

ARTICLE

Vegetation Ecology

Large mammalian herbivores disrupt demographic compensation along an aridity gradient

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Abstract

Ecologists often assume that demographic rates such as survival and reproduction vary in concert along abiotic gradients, but growing evidence suggests that these rates may change in opposition, leading to demographic compensation. However, it is unclear how biotic interactions such as herbivory may affect the presence or strength of demographic compensation. Here, we employ a series of strong tests for demographic compensation for a common forb species in the presence and absence of large mammalian herbivores. Namely, we test for demographic compensation in *Hibiscus meyeri* across a rainfall gradient using a large-scale exclosure experiment that includes or excludes large mammalian herbivores of various sizes (i.e., small, meso-, and megaherbivores). We found that demographic compensation did not occur while all large mammalian herbivores were present. By contrast, demographic compensation occurred when megaherbivores were excluded, and this discrepancy was driven by an excess of negative correlations between vital rates. Understanding how biotic factors interact with abiotic gradients to modify demographic processes is crucial for understanding the drivers of species population dynamics for broader efforts in conservation and management.

KEYWORDS

abiotic gradients, biotic interactions, demographic compensation, herbivory, large mammalian herbivores, plants, populations

INTRODUCTION

Demographic rates of plant species, such as survival, growth, or reproduction, frequently vary across space. This spatial variation in demographic rates has important

implications for species distribution patterns, as these rates directly influence population growth rate and, consequently, the overall distribution of a species. Many studies have examined how abiotic factors induce spatial variation in demographic rates, but biotic factors

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(e.g., herbivory, predation, and competition) also play a significant, though lesser studied role in influencing demographic rates. Biotic drivers' impacts on demographic rates can be considerable and often vary spatially (Kauffman & Maron, 2006; Maron et al., 2014). Furthermore, biotic and abiotic gradients can interact with one another, such as when biotic interactions limit demographic rates, and thus population growth rate, more strongly in less abiotically stressful environments (Connell, 1972; Dobzhansky, 1950; Louthan et al., 2018). Although biotic factors clearly affect demographic processes, their relative importance in driving spatial variation in population growth rates along abiotic gradients remains uncertain. Here, we explore how herbivory drives spatial variation in population growth rate by examining its role in generating demographic compensation, which occurs when a species' demographic rates are negatively correlated across space, resulting in higher demographic rates at one end of a gradient "compensating" for low demographic rates that reduce population growth rate (Doak & Morris, 2010; Vilellas et al., 2015).

Previous theory has suggested that demographic rates should be positively correlated across space (Pironon et al., 2017). For example, if plant growth is higher at one end of an abiotic gradient, theory suggests that reproduction will also be higher, as both demographic rates might respond similarly to the same favorable abiotic conditions. However, an emerging body of research suggests that demographic rates are not always positively correlated. This phenomenon can occur when spatial variation arises from multiple underlying abiotic or biotic gradients that affect rates differently, or when demographic rates respond in opposite directions to the same gradient, leading to demographic compensation. For example, survival may be high at one end of a gradient while the probability of fruiting is low, reducing spatial variation in population growth rates. Because demographic compensation can act to prevent population growth rates from falling below replacement across a broader range of environments, it has important implications for species distributions.

Abiotic drivers are often assumed to be the primary force behind demographic compensation, and recent studies have attributed demographic compensation to spatial variation in abiotic drivers such as precipitation (Doak & Morris, 2010; García-Camacho et al., 2012; Vilellas & García, 2018) or mean annual temperature (Daco et al., 2021; Sheth & Angert, 2018). Despite the emphasis on abiotic drivers, biotic drivers (e.g., herbivores) affect many demographic rates (Crawley, 1989; Maron & Crone, 2006), either negatively (Doust & Doust, 1988; Vergeer & Kunin, 2011) or positively (Pratt et al., 2005; Trumble et al., 2003). Furthermore, herbivore effects often

vary spatially (Wetzel et al., 2023), either due to changes in plant and herbivore communities across space (Cyr & Pace, 1993), or due to responses of plant performance to underlying abiotic gradients (Louthan et al., 2018). Because most studies showing demographic compensation have not quantified the effect of biotic drivers, it remains unclear whether spatial variation in biotic drivers such as herbivory (or spatial variation in their effects on plants) contributes to demographic compensation.

On the one hand, biotic drivers such as herbivory could generate demographic compensation in plant species whose demographic rates would otherwise be positively correlated due to shared responses to an environmental gradient (e.g., rainfall; Figure 1A, top). For example, if herbivores reduce competition most strongly in high-rainfall, productive areas, and have a stronger

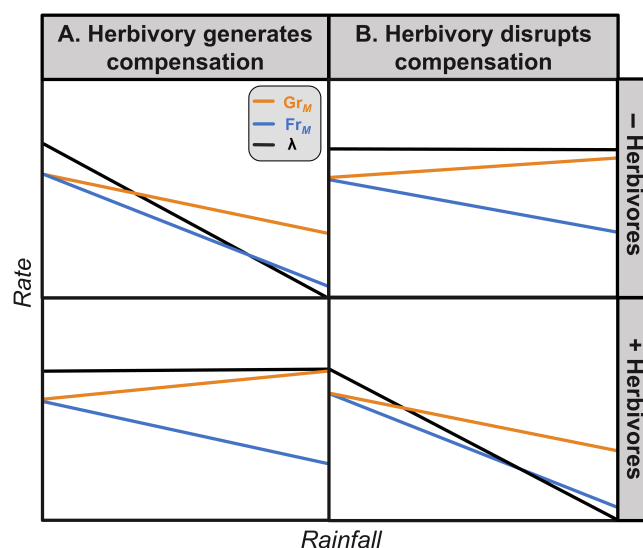


FIGURE 1 Possible effects of herbivory on demographic compensation. (A) Herbivory generates demographic compensation. Without herbivory (– Herbivores), demographic rates such as the growth probability of medium plants (Gr_M , orange line) and the fruiting probability of medium plants (Fr_M , blue line) are positively correlated, resulting in substantial change in population growth rate (λ ; black line) with rainfall. With herbivory (+ Herbivores), demographic rates are negatively correlated, resulting in a minimal change in population growth rate with rainfall. Such an effect could arise if herbivores have stronger effects on certain demographic rates (in this case, growth) in certain environments. (B) Herbivory disrupts demographic compensation. Without herbivory, growth and fruiting probabilities are negatively correlated across a rainfall gradient, resulting in a minimal change in population growth rate with rainfall. With herbivory, growth and fruiting probabilities are positively correlated with one another (i.e., both decrease with increasing rainfall), resulting in a substantial change in population growth rate with rainfall. Such an effect could arise if herbivores have negative effects on multiple demographic rates and these effects differ along environmental gradients.

positive effect on certain demographic rates (such as probability of growth) than on others (such as probability of fruiting), herbivores may create negative correlations among demographic rates and reduce spatial variation in population growth rate (Figure 1A, bottom). On the other hand, biotic drivers such as herbivory could also disrupt demographic compensation. In this scenario, in the absence of herbivory, demographic rates may be negatively correlated due to differing responses to the same abiotic driver (Figure 1B, top). If herbivore effects are greater in high-rainfall, productive areas (Chase et al., 2000; McNaughton et al., 1989) and strongly reduce multiple demographic rates, herbivores could generate positively correlated demographic rates and a loss of demographic compensation (Figure 1B, bottom). Similar effects could arise in the absence of spatial variation in herbivore activity levels; for example, if compensatory responses (as in Maschinski & Whitham, 1989) occur or if the sensitivity of population growth rate to herbivory (as in Louthan et al., 2018) varies across space.

