THE RELATIVE STRENGTH OF ABIOTIC AND BIOTIC CONTROLS ON SPECIES RANGE LIMITS

by

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ABSTRACT

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The Relative Strength of Abiotic and Biotic Controls on Species Range Limits

Thesis directed by Professor Daniel F. Doak

Study of the determinants of species' geographic distributions has a rich tradition in ecology and evolution, and understanding these determinants is becoming increasingly important in the face of climate change. While we know many range limits are set by abiotic stress, species interactions can also be important drivers of range limits. However, we lack any well-tested predictive framework for when and where each of these two broad classes of factors will most commonly set range limits.

A long-standing, but still nearly untested, hypothesis suggests that abiotic stress most often sets range limits in seemingly stressful areas, such as arctic, high-alpine, or arid systems, with species interactions having more influence in apparently benign environments, such as the tropics, low-elevation, or mesic places. In my dissertation, I experimentally tested a fundamental assumption of this hypothesis: namely, that the relative importance of species interactions and abiotic stress for population performance varies systematically with abiotic stress. I tested the relative importance of abiotic stress vs. three species interactions (herbivory, neighbors, and pollinators) for population dynamics of a model plant species in central Kenya, *Hibiscus meyeri,* across a sharp aridity gradient.

I find broad-scale support for Darwin's hypothesis, with stronger effects of herbivores, neighbors, and pollinators on population growth rate in mesic areas v. arid areas. Interestingly, I find universal competitive effects of neighbors (rather than the switch from facilitative to competitive with increasing rainfall predicted by recent theoretical and empirical work). This work suggests that species interactions might be critical drivers of range limits only in unstressful regions of a species range.

This work also has implications for projecting shifts in species' distributions. While in some cases, leaving biotic interactions out of species' distribution models reduces accuracy, the vast majority of projections of shifts in distributions with climate change do not include such interactions. This work suggests that species distribution modelers should include species interactions in their predictions only in abiotically benign portions of a species range.

DEDICATION

In memory of Antony Eschwa.

ACKNOWLEDGEMENTS

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INTRODUCTION

The ecology of species' geographic distributions, including range limits and abundance patterns, has long fascinated ecologists (Darwin 1859), and is becoming increasingly urgent to understand given accelerating climate change. While we know that both abiotic stress and species interactions can set species distributions (Sexton et al. 2009), projections of changes in species' distributions with climate change still largely rely on the assumption that distributions are determined only by abiotic stress, such as freezing or aridity tolerance. In contrast, ecologists have historically predicted that abiotic stress is of primary importance only at some range edges (e.g., northern and high elevation range limits) with geographic limits in apparently more benign locations (southern and low-elevation limits) more strongly controlled by biotic factors, such as parasite load, predation pressure, or herbivory (Darwin 1859, MacArthur 1972, May & MacArthur 1972). This long-standing hypothesis predicts that the strength of species interactions in shaping population growth and persistence will shift systematically with increasing abiotic stress. Determining which of these assumptions or hypotheses is more correct is critical in understanding applied issues such as climate change, as well as fundamental biogeographic patterns.

Despite the fact that ecologists have often suggested that abiotic stress may be a more critical driver of population dynamics in apparently harsher habitats, and biotic factors more influential in abiotically benign environments (Darwin 1859, May & MacArthur 1972, Gross & Price 2000, Grace et al. 2002, Harley 2003), we lack strong empirical evidence supporting this claim (see Chapter 2). Connell's (1961b) classic studies provide perhaps the best support for this hypothesis: in his work, intertidal species' distributions were constrained by abiotic stress in harsh environments and by competition with conspecifics and predation in benign environments. In addition, subsequent work has shown differential effects of interspecific competition, pollinator limitation, and herbivory on individual plant performance across stress gradients (Callaway et al. 2002, Chase et al. 2000, Bingham & Ort 1998). However, many of these studies, including Connell's, address stress gradients at extremely local, rather than geographic scales. In addition, to date, the effects of multiple species interactions have not been combined into a cohesive framework that addresses their relative importance for populations at different levels of abiotic stress. Addressing these multiple effects requires a common demographic modeling framework that explicitly incorporates numerous causal factors, allowing simultaneous analysis of the strength of multiple biotic and abiotic stressors (Caswell 2001, Morris & Doak 2002, Palmer et al. 2010).

My dissertation directly addresses this issue, using experimental approaches to gauge the importance of multiple species interactions (both positive and negative) across stress gradients, thus allowing explicit predictions about how species interactions and climatic stress interact to determine population persistence, abundance, and, ultimately, species' distributions. To construct these predictions, I study the population level effects of herbivory (a negative interaction that decreases fitness), pollination (a positive interaction that increases fitness), and inter-plant interactions (which may shift in sign from negative to positive with increasing stress: Callaway et al. 2002) for a single, model plant species, *Hibiscus meyeri*, across a sharp aridity gradient in an arid sub-Saharan savanna community in East Africa. In this precipitation-driven system, water availability is one of the major gradients in abiotic stress and is thought to strongly influence plant distributions. Traditional theory suggests that population dynamics should be controlled primarily by water stress in arid areas, but by species interactions in more mesic sites. Since largely natural communities of both large and small herbivores and their predators still persist in my study area, this system is uniquely suited to explore the relative strength of multiple biotic factors and climatic stress in a relatively intact ecosystem.

A unique benefit of a demographic approach is the ability to distinguish the demographic mechanisms driving responses to species interactions. In particular, studying individual plant responses to a range of manipulated and quantified species interactions allows me to tease apart three distinct but often confounded mechanisms by which the strength of biotic effects can change across stress gradients: (A) changes in the ratio of number of plants to interactors (e.g. a higher number of herbivores per plant in mesic areas); (B) alterations in the strength of the per capita effect of a given interactor on a plant (e.g., if plants in arid areas are better defended, each herbivore may remove smaller amounts of tissue per plant); or (C) changes in the sensitivity of population growth to an interaction (e.g., lower seedling germination in arid areas reduces the elasticity of population growth to herbivores' reduction of fruit number). My work will distinguish among these different scenarios, thus isolating the effect of aridity on pollinator, herbivore, or neighboring plant population densities from its alterations of life history patterns and hence effects of interactors.

In addition, my focus on aridity as an abiotic stressor is unusual. Predictions about the relative importance of biotic interactions apply to all gradients of abiotic stress, but have largely been invoked for latitudinal or elevational patterns in performance, often thought to mainly result from temperature. In contrast, little work has focused on aridity gradients, though we know precipitation patterns will change drastically with climate change and that these changes will result in as great or greater disruption in ecosystems than will warming alone (IPCC Climate

Change 2007, Crimmins et al. 2011). Further, aridity is one of the most pervasive forms of abiotic stress, with 40% of the world's landmass classified as arid or semi-arid, according to the UNCCD classification system, and nearly 40% of the world's human population living in these areas (White & Nackoney 2003). Aridity is also known to strongly control plant performance and abundance, and is predicted to change drastically with future climate change (Covey et al. 2003). In arid areas, we need to know when and where biotic interactions are critical drivers of individual species' population dynamics, both to anticipate range shifts in natural areas, and to correctly manage controllable interactions, such as cattle grazing, that could either exacerbate or help ameliorate climate-driven shifts in species and community distributions.

In addition to providing a framework for assessing the relative strength of different drivers on population performance, and an empirical test of a long-standing theory on the origins and maintenance of range limits, my dissertation also has direct implications for accurately predicting shifts in species distributions with climate change. Although we know species interactions can be critical drivers of population health and species' distributions (Brown 1971, Gotelli et al. 2010, Jankowski et al. 2010, Sexton et al. 2009), faithfully incorporating them into distribution models is a formidable challenge. As noted above, most "climate envelope" or species distribution modeling approaches implicitly assume that species' distributions are primarily a function of abiotic variables (e.g. temperature and precipitation) and the biotic factors that directly covary with these abiotic variables. Thus, this work will serve to illuminate where and when species interactions should be included in species distribution models, and where and when abiotic variables alone can be used to accurately predict shifts in species range limits.

Together, the following chapters seek to cover the range of topics just outlined. Chapter 2 provides a theoretical and empirical background for the hypotheses of differential mechanisms for range limitation, including predictions for when and where species interactions might be most common and why. This chapter has been published as: Louthan AM, Doak DF, Angert, AL. 2015. Where and When do Species Interactions Set Range Limits? *Trends in Ecology & Evolution* 30, 780-792. Chapter 3 addresses the population-level effects of herbivores on *H. meyeri*; this chapter has been published as: Louthan AM, Doak DF, Goheen JR, Palmer TM, Pringle RM. 2013. Climatic stress mediates the impacts of herbivory on plant population structure and components of individual fitness. *Journal of Ecology* 101, 1074-1083. Chapter 4 presents results on the fitness consequences of neighboring plants and how these effects interact with herbivory. This chapter has been published as: Louthan AM, Doak DF, Goheen JR, Palmer TM, Pringle RM. 2014 Mechanisms of plant – plant interactions: concealment from herbivores is more important than abiotic-stress mediation in an African savannah. Proc. R. Soc. B 281: 20132647. In Chapter 5, I synthesize all of these data to show at what level of aridity species interactions exert stronger effects on *H. meyeri* population performance and why. Finally, a brief concluding chapter summarizes my overall findings.

CHAPTER 2

WHERE AND WHEN DO SPECIES INTERACTIONS SET RANGE LIMITS?

Used with permission from Louthan AM, Doak DF, Angert, AL, Where and When do Species Interactions Set Range Limits?, *Trends in Ecology & Evolution,* 30, 780-792, Elsevier, 2015. See Appendix.

Abstract

A long-standing theory, originating with Darwin, suggests that abiotic forces set species range limits at high latitude, high elevation, and other abiotically 'stressful' areas, while species interactions set range limits in apparently more benign regions. This theory is of considerable importance for both basic and applied ecology, and while it is often assumed to be a ubiquitous pattern, it has not been clearly defined or broadly tested. We review tests of this idea and dissect how the strength of species interactions must vary across stress gradients to generate the predicted pattern. We conclude by suggesting approaches to better test this theory, which will deepen our understanding of the forces that determine species ranges and govern responses to climate change.

Trends

Both climate and species interactions set species range limits, but it is unclear when each is most important.

An old hypothesis, first proposed by Darwin, suggests that abiotic factors should be key drivers of limits in abiotically stressful areas, and species interactions should dominate in abiotically benign areas.

Four distinct mechanisms, ranging from per-capita effects to community-level synergies, could result in differential importance of species interactions across stress gradients.

These mechanisms, operating alone or in tandem, can result in patterns consistent or inconsistent with Darwin's hypothesis, depending on the strength and direction of effects.

The most robust test of this hypothesis, not to date performed in any study, is to analyze how sensitive range limit location is to changes in the strength of one or more species interactions and also to abiotic stressors.

Abiotic and Biotic Determinants of Species Ranges

The ever-mounting evidence of continuing climate change has focused attention on understanding the geographic ranges (see Glossary in Appendix) of species, and in particular how these ranges might shift with changes in climate (Parmesan & Yohe 2003, Loarie et al. 2009). A major complication to these efforts, often mentioned but rarely formalized, is that all populations occur in a milieu of other species, with multiple, often complex species interactions affecting individual performance, population dynamics, and hence geographic ranges. The implicit assumption of most modern work on range shifts is that either directly or indirectly, climate is the predominant determinant of ranges, but interactions among species might also limit species, current and future geographic ranges (Van der Putten et al. 2010, Pigot & Tobias 2013, Wisz et al. 2013). Determining where and when climate alone creates range limits, and where and when it is also critical to consider species interactions, will allow us to identify the most likely forces setting species range limits.

A better understanding of the forces creating range limits is especially important for the accurate prediction of geographic range shifts in the face of both climate change and anthropogenic impacts on species interactions (e.g., introduction of exotic species, shifts in interacting species ranges, and extinction or substantial reductions of native populations; Bois et al. 2013, Gillson et al. 2013, Raffa et al. 2013, Ripple et al. 2014). For example, predictions of shifts in species distributions might only need to consider direct effects of climate to be accurate, but if species interactions also exert strong effects, we must include both climate and these more complex effects in our predictions. Finally, if species interactions are important in some sections of a species range but not in others, we can be adaptive in the inclusion of these effects when formulating predictions.

We frame our discussion of the drivers of range limits around the long-standing prediction that climate and other abiotic factors are far more important in what appear to be abiotically stressful areas, whereas the effects of species interactions predominate in setting range limits in apparently more benign areas; we call this the 'Species Interactions–Abiotic Stress Hypothesis' (SIASH; Table 1). To clarify the evidence and possible causal mechanisms underlying SIASH, we first summarize past work on the drivers of range limits. We then propose a more operational statement of the hypothesis and discuss a series of different mechanisms that could explain systematic shifts in the strength of species interactions across abiotic stress gradients. We end by discussing ways to better test the factors setting range limits.

Cause of cold edge range limit	**Cause of warm edge range limit**	**Pattern generated**
Abiotic stress	Abiotic stress	Only abiotic stress determines species distribution
Species interactions	Species interactions	Only species interactions determine species distribution
Abiotic stress	Species interactions	SIASH
Species interactions	Abiotic stress	Opposite of SIASH

Table 1. Possible patterns in abiotic and biotic causes of range limits**.**

A Brief History of Range Limit Theory

Most early work on range limits emphasized the role of abiotic stress (e.g., von Humboldt & Bonpland 1807, Merriam 1894; see "Causes of Range Limits, below"), but naturalists also speculated that both abiotic stress and species interactions were important determinants of limits (Table 1). For example, Grinnell (1917) observed that the California thrasher (*Toxostoma redivivum*) range is loosely constrained to a specific climatic zone, but in the presence of another thrasher species, it is more tightly constrained. Also, not all authors agreed that the importance of species interactions would vary as predicted by SIASH. Griggs (1914) found that competition sets northern range limits for some plant species, and Janzen (1967) hypothesized that the breadth of abiotic tolerance is narrower in tropical montane species than in temperate montane species, and thus that climate constrains species elevational ranges more tightly in the tropics.

Despite these different ideas, most thinking about the role of species interactions in range limit formation has centered around the predictions of SIASH. As with so many ecological concepts and theories, Darwin, in *On the Origin of Species* (1859), provides the first clear articulation of the idea:

> When we travel from south to north, or from a damp region to a dry, we invariably see some species gradually. . .disappearing; and the change of climate being conspicuous, we are tempted to attribute the whole effect to its direct action. But. . .each species. . .is constantly suffering enormous destruction. . .from enemies or from competitors for the same place and food. . .When we travel southward and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favoured, as in this one being hurt. . .When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements. (Darwin 1859, Chapter 3, p. 66)

Dobzhansky (1950) MacArthur (1972) and Brown (1995) all emphasized geographic patterns arising from SIASH, suggesting that low-latitude range limits are set by species interactions (most commonly negative interactions such as competition or predation) and higher-latitude limits by abiotic stressors.

Tests of the Forces Governing Range Limits

A plethora of correlational studies suggest a major role for abiotic stress in setting range limits (see references in Gaston 2003), but direct effects of abiotic stress on physiological performance or fitness in the context of range limits have been more difficult to document (Sexton et al. 2009; we also note that species find many different conditions ‘stressful’).

There is also abundant evidence that species interactions, both negative and positive (e.g., facilitation or pollination), can and do influence species ranges. In addition to modeling work (e.g., Case et al. 2005), Sexton et al. (2009) found that the majority of empirical studies looking for biotic determinants of range limits found support for these effects. Most commonly, studies addressing biotic determinants of range limits show correlations between density of a focal species and that of their competitors or predators (e.g., Bullock et al. 2000), or attribute a lack of demonstrable abiotic control over nonstressful or trailing range limits to biotic factors (Ettinger et al. 2011, Sunday et al. 2012). Competition, predator– prey dynamics, or hybridization can all constrain occurrence patterns of species (Anderson et al. 2002, Aragón & Sánchez-Fernández 2013, Pigot & Tobias 2013, Tingley et al. 2014), while mutualisms can extend ranges (Afkhami et al. 2014). However, little work measures effects of biotic factors on demographic or extinction–colonization processes (See “Causes of Range Limits”; but see Pennings & Silliman 2005, Kauffman & Maron 2006), and fewer still connect such fine-scale information to geographic range limits (but see Stanton-Geddes et al. 2012).

