Journal of Ecology

DR MELINDA (MENDY) D SMITH (Orcid ID : 0000-0003-4920-6985)
MS MEGHAN AVOLIO (Orcid ID : 0000-0002-2649-9159)
PROFESSOR DAVID J GIBSON (Orcid ID : 0000-0002-0308-7506)
MS AVA M HOFFMAN (Orcid ID : 0000-0002-1833-4397)
DR DAVID LEWIS HOOVER (Orcid ID : 0000-0002-9326-9791)
DR KIMBERLY J LA PIERRE (Orcid ID : 0000-0001-7056-4547)

Article type : Research Article

Handling Editor: Etienne Laliberté

Mass ratio effects underlie ecosystem responses to environmental change

Authors: Melinda D. Smith[1*], Sally E. Koerner[2], Alan K. Knapp[1], Meghan L. Avolio[3], Francis A. Chaves[1], Elsie M. Denton[4], John Dietrich[1], David J. Gibson[5], Jesse Gray[1], Ava M. Hoffman[1], David L. Hoover[6], Kimberly J. Komatsu[7], Andrea Silletti[8], Kevin R. Wilcox[9], Qiang Yu[10], John M. Blair[11]

Affiliations:

[1] Department of Biology and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523

[2] Department of Biology, University of North Carolina Greensboro, Greensboro, NC 27402

[3] Morton K. Blaustein Department of Earth & Planetary Sciences, Johns Hopkins University, Baltimore, MD, 21218

[4] USDA Eastern Oregon Agricultural Research Center, Burns, OR 97720

[5] Department of Plant Biology, Center for Ecology, Southern Illinois University, Carbondale, IL

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2745.13330

62901
[6] USDA-ARS Rangeland Resources Research Unit, Fort Collins, CO 80526
[7] Smithsonian Environmental Research Center, Edgewater, MD 21037
[8] Odum School of Ecology, The University of Georgia, Athens, GA 30602
[9] Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071
[10] Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing, China 100081
[11] Division of Biology, Kansas State University, Manhattan, KS 66506

*Correspondence to:
Melinda D. Smith
Colorado State University
Department of Biology
1878 Campus Delivery
Fort Collins, CO 80523
+1 970-491-7155
melinda.smith@colostate.edu

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*, is 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, species richness, uncommon species

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 et al., 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 (Hector et al., 1999, Tilman et al., 2001, Cardinale et al., 2011, 2012, Hooper et al., 2012), with these effects equivalent to or exceeding those caused by other human-driven environmental changes (Hooper et al., 2012, Tilman et al., 2012, Hautier et al., 2015). Yet, a vigorous debate continues to surround the interpretation of results from BEF experiments (Pillai and Gouhier, 2019) and their relevance for 'real-world' ecosystems (Wardle, 2016, van der Plas, 2019).

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 et al., 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 (Thomas, 1994, Leach and Givnish 1996, Fischer and Stocklin, 1997, Wilsey and Polley, 2004), whereas common species are least likely to be lost due to their high abundances (Duncan and 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 vs.

common species should have dramatically different effects on ecosystem functioning (Sala et al., 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 (Tilman and Haddi, 1992, Hoover et al., 2014) and altered disturbance regimes (Koerner et al., 2014), whereas loss of common species has been found with chronic nutrient deposition (Isbell et al., 2013, Avolio et al., 2014) 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 (Zobel and Zobel, 1994, Smith and Knapp, 2003, Smith et al., 2004, Zavaleta and Hulvey, 2004, Losure et al., 2007, Isbell et al., 2008). In the few cases where non-random loss has been considered experimentally, richness effects on ecosystem functioning can be smaller (e.g., Smith and Knapp, 2003) or larger (e.g., Zavaleta and 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 (Grace et al., 2007, Adler et al., 2011), 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 vs. those simulated in the majority of BEF experiments (Wardle et al., 2011, Wardle, 2016). 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 yrs., 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 et al., 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: 1) rare species are lost first, and thus species loss is inversely related to abundance (Leach and Givnish 1996, Fischer and Stocklin 1997, Wilsey and Polley 2004) or frequency or occurrence in the community (Smith and Knapp, 2003) or 2) 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 (Hooper et al., 2012, Tilman et al., 2012, Hautier et al., 2015). Furthermore, we expected the effects of dominant species loss would have comparable or even larger effects on ecosystem function than other anthropogenic environmental changes.