In this study, we examined whether large mammalian herbivores generated, disrupted, or had no effect on demographic compensation in *Hibiscus meyeri* (Malvaceae), a representative subshrub in sub-Saharan Africa. We used a long-term herbivore exclusion experiment in which various size guilds of large mammalian herbivores are excluded from plots across a rainfall gradient. We estimated the effects of rainfall level and herbivore exclusion treatment on the population growth rate of *H. meyeri*, and then tested for demographic compensation in the presence and absence of a suite of large mammalian herbivore guilds. Finally, we quantified the herbivore-induced changes in demographic rates that resulted in effects on demographic compensation.

METHODS

Study system

Mpala Conservancy (hereafter, “Mpala”) is a 20,000-ha conservancy located near the equator in central Kenya (0°17' N, 37°52' E), composed primarily of semi-arid savanna and acacia bushland. Mpala houses a large diversity of large mammalian herbivores. Rainfall is weakly triannual (Goheen et al., 2013). Mpala is situated along a rainfall gradient with mean annual 2008–2012 rainfall ranging from ~440 mm/year in the north to ~640 mm/year in the south (Goheen et al., 2013). Soil characteristics and elevation do not change significantly across the gradient, allowing a fair comparison of rainfall effects on plant populations and communities (Goheen et al., 2013).

The Ungulate Herbivory Under Rainfall Uncertainty experiment (hereafter, “UHURU”), established in 2008, includes replicated size-based herbivore exclusion treatments at three rainfall levels spanning the Mpala rainfall gradient (hereafter, “Mesic,” “Intermediate,” and “Arid” sites). While there is substantial intra-annual variation in rainfall, seasonal rainfall is consistently highest at the Mesic site and lowest at the Arid site. At each rainfall level, four treatments (complete large mammalian herbivore exclusion, meso- and megaherbivore exclusion, megaherbivore exclusion, and an open control) are replicated three times in a randomized blocked design. Complete large mammalian herbivore exclusion (LMH plots) excludes all herbivore species taller than 50 cm, allowing access by small herbivores such as hares; mesoherbivore exclusion (MESO plots) excludes all herbivore species taller than 120 cm, allowing access by dik-dik (*Madoqua cavendishi*) and warthog (*Phacochoerus africanus*); megaherbivore exclusion (MEGA plots) excludes only megaherbivores such as elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis*); and control plots are open to all herbivores (Goheen et al., 2013).

Demographic data collection

H. meyeri, a common water-limited subshrub, occurs at all rainfall levels in UHURU. *H. meyeri* is consumed by multiple herbivore species and exhibits no known physical or chemical defenses against large mammalian herbivory (Louthan et al., 2018). Within the UHURU experiment, we conducted biannual demographic surveys between June 2011 and February 2015 to quantify herbivore and rainfall effects on *H. meyeri*. Our demographic monitoring methods are described Louthan et al. (2018). Briefly, we searched exhaustively for *H. meyeri* individuals at each rainfall level × herbivore exclusion treatment × block combination in June 2011. We then conducted a biannual census (after the wet season in July–August and after the dry season in January–February) to score plants' survival, measure size (height and basal area, which together correlate well with biomass; Louthan et al., 2018), count the number of fruits, and mark new plants to replace any that died or could not be relocated. Note that these data were collected biannually, rather than annually as in Louthan et al. (2018). Further, fruiting rates are reflective of herbivory (including seed and flower predation), and thus reflect the demographic consequences of herbivory rather than only potential output. We also quantified the number of seedlings produced per fruit (i.e., recruitment) by counting all seedlings in a 2-m radius around reproductive plants

following one wet season. Hereafter, we call each of our seven unique six-month time intervals between subsequent censuses a “transition.”

Modeling demographic rates and population growth rates

We used these data to estimate the effects of rainfall level, herbivore exclusion treatment, block, and transition identity on *H. meyeri* performance. We first synthesized the data into five metrics of performance for each transition: survival, probability of producing fruits, the logged number of fruits per biomass (given fruits were produced), growth (i.e., size difference between censuses), and variance in growth.

We then tested for the effects of size, block, and transition on each rainfall level and herbivore exclusion treatment-specific performance metric using a model selection approach to generate a demographic rate function. We created demographic rate functions for each rainfall level and herbivore exclusion treatment, where global models included size in initial census as a fixed effect, with transition and block as random effects. Probability of survival and of fruiting were fit using a binomial error term and all other demographic rate functions were fit using a normal error term. To assess which fixed effects best predicted demographic rates, we used corrected Akaike information criterion (AIC_c) to compare all possible subsets of each global model, including random effects in all models (Hurvich & Tsai, 1989; Appendix S1, Table S1). If the model fit was singular, we refit global models with transition and block as fixed effects, then repeated the model selection process.

We used the best-fit models for each rainfall level and herbivore treatment-specific demographic rate function to construct 60 herbivore exclusion $\times$ rainfall level-specific integral projection model (IPM) kernels (four herbivore exclusion treatments $\times$ three rainfall levels). If the best-fit model included block or transition as a random effect, we did not include random effects in demographic rate predictions. If it included block or transition as fixed effects, we predicted demographic rates as the across-block or across-transition average response, averaging first across timepoint, then block. The parameters included in best-fit demographic rate functions are shown in Appendix S1: Table S2. We represented recruitment as rainfall level-specific values (as in Louthan et al., 2018) because recruitment did not vary across herbivore exclusion treatments, and we assumed that fruits transitioned to the smallest size class in the subsequent time step. We chose to use IPMs rather than traditional

matrix models to increase precision of demographic rate estimates (Doak et al., 2021; Ramula et al., 2009). However, given our need to assess correlations among a limited number of demographic rates, we chose to limit the number of mesh points to four, selected to generate three size classes equally spanning the range of sizes observed in our study (biomass <24.09, 24.09–<48.18, and 48.18–72.28) in addition to one discrete state (fruits). Hereafter, we refer to our three size classes as small, medium, and large (S, M, and L), and refer to growth rates as transitions between size classes (e.g., M-S regression indicates shrinkage of medium plants to the small size class, M-M stasis indicates medium plants remaining in the medium size class, and M-L growth indicates the growth of medium plants to the large size class, and so on).

We used the IPMs to estimate deterministic population growth rate (λ) for each herbivore exclusion treatment $\times$ rainfall level combination using standard methods (Morris & Doak, 2002). To generate CIs on these estimates that incorporate parameter uncertainty, we sampled from the multivariate normal distribution of the fixed-effect parameter estimates of best-fit demographic rate functions and recalculated λ , repeating this process 10,000 times. We used these estimates to generate 95% CIs on population growth rate.

