–2012 (4 years)	La Pierre et al. (2015)
Invertebrate herbivory	**Untreated** or insecticide aboveground	1985–1986 (2 years)	Gibson et al. (1990)
Invertebrate herbivory	**Untreated** or insecticide belowground	1985–1986 (2 years)	Gibson et al. (1990)
Dominance removal	**Control**, 100% *Andropogon gerardii* removal, or 100% *Sorghastrum nutans* removal	1998–1999 (2 years)	Silletti et al. (2004
Richness decrease	**Untreated (14–16)**, 10–12, 7–9, or 4–6 species	2000–2001 (2 years)	Smith & Knapp (2003)

Note. For each experimental variable, the treatment listed in boldface was designated as the reference (control). Detailed methods for each experiment can be found in the publication listed under Source.

[a] Description of methods are available online: http://lter.konza.ksu.edu/Methods%20Manual.

2 MATERIALS AND METHODS

The 23 datasets utilized in this analysis are from 16 experiments (Table 1) performed at the Konza Prairie Biological Station, a National Science Foundation Long-Term Ecological Research (LTER) site. Konza Prairie is a 3,487-ha tallgrass prairie preserve located in the Flint Hills region of northeastern Kansas on the western edge of the historic tallgrass prairie distribution (39.11°N, 96.61°W). Data were collected over the period of 1983–2012. We chose this time period because it encompassed the greatest number of experimental manipulations. Some experiments span that entire time frame, while others were as short as 2 years (Table 1). Experiments included in this study either altered resource availability or manipulated the plant community. The latter was done by either removing 100% of a dominant grass species (either *Andropogon gerardii* or *Sorghastrum nutans*) or non-randomly reducing richness from an average of ~16 species per 0.5 m^2 plot to either 4–6, 7–9 or 10–12 species per 0.5 m^2 plot by removing species based on their rank abundance (relative frequency in the community) from the lowest rank (least frequent species) until the target range of richness was achieved (see Smith & Knapp, 2003 for further details). For most experiments, treatment response (ANPP and plant community richness) was measured annually.

To evaluate responses of productivity to different drivers, we utilized 22 datasets comparing mean annual net primary production (ANPP) in reference plots with plots manipulating: available soil nitrogen (N), available soil phosphorus (P), available soil potassium (K), precipitation amount (both addition and reduction), atmospheric CO_2 concentration, air temperature, fire, grazing by large ungulates (bison), herbivory by deer and small mammals, herbivory by invertebrates, plant species richness and dominant species abundance (Table 1). These analyses use the mean ANPP across all replicates of a treatment for a given year. By comparing multiple years of annual treatment means, we were able to test for consistent differences between responses of 13 different environmental change drivers. For each sampled year of an experiment, we use mean ANPP across all replicates of a treatment to derive a metric to test for ANPP response to environmental change following Tilman et al. (2012). The log response ratio was calculated for each year of each experiment using the equation:

$$\ln(RR)_{ANPP} = \left| \ln \left(\frac{ANPP_m}{ANPP_c} \right) \right| \qquad (1)$$

where $ANPP_m$ represents the annual average of productivity in manipulated plots of an experiment in a certain year, and $ANPP_c$ represents the annual average of ANPP in reference (control) plots of the same experiment and year. Reference plots were unmanipulated or in the case of fire, unburned, or for grazing, grazed. In addition, control plots with ambient (unmanipulated) plant richness (~average of 16 species per 0.5 m^2; Smith & Knapp, 2003) and naturally high abundance (>80% cover; Silletti & Knapp, 2002) of the dominant, productive C$_4$ grasses (*Andropogon gerardii* and *Sorghastrum nutans*) were compared to those in which either richness was non-randomly reduced (i.e. richness decrease treatments: 10–12, 7–9 or 4–6 target richness) or where a dominant plant species was removed completely (i.e. dominant species removal treatments: 100% of either *A. gerardii* or *S. nutans*).

Following Tilman et al. (2012), the absolute values of the response ratio were used to estimate the magnitude of response of manipulated compared with reference plots without the potentially confounding impact of including directionality of responses. Log response ratios were averaged

across years and experiments for each driver type and compared using a one-way ANOVA and Tukey-adjusted multiple comparison of least-square means using proc MIXED in SAS (Version 9.3).

Similarly, we explored the responses of plant species richness (the number of species within a plot) to 12 different types of anthropogenic drivers (no species composition data was available for CO_2). Here we used species composition data from 20 datasets. We calculated the log response ratio of richness $(ln(RR)_{Rich})$ using Equation (1) and then ran the same statistical tests.

