

RESEARCH ARTICLE

High among-species variability in the context dependence of herbivory across disturbance, weather and topographic gradients

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Abstract

1. Species interaction effects on populations can vary in both magnitude (i.e. strong vs. weak) and sign (positive, negative, or no effect). Context-dependent effects of species interactions occur when the sign or strength of the interaction's effect on population growth rate changes across abiotic gradients.
2. We know that species can vary substantially in the degree of context dependence they exhibit, even across similar abiotic gradients. However, few studies have characterised context dependence of co-occurring species, limiting our ability to understand the implications of context dependence for species interaction effects on community composition.
3. Using over three decades of data collected for 13 tallgrass prairie forbs at the Konza Prairie Biological Station, we parameterise density structured population models that predict population dynamics as functions of abiotic conditions and bison herbivory. We use these models to estimate the degree of context dependence in responses to bison herbivory for 13 species across three abiotic gradients: weather, fire frequency and soil type.
4. All species showed significant context dependence for fire frequency in the same direction, though with variable magnitude, such that herbivory increased cover with more frequent fires. Context dependence with weather and soil type varied dramatically across species in both direction and magnitude. For example, herbivory effects on 3/13 species were stronger in wet conditions, but herbivory effects on 5/13 species were stronger in dry conditions. Thus, context dependence exhibited by individual species, as opposed to effects of abiotic conditions on the relative abundances of species, could generate much of the weather-dependent effects of herbivory on community composition.
5. *Synthesis*: Our work suggests that species can vary dramatically in the presence, direction and magnitude of context dependence, even when occurring in the same community and when considering the same species interaction (i.e. response to a herbivore). In addition, we find that context dependence could

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drive substantial variation in the effect of species interactions on community characteristics (e.g. composition) across multiple abiotic gradients.

KEYWORDS

climate change, density structured models, forbs, herbivory, population, population dynamics, tallgrass prairie

1 | INTRODUCTION

Quantifying how species interactions impact the distribution and abundance of plants is a common goal of plant ecology. A wide variety of experimental and observational work has shown that herbivores, competitors, pathogens and mutualists can have substantial impacts on population dynamics (Fowler et al., 2023; Louthan et al., 2018; Maron & Crone, 2006; Morris et al., 2020). However, the effects of species interaction on populations can be highly variable across space and time, a phenomenon generally known as context dependence in population ecology (Maron et al., 2014). More specifically, we define a species interaction as context-dependent if the outcome of a species interaction (i.e. the difference in population growth rate or abundance in the presence vs. absence of that species interaction) varies across space or time (assuming rigorous study design and sufficient sample size to statistically detect these differences; Catford et al., 2022). Most often context dependence is assumed to arise due to spatiotemporal variation in the environment (Maron et al., 2014). For example, in the case of plant-herbivore interactions, multiple aspects of the abiotic environment can change the outcome of herbivory from weakly to strongly negative (e.g. precipitation; Louthan et al., 2018, sunlight; Harrison, 1987) or even from negative to positive (nutrient limitation; Souza Lima et al., 2018). Most often, however, studies do not implicate a causal mechanism driving context dependence (Catford et al., 2022), limiting our ability to understand for which locations or for which species context dependence might occur.

Further limiting our understanding of context dependence is the dearth of studies comparing the magnitude of context dependence among species. Most studies quantifying context dependence estimate spatial or temporal variation in outcomes for a single species (Chamberlain et al., 2014). Context dependence could be similar across species if they respond in a consistent way to environmental conditions. For example, two species, A and B, co-occurring across a precipitation gradient might have higher recruitment rates in wet years or in wetter locations. If herbivores preferentially consume seedlings, the strength of herbivory on species A and B population dynamics (i.e. the outcome of herbivory) will be higher in wet years for both species (e.g. Louthan et al., 2018). Similarly, if wet years reduce recruitment for both species A and B (e.g. by increasing competition for light), and herbivores preferentially consume seedlings, the outcome of herbivory will be lower in wet years for both species. By contrast, if recruitment increases in wet years for species

A but not species B, we might expect context-dependent herbivory in species A (Figure 1a) but not species B (Figure 1b). Meta-analyses suggest some variation in the degree of context dependence across species (Chamberlain et al., 2014), but these analyses synthesise data on outcomes from species occurring at disparate sites, limiting our ability to control for across-site abiotic and biotic variation. Namely, context dependence of each species is assessed at a unique set of sites, meaning that differences in the magnitude of context dependence could arise from differences in abiotic environment across each set of sites, rather than species identity. We currently lack studies that control for among-site variation in abiotic drivers by quantifying the outcome of a species interaction for multiple species occurring across the same suite of sites (but see Lynn et al., 2019).

Understanding whether species exhibit similar context dependence is critically important to predicting responses of communities to species interactions in a changing climate. For example, if context dependency of herbivory is similar across species and there is no effect of climate change on the relative abundances of species in a community, the effect of herbivory on community composition will be similar in current and future climates (Figure 1a). When context dependency is similar across species but there is an effect of climate change on the relative abundances of species in the community, the effect of herbivory on community composition will differ in current versus future climates (Figure 1c). However, the effect of herbivory on community composition will differ in a current versus future climate, even without climate change-induced changes in the relative abundances of species (Figure 1b), if species differ in the degree of context dependence (i.e. some species experience stronger impacts of herbivory in a future climate, but others experience weaker impacts). Thus, across-species variation in context dependence could result in changes in species interactions' effect on community composition across abiotic gradients, irrespective of effects of the abiotic environment on species' relative abundances.