Testing for demographic compensation

We used these IPM kernels and demographic rates to test for demographic compensation (Appendix S1), focusing on 15 size-specific demographic rates: survival of S, M, and L; fruiting rate (probability of fruiting $\times$ number of fruits produced given fruiting) of S, M, and L; and transitions among all size classes (i.e., S to S, M, or L). No plants were observed to grow from S to L size class, so we excluded that rate from our analyses (Appendix S1: Table S2).

This test involved two steps. First, we calculated Life Table Response Experiment (LTRE) contribution values for each demographic rate at each rainfall level $\times$ herbivore exclusion treatment. These values, describing the contribution of each rate to differences in population growth rate across rainfall levels within an herbivore exclusion treatment, are estimated as:

$$C_{r,h} = (v_{r,h} - \bar{v}_{r,h}) \times S_{r,h}, \quad (1)$$

Here, $v_{r,h}$ represents the demographic rate v at rainfall level r and herbivore exclusion treatment h , $\bar{v}_{r,h}$ indicates the across-rainfall level mean value of demographic rate v at herbivore exclusion treatment h , and $S_{r,h}$ corresponds

to the sensitivity of λ to the across-rainfall level mean value of demographic rate v for herbivore exclusion treatment h . Thus, $C_{r,h}$ describes the contribution of a given demographic rate to differences in population growth rate across rainfall levels, calculated separately for each herbivore exclusion treatment.

To obtain LTRE contributions, we first estimated the sensitivity of population growth to changes in the across-rainfall level mean demographic rates (Appendix S1: Table S3). For each herbivore enclosure treatment, we estimated these sensitivities using a perturbation approach, perturbing an IPM kernel constructed using the across-rainfall level mean values for each demographic rate (Morris & Doak, 2002). These sensitivity values were multiplied by the difference between the across-rainfall level mean demographic rate and the rainfall-level specific value of a demographic rate for each herbivore exclusion treatment to obtain the LTRE contribution.

Next, we used the LTRE contributions to test for evidence of demographic compensation within each herbivore exclusion treatment (Appendix S2). First, we calculated the Pearson product moment correlations between all pairwise combinations of $C_{r,h}$ values for each herbivore exclusion treatment to obtain “observed” proportions of positive and negative correlations between LTRE contributions of demographic rates (Appendix S2: Figure S1A). We highlight that because our data included data from only three sites, each of these correlations was represented by only three data points. Because such correlations are unstable, we emphasize that our results should be interpreted with caution (Appendix S2: Figure S3). However, these data come from a multi-year demographic study with replication across rainfall and herbivore exclusion treatments, and therefore likely capture underlying demographic patterns well. After generating observed proportions of positive and negative correlations, following Villellas et al. (2015), we used a randomization approach to generate null distributions for the proportions of positive and negative correlations between LTRE contributions of demographic rates across the rainfall gradient. For each demographic rate, we randomized $C_{r,h}$ values across rainfall levels and recalculated Pearson correlations among randomized contributions (Appendix S2: Figure S1B). We repeated this process 10,000 times to generate null distributions for the proportions of positive and negative correlations. We then compared the observed proportions of positive ($P_{\text{obs},+}$) and negative ($P_{\text{obs},-}$) correlations for each herbivore exclusion treatment to their respective null distributions. We assumed that having either more negative correlations than expected by chance (i.e., $P_{\text{obs},-}$ was greater than or equal to the 95th percentile of the null distribution of

negative correlations) or fewer positive correlations than expected by chance (i.e., $P_{\text{obs},+}$ was less than or equal to the 5th percentile of the null distribution of positive correlations) indicated evidence for demographic compensation (Villellas et al., 2015). We quantified the mechanism of large mammalian herbivore effects on demographic compensation by comparing correlations among pairs of demographic rates in each herbivore exclusion treatment (Appendix S2: Figure S1C).

RESULTS

Effects of drivers on demographic rates and population growth rates

Demographic rate functions for survival, growth and probability of fruiting almost always included size (40/48; Appendix S1: Table S1), whereas functions for number of fruits per biomass usually did not (2/12). M and L survival rates increased from the Arid to the Mesic site, whereas S survival rates remained relatively similar across the gradient, and survival rates were similar on average across herbivore exclusion treatments (Appendix S1: Table S2, Figure S1). S, M, and L fruiting rates showed no consistent response to rainfall and were similar on average across herbivore exclusion treatments. Growth rates varied considerably across the rainfall gradient. Stasis of M and L plants increased toward the Mesic site for most herbivore exclusion treatments except for LMH plots, which declined slightly. Stasis of S plants increased toward the Mesic site for all herbivore exclusion treatments except for the control plots, which indicated no change in S stasis across the gradient. The growth of S to M also declined toward the Mesic site, whereas the growth of M to L varied little across the gradient; these patterns were consistent across herbivore exclusion treatments. The growth of S to L was consistently zero across the gradient. The regression of L to M increased toward the Mesic site for LMH plots but declined for the control, MEGA, and MESO plots. Conversely, the regression of L to S declined toward the Mesic site for MEGA, MESO, and the control plots, but increased for the LMH plots. The regression of M to S declined toward the Mesic site for LMH, MEGA, MESO, and control plots. Recruitment of fruits declined toward the Mesic site for all herbivore exclusion treatments (Appendix S1: Table S2, Figure S1).

Population growth rate was higher on average in the LMH, MEGA, and MESO plots compared to the control plots; however, overlapping CIs for site-specific estimates indicate that these differences were not significant overall (Table 1). The only exception to this was at the Mesic site,

TABLE 1 Population growth rate (λ) of *Hibiscus meyeri* for all herbivore exclusion treatments.

Herbivore exclusion treatment	Rainfall level		
	Arid	Intermediate	Mesic
LMH	1.12 [1.02, 1.26]	1.02 [0.98, 1.07]	1.58 [1.30, 1.97]
MESO	1.16 [1.08, 1.25]	1.07 [1.01, 1.11]	1.31 [1.17, 1.47]
MEGA	1.10 [1.04, 1.18]	1.03 [0.98, 1.08]	1.12 [1.02, 1.26]
Control	1.03 [0.995, 1.06]	1.02 [0.97, 1.08]	1.34 [1.13, 1.66]

Note: Deterministic λ predicted by rainfall level- and treatment-specific integral projection model kernels, with the 95% CIs (which incorporate parameter uncertainty) in brackets are shown. Herbivore exclusion treatments are the complete absence of large mammalian herbivores (LMH), absence of meso- and megaherbivores (MESO), absence of megaherbivores (MEGA), and presence of all large mammalian herbivores (control).

where population growth was lower within the MEGA treatment compared to the LMH treatment. In all herbivore exclusion treatments, population growth rate was generally higher at the Mesic site compared to the Intermediate and Arid sites, although those differences were only significant within the LMH and control treatments.

