Received: 10 February 2023 | Accepted: 21 August 2023

DOI: 10.1111/1365-2745.14198

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Nothing lasts forever: Dominant species decline under rapid environmental change in global grasslands

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Funding information
Institute on the Environment, University of Minnesota, Grant/Award Number: DG-0001-13; National Science Foundation, Grant/Award Number: NSF-DEB-1042132 and NSF-DEB-1234162

Handling Editor: Jonathan Henn

Abstract

1. Dominance often indicates one or a few species being best suited for resource capture and retention in a given environment. Press perturbations that change availability of limiting resources can restructure competitive hierarchies, allowing new species to capture or retain resources and leaving once dominant species fated to decline. However, dominant species may maintain high abundances even when their new environments no longer favour them due to stochastic processes associated with their high abundance, impeding deterministic processes that would otherwise diminish them.
2. Here, we quantify the persistence of dominance by tracking the rate of decline in dominant species at 90 globally distributed grassland sites under experimentally elevated soil nutrient supply and reduced vertebrate consumer pressure.
3. We found that chronic experimental nutrient addition and vertebrate exclusion caused certain subsets of species to lose dominance more quickly than in control plots. In control plots, perennial species and species with high initial cover maintained dominance for longer than annual species and those with low initial cover respectively. In fertilized plots, species with high initial cover maintained dominance at similar rates to control plots, while those with lower initial cover lost dominance even faster than similar species in controls. High initial cover increased the estimated time to dominance loss more strongly in plots with vertebrate exclosures than in controls. Vertebrate exclosures caused a slight decrease in the persistence of dominance for perennials, while fertilization brought perennials' rate of dominance loss in line with those of annuals. Annual species lost dominance at similar rates regardless of treatments.
4. *Synthesis*. Collectively, these results point to a strong role of a species' historical abundance in maintaining dominance following environmental perturbations. Because dominant species play an outsized role in driving ecosystem processes, their ability to remain dominant—regardless of environmental conditions—is critical to anticipating expected rates of change in the structure and function of grasslands. Species that maintain dominance while no longer competitively favoured following press perturbations due to their historical abundances may result in community compositions that do not maximize resource capture, a key process of system responses to global change.

KEYWORDS
determinants of plant community diversity and structure, dominance, fertilization, global change ecology, historical contigency, plant population and community dynamics, plant–herbivore interactions

1 | INTRODUCTION

Plant community responses to global change can have important consequences for ecosystem processes, especially the responses of numerically and spatially dominant taxa whose high abundance means that they regulate limiting resources for themselves and all other taxa (Smith et al., 2009). Given their role in resource regulation, dominant species are critical in dictating responses to environmental changes (Avolio, Forrestel, et al., 2019). On the one hand, they may buffer such changes if they can maintain high abundances even when the environment becomes unfavourable (Von Holle et al., 2003). By consuming limiting resources, dominant taxa can resist invasion by taxa that might otherwise be better suited to the new environment (Chesson, 2000; Tilman, 2004).

On the other hand, environmental change can drive an 'ecological meltdown' if widespread dominant taxa are rapidly displaced (MacDougall et al., 2013). While dominant species receive proportional attention in the literature, abiotic conditions and biotic characteristics that determine the rate of dominant species' persistence or collapse are underexplored factors underpinning these outcomes.

When environmental changes create newly unfavourable conditions for dominant species, an interplay of stochastic and deterministic factors will determine whether the dominants remain or rapidly collapse. Were species to have equal fitness, ecological drift is the central mechanism by which species abundances change through time (Hubbell, 2001). Functionally, this means the only predictive element of a species' abundance in a given year would be its abundance in the year prior. Thus, the expectation for dominant species would be that they stay dominant regardless of temporal variation in biotic and abiotic conditions. The opposing counterfactual is that stochastic processes like ecological drift yield strictly to deterministic processes like plant competition. In this case, strong environmental perturbations that shift competitive advantages to new species would cause the prior years' abundance of a species to have no predictive power on its current abundance, and deterministic replacement by invading or subordinate species would be expected to occur rapidly (Tilman et al., 1997). Nature lies in between these two hypothetical extremes, with both stochastic and deterministic processes controlling species abundance trajectories, and thus community change, through time (Germain et al., 2013; Shoemaker et al., 2020; Vellend, 2010).

