

## RESEARCH ARTICLE

# Mass ratio effects underlie ecosystem responses to 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 tall-grass 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.

## KEYWORDS

anthropogenic change, biodiversity, climate change, dominant species, ecosystem function and services, global change ecology, mass ratio hypothesis, non-random species loss

## 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<sub>2</sub>, 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

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

<sup>a</sup>Description of methods are available online: <http://lter.konza.ksu.edu/Methods%20Manual>.

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.

## 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<sup>2</sup> plot to either 4–6, 7–9 or 10–12 species per 0.5 m<sup>2</sup> 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<sub>2</sub> 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:

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

where ANPP<sub>m</sub> represents the annual average of productivity in manipulated plots of an experiment in a certain year, and ANPP<sub>c</sub> 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<sup>2</sup>; Smith & Knapp, 2003) and naturally high abundance (>80% cover; Silletti & Knapp, 2002) of the dominant, productive C<sub>4</sub> 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<sub>2</sub>). 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.

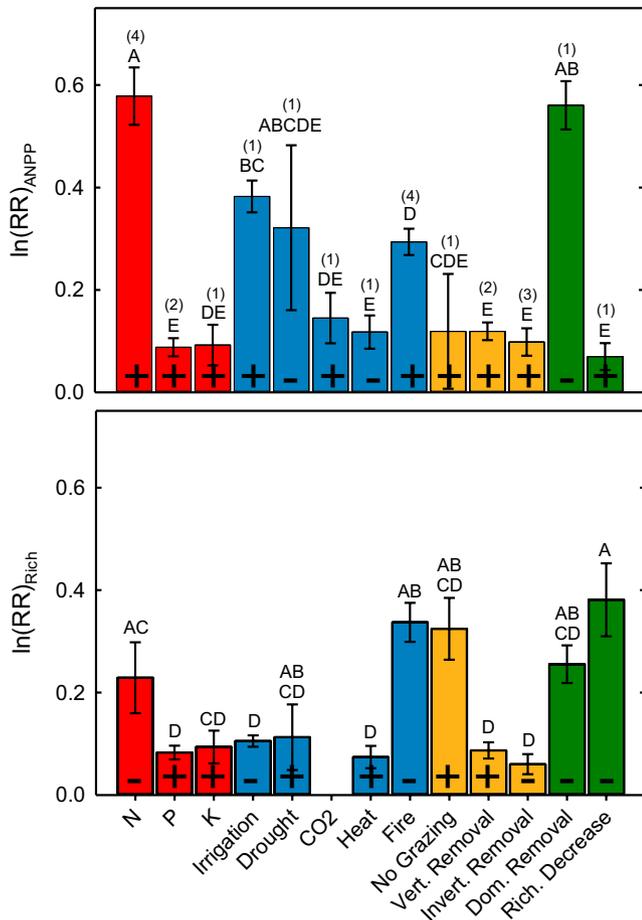
Finally, we examined community compositional shifts with the long-term manipulations of nitrogen, precipitation amount and fire frequency. To identify community shifts, plant community composition data after 15 years of manipulation were analyzed. We first visualized differences in community composition 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<sub>2</sub>, 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.

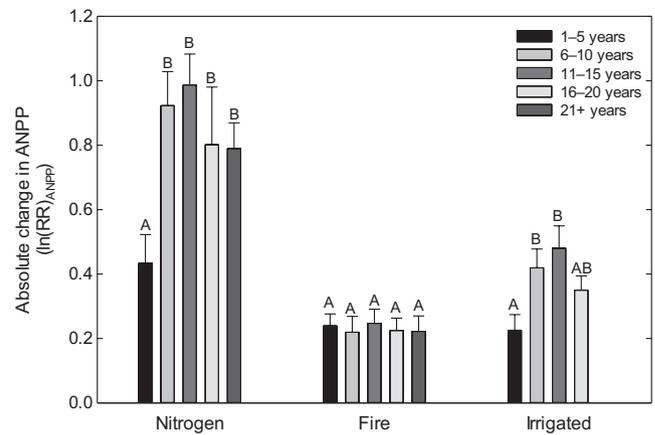
Of the anthropogenic drivers in which there were long-term records of plant community composition (N, fire and water addition), all three drivers significantly shifted plant species composition (Figure 3). In the case of water and N additions, compositional shifts were driven primarily by a large increase in abundance of the productive, perennial C<sub>4</sub> grass *Panicum virgatum* (Table 2). In contrast, compositional shifts with fire resulted primarily from the loss of the less productive perennial C<sub>3</sub> grass *Poa pratensis*, and increased abundance of other, more productive perennial C<sub>4</sub> grasses *S. nutans* and *Schizachyrium scoparium* (Table 2).