Results of test for demographic compensation

The presence of large mammalian herbivores often led to weaker correlations between demographic rates (Appendix S2: Figure S3). As a result, we found strong evidence for demographic compensation only when large mammalian herbivores were excluded (Appendix S3: Table S1). Namely, we found evidence for demographic compensation generated by more negative correlations than expected by chance in the LMH (Figure 2B), MESO (Figure 2D), and MEGA (Figure 2F) plots, but not the control plots (Figure 2H). In particular, the LMH plots exhibited the greatest number of significant negative correlations (21 significant negative correlations; Figure 3A), followed by the MESO and MEGA plots (10 significant negative correlations; Figure 3B,C). Only four pairs of demographic rates in the control plots were significantly negatively correlated (Figure 3D). Negative correlations frequently appeared between either growth or regression versus stasis within a size class, likely reflecting probabilistic constraints on transitioning to a different size class versus stasis in the same size class (Figure 3). The extent and significance of negative correlations varied by treatment, and the LMH plots in particular had many significant negative correlations between fruiting and regression rates, suggesting that the complete absence of large mammalian herbivores might exacerbate trade-offs

in the role of reproduction versus shrinkage between environments.

The proportion of observed positive correlations was never significantly lower than we would expect by chance for all herbivore exclusion treatments (Figure 2A,C,E,G; Appendix S3: Table S1). Across all herbivore treatments, we frequently observed significant positive correlations between similar demographic processes, such as between survival, stasis, regression, or fruiting rates of differing size classes (Figure 3). Additionally, fruiting rate often exhibited positive correlations with stasis, reflecting a link between increased reproductive output and reduced probability of growth. Positive correlations were more common in the LMH (16 significant positive correlations; Figure 3), MESO (12 significant positive correlations), and MEGA plots (11 significant positive correlations) treatments compared to the control plots (6 significant positive correlations), suggesting that the exclusion of larger herbivores reduces positive correlations between demographic rates.

DISCUSSION

Herbivores can profoundly affect plant population dynamics through their influence on demographic rates. In our study, we found that large mammalian herbivores modified correlations among demographic rates. Namely, the presence of all large mammalian herbivore size guilds nullified demographic compensation (as in Figure 1B). Demographic compensation, which occurred only in herbivore exclusion treatments, was driven by negative correlations between LTRE contributions of demographic rates (Figure 2). While the absence of any large mammalian herbivore size guild generated demographic compensation, the effect of megaherbivore exclusion alone was strong enough to generate demographic compensation. The following paragraphs place these findings in the context of previous literature and explore their broader implications.

Large mammalian herbivores had strong effects on demographic rates of *H. meyeri*. This result is consistent with previous work, which has shown that large herbivores strongly affect plant population dynamics, though the direction of these effects can vary across space (Koerner et al., 2014, 2018; Maron & Crone, 2006). In some cases, herbivores largely affect plants through reductions in growth, with minimal impacts on survival (Townsend & Meyer, 2002; Van Der Wal et al., 2000), whereas in others, herbivores can greatly reduce adult (Pisanu et al., 2012) and seedling (Opedal et al., 2021) survival. Similarly, while herbivores sometimes negatively affect reproduction via consumption (Anderson et al., 2001), they can also reduce competition from neighboring plants, thereby increasing the probability of

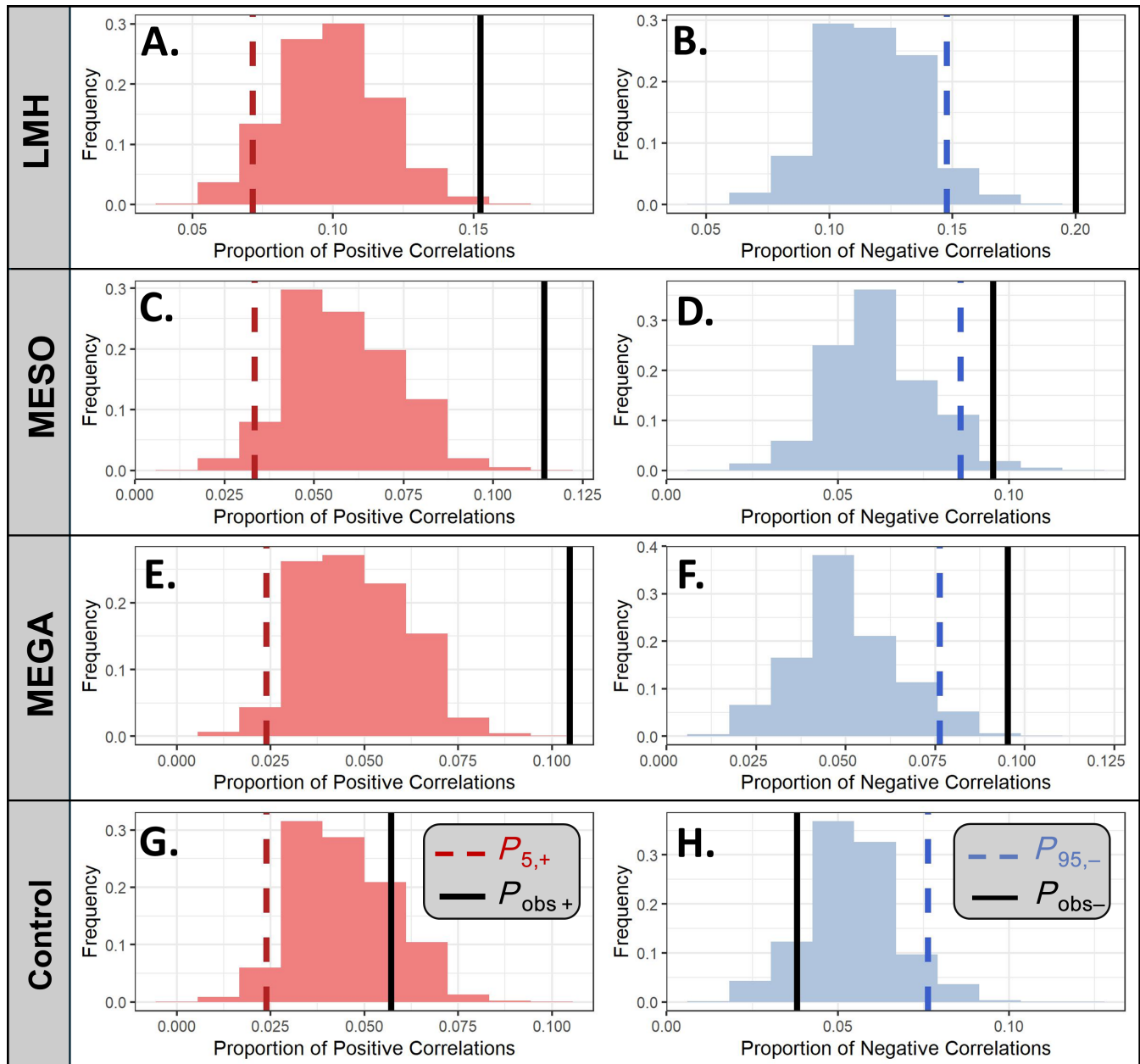


FIGURE 2 Results of tests for demographic compensation. We show null distributions of the proportion of significant (A, C, E, G) positive and (B, D, F, H) negative correlations between Life Table Response experiment contributions for four herbivore exclusion treatments, large mammalian herbivores (LMH), meso- and megaherbivores (MESO), megaherbivores (MEGA), and Control. Null distributions were obtained via randomization following Villellas et al. (2015). In (A), (C), (E), and (G), red dashed lines indicate the 5th percentile of the null distribution of significant positive correlations ($P_{5,+}$) and solid black lines indicate the observed proportion of significant positive correlations ($P_{obs,+}$) in a given herbivore exclusion treatment. If $P_{obs,+} \leq P_{5,+}$ (A, C, E, G), there is evidence for demographic compensation in that herbivore exclusion treatment because there are fewer positive correlations between demographic rates than expected by chance. In (B), (D), (F), and (G), blue dashed lines indicate the 95th percentile of the null distribution of significant negative correlations ($P_{95,-}$) and solid black lines indicate the observed proportion of significant negative correlations ($P_{obs,-}$) for an herbivore exclusion treatment. If $P_{obs,-} > P_{95,-}$, there is evidence for demographic compensation in that treatment because there are more negative correlations between demographic rates than expected by chance. Herbivore exclusion treatments are the complete absence of LMH, absence of MESO, absence of MEGA, and presence of all large mammalian herbivores (control).