Here, we quantify context dependence of large mammal herbivory (hereafter, herbivory) for 13 plant species across three gradients in abiotic drivers, weather, fire return interval (FRI) and soil type, at Konza Prairie Biological Station (KPBS). We measure context dependence of these species in sympatry, meaning that populations of each species are subject to identical abiotic drivers. Our modelling approach also allows us to identify abiotic drivers of variation in outcomes across multiple co-occurring abiotic gradients (i.e. weather, soil type and FRI). Importantly, measuring outcomes of herbivory for multiple species in one community allows us to predict how herbivore reintroduction or extirpation might impact community composition

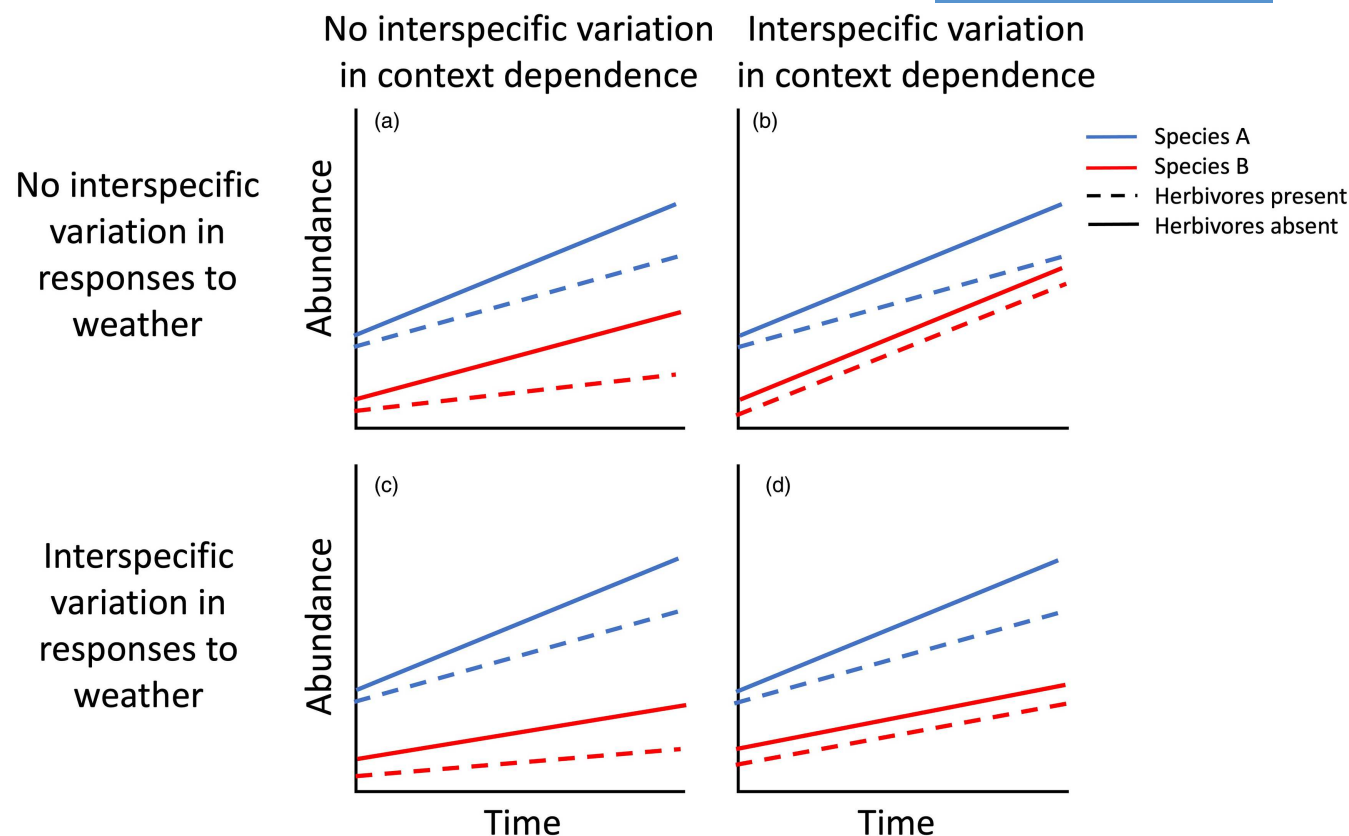


FIGURE 1 Interacting effects of across-species variation in context dependence (columns) and weather effects on species abundances (rows). We show hypothetical results from a simple community comprised of two species, A and B, and quantify the effect of herbivory on each species abundance over time. We also show the proportion of total abundances comprised by species A and B, for both herbivores absent and present, enclosed in boxes. Panel (a) shows no effect of weather on relative abundances (species A is always ~30% more abundant) and similar context dependence (for both species herbivory outcomes increase in response to changing weather conditions). In this scenario, herbivore effects on community composition (i.e. the proportion of total abundance comprised by species A) does not vary with weather. Panel (b) shows no effect of weather on relative densities, but different context dependence across species. In this scenario, the effect of herbivores on community composition increases as weather changes. Panel (c) shows an effect of weather on relative abundances, with similar context dependence across species; in this scenario, herbivore effect on community composition does not vary with weather (but species relative abundance does vary with weather). In Panel (d), weather differentially affects relative abundances and species differ in the degree of context dependence (panel d), resulting in changes in species relative abundance and increases in herbivore effects on community composition as weather conditions change; of course, much more complex patterns are possible in a multi-species community and when considering species additions and losses.

across different weather conditions, including in a future climate (Figure 1c,d). Effects on plant abundance were quantified using a 37-year dataset of plant abundance across extreme weather events (e.g. drought and wet years; Ratajczak et al., 2022), soil types, fire return intervals (FRI) and large-scale experimental manipulations of herbivore presence. We used these long-term data to parameterise density structured models that use environmental drivers to predict multinomial transitions among ordinal cover classes for each species, allowing us to quantify context dependence across three abiotic gradients (weather, FRI and soil type).

2 | METHODS

Our study was based at KPBS (39°05' N, 96°35' W) located in eastern Kansas, USA, a large tallgrass prairie remnant in the Flint Hills

ecoregion. KPBS has been divided into 54 management units ('watersheds'), each assigned to different FRI and herbivory regimes (1, 4 and 20-year FRIs, Great Plains bison (*Bison bison*) present or absent; Collins et al., 2021). FRI and large mammal herbivory ('herbivory', from hereon) are replicated across the landscape in a fully factorial design, with 1–2 large scale (~60ha) replicates of each FRI×herbivory combination. Bison were established on KPBS between 1987 to 1992 (Table S1), and bison are allowed free access to watersheds from all FRI treatments. Once introduced at KPBS, bison population abundance has remained stable at ~260 individuals (Knapp et al., 1999; Ratajczak et al., 2022). In bison absent watersheds, perennial *C₄* grasses comprise most of above-ground cover (Knight et al., 1994) with forb cover and diversity higher in bison present watersheds (Ratajczak et al., 2022). We focus on forbs because in this system, because they contribute substantially to species diversity, comprising a majority of overall richness (O'Keefe & Nippert, 2017;

Towne, 2002) and are critical for maintaining pollinator populations (Welti et al., 2017).