Finally, we examined community compositional shifts with the long-term manipulations of nitrogen, precipitation amount and fire frequency. To identify community shifts, plant community composition data after 15 years of manipulation were analyzed. We first visualized differences in community composition using non-metric multidimensional scaling (NMDS) plots. Second, we tested for significant differences ($\alpha = 0.05$) between mean centroids of treatment and control communities for each experiment by conducting a PERMANOVA (Anderson, 2001) analysis using a Bray–Curtis resemblance matrix and 999 simulations. Lastly, we conducted a similarity percentage analysis (SIMPER; Clarke, 1993) to quantify the relative contributions of each species to the divergence of community composition between manipulated and control plots. All multivariate analyses were conducted in PRIMER 6 (Version 6.1.13).

3 RESULTS

Across all years of the 16 experiments, ANPP was affected the most by the addition of N (100 kg/ha) or the complete removal of a dominant species (Figure 1a). The overall effect of N addition was to significantly increase productivity, whereas removal of a dominant species had the opposite effect. Precipitation manipulations, either as irrigation or imposed drought, and fire were intermediate in their effects on productivity (Figure 1a). Both water addition and fire significantly increased productivity while drought decreased productivity. There were no long-term temporal trends in the effects of nitrogen addition, water addition or fire (Figure 2). On the other hand, the loss of uncommon species (richness decrease, Figure 1a) had a relatively small, yet positive effect on productivity. This effect was not significantly different from any of the other treatments, including manipulations of P, K, CO_2, temperature, grazing and invertebrate/vertebrate herbivory.

Species richness responded most strongly to fire, grazing by a native large herbivore and N addition (Figure 1b). Frequent fire, N addition and the removal of grazers led to a significant loss of species. Richness responses to all other treatments, except species removals, were relatively minor and similar in magnitude (though differing in directionality, for example irrigation decreased richness, whereas drought increased richness; Figure 1b). Non-random species loss (removal of uncommon species) resulted in the greatest absolute loss in richness, but the magnitude of this loss did not differ from that of fire, N addition, grazing or removal of a single dominant species.

Of the anthropogenic drivers in which there were long-term records of plant community composition (N, fire and water addition), all three drivers significantly shifted plant species composition (Figure 3). In the case of water and N additions, compositional shifts were driven