reproduction for the remaining individuals (Allcock & Hik, 2004). In our study, large mammalian herbivores reduced rates such as fruiting, survival, and the stasis of

large plants, and had weak negative effects on population growth rate overall (i.e., population growth rate was on average lower in the control plots compared to other

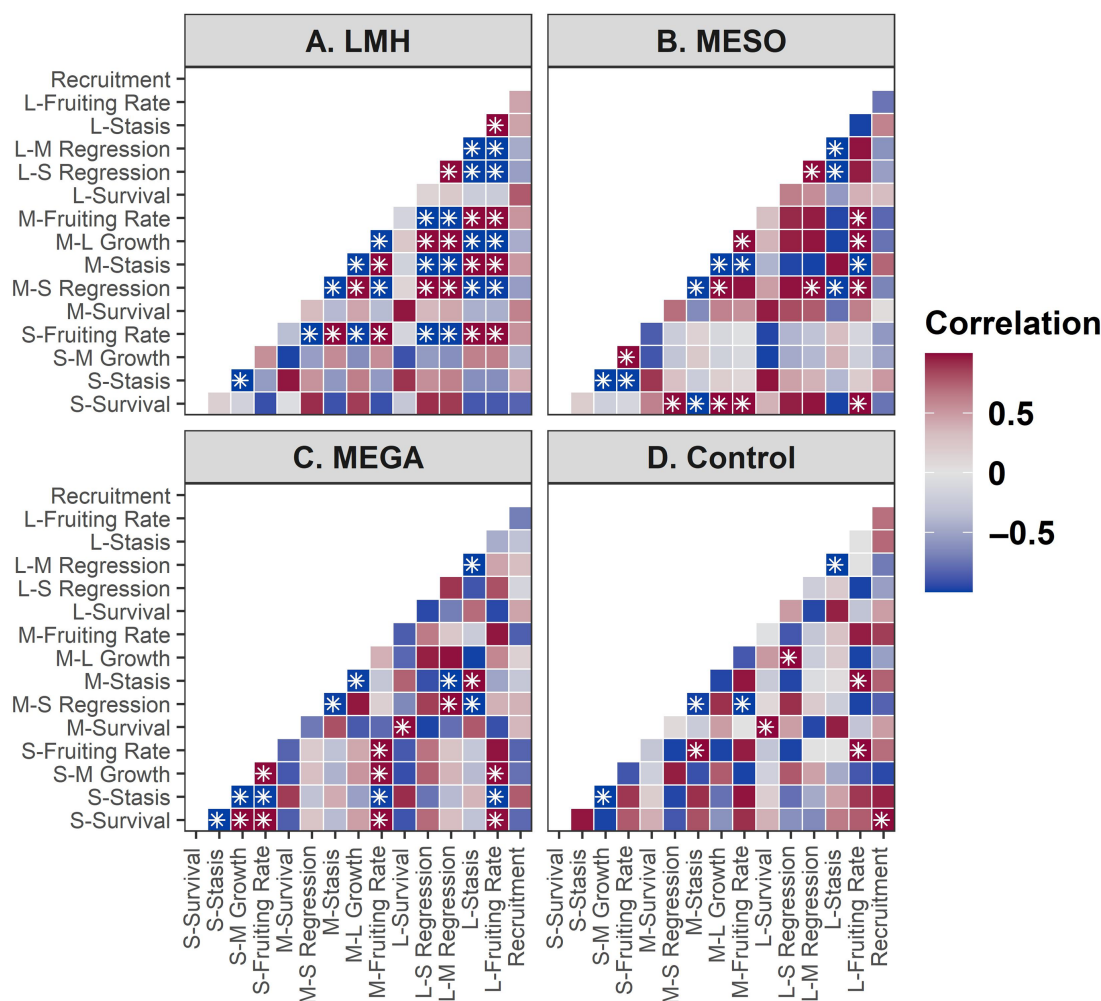


FIGURE 3 Correlations between Life Table Response Experiment (LTRE) contributions of size-specific demographic rates for large mammalian herbivore exclusion treatments. Here, we show across-rainfall gradient Pearson product moment correlations between pairwise combinations of LTRE contributions for demographic rates in four exclusion treatments: (A) the complete exclusion of large mammalian herbivores (LMH), (B) the exclusion of meso- and megaherbivores (MESO), which includes smaller herbivores such as dik-dik, (C) the exclusion of megaherbivores (MEGA), which includes smaller herbivores and mesoherbivores such as gazelle, and (D) the presence of all large mammalian herbivores (control), which include mesoherbivores, smaller herbivores, and megaherbivores such as elephants. S indicates small plants, M indicates medium plants, and L indicates large plants; thus, for transitions among size classes (stasis, growth, and regression), we show transitions from the first size class to the second (e.g., S-M growth indicates transition probability from small to medium). Color indicates the strength and sign of correlations, and white asterisks (*) indicate significance ($p \leq 0.05$). Demographic rates that did not vary across rainfall levels are excluded.

treatments, though these differences were largely non-significant; Table 1).

We found that herbivore effects on population dynamics were sufficient to disrupt demographic compensation, highlighting the importance of considering both biotic and abiotic drivers of demographic compensation. Previous work has assumed that spatial variation in abiotic drivers such as temperature and precipitation (Sheth & Angert, 2018; Villellas & García, 2018; Yang et al., 2022), length of snow-free periods (Doak & Morris, 2010), and soil nutrients (Daco et al., 2021) are the primary drivers of demographic compensation. However, studies examining the effects of abiotic drivers

often overlook how biotic drivers might influence these results. While previous work on demographic compensation has been conducted in relatively depauperate ecosystems without large herbivores, it may be that this phenomenon was less prevalent when they were still present. Further, smaller herbivores or other biotic interactions may be limiting the extent of demographic compensation, suggesting that excluding biotic factors could lead to an overestimation of its prevalence. Consistent with this suggestion, our work suggests that only partial herbivore exclusion is necessary to allow compensation to emerge; the removal of just one large mammalian herbivore guild (i.e., MEGA, which excluded

megaherbivores) was sufficient to generate demographic compensation.