It is even more difficult to quantify the fraction of range limits set by abiotic versus biotic factors, or when and where abiotic versus biotic factors will dominate, much less why such patterns might arise. Doing so is primarily limited by a lack of studies that address both abiotic and biotic determinants of species ranges in the same system. Nonetheless, studies in several ecological systems allow provisional tests of SIASH, although often with a lack of connection between work on local processes and large-scale patterns. At the fine scale, Kunstler et al. (2011) show that tree growth is more reduced by competitors in areas with greater water availability and temperature. Conversely, for an annual plant along a moisture gradient, Moeller et al. (2012) show that plant reproduction is more limited by pollinator service in stressful than in benign locations. There are also many large-scale studies suggestive of SIASH: in conifers, abiotic stress more often limits growth at high elevations, while other factors, presumably species interactions, are more important at low-elevation limits (Ettinger et al. 2011, but see Ettinger & HilleRisLambers 2013, which finds no variation in the strength of competition across elevations), and similar work shows correlations suggestive of SIASH in crabs (DeRivera et al. 2005) and birds (Gross & Price 2000). Stott and Loehle's work (1998) on boreal trees also supports SIASH. In a meta-analysis of over-the-range-limit transplant experiments, Hargreaves et al. (2014) demonstrated that fitness is often reduced beyond high latitude or high elevation limits (consistent with limits set by abiotic stress), whereas fitness remains high beyond most low latitude or low elevation limits (consistent with at least partial control by species interactions). Studies of invasive species, which are often known or suspected of having reduced enemies or competitors in their introduced range, show mixed results. In the tropics, many invasive birds and mammals have very broad geographic ranges, suggesting that their native ranges were tightly controlled by species interactions, consistent with SIASH. However, outside the tropics, most high-latitude invasive species have larger range sizes than extratropical lower-latitude invasive species, inconsistent with SIASH (Sax 2001). Importantly, a minority of these studies use experimental manipulations (Moeller et al. 2012, Hargreaves et al. 2014).

The rocky intertidal offers the best work on the mechanisms settings range limits at both large and small scales. These systems offer clear local stress gradients and harbor many experimentally tractable species, with low adult mobility and clear-cut range limits; all of the studies cited below use experimental manipulations. At the fine-scale, Connell (1961b) found support for SIASH: predation and competition more strongly affect population density in the lower intertidal, which is less abiotically stressful than the upper intertidal. Subsequent work found similar patterns for these and other interactions, including predation (Paine 1974, but see Wootton 1993, one of multiple studies showing large effects of predation by birds in the upper intertidal), competition (Wethey 1984, Wethey 2002), and herbivory (Harley 2003; but see Underwood 1980, where herbivores prevent establishment of algae in the upper intertidal). At the macroecological scale, Sanford et al. (2003) found support for SIASH, with increased frequency of predation on the mussel *Mytilus californianus* in low latitudes (see also Paine 1966, Freestone et al. 2011). Wethey (1983, 2002) has shown that for intertidal barnacles, high-latitude limits are set by competition and low-latitude limits by temperature intolerance, a pattern conforming to the prediction of SIASH regarding abiotic stress, but not the common latitudinal pattern in range limits that assumes stress is lowest in the tropics.

A Clear Definition of SIASH

Although there is an extensive literature on the causes of range limits, and ecologists often assume that SIASH is a strong generality (e.g., Connell 1961b, Ettinger et al. 2011, Hargreaves et al. 2014), a clear operational definition of the hypothesis is lacking. Many of the studies discussed above show evidence that one or more performance measures are differentially affected by biotic or abiotic forces, but not evidence concerning their influence on range limits or expansion or population growth at range margins. An added complication is that ‘stress’ is extremely difficult to define or manipulate (e.g., Helmuth et al. 2006, Crimmins et al. 2011), since multiple conditions can be stressful, many species are known to find both ends of an abiotic gradient stressful (e.g., thermal neutral zones of endotherms and physiological activity ranges of ecotherms), and many abiotic stressors are negatively correlated (e.g., drought stress and freezing stress along an elevational gradient). Before delving further into how the patterns predicted by SIASH could arise, we therefore suggest this definition: ‘amelioration of biotic limits to growth would expand the range much more at the nonstressful than the stressful end of some gradient in abiotic conditions, and conversely for amelioration of abiotic stress’. This definition also has a corollary about the forces governing local population growth at range limits: low density stochastic growth rate ($\lambda_{L.D.}$) of local populations is predicted to be more strongly influenced by species interactions at the nonstressful end of an abiotic gradient, and by abiotic forces near to the stressful end; because population presence or extinction are functions of population growth at low densities, controls on performance under these conditions are the critical metric of effects on range limits. This definition emphasizes the dual pattern that SIASH predicts, has a clear graphical interpretation (Fig. 1), and also can be analyzed using standard demographic methods (See “Formulating Demographic Tests of SIASH”). We also know of no studies that quantify response of range-limit growth rate to different drivers while accounting for density to arrive at estimates of low-density growth rate.

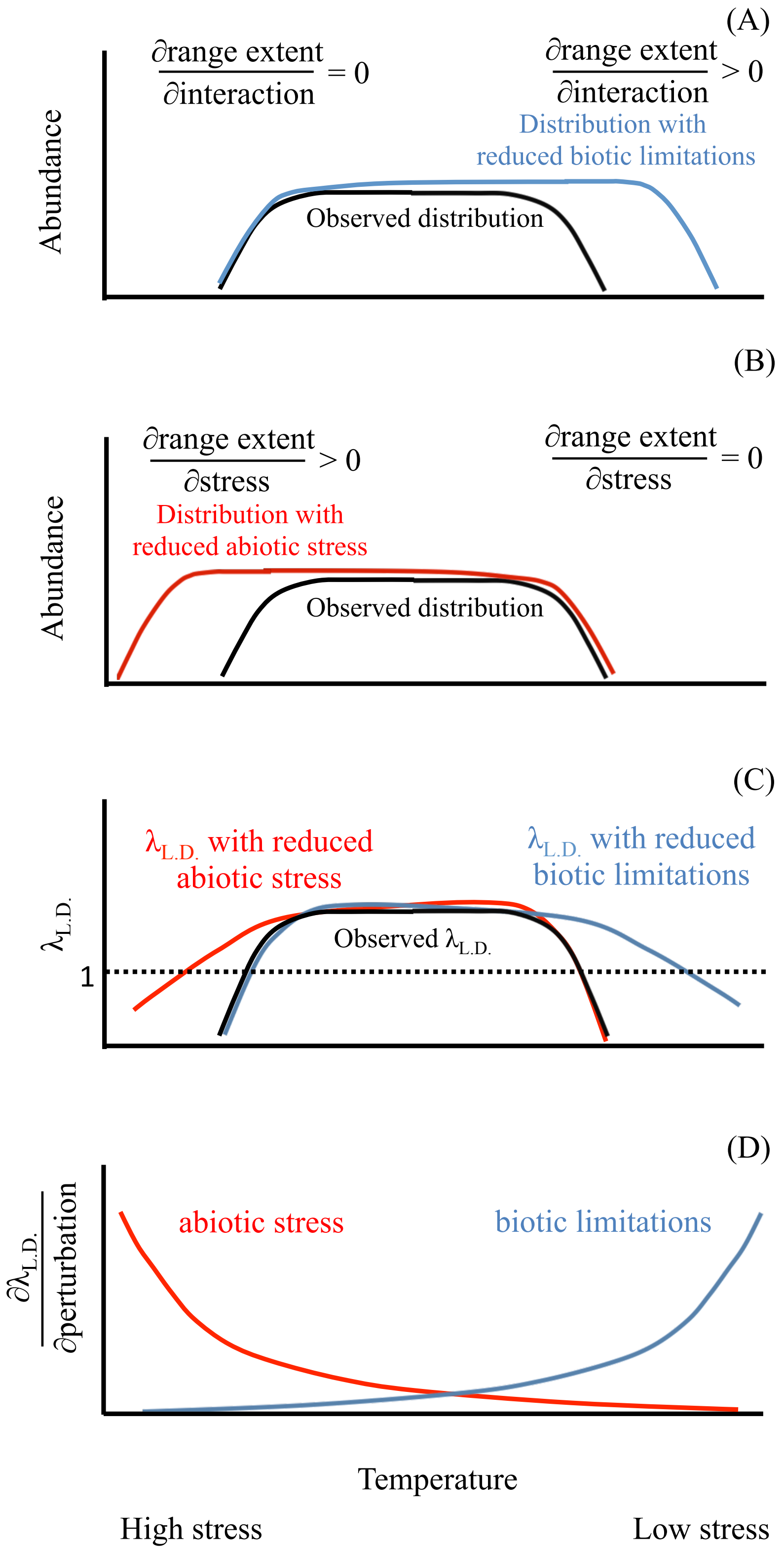
(A)
∂range extent / ∂interaction = 0
∂range extent / ∂interaction > 0
Distribution with reduced biotic limitations
Observed distribution
Abundance
(B)
∂range extent / ∂stress > 0
∂range extent / ∂stress = 0
Distribution with reduced abiotic stress
Observed distribution
Abundance
(C)
λL.D. with reduced abiotic stress
λL.D. with reduced biotic limitations
Observed λL.D.
λL.D.
1
(D)
abiotic stress
biotic limitations
∂λL.D. / ∂perturbation
Temperature
High stress
Low stress

Figure 1. A Functional Definition of Species Interactions–Abiotic Stress Hypothesis (SIASH) Patterns and Predictions. SIASH predicts that the sensitivity of range extent to species interactions (∂range extent/∂interaction) is high at the nonstressful end of a species range. At the nonstressful end, species interactions drive local abundances to zero (i.e., set the range limit), so that release from these limitations (blue line) would lead to significant, stable expansion from the observed distribution (black line). (B) Conversely, SIASH predicts that sensitivity of range extent to stress (∂range extent/ ∂stress) is high at the stressful end of a species range, such that release from these limitations (red line) will result in stable range expansion from the observed distribution (black line). (C) While conducting experiments to measure actual range expansion is generally difficult (Connell's experimental work on barnacles, 1961b, is perhaps the best example of such a study), under realistic assumptions, sensitivities of low-density population growth rate ($\lambda_{L.D.}$) mirror sensitivities of range extent, such that alleviation of biotic limitations or stress results in range expansion (species is extant where $\lambda_{L.D.} \geq 1$; colors as in A and B). (D) SIASH can be tested by assessing the sensitivity of $\lambda_{L.D.}$ to perturbations in both species interactions and abiotic stress ($\partial\lambda_{L.D.}/ \partial$perturbation; red is sensitivity to abiotic stress and blue to biotic limitations).

Possible Mechanisms Determining Species Interaction Strength across Stress Gradients

It is evident (and perhaps even tautological) that abiotic stress will be limiting in places that are abiotically stressful. The less obvious aspect of SIASH is why species interactions should be weak in stressful areas and strong in abiotically benign areas. Understanding if these patterns hold is therefore a key part of testing the generality of SIASH. There are a number of aspects or levels of species interactions, not all of which necessarily lead to SIASH, but few statements of the theory are specific about what component of species interactions are alleged to change across stress gradients. For example, SIASH predicts that parasitism should exert stronger effects on range limits in less stressful areas. However, one might predict that where stress is high, there should be larger effects of a given parasite load on host performance because of decreased ability to recover from infection. Where stress is low, conversely, there might be weaker effects of that same parasite load due to increased reproductive rates that compensate for negative effects of parasites. In this scenario, we would actually expect that parasitism will have larger effects in stressful places, contrary to the predictions of SIASH. To further complicate matters, variation in parasite load, parasite infection rate, and parasite species diversity will also influence the net effect of the interaction.

There are at least four nonexclusive mechanisms underlying any species interaction that together control whether and how the effect of the interaction will vary across stress gradients (Fig. 2). For clarity, we illustrate these different mechanisms using herbivore effects on plants (see “The Breakdown of Species Interactions Effects for Herbivory” for a review of empirical plant–herbivore interactions in the context of SIASH), but the same breakdown applies to other interactions, as follows.

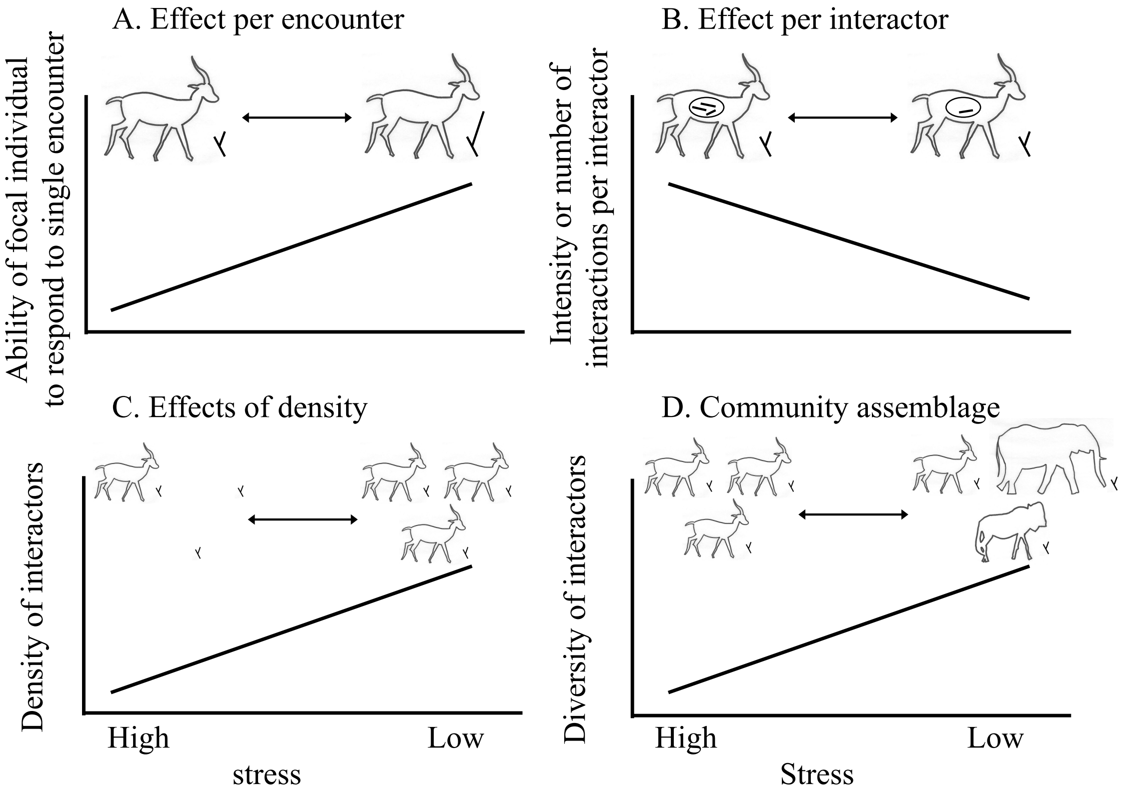

Figure 2. Four Mechanisms Dictating the Strength of Species Interactions. At least four mechanisms combine to influence how the strength of species interactions will vary across stress gradients, as shown here for plausible patterns in plant–herbivore interactions. Each level of the interaction is expected to respond to a gradient of decreasing stress, as might occur with

increasing temperature, rainfall, or nutrient availability. Inset pictographs illustrate these mechanisms for interactions between a focal food plant and its gazelle herbivore. (A) Effect per encounter. The impact of a single feeding bout on the fitness of an individual plant, with increased plant regrowth following herbivory in low-stress areas. (B) Effect per interactor. Cumulative effects of a lifetime of interactions between one gazelle and one plant, with higher consumption, and hence impact, in high-stress areas. (C) Effects of density. The effect of a population of gazelle on the population of a focal plant, with higher gazelle-to-plant ratio in low-stress areas. (D) Community assemblage. Effects of a guild of interactors on a plant population, with greater diversity of herbivore species in low-stress areas. The direction of each mechanism across a stress gradient might be positive or negative, and will not necessarily conform to the pattern shown in these panels (see text for more details).

Mechanism 1: Effect per Encounter

The demographic effect of each interspecific encounter (e.g., one bite from one herbivore) changes across stress gradients, such that focal individuals respond differentially to an encounter as a function of abiotic stress level. For example, the ability of an individual plant to maintain $\lambda = 1$ following one feeding bout by one herbivore appears likely to decrease as stress increases (Fig. 2), opposing SIASH.

Mechanism 2: Effect per Interactor

The effect of an individual interactor on a focal individual (e.g., the effect of one herbivore on one plant over their lifetimes) varies across stress gradients. For example, colder conditions are likely to mean greater energetic needs for endothermic herbivores and hence higher feeding rates (Fig. 2); this would contradict SIASH. Alternatively, a generalist herbivore might feed on a variety of plant species in stressful, low-primary-productivity environments, but specialize on a focal plant species in nonstressful, high-productivity environments; this could support SIASH.

Mechanism 3: Effects of Density

The ratio of the population densities of two species changes across stress gradients, such that population-level effects of the interaction vary. For example, herbivore-to-plant ratios might increase with increasing temperature or rainfall, supporting SIASH (Fig. 2), or show the opposite pattern, contradicting SIASH.