We used a long-term dataset of plant cover data that has been collected annually at 820 plots across 11 watersheds since 1983 (Hartnett et al., 2023). In each watershed, five 10m² circular sampling plots are evenly distributed along four 50m long transects in each of two soil types, upland and lowland soils ($n=40$ plots/watershed/year, except in one watershed; Table S1). Upland soils are shallow but variable in depth (5–200cm) and lowland soils are deeper (>2.5m in depth; Nippert et al., 2012). Each year, percent cover of all species of vascular plants is measured using a modified Daubenmire cover scale (Bailey & Poulton, 1968) and assigned to one of seven density classes (<1%, 2%–5%, 6%–25%, 26%–50%, 51%–75%, 76%–95%, 95%–100%). We restricted our analyses to forb species that were present in all of the 11 watersheds and had at least 1400 observations across all watersheds, resulting in 13 species total (Table S2). Perennial forb species included in our analysis were from six families: Asteraceae (*Ambrosia psilostachya*, *Artemisia ludoviciana*, *Symphyotrichum oblongifolium*, *Ratibida columnifera*, *Solidago altissima*, *Solidago missouriensis*), Asclepiadaceae (*Asclepias verticillate*, *A. viridis*), Fabaceae (*Mimosa quadravalvis*, *Lespedeza violacea*), Oxalidaceae (*Oxalis stricta*), Acanthaceae (*Ruellia humilis*) and Lamiaceae (*Salvia azurea*).

Our modelling approach was comprised of five steps: (1) quantifying impacts of abiotic gradients (weather, fire and soil type) and herbivory on changes in each species' density class by regressing the multinomial probability of observing a species in a given density class against values of abiotic drivers and herbivory experienced over the previous year; (2) using these multinomial probabilities to parameterise density structured population models. Density structured models are similar in structure to a matrix population model, but predict changes in the frequency of plots occupying a given density class, rather than changes in the frequency of individuals in a given size class (Freckleton et al., 2011; Queenborough et al., 2011); (3) using these population models to project changes in density class for various hypothetical combinations of all four drivers; (4) using these projections to estimate the degree of context dependence to herbivory across weather conditions, FRI gradients and soil type for each species; (5) testing whether variability in context dependence in these 13 species contributes to changes in herbivore effects on community composition across each of these three abiotic gradients. We outline each step in more detail below.

2.1 | Quantifying impacts of abiotic drivers and herbivory on multinomial probabilities

We used a model selection approach to test for species-specific effects of weather, fire, soil type and herbivory on the probability of attaining a given density class. Given that a species can attain one of eight density classes in each plot, we used multinomial logistic regression to parameterise this response. We did not use an ordinal regression because the density classes were of unequal size, and

because we did not want to assume that changes in density classes exhibited a central tendency. Our multinomial logistic regressions predict the multinomial probability of observing a species at the seven non-zero density classes in each year, given: (1) its density class in the previous year; (2) herbivore presence or absence, FRI and soil type at that plot; and (3) weather and fire events (distinct from FRI, see below). Specifically, our global model included density class in the previous year, herbivory, FRI, soil type and species identity. Our global model also included a numeric term describing weather throughout the growing season; namely, we used the first principal component score (PC1) of a principal component analysis of mean daily temperature and total daily precipitation at KPBS during the 1983–2019 growing seasons (Nippert et al., 2022); the first PCA axis corresponds very well to a gradient of warm and dry to cool and wet conditions (Supporting Information). Interactions between these variables were also included in the global model and are described below.

In our global model we also included a term representing time since fire effects. Time since fire and FRI effects on forb populations could differ, because long-term management for a particular FRI can affect soil characteristics (Slette et al., 2021) or woody cover (Briggs et al., 2005), which could have qualitatively different effects than time since fire. We assessed support for two alternative representations of time since fire: (1) whether the watershed containing a plot was burned in the year prior; and (2) linear and quadratic effects of years since fire (i.e. number of years since the watershed containing the plot was burned, including both prescribed fires and infrequent wildfires). We constructed two global models that used these alternative representations of time since fire effects (in addition to the predictor variables outlined in the previous paragraph). Both global models included all two-way interactions between species identity, weather, FRI, soil type, herbivore presence or absence, and our time since fire terms. These interactions allow responses of species to weather, fire, herbivory and soil type to vary among species. We provide detailed descriptions of biological rationale for all other interaction terms (Supporting Information).

We then used a model selection approach to compare all possible subsets of each of the two global models using AICc. The top model between these two suites of models was then used in all subsequent analyses (Table S3). All models were fit using nnet (Venables & Ripley, 2002) in R (version 4.1.1; R Core Team 2021).

2.2 | Constructing density structured population models

We constructed density structured population models (Freckleton et al., 2011; Queenborough et al., 2011) using the predictions of the best-fit multinomial logistic regression model. A density structured population model predicts $s(t+1)$, the proportion of plots occupying each of k density classes in time $t+1$, as a function of $\mathbf{T}$, a $k \times k$ transition matrix and $\mathbf{s}(t)$, the proportion of plots occupying each of k density classes in time t . Namely, $\mathbf{s}(t+1) = \mathbf{T} \cdot \mathbf{s}(t)$. Entries in

column i and row j of the T matrix represent the probability that a plot at density class i in time t transitions to density class j at time $t + 1$ (see [Supporting Information](#) for additional information about density structured models). Such transitions can include survival and growth of extant plants, as well as recruitment from seed (or a seedbank). To our knowledge, all previous formulations of these models calculate transition probabilities among density classes from raw data (e.g. Goodsell et al., 2021; Mieszkowska et al., 2013; Queenborough et al., 2011), but here we adopt a novel methodology to construct density structured models in which transition probabilities—predicted from the multinomial logistic regression model—can be functions of drivers such as weather, fire, soil type, or herbivory. These density structured models reflect the ordinal nature of the data collection and account for unequal bin sizes, a strength of previous formulations of density structured models, while allowing for population dynamics to explicitly depend on drivers, a strength of regression-based approaches (Merow et al., 2014). We did not include a density class of 0% cover as a class in our multinomial regression, as high proportions of unoccupied plots led to problems with convergence. Instead, we used the raw data to parameterise colonisation and extirpation of plots over the entire course of our study ([Supporting Information](#)).