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 two 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:

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

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 and Knapp, 2003) and naturally high abundance (>80% cover; Silletti and 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, Cary, NC, USA).

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 Eq. 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; Plymouth, UK).

Results

Across all years of the 16 experiments, ANPP was affected the most by the addition of N (100 kg ha^{-1}) or the complete removal of a dominant species (Fig. 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 (Fig. 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 (Fig. 2). On the other hand, the loss of uncommon species (richness decrease, Fig. 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 (Fig. 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, *e.g.,* irrigation decreased richness, whereas drought increased richness; Fig. 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 (Fig. 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 *Schizachryium scoparium* (Table 2).

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 et al., 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 and 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 (Stachowicz, 2001, Smith and Knapp, 2003), suggesting that in this system dominant species may play a foundational role by modifying environmental conditions to allow co-existence of less abundant species (Ellison et al., 2005). However, other studies have found an increase in richness with removal of a dominant species (Lepš, 1999, Avolio et al., 2019). Therefore, the effects of loss of dominants on richness may depend on whether the dominant plays a facilitative vs. 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^{-1} and herbivore removal both

decreased richness, while 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 (Hooper et al., 2012, Tilman et al., 2012, Hautier et al., 2015) 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 (Wilsey and Polley, 2004, Sonkoly et al., 2019) or reducing abundance of a dominant

species (Smith and Knapp, 2003, Isbell et al., 2008), 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 and colleagues (2009) 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 et al., 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 (Tilman et al., 2012, Hautier et al., 2015, Flombaum et al., 2017, Duffy et al. 2017). 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., Leach and Givnish 1996, Lepš, 2004, Gaston, 2010, 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.

Acknowledgements

We thank the reviewers and editors for their comments on the manuscript. We gratefully acknowledge the numerous scientists, graduate and undergraduate students, and research technicians for their contributions to this research. Tom van Slyke, Patrick O'Neal, and Jim Larkins provided logistical and technical support. This work was supported by the National Science Foundation (NSF) Long-term Ecological Research Network Program at the Konza Prairie Biological Station, the NSF Ecosystem Science Program, the Department of Energy Terrestrial Ecosystem Science and NIGEC/NICCR Programs, the USDA NRI Program, and the Andrew Mellon Foundation.

Author Contributions

MDS conceived the study, SEK conducted the meta-level analyses, and MDS and SEK wrote the manuscript. AKK, MLA, FAC, EMD, JD, DJG, JG, AMH, DLH, KJK, AS, KRW, QY, JMB 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., Harpole, W. S., O'Halloran, L. R., Grace, J. B., Anderson, T. M., Bakker, J. D., Biederman, L. A., Brown, C. S., Buckley, Y. M., Calabrese, L. B., Chu, C. J., Cleland, E. E., Collins, S. L., Cottingham, K. L., Crawley, M. J., Damschen, E. I., Davies, K. F., DeCrappeo, N. M., Fay, P. A., Firn, J.,

Frater, P., Gasarch, E. I., Gruner, D. S., Hagenah, N., Lambers, J. H. R., Humphries, H., Jin, V. L., Kay, A. D., Kirkman, K. P., Klein, J. A., Knops, J. M. H., La Pierre, K. J., Lambrinos, J. G., Li, W., MacDougall, A. S., McCulley, R. L., Melbourne, B. A., Mitchell, C. E., Moore, J. L., Morgan, J. W., Mortensen, B., Orrock, J. L., Prober, S. M., Pyke, D. A., Risch, A. C., Schuetz, M., Smith, M. D., Stevens, C. J., Sullivan, L. L., Wang, G., Wragg, P. D., Wright, J. P. & Yang, L. H. (2011) Productivity Is a Poor Predictor of Plant Species Richness. *Science,* **333,** 1750-1753.

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.

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.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature,* **486,** 59-67.

Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M. I. & Gonzalez, A. (2011) The functional role of producer diversity in ecosystems. *American Journal of Botany,* **98,** 572-592.