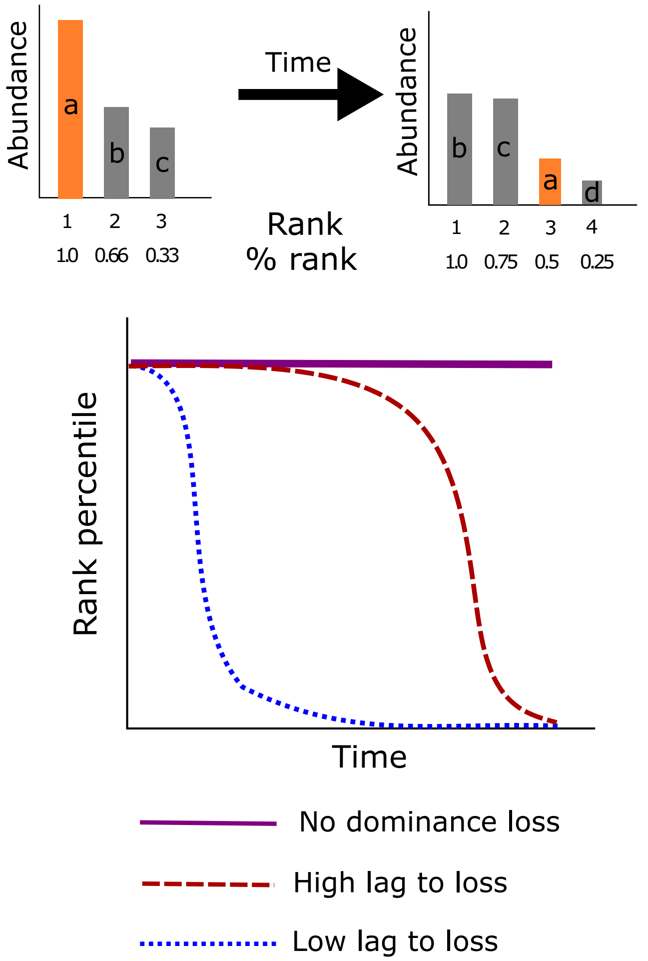

FIGURE 1 Conceptual diagram. Initial dominants' abundances (orange bar, top) are converted to a rank percentile which allows a standardized response range (0–1) across plots through time. Defining initial dominants in this manner means rank percentile can only remain the same or decay through time. Species fated to lose dominance may do so at different rates following the onset of press perturbations. The hypothetical red and blue species in the bottom graph both move towards extirpation, but the red species is able to maintain dominance for some time before beginning to decline. Alternatively, species may not lose their competitive advantage and simply maintain dominance (purple line).

Species may persist in environments no longer favourable to them due to a legacy of high abundance reflecting a previously favourable environment, creating a temporal lag between perturbations and species' responses (Figure 1; Gorham, 1957; Von Holle et al., 2003). The role of historical species' abundances is expected to be stronger for press perturbations such as global warming, eutrophication or loss of wild herbivores than for discrete disturbance events such as fires or habitat destruction. Although both can dramatically change the resource availability of a system, a key distinction is the carryover of biotic material following the onset of each event. Where press perturbations do not directly alter the biotic legacy of a system, disturbance events are defined by the physical removal of biomass, including that of dominant species (White & Jentsch, 2001). As such, disturbance events are more likely to disrupt species dominance, cause rapid community reassembly (Arnillas & Cadotte, 2019; Kreyling et al., 2011) and be characterized by priority effects (Fukami & Nakajima, 2011) or disturbance tolerance (Jentsch & White, 2019), while press perturbations are more likely to be characterized by the lag between the perturbation onset and pre-existing species yielding dominance to newly favoured species (Von Holle et al., 2003). This lag effect links to theory bridging deterministic and stochastic models of community change, where established plant populations may impede establishment and growth of newly favoured plant species by having physically larger individuals, longer lifespans or larger populations (Tilman, 2004). Extending this suggests that with the onset of press perturbations, species with greater relative abundances should maintain dominance longer as they more effectively reduce resource availability to colonists attempting to establish and outcompete the previous residents, even when these colonists are ultimately favoured.

Dominant species have a proportionately larger impact on community assembly (Avolio, Forrestel, et al., 2019; Grime, 1998) and tend to have higher persistence, although press perturbations can weaken persistence of dominant and subordinate species alike (Wilfahrt et al., 2021). This observed higher persistence of dominant species in response to a change in the resource environment can arise from inherent traits such as their lifespan (i.e. annual vs. perennial), growth form, or from their initial abundances. Furthermore, species' ability to maintain dominance following press perturbations could influence community assembly, as their persistence or decline following environmental perturbations influences how subordinate species change in rank abundance (Arnillas & Cadotte, 2019; Avolio et al., 2021; Mortensen et al., 2018). Negative density dependence acts as a countervailing force to the persistence of dominance (Chesson, 2000). Negative density dependence may be exacerbated by perturbations that allow population growth of a species to a point where it limits resources to its own juveniles (Tilman & Wedin, 1991) or alleviated by perturbations that limit a species population growth such as a novel predator introduction (Paine, 1966). Thus, the rate at which dominant species lose dominance status following a perturbation may be best understood in relation to their population trajectories under ambient conditions, where positive and negative density dependencies play out independently of the perturbation.