2.3 | Testing for context dependence

We used our density structured models to predict each species' density class across a series of hypothetical combinations of driver values representing scenarios of interest. We predicted species-specific density class for all possible combinations of: herbivory, FRI, soil type and three weather quantiles representing cool/wet, median and warm/dry weather conditions (the 5th, 50th and 95th quantile of PC1 scores; [Supporting Information](#)); hereafter we refer to these conditions as cool/wet, median and warm/dry. For each combination of driver values, we projected population dynamics using a simulation approach (following Easterling et al., 2000) simulating FRIs of 1, 4 or 20 years by iterating matrices in the appropriate sequence (Doak et al., 2021; deterministic FRI is reflective of fire management in this system). We initialised each projection from a uniform distribution of plots across density classes and simulated 10,000 years of population dynamics. We discarded the first 2000 years to account for any transient effects. For the last 8000 years of our simulation, we calculated the proportion of plot $\times$ year combinations that attained each density class. We assumed that a plot that attained a given density class actually attained the midpoint of the density class (e.g. the first density class represented 0%–1% cover, so we assumed that all plots attaining this density class attained 0.5% cover). Thus, we calculated predicted mean percent cover, for the last 8000 years of our simulation, using a weighted average of the midpoints of each density class, where the weights were the proportion of plot $\times$ year combinations that attained a given density class. We incorporated parameter uncertainty into our estimates of predicted

mean percent cover by generating 500 sets of parameter estimates (Louthan et al., 2022), taking Monte Carlo samples from the multivariate normal approximation to the joint posterior probability distribution of the best fit model's coefficient estimates, and recalculating mean percent cover for each set of coefficient estimates. This multivariate normal distribution reflects the variance–covariance matrix of the coefficient estimates derived from the neural network approach used to fit our multinomial logistic regression. The variance–covariance matrix was obtained using the `vcov.multinom` function from the `nnet` package (Venables & Ripley, 2002). We show the mean and 95% confidence interval across these 500 coefficient estimates in our results; thus our 95% confidence intervals represent parameter uncertainty.

To test whether each species exhibited context dependence, we asked whether the outcome of herbivory varied with weather, FRI or soil type. For each species, we calculated the outcome of herbivory as the log response ratio (LRR) of predicted percent cover with herbivores present vs. absent, for a given weather condition, FRI and soil type:

$$\text{LRR} = \log \left(\frac{\text{percent cover when herbivores present}}{\text{percent cover when herbivores absent}} \right)$$

LRR has been used for similar studies (e.g. Morris et al., 2020) and reflects the multiplicative nature of population growth (Spake et al., 2023). We calculate the species-specific LRR at each level of each abiotic gradient (weather: cool/wet, median and warm/dry, FRI: 1, 4 and 20, soil type: upland or lowland), then present the mean and 95% confidence intervals on these LRRs, calculated across the 500 replicates. When at least one pair of abiotic gradient levels' confidence intervals did not overlap, we assumed that LRR varied significantly across that abiotic gradient (i.e. the outcome of herbivory was context dependent across that gradient). For example, if the 95% confidence intervals of cool/wet LRR and warm/dry LRR did not overlap, the outcome of herbivory was deemed context dependent. When considering weather gradients, we fixed FRI at 1 and soil type at upland. When considering FRI, we fixed weather at the median value and soil type at upland, and when considering soil type, we fixed weather at the median and FRI at 1. Finally, we characterised interspecific variation in context dependence at the family level to quantify if closely related species exhibit similar context dependence across each abiotic gradient. Namely, we assessed whether species were similar in the presence or direction of context dependence (i.e. if context dependence was present, and if so, whether herbivory outcomes increased or decreased along the abiotic gradient).

2.4 | Implications of context dependence for species composition

We used our predictions of percent cover, derived from the density structured models, to estimate how herbivory effects on species composition varied across each of our abiotic gradients for this subset of the community. For each of our three weather conditions (i.e. cool/wet,

median and warm/dry), we calculated a Bray-Curtis distance between community composition with versus without herbivory at each of our three weather conditions (fixed at an FRI of 1 and an upland soil type). We repeated this procedure to estimate herbivory effects on species composition across our three FRIs (for median weather conditions and an upland soil type) and across soil types (for median weather conditions and an FRI of 1). We show 95% confidence intervals, calculated across parameter estimates, for these dissimilarity scores.

Ethical approval was not required for our study as we were working exclusively with long-term data that had already been collected.

3 | RESULTS

3.1 | Effects of herbivory, FRI and weather on percent cover

Mean percent cover of forb species varied widely among species, as did effects of abiotic drivers and herbivory. Most (11/13) species in our analysis remained at low percent cover (mean cover across all years <20%) throughout the entire time series, across all FRI

and herbivory combinations and regardless of weather conditions (Table S4). Weather, FRI and herbivory all contributed to variation in percent cover, though the effects differed across species (Table S3). For example, *Ambrosia psilostachya* had an average percent cover of 12.8% when herbivores were present, but 5.9% when herbivores were absent. In contrast, *Symphyotrichum oblongifolium* had higher average percent cover when herbivores were absent (9.5% vs. 4.8%). Similar interspecific variation was also observed among FRI. Reflecting the discrepancy in species' responses to abiotic drivers and the interacting effects of abiotic drivers and herbivory, our best-fit multinomial logistic regression model included effects of species, weather, FRI and herbivory, whether a plot was burned in a given year, soil type and all two-way interactions between these variables (Table S3).