primarily by a large increase in abundance of the productive, perennial C_4 grass *Panicum virgatum* (Table 2). In contrast, compositional shifts with fire resulted primarily from the loss of the less productive perennial C_3 grass *Poa pratensis*, and increased abundance of other, more productive perennial C_4 grasses *S. nutans* and *Schizachyrium scoparium* (Table 2).
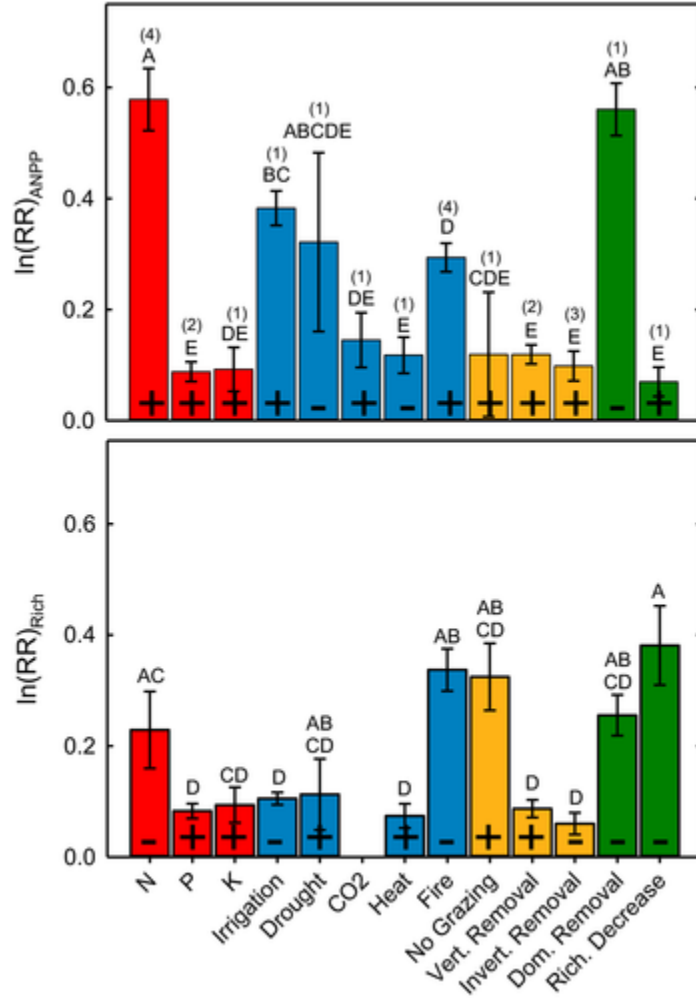
Figure 1. Relative effects (log response ratio) of anthropogenic environmental drivers (*red*, *blue* and *yellow bars*; see Table 1), non-random species loss (*green bars*; dom. removal = removal of the dominant species only; rich. decrease = removal of rare or uncommon species only) on (*top*) ecosystem productivity and (*bottom*) plant community richness. Shown are means (±1 *SE*) of absolute values of the log response ratios for aboveground net primary productivity (ln(RR)$_{ANPP}$) and species richness (ln(RR)$_{Rich}$; see text for details). Note, richness data were not available for the CO_2 experiment. All statistical results are from one-way ANOVAs (ANPP: $F_{12,239} = 9.07$, $p < .001$; Rich: $F_{11,149} = 5.64$, $p < .001$). Significant differences ($\alpha = .05$) between treatments are represented by different letters. ±Symbols represent the direction of the mean effect of a treatment. Numbers in parentheses above bars indicate the number of studies per manipulation category for both panels
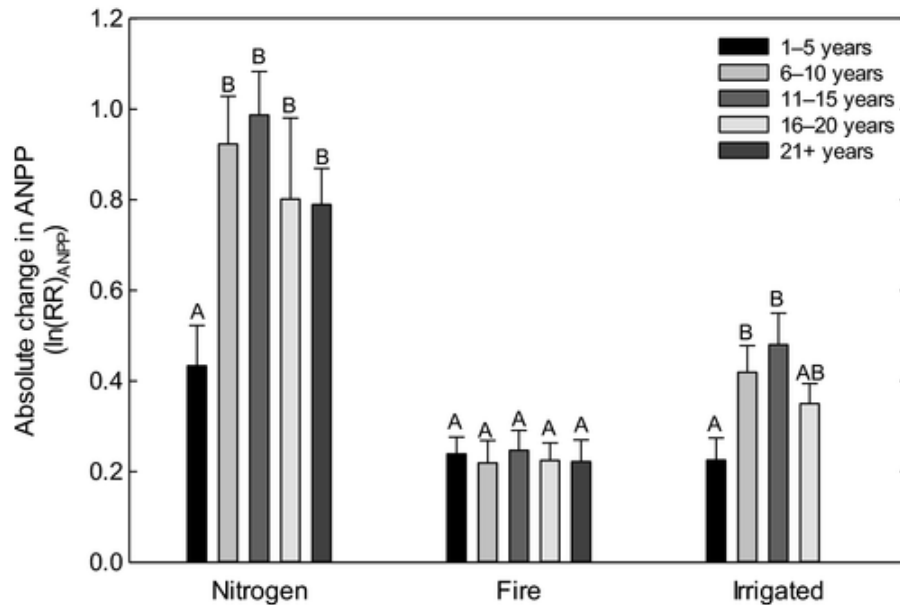
Figure 2. Temporal trends in effect sizes of aboveground net primary production (ANPP) for three anthropogenic drivers (±1 *SE*). Significant differences ($\alpha \leq .05$) between time periods are represented by different letters. N: $F_{4,22} = 3.42$, $p = .026$; Fire: $F_{2,49} = 0.07$, $p = .991$; Water: $F_{3,36} = 3.80$, $p = .018$
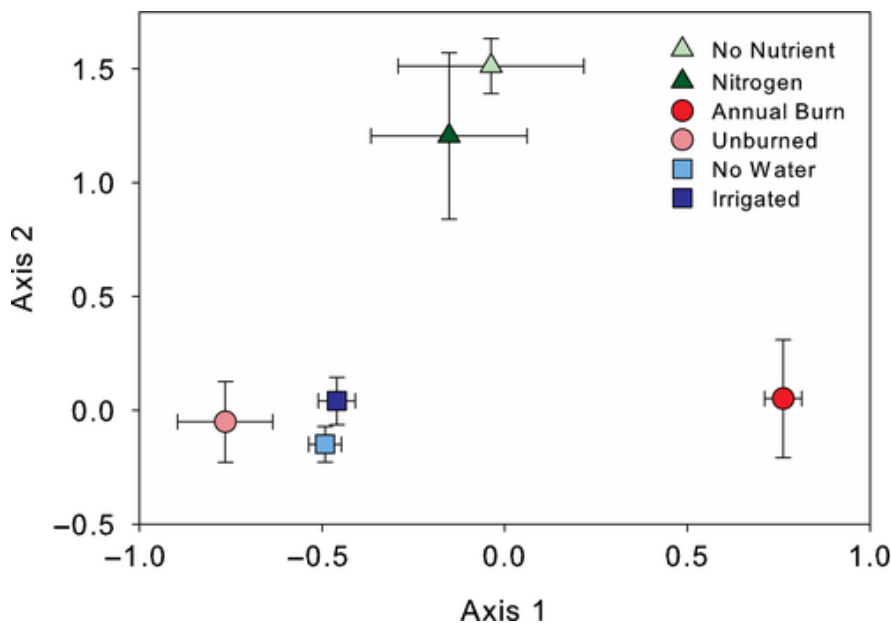
Figure 3. Non-metric multidimensional scaling based on Bray–Curtis dissimilarity for long-term fire (*red circles*), irrigation (*blue squares*) and nitrogen (*green triangles*) experiments. Each point is the centroid for a given cluster of points (±1 *SE*). The light colours are the centroids of the reference plots for each experiment, while the dark colours are the treatment plots for each experiment. This is a snap shot in time showing how the control and treatment plots are different after 15+ years of manipulation. All treatment communities are significantly different than reference communities based on PERMANOVA analysis (Nitrogen: $df = 1,6$, Pseudo-$F = 14.278$, $p = .0127$; Irrigation: $df = 1,40$, Pseudo-$F = 3.505$, $p = .011$; Fire: $df = 1,14$, Pseudo-$F = 8.407$, $p = .001$)