Increased soil nutrient supply and decreased consumer pressure are two press perturbations expected to shift competitive hierarchies, potentially to the disadvantage of initially abundant species (Heckman et al., 2017; Holt et al., 1994; Wilfahrt et al., 2020).

Here, we examine the conditions that affect the rate of dominance loss for initially dominant species and the conditions that alter lags in the loss of dominance in response to these two press perturbations. Our central hypothesis is that initially dominant species that have a higher initial relative cover will maintain their dominance longer following experimentally induced press perturbations, specifically nutrient addition and vertebrate exclusion. We then explore the biotic and abiotic conditions (Box 1) that might also alter the persistence of dominant species in response to nutrient addition and vertebrate exclusion.

2 | METHODS

The Nutrient Network (NutNet) is a coordinated, globally distributed experiment manipulating soil resource supply to plants and vertebrate herbivore access in 5 x 5 m plots with standardized treatment and data collection protocols (Borer et al., 2014). The soil resource supply treatment consists of yearly application of slow-release nitrogen, phosphorus and potassium at a rate of 10 g m^{-2} and an initial application of micronutrients (herein NPK). Herbivore access was reduced by constructing 2.3 m tall wire fences with 1 cm mesh fencing around the bottom 0.9 m. Plant cover was determined yearly by estimating the aerial percent cover of each species rooted in a permanent quadrat of 1 × 1 m size with a minimum 0.5 m buffer from the plot edge; this means total plant cover can, and often does, exceed 100% due to overlapping species' canopies. No permits were required for fieldwork. We used plant cover data from control, +NPK, Fence and +NPK & Fence plots from any site that met three criteria: (1) recorded pretreatment cover data, (2) had at least 1 year of post-treatment cover data, (3) had NPK treatments, fencing treatments or both. This resulted in 90 sites ranging in duration from 1 to 15 years of treatment data (Table S1).

We converted yearly species cover values within a plot into percentage rank abundances. Rank abundance curves array species within a plot ordinally from most (1) to least (*n*) abundant and provide a numerically convenient approach for understanding the role of abundant species across sites (Avolio, Carroll, et al., 2019). Recasting the ordinal rank abundance as a percentage rank (where 1 is the most abundant species, 0.5 indicates a species less abundant than 50% of co-occurring species and 0 indicates absence) provides a continuous metric for analysis with a range independent of species richness. Species tied for highest cover in the pretreatment year were both included in further analyses. Percent cover has an artificial cap of 100, meaning species near 100 at the start can only stay the same or decrease in abundance by this metric while species starting further from 100 have more room to increase even if both hypothetical species increased in abundance (e.g. biomass). Using rank percentiles means the initially most abundant species, the focus of our analyses, all start at 1 and are therefore equally constrained by the same cap (i.e. percentage rank can only decrease or remain the same).

We examined which aspects of initially dominant species and their environments influenced their rate of rank decay following perturbations. Specifically, we evaluated the species' initial relative cover, lifespan, functional group, provenance (native, non-native) and the site's mean annual precipitation (mm, Fick & Hijmans, 2017), precipitation variability (CV, Fick & Hijmans, 2017); and site richness (number of species observed at site in year 0) as environmental covariates. The environmental variables were not correlated strongly with one another (all Pearson's *r*: $-0.22 < r < 0.25$). Lifespan was categorized as annual (annual and biennial) or perennial (perennial and indeterminate; the latter is assigned to species that can switch from annual/biennial to perennial depending on site conditions), enabling a comparison of effectively short-lived and long-lived species. Plant functional group was categorized as graminoid or non-graminoid; 77% of 'non-graminoids' were non-leguminous forbs, 16% were woody shrubs or vines and 7% were legumes. To keep our response bound between 0 and 1, we logit transformed percentile rank, adjusting values of 1 and 0 to 0.99 and 0.01 respectively. We found qualitatively similar results (Table S4) using an arcsin transformation which does not require adjustments to 0 and 1, but has other undesirable qualities (Warton & Hui, 2011).