Our density structured models predicted effects of both abiotic drivers and herbivory on percent cover (Figure 2). First, we found effects of weather on predicted percent cover of many species, with generally higher percent cover under warm/dry than under cool/wet weather conditions (Figure 2). FRI also affected predicted percent cover for many species. Some species (*A. verticillata*, *A. viridis*, *R. columnifera*, *R. humilis*, *M. quadrivalvis*) experienced minimal impacts of weather or FRI; these species tended to have overall low

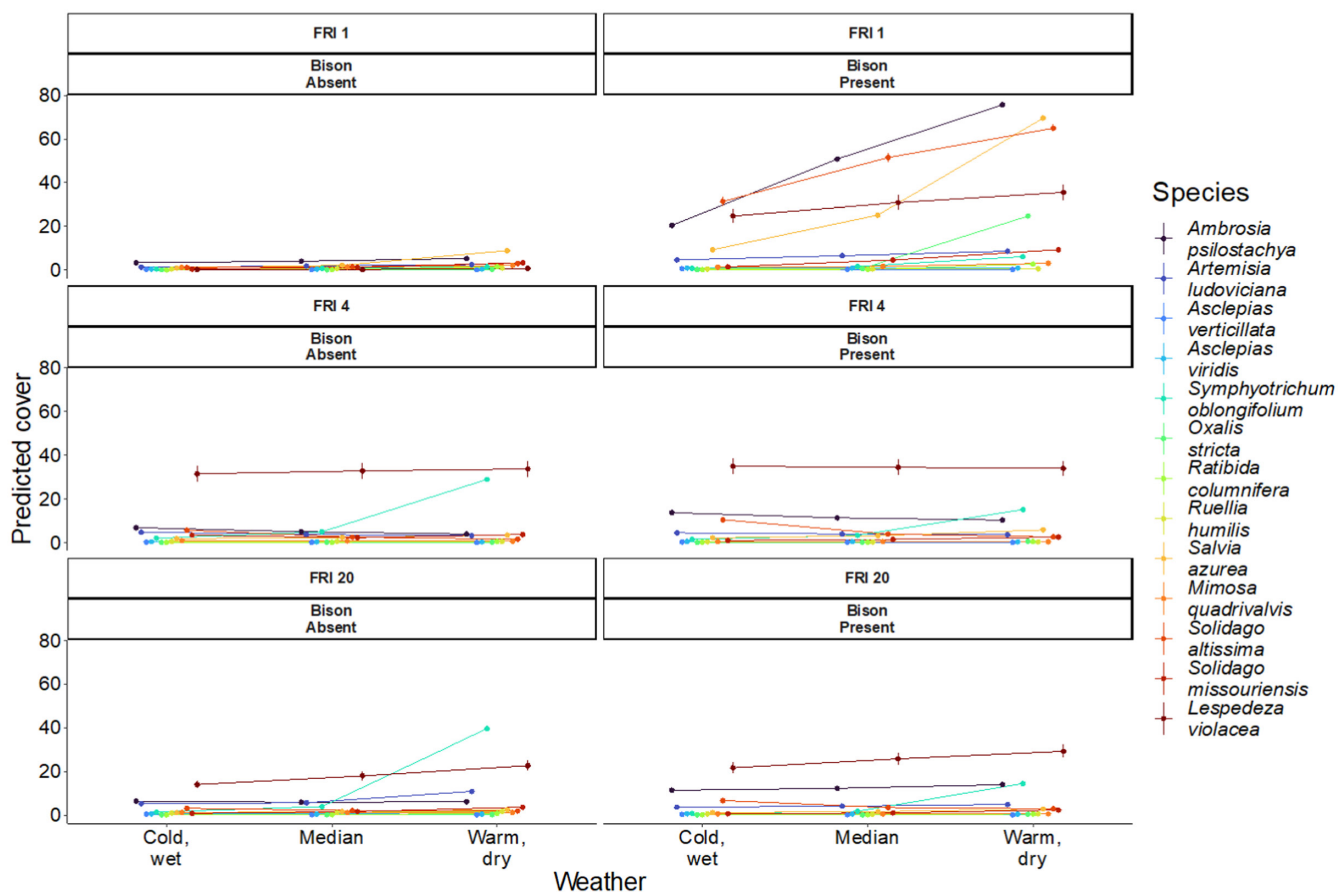


FIGURE 2 Species-specific effects of herbivory, weather and FRI on predicted percent cover in upland soil types. We considered effects of bison presence and FRI at three weather levels that represent cool, wet conditions ("Cold, wet"), median conditions ("Median") and warm, dry conditions ("Warm, dry"). Error bars indicate 95% confidence intervals on predicted percent cover; confidence intervals only include parameter uncertainty, and points are jittered to improve readability. For each panel, FRI (1, 4 or 20) and whether bison were present or absent are indicated by the labels. All predicted percent cover values are shown in Table S4.

predicted percent cover. Herbivores also affected predicted percent cover in most species, with uniformly positive effects of herbivore presence at an FRI of 1 (where bison spend a substantial amount of time; Raynor et al., 2017), likely due to a reduction in competition with grass species, bison's primary food source (Koerner et al., 2018; Ratajczak et al., 2022). Outcomes at longer FRIs were more variable (Figure 2). We present only predicted percent cover for the upland soil type in the main text, as responses were very similar for lowland soil types (Figure S1).

3.2 | Interspecific variation in context dependence

Our metric of herbivory outcomes, LRR, showed context dependence across weather gradients in 10/13 species (Figure 3a). For each of these species, the LRR at one weather level differed significantly from the LRR in at least one other weather level (i.e. their 95% confidence intervals did not overlap). For the remaining species (*A. ludoviciana*, *R. columnifera* and *L. violacea*), LRR did not differ significantly across weather levels. For the 10 species that showed context dependence, the magnitude and direction of the context dependence varied dramatically across species. For example, the outcome of herbivory declined as weather conditions became warmer and drier in three species but increased in five other species. Four species

showed highest LRR at median weather conditions. This interspecific variation in patterns of context dependence resulted in changes in the rank ordering of species' LRRs across weather conditions. For example, *M. quadrivalvis* had the highest LRR at cool/wet and median weather conditions, but *O. stricta* had the highest LRR at warm/dry weather conditions. Family was not a good predictor of the presence or direction of context dependence (Supporting Information). Our metric of weather conditions (namely, position along PCA axis 1) does not include all possible variation in weather (because PCA axis 1 only comprises ~65% of the variance in growing daily temperature and precipitation; Figure S2).