Table 2. SIMPER results for fire, water and nitrogen long-term experiments

Species	Functional group	Av. abundance in reference	Av. abundance w/fire	Contrib.%	Cum.%
(a) Fire					
Poa pratensis	C$_3$ grass	35.19	0.00	15.10	15.10
Andropogon gerardii	C$_4$ grass	55.18	55.13	10.45	25.55
Solidago canadensis	C$_3$ forb	22.67	0.03	9.52	35.07
Sorghastrum nutans	C$_4$ grass	2.78	16.68	6.14	41.21
Lespedeza violacea	Legume	2.99	14.50	5.88	74.09
Schizachyrium scoparius	C$_4$ grass	2.51	15.65	5.63	52.72

Species	Functional group	Av. abundance in reference	Av. Abundance w/irrigation	Contrib.%	Cum.%
(b) Water					
Panicum virgatum	C$_4$ grass	27.57	48.10	22.46	22.46
S. canadensis	C$_3$ forb	7.24	25.14	13.84	36.29
A. gerardii	C$_4$ grass	62.24	66.14	11.50	47.79
S. nutans	C$_4$ grass	19.57	19.00	10.47	58.26
Amorpha canescens	Legume	8.05	16.10	8.75	67.02
S. scoparium	C$_4$ grass	10.48	2.24	5.47	72.48

Species	Functional group	Av. Abundance in reference	Av. abundance w/nitrogen	Contrib.%	Cum.%
(c) Nitrogen					
P. virgatum	C$_4$ grass	33.31	95.94	32.81	32.81
A. gerardii	C$_4$ grass	41.00	3.56	18.70	51.51
Helianthus annuus	C$_3$ annual forb	0.06	31.00	14.71	66.22
S. scoparius	C$_4$ grass	11.81	0.00	6.54	72.76
S. nutans	C$_4$ grass	10.38	0.00	5.31	78.07

Note. Results are for the last year of available data. Only species that contributed more than 5% to the difference between treatment and control plots were included. All species are perennial unless otherwise noted.

4 DISCUSSION

Our analysis provides strong evidence that the complete loss of a dominant plant species or a shift in abundance and identity of dominant species (without loss) can cause large reductions (or increases) in productivity (ANPP), a key ecosystem function in grasslands. Importantly, mass ratio effects, resulting from the removal of a dominant or altered abundance or identity of dominants, can far exceed the effects of non-random loss of uncommon and rare species on ecosystem functioning. We found that removal of a single dominant species strongly reduced productivity, as predicted by the mass ratio hypothesis (Grime, 1998) and as found in other dominant species removal studies (Avolio et al., 2019). The magnitude of this effect on ANPP was comparable to that resulting from chronic N addition and irrigation, though opposite in directionality. This contrasting effect was due to chronic N and water additions causing the replacement of the co-dominant grasses by a single and more productive C$_4$ grass (*P. virgatum*; Wilcox, Blair, Smith, & Knapp, 2016), as well as a highly productive annual forb species (*H. annuus*). As further support for the importance of mass ratio effects, the removal of uncommon and rare species had much smaller impacts on productivity than the loss of a single dominant species or other anthropogenic changes, such as fire, N and water additions. Moreover, removal

of uncommon and rare species surprisingly *increased* productivity, rather than reducing ecosystem function as widely observed with simulated random loss of species (Cardinale et al., 2012; Hooper et al., 2012; Tilman et al., 2012). This increase in productivity was due to an increase in biomass of the dominant C_4 grasses with the loss of uncommon and rare species (Smith & Knapp, 2003).