In order to test how dominance decayed over time in response to press perturbations, we tested the linear relationship with the logit transformed rank percentile as a response to a three-way interaction between (1) year of experimental treatment (0–15, continuous variable), (2) NPK addition and (3) fencing. We additionally tested how covariates (species' initial relative cover, lifespan, functional group, provenance, mean annual precipitation, precipitation variability and site richness) influenced the foundational three-way interaction by adding each as a fourth interactive term (i.e. the full model had seven, four-way interactions). We used a linear mixed effects model with a Gaussian error distribution (nlme package, Pinheiro et al., 2016) with species nested in plot nested in site as a random intercept. Given the complexity of this model, we tested whether each of the seven covariates improved model fit by simultaneously removing all eight model terms associated with that

BOX 1 Hypotheses for drivers of dominance loss.

Time—Even in the absence of press perturbations and disturbances, initially dominant species in grasslands may cede dominance due to succession (Meiners et al., 2015), stochasticity (Shoemaker et al., 2020) or negative density dependence (Chesson, 2000).

Soil resource supply—Sustained increases in soil resource supply shift the competitive balance towards species with lower nutrient use efficiencies. Therefore, there should be a more rapid loss of dominance for initially dominant species following the onset of this press perturbation (Harpole et al., 2016; Wilfahrt et al., 2021).

Consumer pressure—Initially dominant species that gained dominance while tolerating vertebrate herbivory may be further advantaged. Evidence suggests that reduced vertebrate consumer pressure leads to increased dominance that further disadvantages subordinate species (Mortensen et al., 2018), thus reduced consumer pressure should allow initially dominant species to maintain dominance longer.

Soil resources and consumer interaction—Dominant species tend to be diminished with increased soil resource supply (Wilfahrt et al., 2021) whereas their dominance is often reinforced by reduced consumer pressure (Mortensen et al., 2018). Thus, the simultaneous onset of these two press perturbations should lead to sub-additive interactions when one perturbation exerts more influence than the other or additive interactions if these two press perturbations act to neutralize each other's effects on initial dominants.

Covariates

Initial abundance (*relative cover*)—Initially dominant species that occupy a larger area should benefit both from stochastic processes (Shoemaker et al., 2020) and by being able to capture larger shares of resource pools (including light) and preclude the growth of newly favoured but previously subordinate species (Tilman, 2004). Collectively, this allows the initial dominants to maintain their dominance longer even when they are fated to decline (Von Holle et al., 2003).

Lifespan—Perennial species can resprout from developed root systems each growing season, meaning initially dominant perennial species have a greater reserve of biomass to draw on even when environments become less favourable for those species. Annual individuals must develop from seeds each growing season, reducing the amount of biomass they can carry over between growing seasons, giving them fewer reserves to maintain dominance in the face of resource shifts (Eskelinen et al., 2021).

Provenance—Increased soil resource supply and reduced consumer pressure often advantage non-native species (Seabloom et al., 2015), meaning initially dominant non-native species may maintain dominance longer than native species following these press perturbations.

Functional group—Graminoids tend to have higher persistence than other herbaceous species in grasslands (Wilfahrt et al., 2021) and grasses in particular tend to benefit from nutrient addition likely due to better competitive ability for light and nutrients (You et al., 2017). Initially dominant grasses should maintain dominance longer than initially dominant forbs, particularly following press perturbations.

Mean annual precipitation—Deterministic processes are expected to be more influential than stochastic processes in harsher environments (Chase, 2007), so initially dominant species in low precipitation environments are more likely to maintain dominance compared to higher precipitation environments.

Annual precipitation variability—Systems with higher abiotic heterogeneity through space or time should reduce the ability of species to maintain dominance. This arises because the inconstant environment and changing conditions favour the growth of different species through time via the storage effect (Melbourne et al., 2007).

Site richness—Maintenance of dominance may decline in areas with high richness because the likelihood of displacement by a species better suited to the altered resource environment increases in environments with a larger species pool (Chase, 2003).

covariate (i.e. covariate, covariate × NPK, covariate × fence, covariate × NPK × fence, covariate × year, covariate × NPK × year, covariate × fence × year, covariate × NPK × fence × year) and comparing the AIC of this reduced model and the full model. If the full model did not improve on a reduced model by more than the AIC penalty terms (2 × 8), we did not include that covariate or its interactions in the final model (Zuur et al., 2009). We assessed the goodness of fit for our reduced model by estimating R^2 values for fixed and random effects (MuMIn package, Nakagawa & Schielzeth, 2013). We quantified the time to dominance loss by determining the number of years after treatment when model estimates of initially dominant species' rank percentile first fell below the mean of all species' rank percentiles in our initial dominants data set with one or more treatment years (0.70); we did this for each covariate used in our final model under different treatments. To illustrate model results of any continuous covariates, we extracted model estimates for these covariates' 0.05

and 0.95 quantiles within our data set (emmeans package, Lenth et al., 2018). All analyses were performed in R v 4.1.2.