Mechanism 4: Community Assemblage

Finally, the richness or diversity of species within a guild changes across stress gradients, with resulting changes in the limitations imposed on species the guild interacts with. For example, a plant suffering more types of damage from a richer herbivore community might be more strongly impacted than one living with a less diverse set of consumers (Fig. 2). If herbivore communities are richer in low-stress areas than in high-stress areas, this would support SIASH.

The most fundamental difference among the above mechanisms is between effects generated by the interactions between pairs of individuals (mechanisms 1 and 2) versus effects generated by the populations and communities of interacting species (mechanisms 3 and 4). The original proponents of SIASH (Darwin 1859, Dobzhansky 1950, MacArthur 1972, Brown 1995) emphasized that gradients in interactor density or richness, mechanisms 3 and 4, are common along gradients in abiotic stress. Similarly, Menge and Sutherland's formulation of this hypothesis (1987) relies on increased food web complexity in nonstressful areas. A recent review by Schemske et al. (2009) suggests that, concomitant with the well-known decreases in species richness with latitude, the frequency of many types of species interactions also decrease with latitude for a wide variety of species. We might predict that increases in interactor density and species richness with decreasing stress (and by extension, increased number and diversity of interactions) might make SIASH very common in nature. However, variation in interaction strength (mechanisms 1 or 2) could strongly influence this conclusion. For example, if a prey's risk of capture increases with stress (mechanism 1), but, simultaneously, predator density decreases with stress (mechanism 3), the net effect of predation might not vary. Similarly, if predators require more food in stressful areas to maintain body condition (mechanism 2), but predator density decreases with stress (mechanism 3), the net effect of predation might vary in either direction. Different combinations of these mechanisms can generate an overall pattern consistent or inconsistent with SIASH (See “A Simple Model”, Fig. 3).

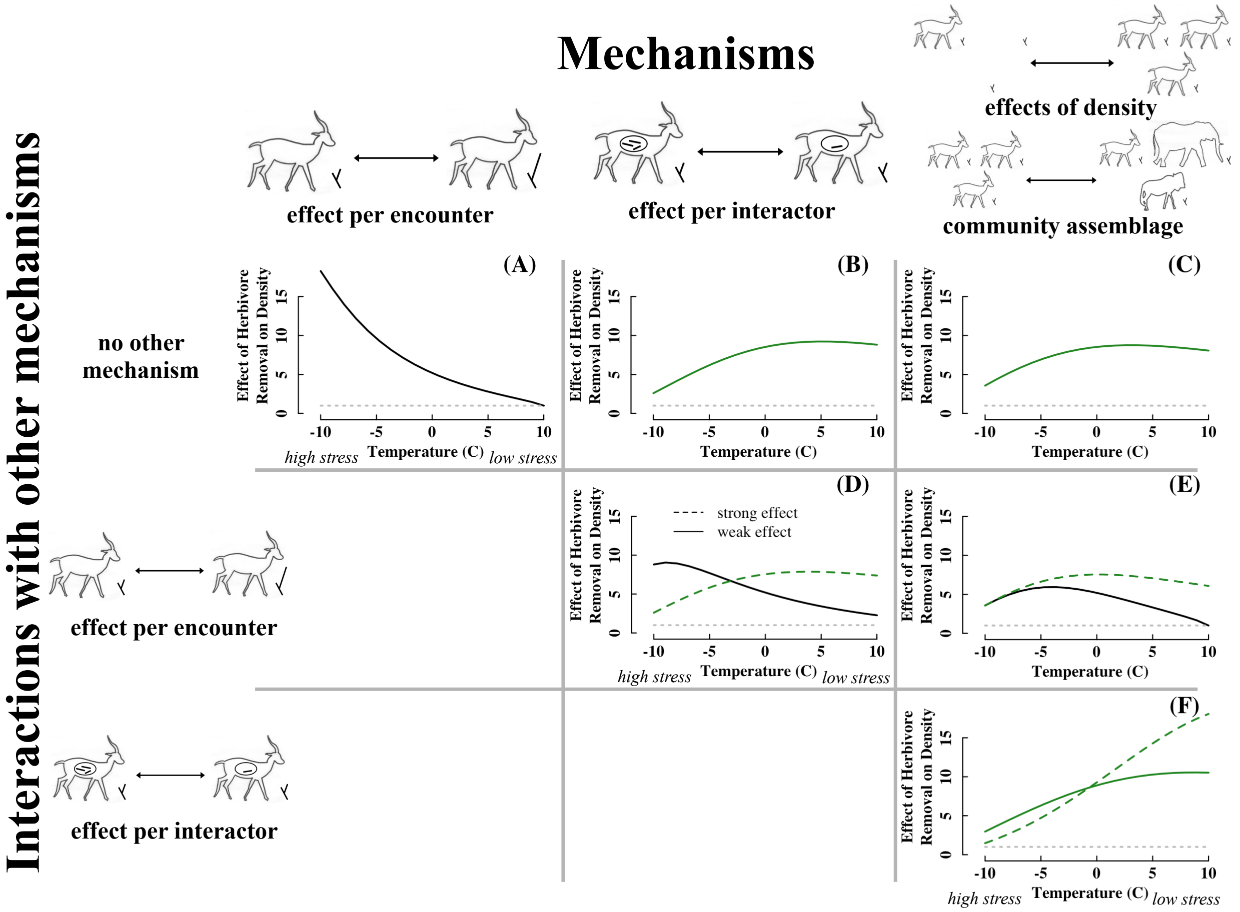

Figure 3. *A Priori* Support for SIASH Is Mixed when considering the Mechanisms Underlying Species Interactions, with Some Mechanisms Leading to the Predicted SIASH Pattern and Others Opposing it. Lines in each subplot show the effect of herbivores on relative plant density (density in the absence of herbivores/density in the presence of herbivores) across a temperature gradient that ranges from highly stressful at low temperatures to nonstressful at warmer temperatures; predictions come from a Nicholson–Bailey predator–prey model modified to reflect plant– herbivore interactions (See “A Simple Model”). High effect values indicate strong suppression of plant abundance by herbivores, while a value of 1 indicates no effect of herbivory (gray dashed line). Lines in green indicate mechanisms and scenarios conforming to the SIASH pattern, whereas those in black show results that oppose SIASH predictions. We show the effects

of each mechanism in isolation (A–C), as well as in combination (D–F), for both weak (solid line; shallow gradient in the numerical difference between mechanism strengths) and strong (dashed line; steep gradient) effects. We group mechanisms 3 and 4 together because they will show the same pattern of effects if different herbivore species have additive or synergistic effects. Importantly, not all mechanisms operating alone result in patterns consistent with the SIASH. Further, when multiple mechanisms operate simultaneously, a pattern consistent with the SIASH is sometimes generated (e.g., F), but sometimes not (e.g., E, black line), and in some cases, whether or not the SIASH pattern occurs depends on the strength of the mechanisms operating (e.g., D). While we illustrate these patterns with effects on equilibrium densities, the same approach can be used to look for effects on $\lambda_{\mathrm{L.D.}}$ (and most results for the parameter combinations used here are qualitatively similar). In all cases, k = 0.25, M= 10000, K_H= 1000, and with increasing rainfall, r_N increases linearly from 0.1 to 0.5 and K_N increases from 5 x10^4, plateauing at 10 x 10^4. In (A), a_1 increases linearly from 0 to 0.01, a_2= 0.01, and e^{r_H}= 0.01. In (B), a_1= 0, a_2 increases linearly from 0.004 to 0.016, and e^{r_H}= 0.01. In (C), a_1= 0, a_2= 0.01, and e^{r_H} increases linearly from 0.005 to 0.015. In (D), a_1 increases linearly from 0 to 0.01 (weak) or 0 to 0.003 (strong), a_2 increases linearly from 0.008 to 0.012 (weak) or 0.004 to 0.016 (strong), and e^{r_H}= 0.01. In (E), a_1 increases linearly from 0 to 0.01 (weak) or 0 to 0.003 (strong), a_2= 0.01, and e^{r_H} increases from 0.005 to 0.015. In (F), a_1 = 0, a_2 increases from 0.008 to 0.012 (weak) or 0.0045 to 0.016 (strong), and e^{r_H} increases linearly from 0.0055 to 0.015.

The different mechanisms by which stress affects species interactions, and how these effects could in turn generate or suppress the SIASH pattern, emphasize that studies of interaction frequencies (say, leaf damage rates) or of single components of fitness (say, individual reproductive success) are not in and of themselves sufficient to determine what factor is primarily determining any given range limit, and thus to fully test the generality of SIASH. Some of the most convincing studies of latitudinal gradients in species interactions address mechanisms 1 or 2 above, showing that attack rates of a herbivore or predator are higher per unit time with decreasing latitudes (e.g., higher annual herbivory on tropical versus temperate broad-leaved forest trees, Coley & Aide 1991, and 18 times higher predation pressure on tropical versus temperate insects, Novonty et al. 2006). But these results by themselves do not show that these interactions control occurrence patterns of victims more strongly in the tropics. Ideally, studies of the generation of range limits should quantify all four mechanisms, although we recognize that this is a tall order. A well-designed study of SIASH for aridity and herbivory might assess sensitivity of $\lambda_{L.D.}$ to rainfall and herbivore density at range limits and conduct over-the-range-limit transplants with and without supplemental watering treatments and herbivore exclosures ("Formulating Demographic Tests of SIASH"). Support for or against SIASH might arise due to any of the four mechanisms detailed above.

Concluding Remarks and Future Directions

Understanding why range limits are where they are, and predicting how climate change, species losses, and other global changes will alter them are key questions in applied and basic ecology. While SIASH is a long-standing hypothesis, there are still few thorough tests of its predictions. Whether or not SIASH provides a strong generality depends on the relative strength of different mechanisms that will combine to create or negate patterns in the importance of abiotic versus biotic limitations to population persistence (Fig. 3). However, we currently lack empirical tests of the underlying processes or exact predictions of the hypothesis that would be needed to judge support for SIASH (see "Outstanding Questions").

We see three avenues to increase our understanding of when and where SIASH is a useful generality. First, field studies that quantify the strength of each of the four interaction mechanisms affecting population growth rate could be used to parameterize simple models (e.g., "A Simple Model") to assess support for SIASH. Such work could use relatively simple experiments replicated across broad-scale geographic gradients to fill in information in already well-studied systems (Maron et al. 2014).

A second need is for studies of how demographic processes vary with stress, or multiple stressors, across a species range, and thus the effect of stress in limiting low-density population growth rates. For example, if seedling germination is already limited by abiotic determinants of safe site abundance, reduction of plant fecundity by herbivores might have muted effects on plant abundance; conversely, if recruitment is not safe site-limited, reduction of fecundity by herbivores will have large population-level effects (Maron et al. 2014). Few studies address variation in vital rates and sensitivity of population growth rate to those vital rates across broad geographic ranges (but see Angert 2009, Doak & Morris 2010, Eckhart et al. 2011, Villellas et al. 2012), and even fewer quantify the factors driving variation in these rates (e.g., Doak & Morris 2010, Fisichelli, Frelich & Reich 2012), Stanton-Geddes et al. 2012) or consider density effects.

Finally, even if the predictions of SIASH are supported, there are very few studies that directly address whether simple reductions in local population performance are usually the key factor limiting ranges ("Causes of Range Limits"), (Angert 2009, Doak & Morris 2010, Eckhart et al. 2011). In particular, we have little empirical evidence showing how metapopulation dynamics affect range limits (Fukaya et al. 2014). In addition, it is unclear if small-scale determinants of species range limits at the local scale are governed by mechanisms similar to determinants that operate at geographic scales. Thus, studies trying to address determinants of range limits should clearly articulate the scale of their work relative to the range of the study species (e.g., Emery et al. 2012).

Predicting where and when the inclusion of species interactions will meaningfully improve range limit predictions is critical to predicting the ecological consequences of climate change (Guisan & Thuiller 2005, Angert et al. 2013), but we have evidence that there is wide variation in how important these species interactions are (Godsoe et al. 2015). Focusing on the relative importance of different factors in driving ranges and their dynamics are particularly important because species might shift their ranges idiosyncratically with climate, resulting in novel communities, and because many climate change-caused extinction events have been suggested to arise via altered species interactions, rather than climate shifts per se (Harley 2011, Cahill et al. 2013, Tunney et al. 2014). While the predictions of SIASH might or might not prove robust to empirical tests, the four mechanisms underlying SIASH provide a framework for testing the most likely forces setting species range limits in a variety of systems and thus could help us more accurately predict shifts in geographic ranges.

Outstanding Questions

Do abiotic stress or species interactions have a strong influence on species range limits? Whereas there is ample evidence from the literature that both abiotic stress and species interactions can set limits, some species limits may be caused by dispersal limitation, or ranges may not be at equilibrium. Thus, we encourage ecologists to devote substantial time to observing causes of reduced performance at range limits, and assessing whether abiotic and biotic factors are likely drivers, before quantifying their influence on population growth.

What is the effect of both abiotic and biotic forces on fitness or population growth? Many existing studies quantify responses of only one fitness component to abiotic or biotic forces, but not overall population growth, especially at low densities, and hence range limits.

What is the total effect of a given species interaction across abiotic gradients, considering potentially different trends at multiple levels of the interaction, including individual responses, as well as density and community assemblage effects? The four mechanisms we outline here are a starting point to consider effects at multiple levels; measuring the strength of poorly studied mechanisms in well-studied systems that have already measured some mechanisms could be especially productive.

How do different demographic processes vary with abiotic stress? We have a poor understanding of how abiotic stress affects vital rates for many species, and thus a limited ability to predict how species interactions will influence population growth.

Are reductions in local population performance or metapopulation persistence the key driver of range limits? Conducting more studies comparing these two forces would both increase our ability to predict whether SIASH is a strong generality, as well as further our understanding of all species range limits and geographic shifts in those limits with climate change.

Causes of Range Limits

In addition to simple dispersal limitation, three demographic processes can set range limits (Holt & Keitt 2000, Holt et al. 2005): (i) a reduction of average deterministic growth rate such that a population can no longer be established or survive; (ii) increased variability in demographic rates, such that stochastic growth rates are too low for establishment or persistence (Boyce et al. 2006); and (iii) increasingly patchy habitat distributions or lower equilibrium local population sizes, so that extinction–colonization dynamics will no longer support a viable metapopulation. For simplicity, we emphasize declines in mean performance in our presentation, but both of the other processes can also enforce range limits, through similarly interacting effects of species interactions and abiotic variables on demographic rates. Both empirical and modeling work suggest that all of these demographic processes can operate in nature, but this breakdown of demographic causes of range limits is agnostic with respect to underlying abiotic or biotic drivers.

Anywhere a species is extant, we expect that, over the long term, populations are able to grow from small numbers to some stable population density (although not necessarily the same density everywhere), but the demographic reasons that this condition is not met – and hence a range limit is hit – can vary geographically. For example, survival rates could decline at high temperatures, while reproduction fails at low temperatures, such that population growth rates are higher at intermediate temperatures, but fall at both extremes. Similarly, different abiotic stressors might simultaneously vary over a single geographic gradient: at high elevations cold can reduce survival, while at low elevations, drought can do the same (e.g., Morin et al. 2007: for aspen, drought is stressful in southern populations, but cold is stressful in northern populations). In contrast to these examples, the classic assumption behind SIASH, and most tests of SIASH, is that abiotic stress gradients are one dimensional and monotonic in their effects on population growth, either increasing or decreasing along a latitudinal or elevational gradient. SIASH also assumes that each range limit arises either from abiotic or biotic factors, while it is quite likely that many range limits result from strong synergies between abiotic and biotic factors, rather than just one class of factors alone.

Formulating Demographic Tests of SIASH

SIASH is sometimes phrased in a way that denies contradiction: a range limit at the stressful end of an abiotic gradient is determined by stress, and the range limit at the other, nonstressful end of the gradient is determined by something else (species interactions), because there is no abiotic stress there. Stress gradients are also often assumed to follow what humans might see as stressful versus nonstressful conditions. However, both ends of even a simple abiotic gradient can pose difficulties for a species, and many stress gradients are nonlinear or polytonic. Finally, range limits can be determined by multiple, interacting factors, with biotic and abiotic factors exerting some control over population performance across a species range.

Given these difficulties, the most robust test of SIASH is analyzing how sensitive range limit location is to changes in the strength of one or more species interactions (in the currency of any of the four mechanisms we outline) versus abiotic stressors. SIASH predicts that the sensitivity of range limit expansion to the alleviation of a biotic limitation (reduction of a negative interaction or increase in a positive one) will be much greater at the low-stress end of a geographic range than the other, with a converse sensitivity to abiotic stress alleviation (Fig. 1) over the long term.