With respect to richness effects, the largest change in richness occurred with non-random species loss, either because of removal of uncommon/rare species or a single dominant species. In both cases, richness decreased significantly. The facilitative role that dominant species may play in maintaining richness has been noted previously (Smith & Knapp, 2003; Stachowicz, 2001), suggesting that in this system dominant species may play a foundational role by modifying environmental conditions to allow coexistence of less abundant species (Ellison et al., 2005). However, other studies have found an increase in richness with removal of a dominant species (Avolio et al., 2019; Lepš, 1999). Therefore, the effects of loss of dominants on richness may depend on whether the dominant plays a facilitative versus competitive role in the community. The reduction in richness that we observed with the loss of the dominant species did not differ, however, from that resulting from other anthropogenic changes. Indeed, fire, grazing by bison and N addition resulted in similar changes in richness as observed with non-random species loss. Hautier et al. (2015) found similar responses of richness. In their case, addition of 95 kg N/ha and herbivore removal both decreased richness, whereas removal of fire increased richness. Thus, short-term manipulations of richness and dominance resulted in either direct or indirect declines in richness that were comparable to losses observed with long-term annual burning and N addition. However, despite similar losses in richness, only the removal of dominant species significantly affected productivity. This effect of dominant species removal suggests that declines in richness are likely not driving the productivity responses observed.

Our findings build on previous experiments (Hautier et al., 2015; Hooper et al., 2012; Tilman et al., 2012) to provide additional mechanistic insight into the relationship between 'real-world' patterns of species loss and altered ecosystem functioning. As proposed by Grime (1998), we found that mass ratio effects rather than declines in richness per se is a key mechanism driving loss in function and underlying ecosystem responses to anthropogenic drivers in natural plant communities. There are several lines of evidence to support this hypothesis. When richness was directly manipulated with removal of uncommon/rare species, the largest richness loss occurred, but productivity increased rather than decreased. When species were lost with long-term fire, irrigation and N additions, the impacts of these changes in richness on productivity were inconsistent. Long-term annual burning resulted in some of the largest declines in richness, yet productivity was increased rather than reduced. Similarly, chronic N additions caused a moderate decrease in richness, but the largest increase in productivity. In contrast, although irrigation increased productivity, there was little change in richness. When delving deeper into the effects of these anthropogenic changes on plant community composition, what is clear is that composition changed significantly with these manipulations and that the primary determinant of the compositional change was not richness change but rather reduced abundance of dominant species, a change in their identity and/or complete loss of a dominant.

Collectively, our results suggest that future research aimed at understanding the impacts of anthropogenic change on ecosystem function should elucidate the nature of plant community

change, particularly the identity and degree of change of species abundances and dominance, and in turn, how these different ways of altering composition may affect ecosystem functioning (Magurran, 2016). Several studies have examined the effects of changes in species evenness via either changing species abundances (Sonkoly et al., 2019; Wilsey & Polley, 2004) or reducing abundance of a dominant species (Isbell et al., 2008; Smith & Knapp, 2003), with varying results. Wilsey and Polley (2004) found that a change in evenness from a maximum level to a realistically low level has little effect on productivity when compared to random loss of species. Similarly, Isbell et al. (2008) found little effect of evenness when comparing realistic extinction scenarios (four vs. a single species = monocultures of a dominant grass). In contrast, Sonkoly et al. (2019) found that a reduction of evenness had a positive effect on productivity, as a result of increased abundance of the perennial dominant grasses. Smith and Knapp (2003) also found that the effects of reducing abundance of the dominant grasses (or increasing evenness) were large, but that non-random species loss had no significant effect on productivity. Clearly, additional research is needed to understand how changes in species evenness may affect ecosystem function (Hillebrand, Bennett, & Cadotte 2008). We contend, however, much less is known about how loss of dominant species or changes in their identity impacts ecosystem function (Avolio et al., 2019), and future research should be devoted to understanding the consequences of this and other dimensions of plant compositional change for ecosystem functioning and stability.

In summary, the results presented here are in direct opposition to the numerous studies suggesting that random losses of richness decrease ecosystem function as much or more than other anthropogenic changes (Duffy, Godwin, & Cardinale, 2017; Flombaum, Yahdjian, & Sala, 2017; Hautier et al., 2015; Tilman et al., 2012). However, an important difference between our study and others is that we manipulated richness non-randomly to mimic scenarios of species loss that occur in natural systems (e.g. Gaston, 2010; Leach & Givnish, 1996; Lepš, 2004; Wardle, 2016). As such, our results can resolve conflicts regarding the generality of the impact of biodiversity on the function of ecosystems (Duffy et al., 2017). We propose that much of the effect of species loss in natural systems is likely indirect via mass ratio effects (Grime, 1998), which may cascade to alter species richness. Indeed, because direct removal of a dominant species and anthropogenic changes (e.g. irrigation and N additions) lead to both large shifts in the abundance and identity of dominant species, as well as in alterations in richness, this has likely confounded attribution to changes in ecosystem function and stability in the past. Our work suggests that conservation efforts should focus on identifying those dominant plant species that are crucial for maintaining ecosystem function, as well as other aspects of biodiversity (e.g. species richness; Koerner et al., 2018). Given that a universal feature of natural communities is an uneven distribution of species abundances in which only a few species dominate (Whittaker, 1965), the management or restoration of these important dominant species and consideration of their identity, rather than simply focusing on the number or evenness of species in a community, will be critical for maintaining ecosystem functioning and services in the face of global environmental change.