3 | RESULTS

The loss of rank percentile through time of initially dominant species was affected by fertilization, exclusion of vertebrate herbivores, species' initial cover and species' lifespan (Table 1, Table S2); provenance marginally improved model fit while functional group and site characteristics did not improve model fit and all were removed from the final model (Table S3; final model conditional pseudo-$R^2=0.59$; marginal pseudo-$R^2=0.23$). In control plots, initially dominant species with high initial relative cover maintained their rank longer than those with lower initial relative cover (Figure 2), with species having initial relative cover values near 1 (0.95 quantile; i.e. near monocultures) staying dominant, on average, for 6 more years than species having low relative cover values (0.05 quantile; i.e. 'dominants' from highly even communities; Table 1). Species with low initial relative cover in treatment plots maintained dominance for shorter periods of time relative to controls (Table 1, Figure S1). Species with high initial relative cover, however, had divergent trajectories following perturbations; fencing increased time to dominance loss by 84% relative to controls, while nutrient addition did not significantly change time to dominance loss (Table 1, Figure 2, NPK: 4.2%, NPK + Fence: −11%). In all plots, having higher initial relative cover conferred higher time to dominance loss, though this was most pronounced in fenced plots (from low (0.05 quantile) to high (0.95 quantile) initial relative cover: control: +95%, Fence: +466%, NPK: +177%, NPK + Fence: +316% (Figure 2, Table S2, initial_cover × year × fence × NPK: $p=0.002$). Initial dominants in 14.1% of observed plots maintained a rank of 1 (dominant) in all observed years (Control: 16.7%, Fence: 16.2%, NPK: 11.6%, NPK + Fence: 11.6%). Across all plots, species that maintained a rank of one in all observed years had a mean initial relative cover of 57.3%, while those that dropped in rank in any year had a mean initial relative cover of 43.1%.

TABLE 1 Table showing how model predictors change the time to dominance loss of initially dominant species, where time to dominance loss is defined as the number of years until the rank percentile of those species was estimated to have fallen below the global mean of all rank percentiles in our initial dominants data set in post-treatment years (0.70). For continuous predictors, 'low' and 'high' refer to the 0.05 and 0.95 quantiles, respectively, of the observed distribution of that predictor in the dataset. Asterisks indicate treatment effects' 95% confidence intervals did not include the control value at the indicated predictor level; crosses indicate that the given level of a covariate's 95% confidence interval did not contain the value above it (i.e. the within treatment estimate of the alternative covariate level).

Predictor	Control	Fence	NPK	NPK + fence
Model average	8.3	7.3	6.6*	5*
Low initial cover	6	3.8*	4.4*	2.5*
High initial cover	11.7†	21.5†	12.2†	10.4†
Annual	6.1	4.8	6.7	4.9
Perennial	12.5†	10.3*†	6.5*	5*

Initially dominant perennial species maintained dominance 104% longer than initially dominant annual species in control plots (Table 1, Table S2, Figure 3). Annual plants had similar rates of rank loss in NPK, Fence and control plots, while perennials in fertilized and fenced plots lost rank more quickly than those in control plots (Figure S2; lifespan × NPK × year: $p<0.001$; lifespan × fence × year: $p=0.016$). There was no interactive effect of fertilization and fences on rate of dominance loss based on lifespan (lifespan × NPK × fence × year: $p=0.36$). Overall, perennials' extended dominance in control plots did not translate to increased persistence of dominance relative to annuals following NPK addition, with perennials maintaining dominance 114%, −3.1% and 2.0% longer than annuals in Fence, NPK and NPK + Fence plots respectively (Figure 3). In other words, perennial species lost dominance at similar rates to annual species in fertilized plots. Across all plots, initially dominant perennial species maintained a rank of 1 (dominance) across all observed years in 16.3% of the plots they were observed in, while annual species only achieved this in 1.6% of plots (2 of 122 observations). We found qualitatively similar results when we used an arcsin transformation (Table S4) and when we included sites with less than 5 years of treatment data (Table S5).