Outcomes were context dependent across FRI gradients for all species, and the direction of context dependence was similar across species. LRR was highest at an FRI of 1 for all species (Figure 3c). With further increases in FRI (i.e. increases from an FRI of 4 to an FRI of 20), LRR either decreased (10/13 species) or did not change (3/13 species). Variance in LRR was highest at an FRI of 1, reflecting high among-species variability in the outcome of herbivory, and lower at longer FRIs, reflecting lower among-species variability in the outcome of herbivory.

Outcomes showed significant context dependence across soil types for 8/13 species, though the direction of context dependence varied across species (Figure 3b). Unlike weather or FRI gradients, the rank order in species LRR did not change with soil type.

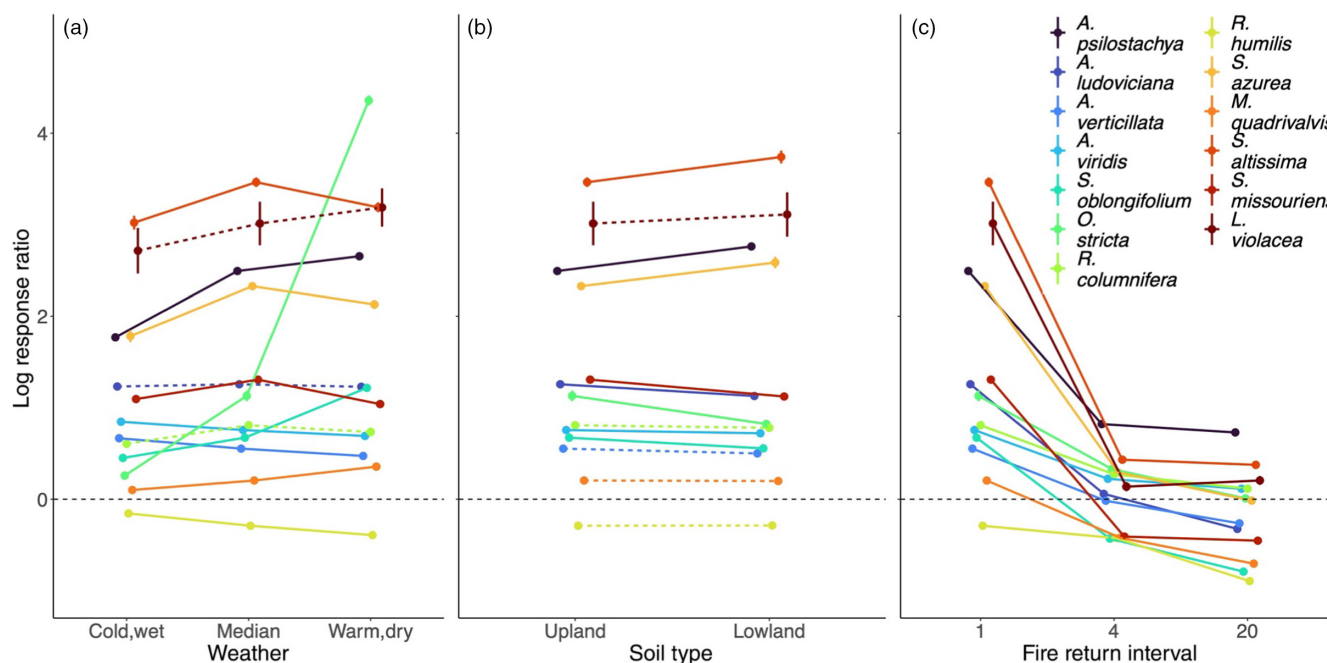


FIGURE 3 Interspecific variation in context dependence across weather (a), soil type (b) and fire return interval (c) gradients. Each coloured line represents log response ratio (LRR; $LRR = \log(\text{cover with herbivore} / \text{cover without herbivore})$) of one species. Species represented by a solid line show significant context dependence (i.e. LRR of at least one pair of abiotic drivers are significantly different from one another at the 95% level); species represented by dashed lines do not show significant context dependence (i.e. no LRRs differ significantly from one another). Dots represent the predicted LRR; error bars represent 95% confidence intervals on the LRR; these confidence intervals incorporate only parameter uncertainty. We show an LRR of zero in a dashed black line; positive LRRs indicate that herbivory increased predicted percent cover, negative LRRs indicate that herbivory decreased predicted percent cover, and an LRR of zero indicates that herbivory did not significantly affect percent cover of that species. Points and lines have been jittered to make points more visible.