SIASH could be tested using across-range-limit transplants combined with manipulations of abiotic and abiotic factors. However, such experiments can be difficult, must be conducted over fairly long time periods, and are sometimes inadvisable ethically. An alternative is to evaluate whether $\lambda_{L.D.}$ values of populations at low-stress range limits have greater sensitivity to experimental reduction of biotic limitations than do $\lambda_{L.D.}$ values at high-stress limits (and, whether sensitivity to abiotic stress shows the converse pattern). Low-density growth rates, which determine probability of population establishment or extinction, will best correlate with population presence and persistence even if range limit populations are at high density (Birch 1953). In established populations, short-term focal individual manipulations (e.g., local density reductions) can be used to estimate $\lambda_{L.D.}$. Assuming that this sensitivity is a continuous function of abiotic conditions and such conditions change continuously across range limits, sensitivity of $\lambda_{L.D.}$ to abiotic or biotic factors should mirror the sensitivity of range limitation (Fig. 1). Discontinuities in either abiotic stressors or species interactions across range limits will obviously complicate the interpretation of this measure of range limitation sensitivity.

The Breakdown of Species Interactions Effects for Herbivory

Studies of herbivory, a particularly well-studied set of species interactions, help illustrate how the direction and strength of the four mechanisms can differ along a stress gradient. The Compensatory Continuum Hypothesis (CCH) predicts that stressed plants are less able to compensate for herbivore damage (mechanism 1, Maschinski & Whitman 1989; although Hilbert et al. 1981 predict the opposite, also see Hawkes & Sullivan 2001). Relevant to mechanism 2, herbivore metabolic rate, and thus food intake, is also often higher in thermally stressful areas (Dunbar & Brigham 2010, Dell et al. 2011), but the opposite is true for precipitation (Scheck 1982, Soobramoney et al. 2003). Supporting our illustration of mechanisms 3 and 4, herbivore densities, herbivore/plant ratios, and herbivore species richness are generally higher in dense plant stands and nonstressful areas (Root 1973, McNaughton et al. 1989, Rosenzweig 1995, Ritchie & Olff 1999, Forkner & Hunter 2000, Jones et al. 2011, Salazar & Marquis 2012).

Some studies of herbivory also quantify the relative strength of multiple mechanisms. Pennings et al. (2009) found very high herbivory rates on low latitude salt marsh plants, consistent with SIASH, resulting from a combination of higher herbivore feeding rates (mechanism 2) and much higher herbivore densities (mechanism 3) in low latitudes than in high latitudes (but high herbivore densities have also been shown to drastically impact salt marsh plants in the high arctic; Handa et al. 2002). However, differences in the strength and direction of these very same mechanisms can lead to net effects inconsistent with SIASH: in *Piper* plants, herbivore densities are highest at the equator, but lower herbivore feeding rates in these same areas (possibility due to higher plant defenses) mean that herbivory rates do not differ with latitude (Salazar & Marquis 2012).

Different mechanisms can also exert strong feedback on one another, further complicating efforts to predict when we expect to see SIASH-like patterns. Miller et al. (2009) showed that cactus (*Opuntia imbricata*) herbivores were most abundant at low elevations (mechanism 3); in turn, this high herbivore pressure acted to reduce cactus densities, thus increasing per-capita effect of herbivores (mechanism 2) due to lack of food. These examples serve to illustrate that mechanisms can exacerbate or nullify one another and, that in some cases, the pattern generated by multiple mechanisms is extremely difficult to predict using only limited data on single mechanisms.

A Simple Model

We use a simple heuristic model of plant response to herbivory to show how the four mechanisms composing a species interaction could contribute to the generation of range limits. We simplify herbivory, the only species interaction in this example, to a simple consumptive effect that results in an immediate reduction in plant size and growth. We use this model to explore how different mechanisms contribute to the sum effect of herbivory on plant populations across a temperature gradient.

We base our model on the modified Nicholson–Bailey predator–prey dynamics (Nicholson 1933, Nicholson & Bailey 1935) that incorporate spatial clumping of the herbivore (May 1978), as well as density dependence of both the plant (after Beddington et al. 1978, Kang et al. 2008) and the herbivore. We model N_t, the density of a focal plant species, and H_t, the density of a generalist herbivore, across a gradient of increasing temperature:

$$N_{t+1} = N_t e^{\left(r_N - r_N \frac{N_t}{K_N}\right)} \left[\left(1 + (a_2 - a_1)\frac{H_t}{k}\right)^{-k}\right] \tag{1}$$

$$H_{t+1} = H_t \left[\left[(N_t + M)\left(1 - \left(\left(1 + a_2 \frac{H_t}{k}\right)^{-k}\right)\right)\frac{e^{r_H}}{H_t}\right]^{\left(1 - \frac{H_t}{K_H}\right)}\right] \tag{2}$$

Here, a_2 is the average reduction in plant size following an encounter with one herbivore, and a_1 governs the extent of compensatory regrowth following that encounter. r_N represents the intrinsic rate of increase of the plant, K_N the carrying capacity, and k the spatial clumping of herbivores. Analogously, r_H represents the conversion rate of plants to herbivores and K_H herbivore carrying capacity; M is the density of other food sources of herbivores. We model mechanism 1 (effect per encounter) by increasing a_1 with temperature, mechanism 2 (effect per herbivore) by increasing a_2 with temperature, and mechanisms 3 and 4 via increasing r_H with temperature.

We first consider each mechanism in isolation, assuming what seem to us plausible directions for these effects with increasing temperature, and then explore combinations of mechanisms. While effects of each mechanism in isolation are relatively easy to predict (Fig. 3A–C), when considering multiple mechanisms, support for SIASH is highly contingent on the strength of individual effects (Fig. 3D–F), illustrating that the conditions under which SIASH is supported or refuted will depend on the strength and exact pattern of each of the four mechanisms and how they vary with stress. These results suggest that the net pattern generated by multiple mechanisms is impossible to predict in the absence of quantitative data on the relative strength of different mechanisms. No empirical study to our knowledge measures the strength of all of these mechanisms for any one species or type of interaction.

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CHAPTER 3

CLIMATIC STRESS MEDIATES THE IMPACTS OF HERBVIORY ON PLANT POPULATION STRUCTURE AND COMPONENTS OF INDIVIDUAL FITNESS

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Summary

Past studies have shown that the strength of top-down herbivore control on plant physiological performance, abundance and distribution patterns can shift with abiotic stress, but it is still unclear whether herbivores generally exert stronger effects on plants in stressful or in nonstressful environments. One hypothesis suggests that herbivores' effects on plant biomass and fitness should be strongest in stressful areas, because stressed plants are less able to compensate for herbivore damage. Alternatively, herbivores may reduce plant biomass and fitness more substantially in nonstressful areas, either because plant growth rates in the absence of herbivory are higher and/or because herbivores are more abundant and diverse in nonstressful areas. We test these predictions of where herbivores should exert stronger effects by measuring individual performance, population size structure and densities of a common subshrub, *Hibiscus meyeri*, in a large-scale herbivore exclosure experiment arrayed across an aridity gradient in East Africa. We find support for both predictions, with herbivores exerting stronger effects on individual-level performance in arid (stressful) areas, but exerting stronger effects on population size structure and abundance in mesic (nonstressful) areas. We suggest that this discrepancy arises from higher potential growth rates in mesic areas, where alleviation of herbivory leads to substantially more growth and thus large changes in population size structure. Differences in herbivore abundance do not appear to contribute to our results. Synthesis: Our work suggests that understanding the multiple facets of plant response to herbivores (e.g. both individual performance and abundance) may be necessary to predict how plant species' abundance and distribution patterns will shift in response to changing climate and herbivore numbers.

Introduction

Where, when and how top-down forces are important in structuring populations and communities is an enduring topic in ecology. Trophic interactions such as predation and herbivory affect primary productivity and species composition in a variety of systems, both through direct reductions in prey or producer biomass (e.g. Estes & Palmisan 1974; McNaughton 1985; Olff & Ritchie 1998), as well as via indirect effects mediated through prey risk perception or through plant and prey establishment patterns (e.g. Schmitz 2005; Riginos & Young 2007). While much of the literature on top-down control focuses on trophic cascades, with effects of predators transmitted through herbivores to primary producers, we also know that climatic and other abiotic factors affect the strength of herbivore control of plant productivity and performance. However, most of this work has been conducted in artificial settings or via simulated herbivory, and most studies have addressed herbivores' effects on individual performance. Here, we ask whether climate influences the degree to which herbivory shapes both individual plant performance and population structure using a large-scale exclosure experiment arrayed across a natural rainfall gradient in an East African savanna.

Herbivores affect plant communities in a variety of ways, including consumption of biomass, suppression of competitively dominant or highly palatable species, and alteration of habitat structure (Olff & Ritchie 1998). Although we know that the strength of these effects can be contingent on abiotic context (Maschinski & Whitham 1989; Anderson et al. 2007; Pringle et al. 2007; Schmitz 2008), results from past studies on the relative direction and magnitude of herbivore effects on plant abundance and composition across stress gradients have been inconsistent. Some studies show that herbivores have weaker effects on plant biomass in areas of lower stress (Chase et al. 2000), but, conversely, denser and more diverse herbivore communities (Cyr & Pace 1993) or higher plant growth rates in lower-stress areas may result in stronger herbivore suppression of potential plant biomass in these sites. Similarly, while most studies find that herbivores exert stronger effects on community composition in less stressful areas (e.g. Chase et al. 2000; Bakker et al. 2006), others show that herbivores alter plant species composition most markedly in areas of intermediate or even low rainfall (Anderson et al. 2007). The apparent inconsistency of these results stems in part from a poor understanding of how the relatively well-studied individual-level responses to herbivory translate into changes in population abundance and structure across stress gradients at a broader scale (Anderson & Frank 2003). This lack of knowledge limits our ability to predict how variation in abiotic stress and herbivory regimes will drive shifts in plant populations and communities.

From past work, three hypotheses about how herbivores affect plants across abiotic stress gradients generate competing predictions; we call these the ‘Compensatory Continuum Model’ (following Maschinski & Whitham 1989), the ‘Herbivore Pressure Hypothesis’ and the ‘Differential Growth Rate Hypothesis.’ The Compensatory Continuum Model predicts that in less productive areas, plants will suffer a reduced ability to compensate for herbivory (e.g. Josefsson 1970; Louda & Collinge 1992; Joern & Mole 2005), and the combination of stress and herbivory will therefore generate synergistic effects that strongly reduce plant performance and abundance. In more productive areas, plants can better tolerate and/or compensate for the effects of herbivory (e.g. via plant regrowth or sustained recruitment of new individuals following herbivory), and thus, the impacts of herbivory on plant biomass should be low (White 1984). In contrast, the Herbivore Pressure and Differential Growth Rate Hypotheses predict that herbivores exert stronger effects on biomass in less stressful areas. This phenomenon occurs either because herbivores are generally more abundant and diverse in less stressful areas (Cyr & Pace 1993, here called the Herbivore Pressure Hypothesis) or because in less stressful areas, potential plant growth in the absence of herbivory is high (Differential Growth Rate Hypothesis). Both of these hypotheses predict that the difference between plant populations with and without herbivores (e.g. individual-, population- and community-level biomass) should be greater in less stressful areas.

Most studies of herbivory effects concentrate on one of two scales: individual plant responses or changes in abundance or biomass at the population level. For example, the Compensatory Continuum model is usually measured at the individual scale, whereas the Herbivore Pressure and Differential Growth Rate Hypotheses are often tested at the population level. Between these two extremes are herbivore effects on the population structure of plants (size, shape or age distribution), which reflect how the responses of individual plants manifest as population-wide effects (Staudhammer & LeMay 2001; Rubin et al. 2006; Drewa et al. 2008; Prior et al. 2011). These distributions provide a straightforward way to capture information on the cumulative effects of herbivory and abiotic stress on populations (Prior et al. 2011), averaged over many years of variation in these factors. This approach is particularly valuable for assessing the long-term effects of herbivores, whose population densities – and thus their effects on plants – can be quite variable from year to year. Thus, examining the consequences of herbivory for population structure is a promising approach with which to augment our understanding of where and how herbivores are important drivers of plant population dynamics.

Here, we examine how herbivory by large mammals affects several aspects of (i) individual performance and (ii) population structure in a common East African savanna plant (the subshrub *Hibiscus meyeri*) using large-scale herbivore exclosures replicated across an abiotic stress gradient of variable rainfall. To assess support for each of the three nonexclusive hypotheses outlined above at both the individual and population scale, we conducted short-term measurements of growth and reproductive rates, and also characterized patterns of population densities and size structures to measure population-wide effects of herbivory and aridity.

Materials and methods

Our study was conducted at the Mpala Research Centre, in the Laikipia District of central Kenya (0°18′ N, 37°54′ E). Rainfall in this semi-arid acacia-dominated savanna falls in a weekly bi- or tri-modal pattern, with little seasonality in temperature. Large common herbivores include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and dik-dik (*Madoqua guentheri*). Elephant, impala and dik-dik attain the greatest biomass densities (2882, 813 and 693 kg km^{-2}, respectively), with zebra a distant fourth at 263 kg km^{-2} (Augustine 2010).

We assessed the effect of herbivores and climate using a largescale herbivore exclusion experiment (Ungulate Herbivory Under Rainfall Uncertainty: ‘UHURU’) established in September 2008 (Goheen et al. 2013). One of four treatments in UHURU is to 1-ha plots in a randomized block design using different configurations of electric fencing: LMH treatments exclude all Large Mammalian Herbivores (> 5 kg); MESO treatments allow dik-diks but exclude mega- and mesoherbivores (> 40 kg); MEGA treatments exclude only megaherbivores (elephants and giraffes); and Control treatments are unfenced, allowing access by all native herbivores. Each treatment is replicated three times at each of three sites (arid, intermediate and mesic) across a 22-km rainfall gradient (Appendix Fig. 1). Total rainfall increases > 45% from the Arid to Mesic site (440 mm/year at the Arid site, 580 mm/year at the Intermediate site and 640 mm /year at the Mesic site). Indirect measures of herbivore activity (quarterly dung counts) show little variation across this gradient. Only two large mammalian herbivores (impala and zebra) show variation in densities across the gradient; impala dung density is significantly greater at the Arid than Intermediate and Mesic sites, and zebra dung density is greater at the Arid than Intermediate sites, neither of which differ significantly from Mesic (Goheen et al. 2013). Major soil texture and nutrient characteristics do not differ systematically across the gradient, although the Intermediate site has lower pH than the Arid and Mesic sites (Goheen et al. 2013). The Intermediate site also suffers from a history of overgrazing (M. Littlewood, Mpala Ranch, pers. comm.).

Hibiscus meyeri is a short-lived subshrub present in all treatment x site combinations in UHURU. *Hibiscus meyeri*'s distribution is extremely patchy, and in the presence of herbivores, it typically occurs near or beneath trees. While some *Hibiscus* species produce extrafloral nectar to attract ants that deter floral herbivores (e.g. Sugiura et al. 2006), and many species produce leaf trichomes, presumably to deter insect herbivores, little is known about *H. meyeri*'s chemical defences, and it is heavily browsed by a variety of mammalian herbivores (A. Louthan, pers. obs.). Plant height can be substantially reduced by herbivory, and compensatory regrowth following browsing is common, with regrowth generally occurring from extant lateral meristems below the damaged apical meristem. Thus, stem diameter at ground level augments height to provide a more reliable and stable measure of past plant size and growth. While individuals are often single stemmed, repeated herbivory events result in a multi-stemmed phenotype that is also common. Together, summed basal area(s) and height provide a good estimate of dry above-ground plant biomass (adjusted $r^2 = 0.92$, $n = 39$). Flowering can occur throughout the year in response to both low- and high-volume rainfall events; fruits mature c.1 month after pollination. *Data collection:* We conducted several small-scale experiments and observations to test whether aridity is a strong driver of performance. To test that differences in performance at the Arid and Mesic sites were driven by rainfall rather than site-specific effects, we watered 12 plants (six at Arid site and six at Mesic site) once with 4.5 L of water during the height of a dry season in January 2012 and, after 17–18 days, compared their performance to an unmanipulated control group using log ratios of post vs. pretreatment fruit number. Additionally, in July 2010, we collected one to three fruits from 47 haphazardly chosen plants ($n = 22$ and 25 at the Arid and Mesic sites, respectively) and counted the nonaborted, nonpredated seeds within each fruit. Finally, in August 2010, we simulated herbivory on 21 plants of varying sizes at the Arid and Mesic sites by removing all leaves and reproductive organs. Two months later, we measured regrowth of floral buds relative to the original number of buds and compared their performance using ln[(final number of reproductive organs +1)/(initial number of reproductive organs +1)].