Clarke, K. R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology,* **18,** 117-143.

De Laender, F., Rohr, J. R., Ashauer, R., Baird, D. J., Berger, U., Eisenhauer, N., Grimm, V., Hommen, U., Maltby, L., Melian, C. J., Pomati, F., Roessink, I., Radchuk, V. & Van den Brink, P. J. (2016) Reintroducing Environmental Chance Drivers in Biodiversity-Ecosystem Functioning Research. *Trends in Ecology & Evolution,* **31,** 905-915.

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.

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.

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J., Orwig, D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. K., Swan, C. M., Thompson, J., Von Holle, B. & 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.

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

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.

Gaston, K. J. (2010) Valuing Common Species. *Science,* **327,** 154-155.

Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hautier, Y., Hillebrand, H., Lind, E. M., Partel, M., Bakker, J. D., Buckley, Y. M., Crawley, M. J., Damschen, E. I., Davies, K. F., Fay, P. A., Firn, J., Gruner, D. S., Hector, A., Knops, J. M. H., MacDougall, A. S., Melbourne, B. A., Morgan, J. W., Orrock, J. L., Prober, S. M. & Smith, M. D. (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature,* **529,** 390-393.

Grace, J. B., Anderson, T. M., Smith, M. D., Seabloom, E., Andelman, S. J., Meche, G., Weiher, E., Allain, L. K., Jutila, H., Sankaran, M., Knops, J., Ritchie, M. & Willig, M. R. (2007) Does species diversity limit productivity in natural grassland communities? *Ecology Letters,* **10,** 680-689.

Grime, J. P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology,* **86,** 902-910.

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.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E. D., Siamantziouras, A. S. D., Spehn, E. M., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S. & Lawton, J. H. (1999) Plant diversity and productivity experiments in European grasslands. *Science,* **286,** 1123-1127.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L. & O'Connor, M. I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature,* **486,** 105-U129.

Hoover, D. L., Knapp, A. K. & Smith, M. D. (2014) Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology,* **95,** 2646-2656.

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.

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,* **110,** 11911-11916.

Koerner, S. E., Burkepile, D. E., Fynn, R. W. S., Burns, C. E., Eby, S., Govender, N., Hagenah, N., Matchett, K. J., Thompson, D. I., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K. & 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.

Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., Knapp, A. K., Lemoine, N. P., Forrestel, E. J., Eby, S., Thompson, D. I., Aguado-Santacruz, G. A., Anderson, J. P., Anderson, T. M., Angassa, A., Bagchi, S., Bakker, E. S., Bastin, G., Baur, L. E., Beard, K. H., Beever, E. A., Bohlen, P. J., Boughton, E. H., Canestro, D., Cesa, A., Chaneton, E., Cheng, J., D'Antonio, C. M., Deleglise, C., Dembélé, F., Dorrough, J., Eldridge, D. J., Fernandez-Going, B., Fernández-Lugo, S., Fraser, L. H., Freedman, B., García-Salgado, G., Goheen, J. R., Guo, L., Husheer, S., Karembé, M., Knops, J. M. H., Kraaij, T., Kulmatiski, A., Kytöviita, M.-M., Lezama, F., Loucougaray, G., Loydi, A., Milchunas, D. G., Milton, S.

J., Morgan, J. W., Moxham, C., Nehring, K. C., Olff, H., Palmer, T. M., Rebollo, S., Riginos, C., Risch, A. C., Rueda, M., Sankaran, M., Sasaki, T., Schoenecker, K. A., Schultz, N. L., Schütz, M., Schwabe, A., Siebert, F., Smit, C., Stahlheber, K. A., Storm, C., Strong, D. J., Su, J., Tiruvaimozhi, Y. V., Tyler, C., Val, J., Vandegehuchte, M. L., Veblen, K. E., Vermeire, L. T., Ward, D., Wu, J., Young, T. P., Yu, Q. & Zelikova, T. J. (2018) Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution,* **2,** 1925-1932.

Leach, M. K. & Givnish, T. J. (1996) Ecological determinants of species loss in remnant prairies. *Science*, **273**, 1555-1558.

Lepš, J. (1999) Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. *Journal of Vegetation Science*, **10**, 219-230.