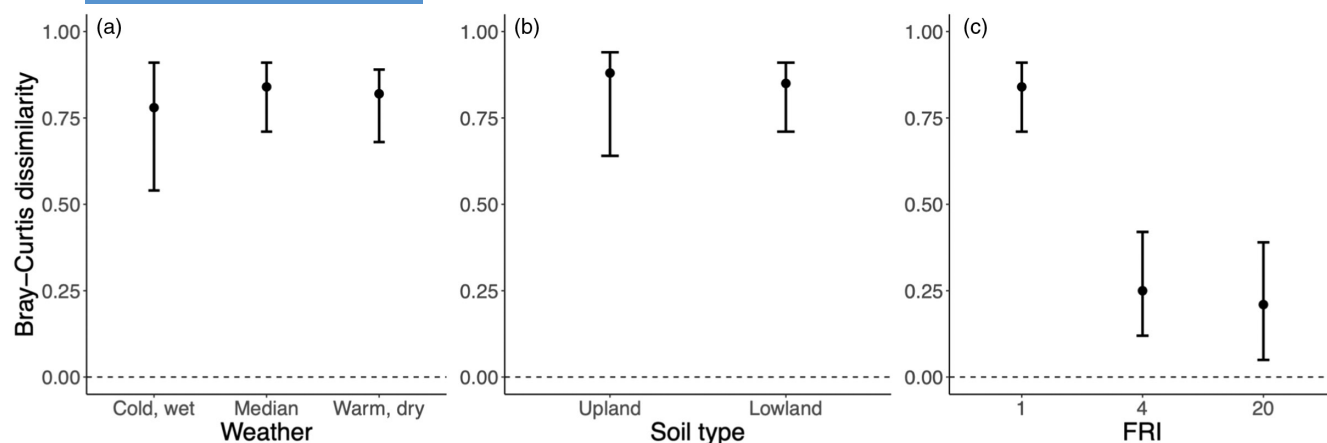


FIGURE 4 Herbivory effects on community composition across weather (a), soil type (b) and fire return interval (c). Herbivory effects on community composition are calculated as the Bray–Curtis dissimilarity between species composition in the presence versus absence of herbivores (using our predicted percent cover estimates of our 13 focal species, a small subset of the understory plant community at this site). Dots represent the mean dissimilarity, averaged over 500 replicates that incorporate parameter uncertainty; error bars represent 95% confidence intervals. We show values of zero in a dashed line; positive values indicate that herbivores changed community composition; a value of zero indicates that herbivores had no effect on community composition.

3.3 | Effect of herbivory on community composition

We were interested in understanding whether context-dependent outcomes of herbivory could, when acting alone, result in changes in the effect of herbivory on species composition across abiotic gradients. Across weather conditions, herbivory's effect on species composition (i.e. the Bray–Curtis dissimilarity between species composition in the presence vs. absence of herbivores) was high across all weather conditions (Figure 4a), meaning that the strength of herbivory effect on species composition was substantial and did not differ significantly with weather. This phenomenon could arise because there is substantial among-species variation in LRR at all weather conditions (Figure 3a), resulting in herbivore-induced shifts in the relative abundance of species regardless of weather. Across FRIs, the effect of herbivory on species composition was significantly higher at an FRI of 1 than for FRIs of 4 and 20 (Figure 4c). This effect likely arises because at an FRI of 1, there is substantial variation in the LRR of these species, resulting in large herbivore-induced changes in species composition. The among-species variation in LRR decreases at longer FRIs, resulting in similar effects of herbivory on all species (and thus little change in their relative abundances and community composition). In both soil types, herbivory's effect on species composition was high and the effect of herbivory on species composition did not vary with soil type (Figure 4b). This result likely occurs because there is high among-species variability in LRR in both soil types (Figure 3b).

4 | DISCUSSION

Our novel modelling framework revealed a wide range of variation in context dependence among co-occurring species across three abiotic gradients. The presence and direction of context dependence across

weather conditions varied across species. All species showed context dependence across FRI gradients, and the direction was similar across all species, with highest LRR to herbivory in annually burned areas. Most species exhibited context dependence across soil types, though the direction of context dependence varied. Finally, we demonstrated that context dependence has the potential to influence community composition. Effects of herbivory on community composition were consistent across weather conditions and soil type, but varied substantially across FRIs, with the largest observed effect of herbivory on community composition in annually burned areas.

The presence, strength and magnitude of context dependence varied dramatically across species for weather and soil type gradients. For those species that showed significant context dependence across weather conditions, many (5/12) experienced the highest LRR to herbivory under warm/dry weather conditions. Such an effect could arise because of commonalities among these species in their response to weather. For example, perhaps for these 5 species warmer and drier weather increases the probabilities of large increases in density class (e.g. from a density class of 0.25% to 80%). If herbivores tend to reduce this particular transition rate (perhaps by preferentially consuming newly abundant species) we will see higher outcomes of herbivory for these species in warmer and drier weather. Such a scenario is congruent with one hypothesised mechanism of context dependence: abiotic drivers impacting components of plant fitness, which then modulate species interaction effects on population growth rate (Maron et al., 2014). For the other seven species that showed context dependence across weather conditions, three showed highest outcomes of herbivory under cool/wet weather conditions, and four showed highest outcomes of herbivory under median weather; similar mechanisms driving these common responses could apply. One species showed no significant context dependence, perhaps due to weak or nonexistent effects of our metric of weather on this species' population dynamics (variance in

weather conditions unexplained by PCA axis 1 might affect context dependence in this species, or any other species).

We see similar patterns across soil type gradients, with high across-species variability in the presence, strength and direction of context dependence, suggesting that plant populations are responding idiosyncratically to differences between soil types, perhaps due to differences in water availability and soil nutrients (O'Keefe & Nippert, 2017). Regardless of the mechanism, substantial interspecific variation in the presence, magnitude and direction of context dependence across these abiotic gradients contrasts with recent predictions that species occurring across similar abiotic gradients should exhibit similar patterns of context dependence simply due to commonalities in plant demographic response to abiotic drivers (Maron et al., 2014). Context dependence does not require that one site, habitat, or environment is more or less 'stressful', which can be defined in many ways, including at the environment or species level (Bertness & Callaway, 1994; Grime, 2006; Maron et al., 2014).

All species showed similar context dependence across FRI gradients, likely driven by covariation between FRI and herbivore activity. For all species, herbivores more strongly increased predicted percent cover at an FRI of 1, with more variable effects of longer FRIs. Positive effects of herbivores on these forb species are likely stronger at an FRI of 1 because herbivores spend more time in recently burned areas (Eby et al., 2014; Raynor et al., 2017), due to higher grass nutrient content following a burn (Simpson et al., 2019). In recently burned areas, bison consume grass and are thought to alleviate competition (Damhoureyeh & Hartnett, 1997; Ratajczak et al., 2022; Raynor et al., 2016). Other effects of bison, such as nutrient deposition and an increase in landscape heterogeneity, could also increase forb performance (Elson & Hartnett, 2017). Our findings also illustrate another hypothesised mechanism that can drive context dependence—namely, higher densities of interacting species in more-productive environments resulting in stronger outcomes of species interactions in those environments (Maron et al., 2014). Our results suggest that this second mechanism of context dependence can generate similar directions and strengths of context dependence across many species. Soil type also influences bison densities, with higher densities in the lowlands following drought years, and higher densities in the uplands following other years (Raynor et al., 2017). Perhaps because of this temporal variation in densities, we do not see consistent directions and strengths of context dependence across upland versus lowland soil types.