We tested for interacting effects of aridity and herbivory by quantifying plant reproductive performance and population size structure at the UHURU sites over a 10-week period in May-August 2011, c. 3 years after the exclosures were built. At each site, we searched all treatments consecutively within one of the three blocks, moving to the next site only after the block in the previous site was completely searched, to ensure that any phenologically driven variability in individual performance or population structure would be confined to among-block effects in our analyses. To facilitate searching and mapping, we divided each plot into fourths; we then conducted independent searches for *H. meyeri* plants > 30 cm tall within each subsection. Searches within each subsection involved scanning sequential 4-m^2 areas in a consistent predetermined pattern, censusing all plants within each 4-m^2 area. We terminated our search when we found at least four plants in a subsection or continued until the entire subsection had been searched. We measured and mapped each plant and searched for seedlings in a 2 m radius around all plants > 30 cm tall. At the Intermediate site, block 1 was searched during this same period, but blocks 2 and 3 were searched over a 2-week period in January-February 2012. We use data from these surveys to analyse population size structure.

We adopted two strategies to increase our confidence in our estimates of individual-level effects of stress and herbivory and to investigate any artefacts arising from the UHURU experiment. First, we increased our sample size by measuring additional, haphazardly selected plants of varying sizes within Control and LMH treatments that were chosen as part of another experiment (in May-August 2011, see Appendix Table 1 for sample sizes). Second, to ensure that plants measured within Control plots in UHURU reflected the general characteristics of plants at each site, in May-August 2011, we measured haphazardly selected plants along two 100 9 15 m belt transects within 300 m (but outside of) the UHURU Arid and Mesic sites. We used data on height, basal area, number of fruits, number of flower buds and flowers, and probability of reproduction from both of these sets of haphazardly selected plants to bolster samples sizes for analyses involving these response variables. We assigned all plants measured within UHURU to the appropriate block and treated the transect plants as a separate (fourth) block. Including these haphazardly selected plants in our analyses of height/basal area ratio, number and probability of reproduction had no qualitative effect on our results.

For each plant sampled, we estimated the percent of leaves with insect damage, counted the total number of broken woody stems (a rough proxy for mammalian herbivory rates) and counted numbers of floral buds, flowers and fruits. We measured height and the diameters of all stems (woody and nonwoody) 1 cm above the ground. We condensed these data into the following metrics of individual size, shape and performance: height, height/basal area ratio (an approximate measure of size relative to age and/or past growth), number of fruits/estimated biomass and reproductive state (plant has produced flower buds, flowers or fruits, or has not).

Statistical analyses: We conducted all analyses using R 2.14.0 (R Development Core Team 2011). We used mixed models to test for fixed effects of site and treatment on the number of fruits per biomass, plant height/basal area ratios and reproduction (flowering or not, with initial plant basal area as an additional fixed effect), with block as a random effect (Appendix). In tests for effects of site (and thus rainfall amount) alone, we restricted analyses to data from the LMH plots. For ease of interpretation, we use the R ANOVA function to estimate the significance of fixed effects in our mixed models by comparing nested mixed models using likelihood ratio tests (Pinheiro & Bates 2000b). We use negative binomial generalized linear models to test for differences in insect folivory rates across the gradient. We restrict analyses of insect folivory to Control areas, for two reasons, both designed to minimize the effect of any size biases in our visual estimation of insect folivory: first, plants in Control treatments are similar in size across the gradient, but those in exclosures are not; second, the size discrepancy between LMH and Control treatments is large at the Mesic site, but small at the Arid site; thus, there are complex interactions between plant size, treatment and site, making analysis of the effect of site alone difficult.

To examine the population-level effects of herbivory, we used stem density (plants m^{-2}), basal area density (total *H. meyeri* stem cover/ m^2) and size distributions of *H. meyeri*. We determined basal area density by calculating the total area covered by *H. meyeri* stems per m^2 searched in each subsection. We determined the effect of site and treatment on density and basal area density using negative binomial general linear models, multiplying basal area density by 100 and rounding up to conform to a negative binomial distribution. We also calculated a difference in mean densities across subsections for each Control–exclosure pair of each block to visually compare the effect of exclosures across sites.

We used a variety of metrics to test whether population structure differed across treatment–site combinations. To compare distributions between Control and exclosure treatments, we used Kolmogorov– Smirnov tests. Then, to determine which characteristics of these distributions do or do not differ, for each site–treatment combination, we calculated multiple metrics of the size distribution that have been proposed or used in the plant ecology literature: coefficient of variation, skewness, kurtosis, structure index based on variance (STVI; a modified Shannon–Weiner index for continuous size classes; Staudhammer & LeMay 2001) and Gini coefficients (a measure of the inequality of an individual trait across a population that is more robust to right-tail outliers than the coefficient of variation). We generated confidence intervals around the difference between Gini coefficients for each Control–exclosure treatment pair at each site using a pooled bootstrapping technique (Dixon et al. 1987).

Finally, to better visualize how herbivore exclosures and aridity alter size structure, we compared smoothed height and basal area distributions for plants in different treatments and sites. We fit third-order logistic functions to the cumulative size distribution for each site-treatment combination and then used these functions to calculate differences in the relative numbers of plants in each size class between each exclosure treatment and its corresponding Control.

Results

Site/ Aridity effects

Rainfall affected individual plant performance, with lower performance in more arid areas. Plants subject to supplemental watering showed an increase (marginally significant) in fruit number at the Arid site compared to an unmanipulated control group (Wilcox, $W_{6,6} = 7$, $P = 0.09$), but did not show a response at the Mesic site ($W_{6,6} = 13$, $P = 0.77$). The number of nonaborted, nonpredated seeds per fruit, averaged for all fruits from each plant, was also higher at the Mesic than at the Arid site (Wilcoxon signed-rank test, $P = 0.004$). Additionally, individuals regrew floral buds faster following simulated herbivory at the Mesic than at the Arid site (Wilcoxon signed-rank test, $P < 0.002$). To examine site (aridity) effects on plant performance, we looked for site effects only in LMH treatments (total herbivore exclusion). In LMH treatments, the probability of initiating reproduction was greatest at the Mesic site, intermediate at the Intermediate site and lowest at the Arid site across all plant sizes (Fig. 1a–c). Similarly, fruit crop per dry gram of biomass followed the same pattern for plants within LMH treatments (Mesic > Intermediate > Arid, Fig. 2; mixed model, site significant at $\chi_2^2 = 13.46$, $P = 0.001$).

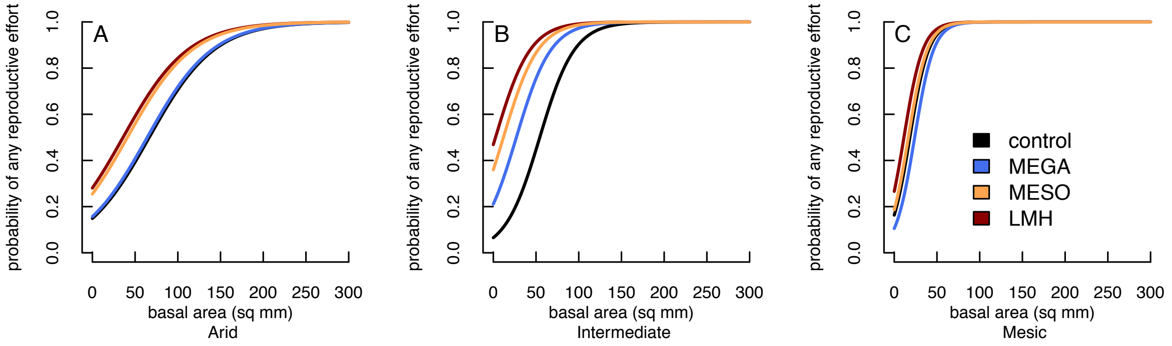

Figure 1. The effect of herbivore exclosures on the probability of initiating reproduction as a function of plant size (basal area), for all treatment and site combinations. Lines represent fitted probability distributions derived from mixed models with block as a random effect (Appendix Table 2). Likelihood ratio tests supported including treatment at all sites (Arid, $\chi^2 = 16.456$, $P = 0.0009$; Intermediate, $\chi^2 = 99.437$, $P < 2.2\text{e-}16$; Mesic, $\chi^2 = 11.984$, $P = 0.007$).

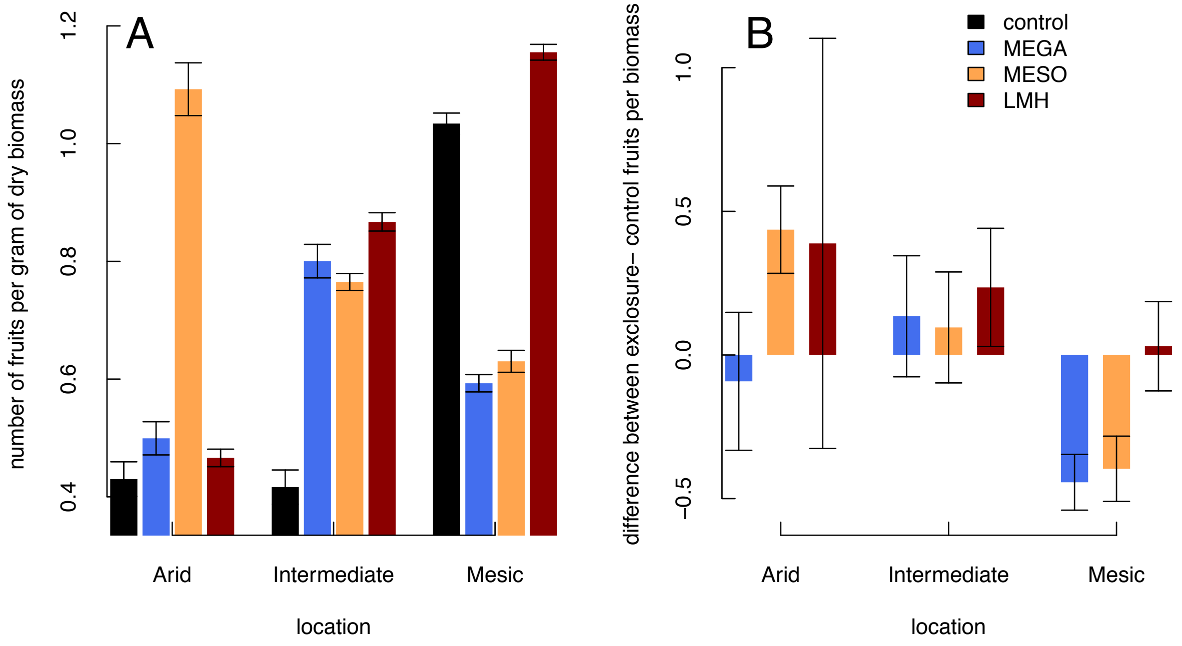

Figure 2. (a) The number of fruits per gram dry biomass (given that an individual produced fruits), as a function of site, treatment and their interaction (mixed model; site: $\chi_2^2 = 13.31$, P = 0.0013; treatment: $\chi_3^2 = 6.29$, $P = 0.098$; treatment*site: $\chi_6^2 = 12.57$, $P = 0.050$, with block as a random effect; Appendix Table 5). (b) Average block-wide differences in mean fruits per gram dry biomass between exclosure treatment and Control for all exclosure–Control pairs and sites. Error bars represent one SE calculated across blocks.

In addition to these individual-level effects, we found strong effects of rainfall on population structure. Although neither stem density nor basal area density differed among sites within LMH treatments (negative binomial general linear models, raw density: $F_{2,32} = 0.35$, $P = 0.70$; basal area density: $F_{2,32} = 0.9701$, $P = 0.38$), we found that site did influence size distribution, with greater fractions of large plants, as well as young recruits, at the Mesic than at the Arid site (basal area; Kolmogorov–Smirnov, $D_{96,59} = 0.3054$, $P = 0.002$; Fig. 3; Appendix Fig. 2), suggesting that both recruitment and plant growth are greater in more mesic areas in the absence of mammalian herbivory.

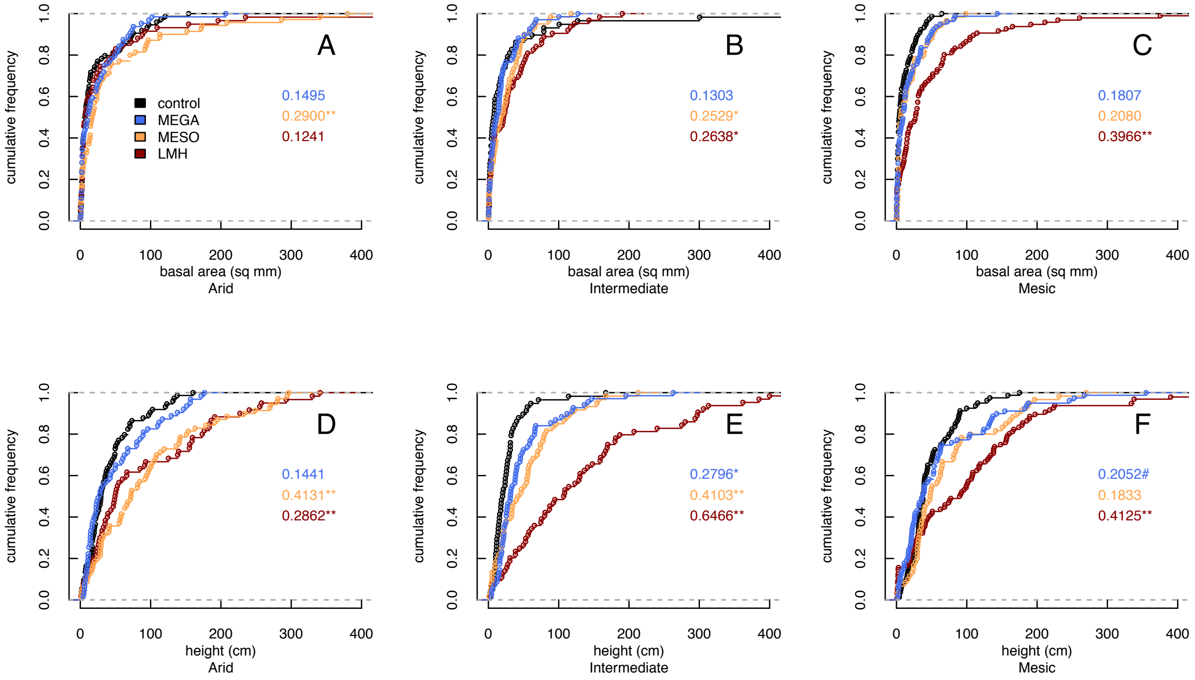

Figure 3. Cumulative probability distributions for size structures at the Arid, Intermediate and Mesic sites, measured for both height and basal area. Colours as in previous figures. D-statistics of Kolmogorov–Smirnov tests between exclosure and control treatments are shown in the colour corresponding to the exclosure treatment; # indicates marginally significant ($P < 0.10$), * indicates significant at the $P < 0.05$ level, ** indicates $P < 0.005$ (see Appendix Table 3). We have conducted 3 Kolmogorov–Smirnov tests for each site–size metric combination; thus,

individual reported *P*-values should be interpreted with caution. See Appendix Fig. 3 for alternative presentations of size distributions.

Insect folivory rates

We did not find evidence of systematic variation in insect herbivory across the gradient. Insect herbivore damage in Control areas did not vary across sites, but larger plants suffered more damage (higher percent of leaves damaged), predominately by chewing folivores (negative binomial general linear model, site: deviance = 0.49, d.f. = 2, $P = 0.78$; block: deviance = 26.86, d.f. = 8, $P < 0.001$; height: deviance = 13.78, d.f. = 1, $P < 0.001$; see Appendix).

Support for stronger effects of herbivores in arid areas

While treatment effects varied in relative magnitude across the gradient, exclosures collectively increased several measures of individual performance, especially at the Arid site. Herbivore exclusion increased the probability of initiating reproduction more at the Arid than the Mesic site, with variable effects at the Intermediate site (Fig. 1 and Appendix Table 2), and exclosure treatments had stronger positive effects on the amount of reproductive effort per biomass at the Arid than at the Mesic site (Fig. 2). Similarly, at the Arid site, plant height/basal area ratios were greater in LMH relative to Control treatments, while the effects of exclosure treatments on height/basal area ratio were weak at the Mesic site (mixed model; Appendix Fig. 3).

Support for stronger effects of herbivores in mesic areas: In contrast to the support for the prediction that herbivores exert stronger effects in arid areas, which we found only with individual plant performance measures, at the population level, we found that herbivores exerted stronger effects in mesic areas. Although neither rainfall nor treatment affected raw individual densities consistently (see Appendix Table 6), the differences in basal area density across treatments were marginally significant across sites (negative binomial general linear model

ANOVA: site $F_{2,139} = 0.957$, $P = 0.38$; treatment $F_{3,136} = 10.06$, $P < 0.00001$; site*treatment; $F_{6,130} = 1.92$, $P = 0.074$, Block; $F_{6,124} = 2.04$, $P = 0.057$): exclosures increase basal area densities (relative to Controls) at the Mesic site but have minimal effects at the Arid site (Fig. 4).