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.

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.

Magurran, A. E. (2016) How ecosystems change. *Science,* **351,** 448-449.

Pillai, P. & Gouhier, T. C. (2019) Not even wrong: the spurious measurement of biodiversity's effects on ecosystem functioning. *Ecology,* **0,** e02645.

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M. & Sexton, J. O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science,* **344,** 1246752.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J. & Paine, R. T. (1996) Challenges in the quest for keystones. *Bioscience,* **46,** 609-620.

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* (eds H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala & E.-D. Schulze), pp. 129-149. John Wiley & Sons Ltd

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.

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.

Smith, M. D. & Knapp, A. K. (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters,* **6,** 509-517.

Smith, M. D., Wilcox, J. C., Kelly, T. & Knapp, A. K. (2004) Dominance not richness determines invasibility of tallgrass prairie. *Oikos*, **106**, 253-262.

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.

Smith, M. D., (2019), Koerner, S. E., Knapp, A. K., Avolio, M. L., Chaves, F. A., Denton, E. M., Dietrich, J., Gibson, D. J., Gray, J., Hoffman, A. M., Hoover, D. L., Komatsu, K. J., Silletti, A., Wilcox, K. R., Yu, Q. & Blair, J. M. (2019). Meta-level analysis of global change experiments, Dryad, Dataset, https://doi.org/10.5061/dryad.j3tx95x8w

Sonkoly, J., Keleman, A., Valko, O., Deak, B., Kiss, R., Toth, K., Miglecz, T., Tothmeresz, B., & Torok, P. (2019) Both mass ratio effects and community diversity drive biomass production in a grassland experiment. Scientific Reports, **9**, 1848.

Stachowicz, J. J. (2001) Mutualism, facilitation, and the structure of ecological communities. *Bioscience,* **51,** 235-246.

Steffen, W., Richardson, K., Rockstrom, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., de Vries, W., de Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B. & Sorlin, S. (2015) Planetary boundaries: Guiding human development on a changing planet. *Science,* **347**.

Thomas, C. D. (1994) Extinction, Colonization, and Metapopulations: Environmental Tracking by Rare Species. *Conservation Biology,* **8,** 373-378.

Tilman, D. & Haddi, A. (1992) Drought and biodiversity in grasslands. *Oecologia,* **89,** 257-264.

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.

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.

van der Plas, F. (2019) Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews,* **0**.

Vetter, D., Rucker, G. & Storch, I. (2013) Meta-analysis: A need for well-defined usage in ecology and conservation biology. *Ecosphere,* **4**.

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.

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.

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.

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.

Wilsey, B. J. & Polley, H. W. (2004) Realistically low species evenness does not alter grassland species-richness-productivity relationships. *Ecology*, **85**, 2693-2700.

Zavaleta, E. S. & Hulvey, K. B. (2004) Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science,* **306,** 1175-1177.

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.

Table 1. Summary of the 16 experiments comprising 23 treatments utilized in the meta-level analyses. 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. *Description of methods are available online: http://lter.konza.ksu.edu/Methods%20Manual.

Experimental Variable	Treatment levels used in analyses	Study period (no. years)	Source
Nitrogen addition	**0** or 100 kg N · ha^{-1} · y^{-1}	2003-2012 (10 y)	Avolio et al. 2014
Nitrogen addition	**0** or 100 kg N · ha^{-1} · y^{-1}	2008-2012 (5 y)	La Pierre et al. 2016
Nitrogen addition	**0** or 100 kg N · ha^{-1} · y^{-1}	1986-2012 (26 y)	Collins et al. 1998
Nitrogen addition	**0** or 100 kg N · ha^{-1} · y^{-1}	1998-1999 (2 y)	Silletti et al. 2004
Phosphorous addition	**0** or 100 kg P · ha^{-1} · y^{-1}	2003-2012 (10 y)	Avolio et al. 2014
Phosphorous addition	**0** or 100 kg P · ha^{-1} · y^{-1}	2008-2012 (5 y)	La Pierre et al. 2016
Potassium addition	**0** or 100 kg K · ha^{-1} · y^{-1}	2008-2012 (5 y)	La Pierre et al. 2016
Water addition	**Non-irrigated** or Irrigated	1991-2011 (21 y)	Collins et al. 2012
Drought	**Ambient rain** or ~66% decrease	2010-2011 (2 y)	Hoover et al. 2014
CO_2	**Chamber ambient** or 100% enrichment (ANPP only)	1989-1996 (8 y)	Owensby et al. 1999
Warming	**Unheated** or ~+2°C year round	2003-2011 (9 y)	Fay et al. 2011
Fire	**Unburned** or annual burn (ANPP only)	1984-2011 (28 y)	*
Fire	**Unburned** or annual burn (ANPP only)	1989-1997 (7 y)	*
Fire	**Unburned** or annual burn	1986-2012 (26 y)	Collins et al. 1998
Fire	**Unburned** or annual burn (Species comp only)	1983-2000 (18 y)	*
Bison grazing	**Unfenced** or bison (large herbivore) exclosure	2007-2008 (2 y)	Knapp et al. 2012, Koerner et al. 2014
Vertebrate herbivory	**Unfenced** or deer and small herbivore exclosure	2009-2012 (4 y)	La Pierre et al. 2014