In our study, demographic compensation when large mammalian herbivores were excluded was driven largely by negative correlations between LTRE contributions of demographic rates along the rainfall gradient. Different abiotic conditions can cause plants to exhibit trade-offs in physiological and life history traits, as traits that are advantageous in some environments may reduce performance in others (Dudley, 1996; Schlichting, 1986). For example, a plant species that invests heavily in vegetative growth under greater growing-season precipitation may instead invest in rapid and high flowering rates under reduced growing-season precipitation, as this trait may allow escape from drought stress occurring later in the growing season (van Kleunen, 2007). Thus, abiotic gradients can elicit demographic compensation through negative correlations, as demographic rates and the sensitivity of population growth rates to different demographic rates may shift along these gradients as plants alter life history strategies across abiotic contexts. Herbivory may be uniquely poised to affect demographic compensation because it can interact with abiotic gradients to affect plant performance and competitive dynamics (Callaway et al., 2002; Hambäck & Beckerman, 2003; Van Der Wal et al., 2000). As herbivores remove biomass and trample plants (Heggenes et al., 2017; Pascual et al., 2017), they may directly increase or decrease growth and the probability of reproduction. Further, changes in competitive dynamics across abiotic conditions (e.g., the stress gradient hypothesis) may be disrupted in the presence of herbivores, which strongly modify competitive dynamics (Hambäck & Beckerman, 2003). Consistent with this prediction, we found that in the herbivore exclusion treatments, negative correlations frequently occurred between LTRE contributions for demographic rates associated with conservative strategies (shrinkage/stasis) and those linked to non-conservative strategies (growth/fruitletting; Figure 3; Appendix S2: Figures S2 and S3). These negative correlations became less frequent in the presence of all large mammalian herbivores (i.e., control plots), suggesting that trade-offs between conservative and non-conservative strategies may become less pronounced with greater herbivore presence (Figure 3; Appendix S2: Figure S3), in turn leading to a disruption of demographic compensation. At the same time, we observed fewer positive correlations between demographic rates in the presence of all large mammalian herbivores, disrupting the expectation that demographic rates responding similarly to abiotic gradients should covary positively. Together, these results indicate that large mammalian herbivores affect the degree of spatial variability in vital rates, reducing both negative and positive

correlations among demographic rates, the former leading to weaker demographic compensation (consistent with Figure 1B; Appendix S2: Figure S3), and the latter reflecting altered responses to abiotic conditions without direct consequences for demographic compensation.

We saw that excluding multiple large mammalian herbivore sizes did not always lead to a greater number of negative correlations between demographic rates (Figure 2). Previous work has shown that herbivores of different sizes can have disparate effects on plant population dynamics. For example, in grassland systems, larger herbivores (>30 kg) can have stronger effects on plant community composition compared to small herbivores (Bakker et al., 2006). Alternatively, in savanna systems, large versus small herbivore effects can be context-dependent, with either group exerting a stronger influence depending on the environmental conditions (Burkepile et al., 2017). We saw that the exclusion of megaherbivores such as elephants and giraffes alone (i.e., the MEGA exclusion plots) was enough to elicit demographic compensation (Figure 2F). This result is consistent with previous work, which shows that megaherbivores have considerable impacts on plant productivity and biomass, particularly in savannah ecosystems (Davies & Asner, 2019; Hyvarinen et al., 2021; Pellegrini et al., 2017). The combined exclusion of megaherbivores, mesoherbivores such as zebra and gazelle, and of smaller large mammalian herbivores such as dik-dik and warthogs, (i.e., the LMH exclusion plots) led to the greatest number of negative correlations, suggesting that the combined exclusion of these size guilds can have similar, additive effects on demographic compensation. However, when only mega- and mesoherbivores were excluded and smaller herbivores were included (i.e., MESO exclusion plots), we saw the same number of negative correlations as when only megaherbivores were excluded. These findings suggest that the exclusion of one large mammalian herbivore size guild modifies the effect of others, perhaps because of ecological interactions among guilds.

Several caveats apply to our study. First, many contemporary ecosystems lack large mammalian herbivores, particularly mega- and mesoherbivores, due to human interference, limiting the applicability of our findings to other systems. Even in cases where large mammalian herbivores have persisted or been reintroduced, they are often not as abundant as they once were historically, meaning their densities may not be high enough to elicit demographic compensation. Second, the statistical power of our test for demographic compensation is limited by the number of populations (three) included in our study (Appendix S2: Figure S3). Most other studies of demographic compensation contain at least six populations

(Villellas et al., 2015), though we note that these studies do not have replicated herbivore exclusion treatments such as ours. Thus, our results should be thought of as preliminary evidence that mammals may influence demographic compensation. We suggest that studies measuring plant demographic rate response to herbivores across a broader array of populations consider conducting a test for demographic compensation to test the generality of our findings.

Conclusion

Our study demonstrates that for *H. meyeri*, large mammalian herbivores play a significant role in shaping population dynamics through affecting spatial variability in vital rates and disrupting demographic compensation. When large herbivores were excluded, *H. meyeri* exhibited strong demographic compensation; conversely, when all large herbivore size guilds were present, demographic compensation was disrupted (Figure 1B). However, rather than disrupting demographic compensation by turning negative correlations between rates to positive (as in Figure 1B), large mammalian herbivores disrupt compensation through reducing variability in LTRE contributions (i.e., diminishing differences in how individual demographic rates influenced population growth across the rainfall gradient; Appendix S2: Figure S3), leading to multiple rates becoming uncorrelated. While this disruption does not significantly alter spatial variation in population growth rate (Appendix S3: Figure S1), at least at the 20-km range over which we conducted our study, it suggests that large mammalian herbivores may exert negative effects on woody plants such as *H. meyeri* not by directly reducing population growth, but rather by eliminating demographic compensation. Our findings emphasize the need to consider both biotic and abiotic drivers when studying demographic compensation. Although large mammalian herbivores non-significantly reduced population growth in our system, herbivores in other contexts may have positive or neutral effects on plant populations by reducing competition (Dyer et al., 2010; Koerner et al., 2018) or inducing overcompensation (Garcia & Eubanks, 2019). Ultimately, understanding the complexity of plant–herbivore interactions is key to predicting population dynamics and species distributions in changing landscapes. Incorporating these insights into conservation planning will be vital for ensuring the long-term persistence of diverse plant communities.

AUTHOR CONTRIBUTIONS

Aleah K. Querns contributed to the conceptualization of this analysis, performed analyses, interpreted data, and led the writing of the manuscript. Allison M. Louthan collected the data, contributed to the conceptualization of the analysis, provided feedback on analyses, contributed

to data interpretation, and contributed to manuscript writing and revisions. Todd M. Palmer and Jacob R. Goheen contributed to funding acquisition for and the design and management of the UHURU experiment and provided feedback on the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Querns, 2025) are available from Zenodo: <https://doi.org/10.5281/zenodo.15319614>.

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REFERENCES

- Allcock, K. G., and D. S. Hik. 2004. "Survival, Growth, and Escape from Herbivory Are Determined by Habitat and Herbivore Species for Three Australian Woodland Plants." *Oecologia* 138(2): 231–241. <https://doi.org/10.1007/s00442-003-1420-3>.