4 | DISCUSSION

The relative cover of a dominant species prior to vertebrate exclusion and nutrient addition (press perturbations) had a clear positive influence on the species' maintenance of dominance in ambient conditions and post-perturbation. Species lifespan additionally interacted with vertebrate exclusion and nutrient addition to affect the rate of dominance loss. Even when species initial abundance and lifespan predicted rank percentile trajectories that eventually approached zero (i.e. loss of species), the lag before rank loss often differed, suggesting that life-history traits and historical abundances confer differing degrees of resistance to dominance loss. Previous nutrient network studies have shown that vertebrate exclusion and nutrient addition diminish species persistence as well as abundance of abundant and rare species (Wilfahrt et al., 2021), that nutrient addition differently affects species gains versus species losses, underlying observed species richness changes (Muehleisen et al., 2023), and that these gains and losses have observable linkages to changes in above-ground biomass (Ladouceur et al., 2022). The temporal order of composition changes, particularly shifts in dominance and lagged responses, is likely an important component of how and when communities and ecosystems respond to perturbations (Komatsu et al., 2019; Smith et al., 2009; Walther et al., 2002). The results presented here provide evidence for the conditions controlling rates of dominance loss in grasslands over decades and across broad environmental gradients.

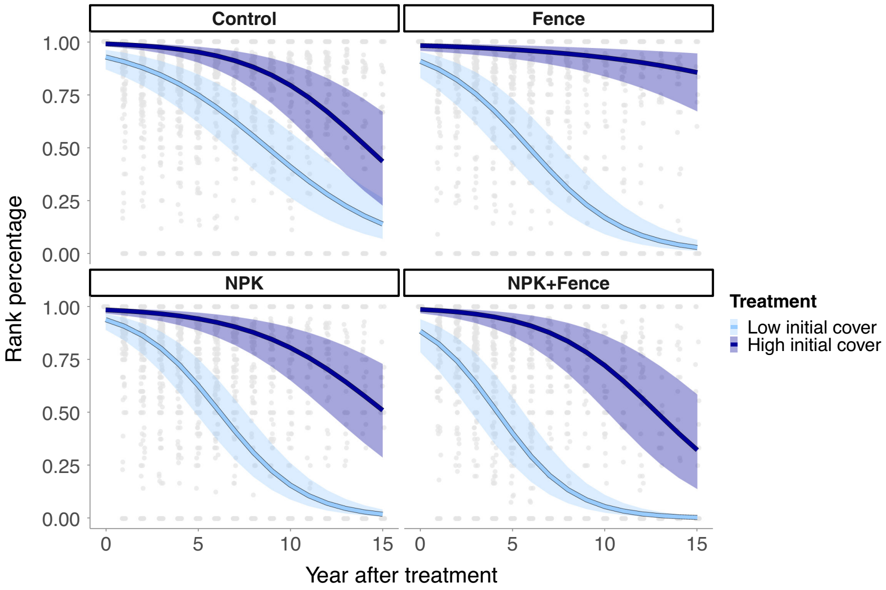

FIGURE 2 Interactions between initial relative cover and treatments through time on rank percentile (Table S2). Coloured lines are extracted estimates from a model with initial relative cover as a continuous variable; high (dark blue) is the 95% quantile of all observed initial relative cover values and low (light blue) is the 5% quantile. Ribbons are 95% confidence intervals at the specified initial cover level. Figure S1 shows alternative graphing with treatments as coloured lines and initial cover as facets for additional comparison.

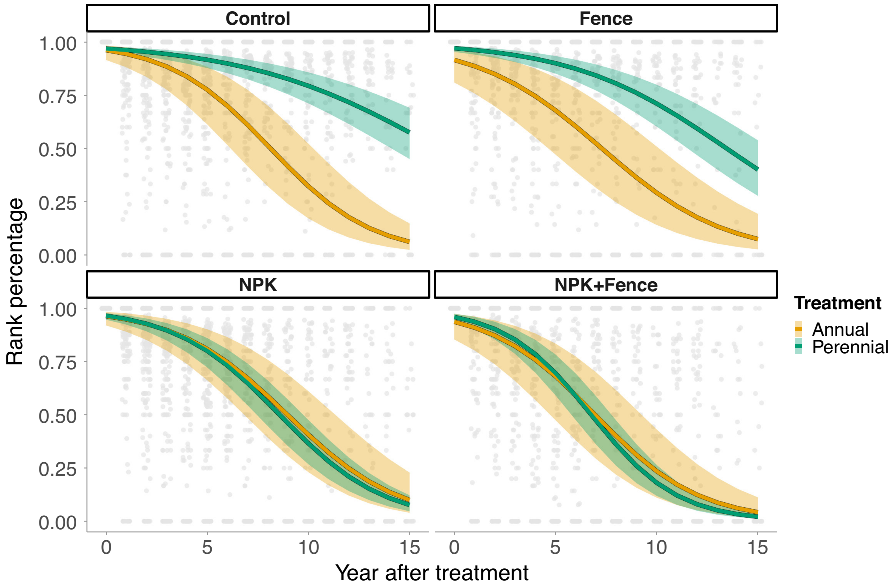

FIGURE 3 Interactions between species lifespan and treatments through time on rank percentile (Table S2). Ribbons are 95% confidence intervals. Figure S2 shows alternative graphing with treatments as coloured lines and lifespan as facets for additional comparison.