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AUTHORS' CONTRIBUTIONS

M.D.S. conceived the study, S.E.K. conducted the meta-level analyses, and M.D.S. and S.E.K. wrote the manuscript. A.K.K., M.L.A., F.A.C., E.M.D., J.D., D.J.G., J.G., A.M.H., D.L.H., K.J.K., A.S., K.R.W., Q.Y. and J.M.B. helped to compile the datasets and/or contributed datasets to the analysis. All authors edited the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j3tx95x8w (Smith et al., 2019).

REFERENCES

Adler, P. B., Seabloom, E. W., Borer, E. T., Hillebrand, H., Hautier, Y., Hector, A., … Yang, L. H. (2011). Productivity is a poor predictor of plant species richness. *Science*, **333**, 1750– 1753. https://doi.org/10.1126/science.1204498 Google Scholar

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32– 46. Google Scholar

Avolio, M. L., Forrestel, E. J., Chang, C. C., La Pierre, K. J., Burghardt, K. T., & Smith, M. D. (2019). Demystifying dominant species. *New Phytologist*, **223**, 1106– 1126. https://doi.org/10.1111/nph.15789 Google Scholar

Avolio, M. L., Koerner, S. E., La Pierre, K. J., Wilcox, K. R., Wilson, G. W. T., Smith, M. D., & Collins, S. L. (2014). Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. *Journal of Ecology*, **102**, 1649– 1660. https://doi.org/10.1111/1365-2745.12312 Google Scholar

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, **486**, 59– 67. https://doi.org/10.1038/nature11148 Google Scholar

Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., … Gonzalez, A. (2011). The functional role of producer diversity in ecosystems. *American Journal of Botany*, **98**, 572– 592. https://doi.org/10.3732/ajb.1000364 Google Scholar

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117– 143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x Google Scholar

Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M., & Steinauer, E. M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, **280**, 745– 747. https://doi.org/10.1126/science.280.5364.745 Google Scholar

Collins, S. L., Koerner, S. E., Plaut, J. A., Okie, J. G., Breese, D., Calabrese, L. B., … Nonaka, E. (2012). Stability of tallgrass prairie during a 19-year increase in growing season precipitation. *Functional Ecology*, **26**, 1450– 1459. https://doi.org/10.1111/j.1365-2435.2012.01995.x Google Scholar

De Laender, F., Rohr, J. R., Ashauer, R., Baird, D. J., Berger, U., Eisenhauer, N., … Van den Brink, P. J. (2016). Reintroducing environmental chance drivers in biodiversity-ecosystem functioning research. *Trends in Ecology & Evolution*, **31**, 905– 915. Google Scholar

Duffy, J. E., Godwin, C. M., & Cardinale, B. J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, **549**, 261– 264. https://doi.org/10.1038/nature23886 Google Scholar

Duncan, R. P., & Young, J. R. (2000). Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology*, **81**, 3048– 3061. https://doi.org/10.1890/0012-9658(2000)081[3048:DOPEAR]2.0.CO;2 Google Scholar

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., … Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, **3**, 479– 486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2 Google Scholar

Fay, P. A., Blair, J. M., Smith, M. D., Nippert, J. B., Carlisle, J. D., & Knapp, A. K. (2011). Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. *Biogeosciences*, **8**, 3053– 3068. https://doi.org/10.5194/bg-8-3053-2011 Google Scholar

Fischer, M., & Stocklin, J. (1997). Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology*, **11**, 727– 737. Google Scholar

Flombaum, P., Yahdjian, L., & Sala, O. E. (2017). Global-change drivers of ecosystem functioning modulated by natural variability and saturating responses. *Global Change Biology*, **23**, 503– 511. https://doi.org/10.1111/gcb.13441 Google Scholar

Gaston, K. J. (2010). Valuing common species. *Science*, **327**, 154– 155. https://doi.org/10.1126/science.1182818 Google Scholar

Gibson, D., Freeman, C., & Hulbert, L. (1990). Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia*, **84**, 169– 175. https://doi.org/10.1007/BF00318268 Google Scholar

Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., … Smith, M. D. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, **529**, 390– 393. https://doi.org/10.1038/nature16524 Google Scholar

Grace, J. B., Anderson, T. M., Smith, M. D., Seabloom, E., Andelman, S. J., Meche, G., … Willig, M. R. (2007). Does species diversity limit productivity in natural grassland communities? *Ecology Letters*, **10**, 680– 689. https://doi.org/10.1111/j.1461-0248.2007.01058.x Google Scholar