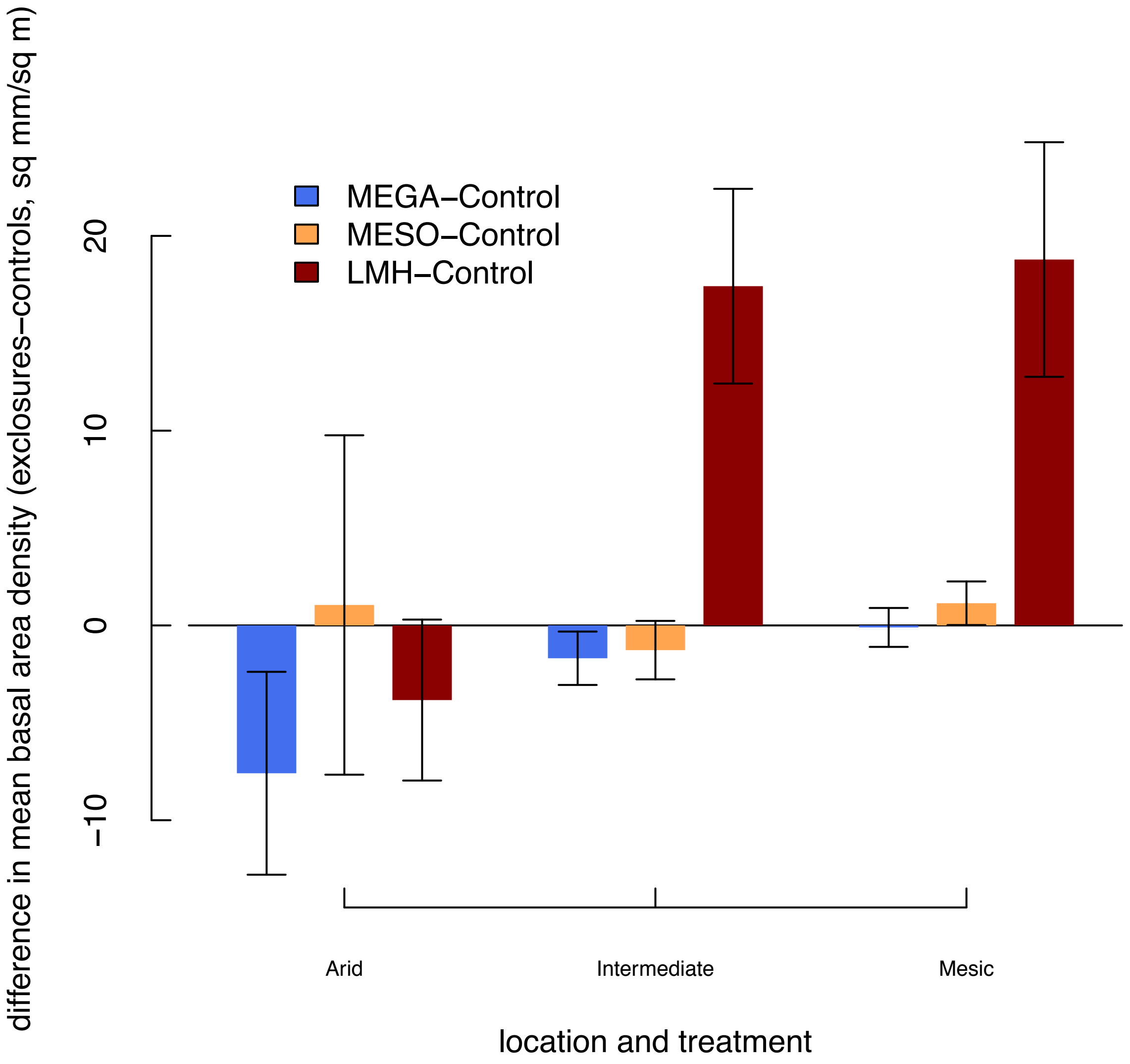

Figure 4. Difference in mean basal area density between exclosure and Control block pairs for all exclosure–Control comparisons (MEGA–- Control, MESO–Control, LMH–Control) and sites. Error bars represent one SE calculated across blocks.

Size distributions of *H. meyeri* populations also differed sharply as a function of both site (rainfall) and treatment (Figs 3, 5 and Appendix Fig. 2), with population structure more affected by exclosure treatments at the Mesic than at the Arid or Intermediate sites. At the Mesic site, basal area distributions in two exclosure treatments differed significantly or marginally significantly from those in the Control (Kolmogorov–Smirnov tests: LMH: $D_{77,96} = 0.397$, $P <$ 0.0001; MESO: $D_{77,60} = 0.208$, $P = 0.108$; Fig. 3, Appendix Table 3). Similarly, basal area distributions in Intermediate exclosures differed from Control (LMH: $D_{58,53} = 0.2638$, $P = 0.03$; MESO: $D_{58,60} = 0.2529$, $P = 0.046$). We found weaker and inconsistent differences in size structure between exclosure and Control treatments at the Arid site, where only MESO differed from Control ($D_{74,70} = 0.252$, $P = 0.005$). The effect of herbivores on height distributions, in contrast, was relatively consistent across the gradient; at the Arid site, LMH and MESO, and at the Intermediate site, LMH and MEGA had significantly different size structures than Control, while at the Mesic site, all exclosure treatments were significantly or marginally significantly different from Control plots (Fig. 3 and Appendix Table 3).

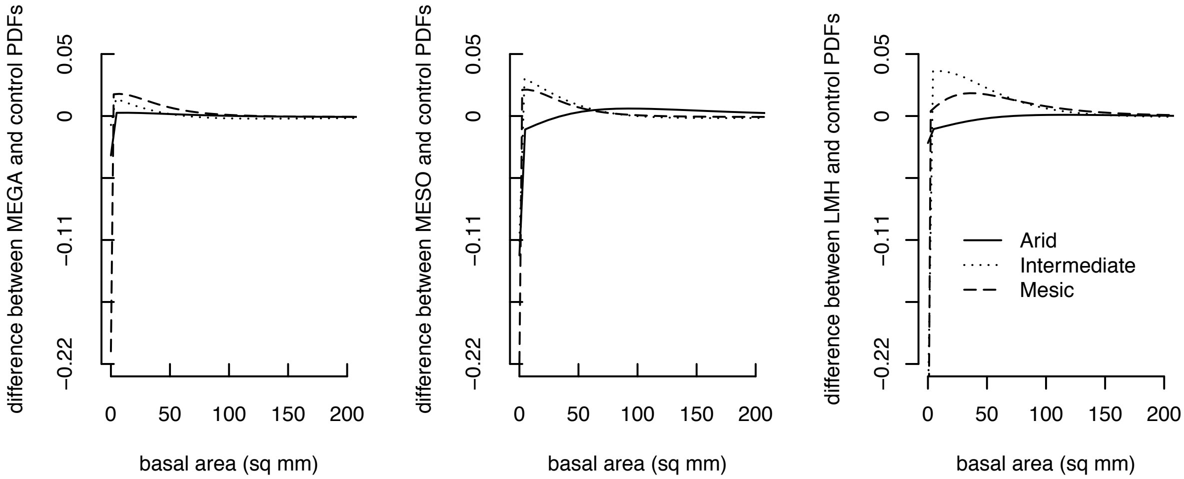

Figure 5. Differences in smoothed size distributions between Control and exclosure treatments, shown using an anti-logged y-axis for clarity. Positive values indicate that the exclosure treatment has a higher fraction of individuals in that size class than does the Control treatment.

We found that the relative effect size of treatments varied across sites, but that LMH treatments consistently have stronger effects on size structure in more mesic areas. To assess which size classes were affected by exclosures at each site, we generated smoothed differences between the plant basal area size distributions in exclosure treatments and their corresponding Control plots. These plots (Fig. 5) indicate that the difference in size distributions between exclosures and Control treatments is driven by consistent increases in the frequencies of small plants at all sites, with corresponding reductions in relative numbers of medium-sized plants, suggesting higher recruitment. These effects are strongest at the Mesic site. At both the Mesic and Intermediate sites, these size structures suggest there was a substantial pulse of young recruits in LMH and, at the Mesic site, the LMH treatment also increased the proportion of very large individuals (Fig. 3). At the Arid site, in contrast, increases in small plants in the LMH treatment were muted (Fig. 5). At the Mesic and Intermediate sites, the most extreme treatment (LMH) had the strongest effects on size structure, but at the Arid site, MESO and MEGA had strong effects relative to LMH.

Consistent with our analyses of full size distributions, we found weaker but similar patterns using traditional summary metrics of size distributions. Most of these metrics showed fairly consistent patterns across sites and supported stronger effects of herbivores at the Mesic site. Exclosures generally increase the CV of height distributions, and the CV and kurtosis of basal area distributions (correlated at > 0.50) at the Mesic and Intermediate sites, reflecting greater numbers of small individuals in these areas (Table 1). We found significant differences in Gini coefficients of height distributions in Control vs. exclosure treatments only at the Mesic site (Appendix Fig. 4), indicating lower dispersion of size structures in exclosure treatments. For basal area size distributions, we found differences between Control and exclosure treatments at the Intermediate site, with no differences at the Mesic or Intermediate sites (Appendix Fig. 4).

	Control	LMH	Difference (LMH-Control)	Control	LMH	Difference (LMH-Control)	Control	LMH	Difference erence (LMH-Control)
height	Arid			Intermediate			Mesic		
CV	89.01	98.24	9.23	98.66	3.80	-94.86	72.24	97.08	24.85
skewness	1.41	1.12	-0.29	3.24	1.13	-2.11	1.44	1.52	0.08
kurtosis	4.37	3.27	-1.09	16.00	3.80	-12.20	5.11	5.65	0.54
STVI	0.92	0.99	0.07	0.59	0.90	0.31	0.81	0.85	0.04
basal area									
CV	149.47	263.61	114.15	288.39	121.65	-166.74	126.83	150.36	23.54
skewness	1.90	5.60	3.70	5.58	1.73	-3.86	1.72	3.11	1.39
kurtosis	5.76	37.56	31.80	36.17	5.70	-30.47	5.46	14.71	9.26
STVI	0.90	0.47	-0.43	0.49	0.89	0.40	0.87	0.60	-0.28
joint									
STVI	0.53	0.26	-0.27	0.14	0.38	0.24	0.27	0.25	-0.02

Table 1. Values for the STVI (structure index based on variance), coefficient of variation (CV), skewness, and kurtosis of height and basal area size distributions in Control and full exclosure plots at Arid, Intermediate and Mesic sites. Correlation coefficients > 0.5 are as follows: $\mathrm{CV}_{\text{basal area}}$ & $\mathrm{skewness}_{\text{basal area}}$: 0.97; $\mathrm{CV}_{\text{basal area}}$ & $\mathrm{kurtosis}_{\text{height}}$: 0.519; $\mathrm{CV}_{\text{basal area}}$& $\mathrm{kurtosis}_{\text{basal area}}$: 0.962; $\mathrm{skewness}_{\text{height}}$ & $\mathrm{kurtosis}_{\text{height}}$: 0.989; $\mathrm{skewness}_{\text{height}}$ & $\mathrm{STVI}_{\text{joint}}$: 0.523; $\mathrm{skewness}_{\text{basal area}}$& $\mathrm{kurtosis}_{\text{basal area}}$: 0.994; $\mathrm{skewness}_{\text{basal area}}$& $\mathrm{STVI}_{\text{joint}}$: 0.541; $\mathrm{kurtosis}_{\text{height}}$ & STVIjoint: 0.547; $\mathrm{kurtosis}_{\text{basal area}}$& STVIjoint: 0.564; $\mathrm{Gini}_{\text{height}}$ & $\mathrm{CV}_{\text{height}}$: 0.989; $\mathrm{Gini}_{\text{basal area}}$& $\mathrm{kurtosis}_{\text{basal area}}$: 0.857; $\mathrm{Gini}_{\text{basal area}}$ & $\mathrm{CV}_{\text{basal area}}$: 0.945. Note that although some of the correlation coefficients of the CV, STVIs and Gini coefficient are < 0.5, all of these metrics are nonindependent and that the joint STVI is not independent from the height STVI or the basal STVI; thus, results should be interpreted with caution. See Appendix Table 4 for values from all treatments**.**

Discussion

Our results show that aridity and herbivores negatively affect both individual plant performance and alter plant population size structure. On different scales, our results support both the Compensatory Continuum Model and Differential Growth Rate Hypothesis outlined in the introduction. We do not find support for the Herbivore Pressure Hypothesis; herbivore densities are not higher in mesic areas. The effects of herbivory vary as a function of aridity, with the strongest individual-level effects of herbivory occurring at our driest site. In contrast, herbivores had the largest effects on population size structure at our wettest site.

Three potential mechanisms may underlie the discrepancy we observe at the individual versus population scale. First, it is possible that there are a higher number of safe sites for seedling establishment in mesic areas, such that smaller increases in reproductive output when herbivores are excluded result in higher numbers of seedlings in mesic areas but not in arid areas. However, we found no differences in total plant densities across sites, which does not support this possibility. Second, as is true for many plant species, increases in reproductive output with size may be nonlinear, such that relatively small increases from, for example, medium to large size classes in mesic areas following herbivore exclusion result in substantial increases in seed number and thus population growth – and conversely, that large absolute increases in the sizes of (smaller) plants in arid areas result in only moderate increases in seed number and thus population growth.

Finally, consistent with the Differential Growth Rate Hypothesis, herbivory may reduce total plant growth more substantially in mesic areas, such that excluding herbivores results in large effects at the Mesic site relative to dampened effects at the Arid site, giving rise to the population-level effects we observed. Under this last scenario, the absolute potential for plant growth in arid areas is low due to constraints imposed by aridity, even when released from herbivory (e.g. Fig. 2). Thus, while herbivores have large individual-level effects on plant reproduction and shape (height/ basal area ratio) in arid areas, low growth rates limit plant response to alleviation of herbivore pressure, leading to small population-level effects, especially when accumulated over time. In mesic areas, higher potential growth and reproductive rates mean that removing herbivore pressure results in substantial increases in total growth and thus large effects on population size structure. In support of this third hypothesis, we found that plants at the Mesic site regrow more quickly following damage, and plants protected from herbivores initiate reproduction at smaller sizes (Fig. 1) and produce more fruits (Fig. 2A) at the Mesic vs. Arid or Intermediate sites. Thus, we hypothesize that herbivores exert strong effects on the individual scale variables we measured in arid areas (supporting the Compensatory Continuum Model), while in mesic areas, herbivores more strongly reduce potential plant growth, largely because of reduced abiotic limitation of growth rates, supporting the Differential Growth Rate Hypothesis at the population level.

Consistent with the predictions of the Compensatory Continuum Model, synergistic effects of herbivory and aridity at the organismal level may result if individuals are less able to tolerate and/or respond to damage when water stressed. A variety of studies have shown a reduced ability to compensate for herbivore damage in the presence of abiotic stress (e.g. Mueggler 1967; Janzen 1974; Willis et al. 1993). However, because we also observed higher numbers of impala at the Arid site, it is unclear if higher densities of herbivores (and likely, increased herbivory) or reduced regrowth is driving the stronger individual-level responses we observed at the Arid site. Our study site is unusual in that we find higher densities of at least one herbivore (impala) in arid areas, contrasting with the usual pattern of greater herbivore densities in more mesic areas (Cyr & Pace 1993). The strong effect of MESO treatments at both the individual and population level at the Arid site suggests that impala herbivory is an important driver of plant performance and might also indicate that herbivore numbers are a driver of stronger individual-level effects at the Arid site.

Our results also provide support for the Differential Growth Rate Hypothesis, showing that plant densities and population size distributions are more strongly affected by herbivory in more mesic areas. In mesic areas, excluding herbivores leads to an increase in basal area density, with weaker effects in more arid areas (Fig. 4). This result suggests that herbivores consume a larger quantity of the potential biomass in mesic areas (i.e. biomass in the absence of herbivory), reducing both total recruit number and the number of large plants (Figs. 3 and 5). In our system, total herbivore densities are not higher in mesic areas; thus, our finding that herbivory more strongly reduces plant biomass in mesic areas is likely not due to increased herbivory, as predicted by the Herbivore Pressure Hypothesis, but rather to some other mechanism, such as a larger number of safe sites, nonlinear increases in reproduction with size, or, most plausibly, differential growth rates, as outlined above. Support for the Differential Growth Rate Hypothesis depends on the fact that *H. meyeri* is an herbivore-tolerant species and regrows quickly following herbivory. For plant species that grow more slowly (e.g. those that invest substantially in defences), we might expect to see weaker or quite different population-level patterns than those observed in *H. meyeri*.