Community composition prior to press perturbations may influence community response rates and trajectories. We show that the degree to which initially dominant species were abundant (i.e. initial relative cover) was the best predictor of their ability to maintain dominance across globally distributed grasslands. The duration of dominance in control plots provides an expected rate of decay in dominance due to ambient environmental fluctuations, density dependence, succession or ecological drift. Higher initial relative cover increased the length of dominance in control plots, suggesting dominant species in less even communities could better withstand displacement. Fertilization led to a decline in the maintenance of dominance for species with low initial relative cover relative to this ambient dominance loss, while fertilization did not affect rate of dominance loss for species with high initial relative cover relative to controls. Moreover, many initial dominants never ceded dominance in our study, and these populations were more likely to have high initial abundances, indicating that high abundance dominant species are more likely to maintain competitive dominance following press perturbations (van Nes & Scheffer, 2004). Even when there was pressure for community reassembly following nutrient addition (i.e. eventual loss of dominance), it was slowed in the presence of highly dominant species. There are two potential non-mutually exclusive reasons for this. First, high relative cover is indicative of species that monopolize pretreatment resource uptake. Even when such species are no longer competitively favoured, they can still inhibit resource uptake of competitively superior species, especially newly establishing propagules, by virtue of being better established populations (Tilman, 2004), size asymmetry (Schwinning & Weiner, 1998) or allelopathy (Wardle et al., 1998). Second, high relative cover, by definition, indicates lower relative cover to be shared among remaining species and often fewer co-occurring species in general. This means that any newly superior competitor must colonize or expand from a small existing population before it can displace the initially dominant species.

Fencing had a negative effect on species with low initial relative cover, but a positive effect for species with high initial relative cover, allowing the latter to maintain dominance for much longer in fenced plots, reinforcing herbivory as a countervailing force to single species dominance (Mortensen et al., 2018). However, fencing effects were negated by fertilization effects, indicating that the benefit highly dominant species gained from alleviation of consumer pressure reduction was subordinate to the importance of nutrient supply at the high rates applied in our experiment. Our results indicate that the responsiveness of communities to press perturbations depends on the degree of dominance in the most abundant species of a community prior to the perturbations beginning. This lag between environmental perturbations and turnover of dominance being predicated on initial dominance has been called biological inertia (Gorham, 1957; Von Holle et al., 2003) and is likely to be an important part of broader system hysteresis in the response to press perturbations (van Nes & Scheffer, 2004).

Beyond the historical abundance of a dominant species, deterministic factors, such as its life-history traits, may dictate the persistence of dominant species (Suding et al., 2005; Wilfahrt et al., 2021). Here, we found that lifespan was the only predictive trait among those we tested. Perennial species may be expected to have higher persistence of dominance than annual species, as perennial individuals retain vegetative structures between growing seasons where annual species must recruit next season's growth from seed, a potential disadvantage in novel resource environments (Eskelinen et al., 2021). However, while dominant perennials in our study maintained dominance longer than dominant annuals in ambient conditions, this advantage was actually lost following fertilization. Two interesting insights emerge from this, first annual initial dominants had similar rates of dominance loss regardless of perturbations, suggesting their ability to continually maintain dominance by recruiting from the seedbank was neither hindered nor enhanced by herbivory or soil resource supply. Second, perennials' inability to maintain dominance longer than annuals following increased soil resource supply could imply that annual species may be able to better rebound following any cessation of press perturbations due to their long-lived seedbanks (Ma et al., 2021).

We found little evidence that abiotic or biotic site conditions had a strong influence on dominant species' rank loss in response to our imposed press perturbations, suggesting that the maintenance of dominance following rapid environmental change is intrinsic to the species and its population. Conversely, site conditions may indirectly affect maintenance of dominance by pre-selecting the dominant species based on life-history characteristics. For instance, we observed a negative correlation (Pearson's $r = -0.399$) between initial relative cover and site-wide species richness. The absence of a prominent site richness effect could potentially indicate that any effect of site richness on rank loss is mediated by the relationship with initial relative cover of dominants. Nonetheless, it does appear that while abiotic site characteristics could possibly affect changes in dominance in ambient conditions, they did not alter the effect of the strong, induced press perturbations of this study.