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, **86**, 902– 910. https://doi.org/10.1046/j.1365-2745.1998.00306.x Google Scholar

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, **348**, 336– 340. https://doi.org/10.1126/science.aaa1788 Google Scholar

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., … Lawton, J. H. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123– 1127. https://doi.org/10.1126/science.286.5442.1123 Google Scholar

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology*, **89**, 1510– 1520. https://doi.org/10.1890/07-1053.1 Google Scholar

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., … O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, **486**, 105– 108. https://doi.org/10.1038/nature11118 Google Scholar

Hoover, D. L., Knapp, A. K., & Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, **95**, 2646– 2656. https://doi.org/10.1890/13-2186.1 Google Scholar

Isbell, F., Losure, D. A., Yurkonis, K. A., & Wilsey, B. J. (2008). Diversity-productivity relationships in two ecological realistic rarity-extinction scenarios. *Oikos*, **117**, 996– 1005. Google Scholar

Isbell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 11911– 11916. https://doi.org/10.1073/pnas.1310880110 Google Scholar

Knapp, A. K., Hoover, D. L., Blair, J. M., Buis, G., Burkepile, D. E., Chamberlain, A., … Zinn, A. (2012). A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. *Journal of Plant Ecology*, **5**, 357– 365. https://doi.org/10.1093/jpe/rts020 Google Scholar

Koerner, S. E., Burkepile, D. E., Fynn, R. W. S., Burns, C. E., Eby, S., Govender, N., … Smith, M. D. (2014). Plant community response to loss of large herbivores differs between North American and South African savanna grasslands. *Ecology*, **95**, 808– 816. https://doi.org/10.1890/13-1828.1 Google Scholar

Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., … Zelikova, T. J. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution*, **2**, 1925– 1932. https://doi.org/10.1038/s41559-018-0696-y Google Scholar

La Pierre, K. J., Blumenthal, D. M., Brown, C. S., Klein, J. A., & Smith, M. D. (2016). Drivers of variation in aboveground net primary productivity and plant community composition differ across a broad precipitation gradient. *Ecosystems*, **19**(3), 521– 533. https://doi.org/10.1007/s10021-015-9949-7 Google Scholar

La Pierre, K., Joern, A., & Smith, M. (2015). Invertebrate, not small vertebrate, herbivory interacts with nutrient availability to impact tallgrass prairie plant community composition and forb biomass. *Oikos*, **124**, 842– 850. Google Scholar

Leach, M. K., & Givnish, T. J. (1996). Ecological determinants of species loss in remnant prairies. *Science*, **273**, 1555– 1558. https://doi.org/10.1126/science.273.5281.1555 Google Scholar

Lepš, J. (1999). Nutrient status, disturbance and competition: An experimental test of relationships in a wet meadow. *Journal of Vegetation Science*, **10**, 219– 230. https://doi.org/10.2307/3237143 Google Scholar

Lepš, J. (2004). What do the biodiversity experiments tell us about consequences of plant species loss in the real world? *Basic and Applied Ecology*, **5**, 529– 534. https://doi.org/10.1016/j.baae.2004.06.003 Google Scholar

Losure, D. A., Wilsey, B. J., & Moloney, K. A. (2007). Evenness-invasibility relationships differ between two extinction scenarios in tallgrass prairie. *Oikos*, **116**, 87– 98. https://doi.org/10.1111/j.2006.0030-1299.15341.x Google Scholar

Magurran, A. E. (2016). How ecosystems change. *Science*, **351**, 448– 449. https://doi.org/10.1126/science.aad6758 Google Scholar

Owensby, C. E., Ham, J. M., Knapp, A. K., & Auen, L. M. (1999). Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO_2. *Global Change Biology*, **5**, 497– 506.

Pillai, P., & Gouhier, T. C. (2019). Not even wrong: The spurious measurement of biodiversity's effects on ecosystem functioning. *Ecology*, **100**(7), e02645. https://doi.org/10.1002/ecy.2645 Google Scholar

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., … Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**, 1246752. https://doi.org/10.1126/science.1246752 Google Scholar

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., … Paine, R. T. (1996). Challenges in the quest for keystones. *BioScience*, **46**, 609– 620. https://doi.org/10.2307/1312990 Google Scholar

Sala, O. E., Lauenroth, W. K., McNaughton, S. J., Rusch, G., & Zhang, X. (1996). *Biodiversity and ecosystem functioning in grasslands functional roles of biodiversity: A global perspective* (pp. 129– 149). In H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, & E.-D. Schulze (Eds.). Chichester: John Wiley & Sons Ltd. Google Scholar

Silletti, A., & Knapp, A. (2002). Long-term responses of the grassland co-dominants *Andropogon gerardii* and *Sorghastrum nutans* to changes in climate and management. *Plant Ecology*, **163**, 15– 22. Google Scholar