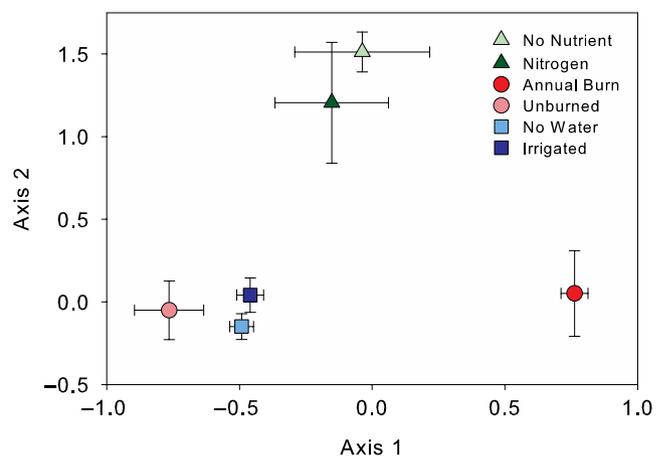
**FIGURE 1** Relative effects (log response ratio) of anthropogenic environmental drivers (red, blue and yellow bars; see Table 1), non-random species loss (green bars; dom. removal = removal of the dominant species only; rich. decrease = removal of rare or uncommon species only) on (top) ecosystem productivity and (bottom) plant community richness. Shown are means ( $\pm 1$  SE) of absolute values of the log response ratios for aboveground net primary productivity ( $\ln(\text{RR})_{\text{ANPP}}$ ) and species richness ( $\ln(\text{RR})_{\text{Rich}}$ ; see text for details). Note, richness data were not available for the  $\text{CO}_2$  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.  $\pm$ 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

## 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



**FIGURE 2** Temporal trends in effect sizes of aboveground net primary production (ANPP) for three anthropogenic drivers ( $\pm 1$  SE). Significant differences ( $\alpha < .05$ ) 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 ( $\pm 1$  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- $F = 8.407$ ,  $p = .001$ )

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

**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.%
<b>(a) Fire</b>					
<i>Poa pratensis</i>	C <sub>3</sub> grass	35.19	0.00	15.10	15.10
<i>Andropogon gerardii</i>	C <sub>4</sub> grass	55.18	55.13	10.45	25.55
<i>Solidago canadensis</i>	C <sub>3</sub> forb	22.67	0.03	9.52	35.07
<i>Sorghastrum nutans</i>	C <sub>4</sub> grass	2.78	16.68	6.14	41.21
<i>Lespedeza violacea</i>	Legume	2.99	14.50	5.88	74.09
<i>Schizachyrium scoparium</i>	C <sub>4</sub> grass	2.51	15.65	5.63	52.72
Species	Functional group	Av. abundance in reference	Av. Abundance w/irrigation	Contrib.%	Cum.%
<b>(b) Water</b>					
<i>Panicum virgatum</i>	C <sub>4</sub> grass	27.57	48.10	22.46	22.46
<i>S. canadensis</i>	C <sub>3</sub> forb	7.24	25.14	13.84	36.29
<i>A. gerardii</i>	C <sub>4</sub> grass	62.24	66.14	11.50	47.79
<i>S. nutans</i>	C <sub>4</sub> grass	19.57	19.00	10.47	58.26
<i>Amorpha canescens</i>	Legume	8.05	16.10	8.75	67.02
<i>S. scoparium</i>	C <sub>4</sub> grass	10.48	2.24	5.47	72.48
Species	Functional group	Av. Abundance in reference	Av. abundance w/nitrogen	Contrib.%	Cum.%
<b>(c) Nitrogen</b>					
<i>P. virgatum</i>	C <sub>4</sub> grass	33.31	95.94	32.81	32.81
<i>A. gerardii</i>	C <sub>4</sub> grass	41.00	3.56	18.70	51.51
<i>Helianthus annuus</i>	C <sub>3</sub> annual forb	0.06	31.00	14.71	66.22
<i>S. scoparium</i>	C <sub>4</sub> grass	11.81	0.00	6.54	72.76
<i>S. nutans</i>	C <sub>4</sub> 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.

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<sub>4</sub> 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 (Sunkoly 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, Sunkoly 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).

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