- Anderson, R. C., E. A. Corbett, M. R. Anderson, G. A. Corbett, and T. M. Kelley. 2001. "High White-Tailed Deer Density Has Negative Impact on Tallgrass Prairie Forbs." *Journal of the Torrey Botanical Society* 128(4): 381–392. <https://doi.org/10.2307/3088670>.
- Bakker, E. S., M. E. Ritchie, H. Olff, D. G. Milchunas, and J. M. H. Knops. 2006. "Herbivore Impact on Grassland Plant Diversity Depends on Habitat Productivity and Herbivore Size." *Ecology Letters* 9(7): 780–88. <https://doi.org/10.1111/j.1461-0248.2006.00925.x>.
- Burkepile, D. E., R. W. S. Fynn, D. I. Thompson, N. P. Lemoine, S. E. Koerner, S. Eby, N. Hagenah, et al. 2017. "Herbivore Size Matters for Productivity–Richness Relationships in African Savannas." *Journal of Ecology* 105(3): 674–686. <https://doi.org/10.1111/1365-2745.12714>.
- Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, et al. 2002. "Positive Interactions among Alpine Plants Increase with Stress." *Nature* 417(6891): 844–48. <https://doi.org/10.1038/nature00812>.
- Chase, J. M., M. A. Leibold, A. L. Downing, and J. B. Shurin. 2000. "The Effects of Productivity, Herbivory, and Plant Species Turnover in Grassland Food Webs." *Ecology* 81(9): 2485–97. [https://doi.org/10.1890/0012-9658\(2000\)081%255B2485:TEOPHA%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081%255B2485:TEOPHA%255D2.0.CO;2).
- Connell, J. H. 1972. "Community Interactions on Marine Rocky Intertidal Shores." *Annual Review of Ecology and Systematics* 3: 169–192. <https://doi.org/10.1146/annurev.es.03.110172.001125>.
- Crawley, M. J. 1989. "Insect Herbivores and Plant Population Dynamics." *The Annual Review of Entomology* 34: 531–564. <https://doi.org/10.1146/annurev.en.34.010189.002531>.
- Cyr, H., and M. L. Pace. 1993. "Magnitude and Patterns of Herbivory in Aquatic and Terrestrial Ecosystems." *Nature* 361(6408): 148–150. <https://doi.org/10.1038/361148a0>.
- Daco, L., G. Colling, and D. Matthies. 2021. "Altitude and Latitude Have Different Effects on Population Characteristics of the Widespread Plant *Anthyllis vulneraria*." *Oecologia* 197(2): 537–549. <https://doi.org/10.1007/s00442-021-05030-6>.
- Davies, A. B., and G. P. Asner. 2019. "Elephants Limit Aboveground Carbon Gains in African Savannas." *Global Change Biology* 25(4): 1368–82. <https://doi.org/10.1111/gcb.14585>.
- Doak, D. F., and W. F. Morris. 2010. "Demographic Compensation and Tipping Points in Climate-Induced Range Shifts." *Nature* 467(7318): 959–962. <https://doi.org/10.1038/nature09439>.
- Doak, D. F., E. Waddle, R. E. Langendorf, A. M. Louthan, N. Isabelle Chardon, R. R. Dibner, D. A. Keinath, et al. 2021. "A Critical Comparison of Integral Projection and Matrix Projection Models for Demographic Analysis." *Ecological Monographs* 91(2): e01447. <https://doi.org/10.1002/ecm.1447>.
- Dobzhansky, T. 1950. "Evolution in the Tropics." *American Scientist* 38(2): 209–221.
- Doust, J. L., and L. L. Doust. 1988. *Plant Reproductive Ecology: Patterns and Strategies*. New York, NY: Oxford University Press.
- Dudley, S. A. 1996. "The Response to Differing Selection on Plant Physiological Traits: Evidence for Local Adaptation." *Evolution* 50(1): 103–110. <https://doi.org/10.1111/j.1558-5646.1996.tb04476.x>.
- Dyer, L. A., D. K. Letourneau, G. V. Chavarria, and D. S. Amoretti. 2010. "Herbivores on a Dominant Understory Shrub Increase Local Plant Diversity in Rain Forest Communities." *Ecology* 91(12): 3707–18. <https://doi.org/10.1890/08-1634.1>.
- Garcia, L. C., and M. D. Eubanks. 2019. "Overcompensation for Insect Herbivory: A Review and Meta-Analysis of the Evidence." *Ecology* 100(3): e02585. <https://doi.org/10.1002/ecy.2585>.
- García-Camacho, R., M. J. Albert, and A. Escudero. 2012. "Small-Scale Demographic Compensation in a High-Mountain Endemic: The Low Edge Stands Still." *Plant Ecology & Diversity* 5(1): 37–44. <https://doi.org/10.1080/17550874.2012.662534>.
- Goheen, J. R., T. M. Palmer, G. K. Charles, K. M. Helgen, S. N. Kinyua, J. E. Maclean, B. L. Turner, H. S. Young, and R. M. Pringle. 2013. "Piecewise Disassembly of a Large-Herbivore Community across a Rainfall Gradient: The UHURU Experiment." *PLoS One* 8(2): e55192. <https://doi.org/10.1371/journal.pone.0055192>.
- Hambäck, P. A., and A. P. Beckerman. 2003. "Herbivory and Plant Resource Competition: A Review of Two Interacting Interactions." *Oikos* 101(1): 26–37. <https://doi.org/10.1034/j.1600-0706.2003.12568.x>.
- Heggenes, J., A. Odland, T. Chevalier, J. Ahlberg, A. Berg, H. Larsson, and D. K. Bjerketvedt. 2017. "Herbivore Grazing—or Trampling? Trampling Effects by a Large Ungulate in Cold High-Latitude Ecosystems." *Ecology and Evolution* 7(16): 6423–31. <https://doi.org/10.1002/ece3.3130>.
- Hurvich, C. M., and C.-L. Tsai. 1989. "Regression and Time Series Model Selection in Small Samples." *Biometrika* 76(2): 297–307. <https://doi.org/10.1093/biomet/76.2.297>.
- Hyvarinen, O., M. Te Beest, E. le Roux, M. Te Beest, E. le Roux, G. Kerley, E. de Groot, R. Vinita, and J. P. G. M. Cromsigt. 2021. "Megaherbivore Impacts on Ecosystem and Earth System Functioning: The Current State of the Science." *Ecography* 44(11): 1579–94. <https://doi.org/10.1111/ecog.05703>.
- Kauffman, M., and J. Maron. 2006. "Consumers Limit the Abundance and Dynamics of a Perennial Shrub with a Seed Bank." *American Naturalist* 168: 454–470. <https://doi.org/10.1086/507877>.
- Koerner, S. E., D. E. Burkepile, R. W. S. Fynn, C. E. Burns, S. Eby, N. Govender, N. Hagenah, et al. 2014. "Plant Community Response to Loss of Large Herbivores Differs between North American and South African Savanna Grasslands." *Ecology* 95(4): 808–816. <https://doi.org/10.1890/13-1828.1>.
- Koerner, S. E., M. D. Smith, D. E. Burkepile, N. P. Hanan, M. L. Avolio, S. L. Collins, A. K. Knapp, et al. 2018. "Change in Dominance Determines Herbivore Effects on Plant Biodiversity." *Nature Ecology & Evolution* 2(12): 1925–32. <https://doi.org/10.1038/s41559-018-0696-y>.
- Louthan, A. M., R. M. Pringle, J. R. Goheen, T. M. Palmer, W. F. Morris, and D. F. Doak. 2018. "Aridity Weakens Population-Level Effects of Multiple Species Interactions on *Hibiscus meyeri*." *Proceedings of the National Academy of Sciences* 115(3): 543–48. <https://doi.org/10.1073/pnas.1708436115>.
- Maron, J. L., K. C. Baer, and A. L. Angert. 2014. "Disentangling the Drivers of Context-Dependent Plant–Animal Interactions." *Journal of Ecology* 102(6): 1485–96. <https://doi.org/10.1111/1365-2745.12305>.
- Maron, J. L., and E. Crone. 2006. "Herbivory: Effects on Plant Abundance, Distribution and Population Growth." *Proceedings of the Royal Society B: Biological Sciences* 273(1601): 2575–84. <https://doi.org/10.1098/rspb.2006.3587>.