Silletti, A. M., Knapp, A. K., & Blair, J. M. (2004). Competition and coexistence in grassland codominants: Responses to neighbour removal and resource availability. *Canadian Journal of Botany*, **82**, 450– 460. https://doi.org/10.1139/b04-016 Google Scholar

Smith, M. D. (2011). An ecological perspective on extreme climatic events: A synthetic definition and framework to guide future research. *Journal of Ecology*, **99**, 656– 663. https://doi.org/10.1111/j.1365-2745.2011.01798.x Google Scholar

Smith, M. D., & Knapp, A. K. (2003). Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, **6**, 509– 517. https://doi.org/10.1046/j.1461-0248.2003.00454.x Google Scholar

Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, **90**, 3279– 3289. https://doi.org/10.1890/08-1815.1 Google Scholar

Smith, M. D., Koerner, S. E., Knapp, A. K., Avolio, M. L., Chaves, F. A., Denton, E. M., … Blair, J. M. (2019). Data from: Meta-level analysis of global change experiments. Dryad Digital Repository, https://doi.org/10.5061/dryad.j3tx95x8w Google Scholar

Smith, M. D., Wilcox, J. C., Kelly, T., & Knapp, A. K. (2004). Dominance not richness determines invasibility of tallgrass prairie. *Oikos*, **106**, 253– 262. https://doi.org/10.1111/j.0030-1299.2004.13057.x Google Scholar

Sonkoly, J., Keleman, A., Valko, O., Deak, B., Kiss, R., Toth, K., … Torok, P. (2019). Both mass ratio effects and community diversity drive biomass production in a grassland

experiment. *Scientific Reports*, **9**, 1848. https://doi.org/10.1038/s41598-018-37190-6 Google Scholar

Stachowicz, J. J. (2001). Mutualism, facilitation, and the structure of ecological communities. *BioScience*, **51**, 235– 246. https://doi.org/10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2 Google Scholar

Steffen, W., Richardson, K., Rockstrom, J., Cornell, S. E., Fetzer, I., Bennett, E. M., … Sorlin, S. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, **347**(6223). https://doi.org/10.1126/science.1259855 Google Scholar

Thomas, C. D. (1994). Extinction, colonization, and metapopulations: Environmental tracking by rare species. *Conservation Biology*, **8**, 373– 378. https://doi.org/10.1046/j.1523-1739.1994.08020373.x Google Scholar

Tilman, D., & Haddi, A. (1992). Drought and biodiversity in grasslands. *Oecologia*, **89**, 257– 264. https://doi.org/10.1007/BF00317226 Google Scholar

Tilman, D., Reich, P. B., & Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 10394– 10397. https://doi.org/10.1073/pnas.1208240109 Google Scholar

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, **294**, 843– 845. https://doi.org/10.1126/science.1060391 Google Scholar

van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews*. https://doi.org/10.1111/brv.12499 Google Scholar

Vetter, D., Rucker, G., & Storch, I. (2013). Meta-analysis: A need for well-defined usage in ecology and conservation biology. *Ecosphere*, **4**(6), 1– 24. https://doi.org/10.1890/ES13-00062.1 Google Scholar

Wardle, D. A. (2016). Do experiments exploring plant diversity-ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems? *Journal of Vegetation Science*, **27**, 646– 653. https://doi.org/10.1111/jvs.12399 Google Scholar

Wardle, D. A., Bardgett, R. D., Callaway, R. M., & Van der Putten, W. H. (2011). Terrestrial ecosystem responses to species gains and losses. *Science*, **332**, 1273– 1277. https://doi.org/10.1126/science.1197479 Google Scholar

Whittaker, R. H. (1965). Dominance and diversity in land plant communities – Numerical relations of species express importance of competition in community function and evolution. *Science*, **147**, 250– 260. Google Scholar

Wilcox, K. R., Blair, J. M., Smith, M. D., & Knapp, A. K. (2016). Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions? *Ecology*, **97**, 561– 568. https://doi.org/10.1890/15-1437 Google Scholar

Wilsey, B. J., & Polley, H. W. (2004). Realistically low species evenness does not alter grassland species-richness-productivity relationships. *Ecology*, **85**, 2693– 2700. https://doi.org/10.1890/04-0245 Google Scholar

Zavaleta, E. S., & Hulvey, K. B. (2004). Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, **306**, 1175– 1177. https://doi.org/10.1126/science.1102643 Google Scholar

Zobel, K., Zobel, M., & Rosén, E. (1994). An experimental test of diversity maintenance mechanisms, by a species removal experiment in a species-rich wooded meadow. *Folia Geobotanica et Phytotaxonomica*, **29**, 449– 457. https://doi.org/10.1007/BF02883143