The coarseness of our data (i.e. wide density classes) may have obscured variability in context dependence between species and limited our ability to identify context-dependent responses. By restricting transitions between density classes, species could only be observed to make a limited number of transitions, which would not be the case if percent cover was treated as a continuous response. Therefore, our observed results are likely conservative estimates of changes in abundance, because with wider density classes there is the potential for changes in abundance to not be detected, even if abundance has changed dramatically within a plot. For example, a change from 30 percent cover to 50 percent cover would have fallen

within a single density class and not resulted in an observed change. This potential problem is offset by the fact that forbs rarely occupy high density classes but this is nonetheless a limitation of density structured models when density classes are uneven. Future studies using density structured models could consider designing more even density classes, or carefully considering possible density classes a focal species may occupy. Additionally, applying treatments at the watershed level means that there is some degree of pseudoreplication, but the added realism of this approach largely outweighs any impact of pseudoreplication on plant populations within a given treatment (Ratajczak et al., 2022).

Species-specific patterns of context dependence manifest into systematic variation in herbivore effects on community composition for some, but not all, abiotic gradients. For weather, high among-species variability in LRR results in consistently strong herbivore effects on community composition across all weather conditions (Figure 4a). Given that the rank order of LRR changes across weather conditions, the community composition of bison-grazed areas under warm/dry weather conditions will differ dramatically from composition of bison-grazed areas in cool/wet conditions, an effect that arises only from context dependence (Figure 1b). For example, herbivory substantially increases percent cover of *S. oblongifolium* in warm/dry conditions, with minimal effects in cool/wet conditions, likely resulting in grazed communities with high *S. oblongifolium* cover in warm/dry weather conditions, and grazed communities with low *S. oblongifolium* cover in cool/wet conditions. Such effects arise irrespective of direct weather effects on *S. oblongifolium* density, and simply due to the context dependence of herbivory (as in Figure 1b). Similar arguments apply to soil type. By contrast, high across-species variation in LRR at an FRI of 1 (Figure 3b) results in strong effects of herbivores on composition at this FRI, with lower across-species variation in LRR at longer FRIs resulting in weaker effects of herbivores on composition (Figure 4b).

Our results suggest that context dependence could be a key, yet underappreciated, driver of why herbivore effects on diversity and richness change across abiotic gradients (Koerner et al., 2018). While many studies implicate changes in plant species composition across abiotic gradients as a driver of changes in herbivore effect size (Chase et al., 2000), as in our Figure 1c, fewer discuss how context dependence might modulate those responses (as in Figure 1d). Single-species studies do find context-dependent herbivory (e.g. Chamberlain et al., 2014; Louthan et al., 2018; Miller et al., 2009), but context dependence has not yet been connected to the rich literature on geographical variation in herbivore effects on diversity (e.g. Koerner et al., 2018). Instead, most studies of herbivore effects on diversity simply look at community-level metrics rather than ask how individual species' responses to herbivory vary across abiotic environment. In fact, seminal literature on this topic assumes that variation in the effect of herbivores on diversity is mediated by differential effects of herbivores on extirpation or colonisation rates, rather than context dependence of species extant across the gradient (Olf & Ritchie, 1998). Our work suggests that changes in herbivore effects on diversity could result from both abiotic effects on

relative abundances and on context-dependent herbivory, but that the pattern of effect depends on the magnitude and variation in LRR across species.

Our work also highlights the difficulty in predicting the outcome of herbivory—or any other species interaction—in a particular population. Studies that rigorously test for context dependence by accounting for confounding variables, including sufficient sample size, and standardised methodology (Catford et al., 2022), particularly when combining data from multiple studies (Spake et al., 2023) are critical to accurately predicting context dependence in new environments. Our work further highlights that any population lies at the confluence of multiple abiotic gradients, such that the outcome of a species interaction at a given population will be a product of that population's position along all underlying abiotic gradients. In order to predict how outcomes will change along multiple concurrent abiotic gradients, we must quantify context dependence across each abiotic gradient. Our work further suggests that multiple mechanisms of context dependence could operate simultaneously—in our system, FRI operates to change the densities of herbivores, while weather could modulate herbivore outcomes by changing aspects of plant demography. Multiple abiotic gradients could therefore both play key roles in the future population dynamics of plant species, particularly in the context of changing land management practices such as fire.

Overall, we see substantial variability in the direction, magnitude and even presence of context dependence across species. We find that gradients that result in variation in densities of interacting species (like FRI) can lead to similar context-dependent patterns, but gradients that do not systematically affect densities (like weather and soil type) do not. We also find support for the idea that interspecific variability in context dependence is high enough that it can result in changes in the effect of a species interaction on community composition across abiotic gradients, even without abiotic effects on species relative abundances. Our work suggests that context dependence could be an important contributor to spatiotemporal variation in the effect size of species interactions on communities.

AUTHOR CONTRIBUTIONS

Alex O. Sutton and Allison M. Louthan conceived of the study, Alex O. Sutton conducted the data analysis, with input from Allison M. Louthan and Zak Ratajczak. All authors contributed to writing the manuscript and providing feedback on drafts. Multiple authors are based at Kansas State University which oversees data collection for the long-term dataset that was the basis of our analysis and as such we included local experts in our analysis.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14390>.

DATA AVAILABILITY STATEMENT

Data are publicly available at the Environmental Data Initiative: PVC02 Plant species composition on selected watersheds at Konza Prairie <https://doi.org/10.6073/pasta/0d591da0aff8bbcc8ec07c160d83d36e> (Hartnett et al., 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. List of watersheds across Konza Prairie Biological Station used in this analysis.

Table S2. List of species used in analysis.

Table S3. Model selection table of top six models from AICc model selection.

Table S4. Predicted percent cover estimates for each species across FRI and herbivory treatments, weather conditions, and soil types.

Figure S1. Species-specific effects of herbivory, weather, and FRI on predicted percent cover in lowland soil types.

Figure S2. Principal component analysis of long-term weather data (mean temperature and cumulative precipitation) collected from Konza Prairie Biological Station.

Figure S3. Principal component 1 score (PC1) over the course of our study. PC1 varied widely but did not change directionally over time.

Figure S4. Principal component 1 score (PC1) frequency across all years of our study.

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