The Intermediate site was an outlier in many respects, where *H. meyeri* shows very low performance in Control treatments with respect to probability of reproduction (Fig. 1), but a high number of fruits per biomass in the absence of herbivores (Fig. 2) and significant reductions in Gini coefficients of basal area size distributions in exclosure treatments (Appendix Fig. 4). This site has a history of overgrazing (M. Littlewood, Mpala Ranch, pers. comm.) and also probably experiences reduced rainfall infiltration relative to the Arid and Mesic sites (Goheen et al. 2013). Reductions in probability of reproducing and increased number of fruits per reproductive event may result from less frequent rainfall infiltration events that can trigger fruiting, such that while reproduction is less common, investment in each fruiting event may be higher. Differences in size distributions may arise from substantial amounts of bare ground in between appropriate understorey habitat. These effects may also be an artefact of reduced sample size at the Intermediate site; there were very low *H. meyeri* densities in the Control treatment in one block, and we did not measure any plants outside of the UHURU experiment at the Intermediate site.

Whereas the total herbivore exclusion treatment (LMH) shows quite consistent and expected patterns of effects relative to Control plots, the other two treatments in our study showed far more variable effects. Large differences in total- vs. mesoherbivore-exclusion treatments at both the Mesic and Intermediate sites suggest that chronic low-intensity herbivory by smaller species (namely dik-dik) is most important in driving the observed population-level effects of mammalian herbivory, both for recruitment and for growth of large plants. It is possible that the high densities of impala at the Arid site obscure this pattern in this location. Based on metabolic allometries (Nagy et al. 1999), dik-diks's energy consumption per unit area is similar to larger mammalian herbivores such as giraffe and elephant (Augustine 2010), suggesting that the amount of biomass per area consumed by dik-dik and by larger herbivores could be similar in our study system. One of the primary effects of these small herbivores is likely to be limitation of plant recruitment; our results indicate that plant populations in LMH treatments exhibit a strong recruitment pulse and an increased proportion of large individuals (Figs. 3 and 5). Together, these results suggest that the frequency of both large and small plants is more strongly affected by chronic, low-severity herbivory pressure than by infrequent-but-catastrophic herbivory events (such as by elephants), as has also been seen in other systems (Sullivan & Howe 2010).

It is also possible that the strong effects of LMH treatments relative to other exclosure treatments could arise if the damage inflicted by multiple species exerts synergistic effects. For example, small-scale but chronic herbivory could make plants more susceptible to infrequent bouts of severe herbivory, or herbivores acting on different life stages could decrease fitness more than reductions in performance in one life stage alone. Supporting this interpretation, the contrasting effects of the MESO and MEGA treatments revealed strong effects of mesoherbivores (likely impala) on height size structure, with weaker effects of this treatment on basal area size structure and recruitment (Fig. 3). Similarly, effects of treatments on basal area density at the Arid site, where impala exclusion (MESO vs. MEGA) leads to increased densities, and dik-dik exclusion (LMH vs. MESO) leads to decreased densities (Fig. 4), suggest that different-sized guilds of herbivores exerted disparate effects. Very few studies have addressed the effect of more than one species or guild of mammalian herbivores on plant performance (Gomez & Zamora 2000; Midgley & Bond 2001; Maclean et al. 2011), but those studies have shown that different species of herbivores can often have synergistic effects (Olff & Ritchie 1998; Maclean et al. 2011).

Our results show that measuring both organismal and population-level responses provides a more complete picture of how herbivory affects performance (Anderson & Frank 2003). We find support for both the Compensatory Continuum Model and the Differential Growth Rate Hypothesis, with herbivores exerting stronger effects at the individual scale in arid areas, but consuming a higher fraction of potential population biomass in mesic areas. These disparate results suggest that quantifying how individual species respond to the interacting effects of herbivory and stress, and how interspecific variation in growth rates affects these responses, is critical to predicting how species will respond to these effects. This understanding will allow us to predict how climatic change (e.g. future changes in aridity) will interact with changes in herbivore distribution (via reduction or extinction of predator populations, livestock stocking rates or extirpation of herbivores through hunting or climate change) to determine the future structure and distribution patterns of plant populations.

Acknowledgements

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CHAPTER 4

MECHANISMS OF PLANT-PLANT INTERACTIONS: CONCEALMENT FROM HERBIVORES IS MORE IMPORTANT THAN ABIOTIC-STRESS MEDIATION IN AN AFRICAN SAVANNAH

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Abstract

Recent work on facilitative plant–plant interactions has emphasized the importance of neighbours' amelioration of abiotic stress, but the facilitative effects of neighbours in reducing plant apparency to herbivores have received less attention. Whereas theory on stress reduction predicts that competition should be more important in less stressful conditions, with facilitation becoming more important in harsh environments, apparency theory suggests that facilitation should be greater in the presence of herbivores, where it is disadvantageous to be conspicuous regardless of abiotic stress level. We tested the relative strength of neighbours' stress reduction versus apparency reduction on survival, growth, reproduction and lifetime fitness of Hibiscus meyeri, a common forb in central Kenya, using neighbour removals conducted inside and outside large-herbivore exclosures replicated in arid and mesic sites. In the absence of herbivores, neighbours competed with H. meyeri in mesic areas and facilitated H. meyeri in arid areas, as predicted by stress-reduction mechanisms. By contrast, neighbours facilitated H. meyeri in the presence of herbivory, regardless of aridity level, consistent with plant apparency. Our results show that the facilitative effects arising from plant apparency are stronger than the effects arising

from abiotic stress reduction in this system, suggesting that plant-apparency effects may be particularly important in systems with extant large-herbivore communities.

Introduction

Recent work on plant–plant interactions has emphasized that neighbours often act as facilitators in stressful conditions, but the role of consumers has received less attention in this literature (Smit et al. 2009). Amelioration of abiotic stress in harsh environments is a well-supported mechanism of facilitation in many communities (Bertness & Callaway 1994, Callaway et al. 2002, Maestre et al. 2002, Daleo & Iribarne 2009). However, neighbouring plants can also facilitate one another via reduced plant apparency (i.e. concealment), in which neighbours reduce herbivory on focal individuals by making them less conspicuous or accessible (Feeny 1976, see Callaway 2007 for a recent review). We know little about the relative strength of these two facilitative mechanisms, or how they interact, since few experimental studies incorporate both variable stress levels and herbivory (Smit et al. 2009, but see Daleo & Iribarne 2009, Bulleri et al. 2011, Graff & Aguiar 2011).

The literatures on abiotic stress reduction and plant apparency make different predictions concerning when and where plant –plant facilitation should be most common or intense. Work on abiotic stress reduction predicts that the frequency or intensity of facilitation conferred by neighbours varies with environmental conditions (Bertness & Callaway 1994): competition should predominate in low-stress environments, with facilitation increasing in strength and/or frequency in high-stress areas. While many authors refer to this pattern as the ‘stress gradient hypothesis’ (SGH, e.g. Callaway et al. 2002), some revisions to the SGH predict slightly different patterns (e.g. hump-shaped, Maestre et al. 2009). Hence, here we refer to the original monotonic relationship as facilitation via stress reduction. Studies conducted across a variety of gradients— including altitudinal (Callaway et al. 2002), aridity (Maestre et al. 2005, Lortie & Callaway 2006) and nutrient gradients (Bakker et al. 2013)—show effects consistent with these predictions. By contrast, plant-apparency theory suggests that rather than varying systematically with abiotic stress, facilitation should be stronger and/or more frequent when neighbouring plants provide safety from herbivores, irrespective of abiotic stress level (Feeny 1976, Riginos & Young 2007, Smit et al. 2009, Graff & Aguiar 2011). Consistent with plant apparency, a variety of studies have shown that facilitation is more common or intense when herbivore pressure is greater (Graff et al. 2007, Alberti et al. 2008, Le Bagousse-Pinguet et al. 2012).

Few studies have addressed the relative strength of, or interactions between, the stress-reduction and plant-apparency mechanisms of facilitation; consequently, we have little empirical data regarding which mechanism is stronger or more common in natural systems. However, recent theoretical models predict that facilitation via plant apparency might, in the presence of herbivores, temper or even overwhelm the competitive– facilitative continuum predicted by the stress-reduction literature (Smit et al. 2009). Consistent with this prediction, Bulleri et al. (2011) found weak support for the competition– facilitation continuum predicted by the stress-reduction literature under moderate herbivore pressure, but these patterns broke down with an increase in herbivory such that neighbours' effects were either neutral or competitive, depending on neighbour density and stress level. By contrast, Crain (2008) found no support for the hypothesis that herbivore pressure alters the predictions of the stress-reduction literature: consistent with stress reduction, in the absence of herbivory, neighbours increased biomass of focal plants in stressful saline environments, but reduced biomass in milder non-saline areas. However, in the presence of herbivores, neighbours exerted the same pattern of effects (facilitative in stressful saline habitats, competitive in less-stressful ones); lack of an herbivore effect in this system was likely due to substantial spatial and temporal variability in herbivore pressure. These contrasting results in different systems underscore the paucity of empirical data on the relative strength of facilitation via plant apparency versus stress-reduction mechanisms under naturally occurring herbivore densities.

Here, we experimentally evaluate the relative strength of these two mechanisms of facilitation on a common subshrub in East Africa, *Hibiscus meyeri* (Malvaceae). Specifically, we tested whether the competition – facilitation continuum predicted by stress-reduction theory was altered by large mammalian herbivores in central Kenya. To do this, we removed *H. meyeri*'s understory neighbours in the presence and the absence of herbivory, using sets of large-scale herbivore exclosures replicated in both arid areas (high stress; Louthan et al. 2013) and mesic areas (low stress). We quantified neighbours' effect on multiple metrics of plant performance, and also synthesized these responses into estimates of plant fitness. Although many studies have measured the effect of neighbours on one or a few response variables, we have a poor understanding of the importance of neighbours for lifetime fitness (Malkinson & Tielbörger 2010). Our work helps to bridge a key gap in the facilitation literature: the need for experiments that illuminate the independent and interactive effects of plant apparency and stress reduction on plant fitness at scales large enough to encompass biologically meaningful variation in the abiotic environment (Callaway 2007).

Material and methods

Study site and experimental design

All fieldwork was conduxcted at the Mpala Research Centre in the Laikipia County of central Kenya (0°18' N, 37°54' E). Rainfall in this acacia-dominated savannah usually falls in a bimodal pattern, with substantial interannual variability in rainfall but little seasonality in temperature.

Data were collected within a large-scale herbivore-exclusion experiment (Ungulate Herbivory Under Rainfall Uncertainty: 'UHURU') established in September 2008 (Goheen et al. 2013). UHURU includes four treatments, which use different configurations of electric fencing around 1-ha plots to exclude different subsets of the large-herbivore fauna. We used the two most extreme treatments in this study: 'total exclosure', which excludes all medium- to large-sized mammalian herbivores of more than 5 kg, and 'control', which is unfenced and allows access by all wild herbivores. Each treatment is replicated three times at either end of a 22-km rainfall gradient, making three 'blocks' of total exclosure/control pairs at each end. From 2009 through 2011, mean annual precipitation increased more than 45% from the North (arid) to the South (mesic) site (440 mm yr^{-1} in arid, 640 mm yr^{-1} in mesic, Goheen et al. 2013). We conducted our experiment between June 2011 and August 2012, during a comparatively wet year (1034 mm yr^{-1} in mesic and 757 mm yr^{-1} in arid).

Major soil-texture and nutrient concentrations do not differ systematically across these sites (Goheen et al. 2013). Common large herbivores include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), eland (*Taurotragus oryx*), buffalo (*Syncerus caffer*), zebra (*Equus quagga*), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and dik-dik (*Madoqua guentheri*). Elephant, impala and dik-dik attain the greatest biomass densities at Mpala (2882, 813 and 693 kg km^{-2}, respectively; Augustine 2010). Activity levels of most herbivores do not vary markedly across these sites: mean number of dung piles in open controls, including dung of all common herbivores listed above, was 48.1 (±9.8 s.e.) in mesic and 73.2 (±19.8) in arid areas, averaged across seven surveys of nine 2 60 m transects in each aridity level between 2009 and 2011 (Goheen et al. 2013). Impala dung counts are significantly higher in the arid site (Goheen et al. 2013). Perhaps most importantly, regular dung counts (Goheen et al.

2013) suggest that dik-dik, which appear to exert the strongest influences on *H. meyeri* performance in this system (Louthan et al. 2013), are equally active in the arid and mesic sites. Total exclosure treatments were highly effective; mean number of dung piles was 58.7 per level in control and 1.4 in total exclosures (total dung of all common herbivores listed above, averaged across seven surveys between 2009 and 2011 and both aridity levels; Goheen et al. 2013).

Hibiscus meyeri is a short-lived, common, perennial subshrub, frequently occurring near or beneath trees. Little is known about its chemical defences (Louthan et al. 2013), but it is consumed by a variety of large herbivores (A. Louthan 2012, personal observation), which often substantially reduce its height and reproductive output. Compensatory regrowth following browsing is common, with extensive branching from the remaining portion of extant stems damaged or removed by herbivores. In the absence of herbivory, *H. meyeri* growth and reproduction are higher in mesic areas and individuals respond more positively to supplemental-watering treatments in arid areas than in mesic areas, suggesting that water limitation is a strong driver of performance (Louthan et al. 2013). *Hibiscus meyeri* is present but patchily distributed in all herbivore exclosure treatments at all aridity levels within the UHURU experiment; densities did not vary systematically across the herbivore-exclusion treatments after 3 years of herbivore exclosure, although there is a weak trend for both higher stem density and higher basal area density in the more arid site (Louthan et al. 2013). Herbivores do exert strong effects on *H. meyeri* population size structure, with significant increases in plant recruitment in the absence of herbivores (Louthan et al. 2013). In this system, neighbours could facilitate *H. meyeri* by ameliorating water stress (e.g. via soil water retention, decreasing runoff or decreasing transpiration through shading; Callaway et al. 2002), or through protection from herbivory (most co-occurring species of grasses and forbs in this system are similar in size to *H. meyeri*; A. Louthan 2012, personal observation).

Field methods

Between 6 June and 7 July 2011, we marked and measured the height and basal area of haphazardly chosen plants in each of the three replicates of exclosures and controls at each site (171 total plants in arid control, 79 in arid exclosure, 185 in mesic control and 55 in mesic exclosure). These plants fell into three size classes: small (mean basal area 4.7 cm^2+0.06 s.e., mean height 21.4 cm ± 0.10 s.e.); medium (16.8 cm^2 ± 0.11 s.e., 50.6 cm ± 0.17 s.e.); and large (50.9 cm^2 ± 0.35 s.e., 91.6 cm ± 0.35 s.e.; see Appendix Table 8). To control for any artifactual effects arising from the location of the UHURU experiment, we also include data on 59 plants marked and measured along two 200-m transects that were located 200–300 m outside of the UHURU experiment at each site, fully accessible to large herbivores; we code these plants as a separate fourth block in our analyses. In total, we measured 543 plants.

We randomly designated half of the plants in each size class (small, medium and large) for neighbour-removal treatments. Between 1 September and 31 November 2011, we initiated neighbour-removal treatments by cutting down all neighbouring understory plants (grass and forbs) in a 30-cm radius around focal plants and carefully applying Roundup herbicide with a paintbrush to the remaining rootstocks to kill neighbours' roots and underground stems. The rapid pace of regrowth in this tropical system necessitated the use of herbicides to maintain removal treatments. We re-measured the height, basal area and number of fruits of all plants between 29 May and 26 August 2012. Although the majority of H. meyeri plants were more than 30 cm from trunks of overstorey shrubs, 6% of plants (33 of 543) were within 30 cm of an overstorey plant trunk. Our results were largely unchanged when presence/ absence of an overstorey plant trunk within a 30 cm radius is included as an independent variable in the analysis; differences are noted in the caption of Table 1. All data will be made publicly available 1 year after publication (Louthan et al. 2014).

response variables	predictor variables									support	
	fixed effects								random effects		
	initial height	*herbivore activity*	*aridity*	*neighbors*	*herbivore activity x aridity*	*herbivore activity x neighbors*	*aridity x neighbors*	*herbivore activity x aridity x neighbors*	*block*	*AICc*	*Akaike weight*
height after annual growth (cm)	+	-	-	+	x	x	x	x	x	3252.3	0.341
annual survival									x	135.9	0.15
annual P(fruit)	+		+						x	292.1	0.263
annual number fruits|fruiting	+	-	+						x	904.3	0.187

Table 1. Best-fit mixed models of vital rates as a function of height, herbivore activity (dung counts), aridity and neighbour presence (fixed effects) and block (random effect; six blocks total). Direction of coefficients for main effects are shown using + and -; the presence of interaction effects in the model is shown using x. While estimating *p*-values for coefficients in mixed models is controversial (Pinheiro & Bates 2000a), red text indicates significant parameter estimates of fixed effects ($p \leq 0.05$), where *p*-values are either estimated using a Wald test (for binomial responses) or an MCMC approach. When including overstorey plant presence/absence in a 30 cm radius as a putative fixed effect in our best-fit model selection, the best supported model for survival includes overstorey plant presence, with higher survival rates when *H. meyeri* is within 30 cm of an overstorey plant trunk. For a list of well-supported models for each vital rate and parameter estimates, see Appendix Table 9.