Vertebrate herbivory	**High vertebrate density** or no vertebrates	1985-1986 (2 y)	Gibson et al. 1990
Invertebrate herbivory	**Untreated** or insecticide aboveground	2009-2012 (4 y)	La Pierre et al. 2014
Invertebrate herbivory	**Untreated** or insecticide aboveground	1985-1986 (2 y)	Gibson et al. 1990
Invertebrate herbivory	**Untreated** or insecticide belowground	1985-1986 (2 y)	Gibson et al. 1990
Dominance removal	**Control**, 100% *A. gerardii* removal, or 100% *S. nutans* removal	1998-1999 (2 y)	Silleti et al. 2004
Richness decrease	**Untreated (14-16)**, 10-12, 7-9, or 4-6 species	2000-2001 (2 y)	Smith et al. 2003

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

(a) Fire

Species	Functional group	Av. Abundance in Reference	Av. Abundance w/ Fire	Contrib.%	Cum.%
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
Schizachryium scoparius	C_4 grass	2.51	15.65	5.63	52.72

(b) Water

Species	Functional group	Av. Abundance in Reference	Av. Abundance w/ Irrigation	Contrib.%	Cum.%
Panicum virgatum	C_4 grass	27.57	48.10	22.46	22.46
Solidago canadensis	C_3 forb	7.24	25.14	13.84	36.29
Andropogon gerardii	C_4 grass	62.24	66.14	11.50	47.79
Sorghastrum nutans	C_4 grass	19.57	19.00	10.47	58.26
Amorpha canescens	Legume	8.05	16.10	8.75	67.02
Schizachryium scoparium	C_4 grass	10.48	2.24	5.47	72.48

(c) Nitrogen

Species	Functional	Av. Abundance in	Av. Abundance w/	Contrib.%	Cum.%

	group	Reference	Nitrogen		
Panicum virgatum	C_4 grass	33.31	95.94	32.81	32.81
Andropogon 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
Schizachryium scoparius	C_4 grass	11.81	0.00	6.54	72.76
Sorghastrum nutans	C_4 grass	10.38	0.00	5.31	78.07

Figure Legends

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 S.E.) 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: $F_{12,239} = 9.07$, $p < 0.001$; Rich: $F_{11,149} = 5.64$, $p < 0.001$). Significant differences ($\alpha = 0.05$) 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 S.E.). Significant differences ($\alpha \leq 0.05$) between time periods are represented by different letters. N: $F_{4,22} = 3.42$, $p = 0.026$; Fire: $F_{2,49} = 0.07$, $p = 0.991$; Water: $F_{3,36} = 3.80$, $p = 0.018$.

Figure 3. Non-metric multidimensional scaling based on Bray-Curtis dissimilarity for long-term fire (*red circles*), irrigation (*blue square*s), and nitrogen (*green triangles*) experiments. Each point is the centroid for a given cluster of points (±1 S.E.). 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-value = 0.0127; Irrigation: df = 1,40, Pseudo-F = 3.505, p-value = 0.011; Fire: df = 1,14, Pseudo-F = 8.407, p-value = 0.001).