Dominant species play a prominent role in driving ecosystem functions and, thus, dictating ecosystem responses to perturbations (Avolio, Forrestel, et al., 2019). Our results suggest high initial abundances of dominant species can create lags of over a decade between the onset of a major perturbation and loss of dominance in grassland species. Given dominant species' prominent role in driving ecosystem functions, these lags may lead to an underestimation of global change effect sizes on ecosystem changes (Komatsu et al., 2019). Moreover, the lag in loss of dominance is likely to be longer in systems with less severe perturbations (e.g. atmospheric nitrogen deposition), longer lived dominants (e.g. forests, coral reefs) or infrequent disturbances (Smith, 1965; Von Holle et al., 2003). The intersection of press perturbations and disturbances is of particular interest (Harris et al., 2018). Where perturbations cause changes to ecosystem functions that are dependent on species turnover, the lag in dominance loss may impede these changes (Von Holle et al., 2003). However, when disturbances overlap with perturbations, disturbances can eliminate any such lag, also interrupting system hysteresis and causing systems under pressure from global changes factors to rapidly approach new system equilibria (DeSiervo et al., 2023; Ratajczak et al., 2018). Absent from disturbance, we demonstrate that in global grasslands, the degree of dominance and lifespan of species differently influence the maintenance of dominance in current and future grasslands. Unravelling the complexity of species composition dynamics and their role in constraining or driving other ecosystem responses is fertile ground for continued study.

AUTHOR CONTRIBUTIONS

Peter A. Wilfahrt analysed the data and wrote the paper; Eric W. Seabloom and Elizabeth T. Borer helped frame the questions; Edwin Pos and Qingqing Chen contributed to analyses and scripting and all other authors contributed data; all authors helped in substantially editing the text over multiple drafts. Full author contributions are listed in Table S6.

ACKNOWLEDGEMENTS

This work was generated using data from the Nutrient Network (http://www.nutnet.org) experiment, funded at the site scale by individual researchers (Table S1). Coordination and data management have been supported by funding to E. Borer and E. Seabloom from the National Science Foundation Research Coordination Network (NSF-DEB-1042132) and Long Term Ecological Research (NSF-DEB-1234162 to Cedar Creek LTER) programmes, and the Institute on the Environment (DG-0001-13). We also thank the Minnesota Supercomputer Institute for hosting project data and the Institute on the Environment for hosting Network meetings. The findings and conclusions of this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

CONFLICT OF INTEREST STATEMENT

No authors report a conflict of interest. Jane Catford is an Senior Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14198.

DATA AVAILABILITY STATEMENT

Data and R code used for this manuscript are available on the Environmental Data Initiative data portal: https://doi.org/10.6073/pasta/c30eb38e801a6db7506bf1e5a5a235ed (Wilfahrt, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Nutrient Network sites included in the current study.

Table S2. Simplified model output (see Table S3) of linear mixed effect models examining rank percentile of four-way interactions between NPK+, fencing, time (main effects in section 1), and each of initial relative cover (section 2), and lifespan (section 3) for sites with 5 or more years of treatment data.

Table S3. The first row shows the AIC of the full model examining the rank percentile response to seven covariates and their interactions with NPK, Fence, and time.

Table S4. Simplified model output of a linear mixed effect models examining rank percentile of four-way interactions between NPK+, fencing, time (main effects in section 1), and each of initial relative cover (section 2), and lifespan (section 3).

Table S5. Simplified model output of linear mixed effect models examining rank percentile of four-way interactions between NPK+, fencing, time (main effects in section 1), and each of initial relative cover (section 2), and lifespan (section 3) in all sites.

Table S6. Authorship contribution table. All authors contributed to at least two categories.

Figure S1. Alternative graph for Figure 2. Interactions between initial relative cover and treatments through time on rank percentile (Table S2).

Figure S2. Alternative graph for Figure 3. Interactions between lifespan and treatments through time on rank percentile (Table S2).

How to cite this article: Wilfahrt, P. A., Seabloom, E. W., Bakker, J. D., Biederman, L., Bugalho, M. N., Cadotte, M. W., Caldeira, M. C., Catford, J. A., Chen, Q., Donohue, I., Ebeling, A., Eisenhauer, N., Haider, S., Heckman, R. W., Jentsch, A., Koerner, S. E., Komatsu, K. J., Laungani, R., MacDougall, A. … Borer, E. T. (2023). Nothing lasts forever: Dominant species decline under rapid environmental change in global grasslands. *Journal of Ecology*, *00*, 1–11. https://doi.org/10.1111/1365-2745.14198