- Maschinski, J., and T. G. Whitham. 1989. "The Continuum of Plant Responses to Herbivory: The Influence of Plant Association, Nutrient Availability, and Timing." *American Naturalist* 134(1): 1–19. <https://doi.org/10.1086/284962>.
- McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. "Ecosystem-Level Patterns of Primary Productivity and Herbivory in Terrestrial Habitats." *Nature* 341(6238): 142–44. <https://doi.org/10.1038/341142a0>.
- Morris, W. F., and D. F. Doak. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sunderland, MA: Sinauer Associates.
- Opedal, Ø. H., K. O. Nystuen, D. Hagen, H. Holien, M. V. Sørensen, S. I. Lang, S. Lindmo, G. R. Strimbeck, and B. J. Graae. 2021. "Herbivores Reduce Seedling Recruitment in Alpine Plant Communities." *Nordic Journal of Botany* 39(2): 1–14. <https://doi.org/10.1111/njb.02989>.
- Pascual, J., J. Alberti, P. Daleo, and O. Iribarne. 2017. "Herbivory and Trampling by Small Mammals Modify Soil Properties and Plant Assemblages." *Journal of Vegetation Science* 28(5): 1028–35. <https://doi.org/10.1111/jvs.12562>.
- Pellegrini, A. F. A., R. M. Pringle, N. Govender, and L. O. Hedin. 2017. "Woody Plant Biomass and Carbon Exchange Depend on Elephant-Fire Interactions Across a Productivity Gradient in African Savanna." *Journal of Ecology* 105(1): 111–121. <https://doi.org/10.1111/1365-2745.12668>.
- Pironon, S., G. Papuga, J. Villellas, A. L. Angert, M. B. García, and J. D. Thompson. 2017. "Geographic Variation in Genetic and Demographic Performance: New Insights from an Old Biogeographical Paradigm." *Biological Reviews* 92(4): 1877–1909. <https://doi.org/10.1111/brv.12313>.
- Pisanu, S., E. Farris, R. Filigheddu, and M. B. García. 2012. "Demographic Effects of Large, Introduced Herbivores on a Long-Lived Endemic Plant." *Plant Ecology* 213(10): 1543–53. <https://doi.org/10.1007/s11258-012-0110-9>.
- Pratt, P. D., M. B. Rayamajhi, T. K. Van, T. D. Center, and P. W. Tipping. 2005. "Herbivory Alters Resource Allocation and Compensation in the Invasive Tree *Melaleuca quinquenervia*." *Ecological Entomology* 30(3): 316–326. <https://doi.org/10.1111/j.0307-6946.2005.00691.x>.
- Querns, A. 2025. "aquerns/Hibiscus_25: Initial Release (v1.0.0)." Zenodo. <https://doi.org/10.5281/zenodo.15319614>
- Ramula, S., M. Rees, and Y. M. Buckley. 2009. "Integral Projection Models Perform Better for Small Demographic Data Sets than Matrix Population Models: A Case Study of Two Perennial Herbs." *Journal of Applied Ecology* 46(5): 1048–53. <https://doi.org/10.1111/j.1365-2664.2009.01706.x>.
- Schlichting, C. D. 1986. "The Evolution of Phenotypic Plasticity in Plants." *Annual Review of Ecology and Systematics* 17: 667–693. <https://doi.org/10.1146/annurev.es.17.110186.003315>.
- Sheth, S. N., and A. L. Angert. 2018. "Demographic Compensation Does Not Rescue Populations at a Trailing Range Edge." *Proceedings of the National Academy of Sciences* 115(10): 2413–18. <https://doi.org/10.1073/pnas.1715899115>.
- Townsend, D. S., and A. D. Meyer. 2002. "Rapid Recovery of Witch Hazel (*Hamamelis virginiana* L.) by Sprouting, Following Release from White-Tailed Deer (*Odocoileus virginianus* zimm.) Browsing." *Natural Areas Journal* 22(4): 290–95.
- Trumble, J., D. Kolodny-Hirsch, and I. P. Ting. 2003. "Plant Compensation for Arthropod Herbivory." *Annual Review of Entomology* 38: 93–119. <https://doi.org/10.1146/annurev.en.38.010193.000521>.
- Van Der Wal, R., M. Egas, A. Van Der Veen, and J. Bakker. 2000. "Effects of Resource Competition and Herbivory on Plant Performance along a Natural Productivity Gradient." *Journal of Ecology* 88(2): 317–330. <https://doi.org/10.1046/j.1365-2745.2000.00450.x>.
- van Kleunen, M. 2007. "Adaptive Genetic Differentiation in Life-History Traits between Populations of *Mimulus guttatus* with Annual and Perennial Life-Cycles." *Evolutionary Ecology* 21(2): 2. <https://doi.org/10.1007/s10682-006-0019-7>.
- Vergeer, P., and W. E. Kunin. 2011. "Life History Variation in *Arabidopsis lyrata* across Its Range: Effects of Climate, Population Size and Herbivory." *Oikos* 120(7): 7. <https://doi.org/10.1111/j.1600-0706.2010.18944.x>.
- Villellas, J., D. F. Doak, M. B. García, and W. F. Morris. 2015. "Demographic Compensation among Populations: What Is It, how Does It Arise and What Are Its Implications?" *Ecology Letters* 18(11): 1139–52. <https://doi.org/10.1111/ele.12505>.
- Villellas, J., and M. B. García. 2018. "Life-History Trade-Offs Vary with Resource Availability across the Geographic Range of a Widespread Plant." *Plant Biology* 20(3): 483–89. <https://doi.org/10.1111/plb.12682>.
- Wetzel, W. C., B. D. Inouye, P. G. Hahn, S. R. Whitehead, and N. Underwood. 2023. "Variability in Plant–Herbivore Interactions." *Annual Review of Ecology, Evolution, and Systematics* 54: 451–474. <https://doi.org/10.1146/annurev-ecolsys-102221-045015>.
- Yang, X., A. L. Angert, P. A. Zuidema, F. He, S. Huang, S. Li, S.-L. Li, N. I. Chardon, and J. Zhang. 2022. "The Role of Demographic Compensation in Stabilising Marginal Tree Populations in North America." *Ecology Letters* 25(7): 1676–89. <https://doi.org/10.1111/ele.14028>.

SUPPORTING INFORMATION

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

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