Analyses

We used four metrics of plant performance to quantify effects of neighbours: survival, growth (difference in height after 1 year of growth), probability of fruiting and (for plants that fruited) the size-corrected fruiting effort (number of fruits/height: $r^2 = 0.27$ for height and fruit number).

Probabilities of survival and fruiting were fit using generalized linear mixed models with a logit link. We generated a series of hypotheses of the drivers of each of these response variables and assessed support for each hypothesis using a model selection framework (Burnham & Anderson 2002). To do so, for each response variable, we selected the best-fitting model using AICc, comparing a suite of nested mixed models that included all possible combinations of initial height, aridity level, neighbour presence (neighbours removed or not), 'herbivore activity' (using dung counts as a proxy; see below), and all possible interactions among aridity level, neighbour presence and herbivore activity as fixed effects; all models also included block as a random effect (with six blocks in total). We used dung counts, a measure of relative herbivore activity (Goheen et al. 2013), as a predictor variable (rather than herbivore presence/absence) owing to substantial variation in herbivore activity levels among blocks within each level of aridity; block-specific dung counts were obtained by averaging total dung counts of all herbivore species over the three dung surveys conducted between June 2011 and May 2012 (Goheen et al. 2013).

To assess effects of aridity, neighbour presence and herbivore activity on total fitness of individuals, and thus their putative effects on population dynamics, we used the best-fit models of each demographic response variable (survival, growth and reproduction) to construct deterministic demographic matrix models (Morris & Doak 2002) for all eight combinations of: arid versus mesic sites, neighbours present versus neighbours removed and no herbivore activity versus mean herbivore activity in control treatments. To incorporate model uncertainty (uncertainty about which model is the best-fit) for each transition matrix, we selected models for survival, growth, binary fruiting probability and number of fruits produced (given fruiting) from among the models that had Akaike weights greater than or equal to 0.1. We selected models with probabilities proportional to each model's Akaike weight (Burnham & Anderson 2002). To incorporate parameter uncertainty, we generated random sets of parameter values for the fixed effects using the multivariate normal distribution, and based on a model's estimated mean parameter values and variance –covariance structure. In the absence of data on seed germination rates, we assumed a 0.09 probability of 'germination' (transition from a seed to the first size class) for all sets of matrices and for all aridity –neighbour –herbivore activity combinations. (Although we lack data on germination rates in the field, a 0.09 probability of germination yielded biologically realistic population growth rate values that span 1; use of other plausible germination rates did not change the relative effect strength of driver variables on overall fitness; Morris & Doak 2002). With this approach, we generated 1000 sets of demographic rates, which incorporated both model and parameter uncertainty, for each of the eight experimental conditions. We used each set of demographic rates to construct a matrix model, and summarized fitness for each model as the expected total offspring number after 5 years (the estimated lifetime of this plant) starting from a single seed. We calculated the mean and variance in fitness by averaging values across the 1000 transition matrices. To assess statistical significance, we conducted a three-way ANOVA on the simulated fitness values of 100 plants in each combination of aridity level neighbour presence herbivore activity.

We used the best-fit parameter estimates of growth in height to determine at what level of herbivore activity the effects of neighbours shifted from the competitive– facilitative continuum (predicted by the stress reduction literature) to facilitative effects across all aridity levels (predicted by plant apparency). We chose growth because it is a common metric of performance in studies of stress amelioration. Assuming that a switch from competitive to facilitative effects of neighbours in mesic areas was indicative of this shift, we plotted the predicted effects of neighbours in the mesic and arid site as a function of herbivore activity and found the x-intercept of the mesic line.

Results

For *H. meyeri* growth in the absence of large herbivores, our best-fitting model predictions were generally consistent with the competition– facilitation continuum predicted by the stress-reduction literature: neighbours slightly increased growth in arid areas and strongly decreased growth in mesic areas (Figure 1a). In the presence of herbivores, however, neighbours increased growth in both arid and mesic sites, with a weak facilitative effect in the arid site and a strong facilitative effect in the mesic site (Figure 1b). In other words, the presence of herbivores eliminated the interaction between neighbour presence and aridity on growth (indicated by support for a three-way interaction among aridity, neighbours and herbivore activity; Table 1 and Appendix, Table 9), suggesting that concealment by neighbours may be more important than stress-mediation as a mechanism of facilitation in this large-herbivore-dominated system.

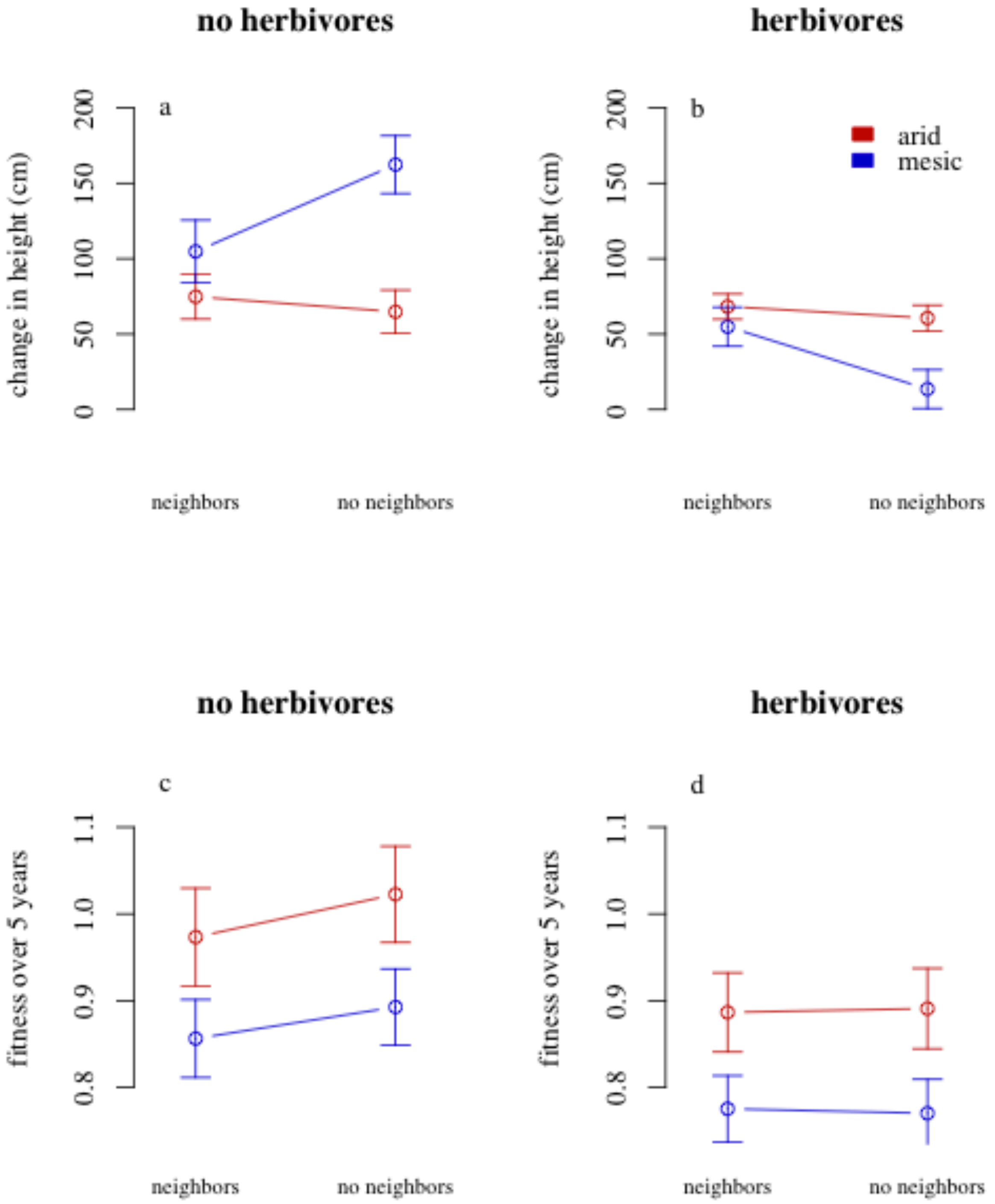

Figure 1. (a,b) Best-fit predictions of growth (height after 1 year of growth-initial height), as a function of neighbour presence, aridity and herbivore activity (no herbivore activity, (a), and average herbivore activity across control treatments, (b). Points show fixed-effect parameter

estimates and bars represent standard errors based on uncertainties of fixed-effect parameter estimates, without random effects. See Appendix Fig. 6 for a presentation of raw data using herbivore activity as a continuous predictor variable. (c,d) Projections of 5-year fitness of an individual seed as a function of neighbour presence, aridity and herbivore activity (zero herbivore activity, (c), and average herbivore activity across control treatments, (d)). Demographic projections incorporate model and fixed-effect parameter uncertainty for change in height, reproduction and survival, including all models with Akaike weights greater than or equal to 0.10. Error bars represent standard deviation across 1000 replicate deterministic projections. According to a three-way ANOVA with aridity, herbivore activity (zero herbivore activity versus average herbivore activity across control treatments) and neighbour presence (and all interactions among these main effects) as predictors, all main effects and the interaction between herbivore activity and neighbour presence are significant ($p \leq 0.05$; Appendix Table 10). These models predict higher 5-year fitness in arid areas because probability of fruiting and number of fruits are higher in arid areas (presumably an evolutionary adaptation to counterbalance low germination probability and seedling survival; Louthan et al. 2013), but we assume similar seed set per fruit and germination rates in all matrices.

In contrast to neighbours' effects on growth, neighbours did not exert strong effects on *H. meyeri* reproduction; instead, negative effects of herbivory and positive effects of aridity were important (Table 1). For survival, neither herbivory, neighbours nor aridity was important (Table 1).

Our results for the effects of neighbours on lifetime fitness were not consistent with the predictions of the stress-reduction literature (Fig. 1c,d; Appendix Table 10). In the absence of large herbivores, neighbours reduced projected fitness at both arid and mesic sites (Fig. 1c). By contrast, there was no net effect of neighbours on fitness in unfenced control plots, suggesting that facilitative effects in the presence of herbivores were strong enough to counterbalance the competitive effects observed in herbivore exclosures (Fig. 1d; significant interaction between neighbour presence and herbivore activity F = 4.3209, $p = 0.038$; Appendix Table 10). This result supports the prediction from plant-apparency theory that neighbours should exert facilitative effects in the presence of herbivores, but not in their absence.

Parameter estimates from our best-fit mixed model for plant growth show that a departure from the predictions of the stress-reduction literature occurs at relatively low levels of herbivore activity (58% of mean herbivore activity in control plots; Fig. 2). The switch from competition with neighbours to facilitation by neighbours in mesic areas that occurs with increasing herbivore activity suggests that the applicability of stress-reduction versus plant-apparency mechanisms is contingent on herbivore pressure. At the arid site, neighbour effects were consistently (and weakly) facilitative, regardless of herbivore activity level (Fig. 2).

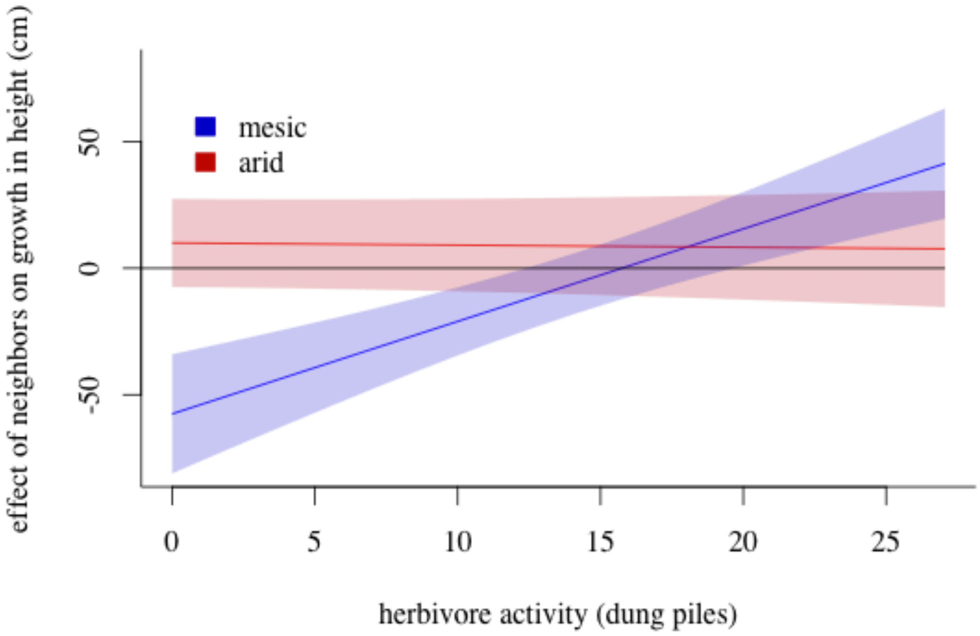

Figure 2. Effect of neighbours on growth as a function of herbivore activity (dung counts), for mesic and arid sites. Solid lines show predictions, derived from the fixed-effect parameter estimates of our best-fit mixed model for growth, of the difference between mean height of plants with versus without neighbours after 1 year of growth; thus, positive numbers suggest facilitation (higher growth with neighbours than without) and negative suggest competition (lower growth without neighbours than with). Shaded area shows the standard error of the difference. X-intercept of the mesic line is at 15.75, 58.2% of mean herbivore activity in control plots, 27.1. See the Appendix Fig. 6 for an alternate presentation showing raw data.

Discussion

In the absence of herbivory, our results for plant growth offer qualified support for the stress-reduction literature, with neighbours weakly facilitating plant growth in arid areas and reducing growth in mesic areas (Fig. 1a). In mesic areas, competitive effects of neighbours outweighed any facilitative effects, such that the net effect of neighbours on plant growth was negative; conversely, the net effect of neighbours was neutral-to-positive in arid areas, suggesting that facilitative effects were at least as strong as competitive ones (Callaway 2007, Brooker & Callaghan 1998, Armas et al. 2011). These competitive effects could include direct uptake of soil water or rainfall interception, whereas facilitative effects could include amelioration of vapour pressure deficit, increased soil water retention or reduced soil evaporation via shading (Holmgren et al. 1997, Tielbörger & Kadmon 2000, Zou et al. 2005, Callaway 2007). Further work would be necessary to establish which of these mechanisms are operating in our study system.

Our results support the predictions of plant apparency in the presence of large herbivores. In the presence of herbivores, neighbours enhanced growth regardless of abiotic stress level (Fig.1b), and herbivores alleviated the competitive effects of neighbours on fitness (Fig. 1c,d). Our work is consistent with the suggestion of Graff et al. (2011) that plant –plant interactions in the presence of herbivores should primarily be facilitative. The effects of plant apparency were strong enough to obscure the competition – facilitation continuum predicted by the stress-reduction literature: in mesic areas, herbivores switched the net effect of neighbours from competitive to neutral or facilitative (for fitness and growth, respectively). Thus, neighbours' concealment of plants in mesic areas was strong enough to match or overwhelm neighbours' stress-mediated competitive effects. In arid areas, facilitative effects were weak in the absence of herbivores, and we did not find additional facilitative effects conferred by plant apparency in the presence of herbivores, perhaps because of lower overall growth rates in arid areas.

Our results are consistent with theoretical predictions that the competition– facilitation continuum predicted by stress reduction can be mitigated or even negated by herbivory (Smit et al. 2009). In spite of these predictions, there have been few empirical tests of the relative strength of stress amelioration versus plant apparency in ecosystems with extant herbivore communities at densities comparable to historical records (Eskelinen 2007, Graff & Aguiar 2011, Solivered et al. 2011). In a salt marsh community, Crain (2008) found that the effects of plant apparency were weaker than those of stress reduction, an effect attributed to low and spatially variable herbivore densities. In the absence of herbivores, Bulleri et al. (2011) found no support for the competitive– facilitative continuum predicted by the stress-reduction literature; instead, interactions between vermetid snails and macroalgae were always competitive. However, in the presence of sea urchin herbivory, vermetids exerted a positive effect on macroalgae at intermediate grazing pressure. These results show that the relative strength and sign of neighbours' effects can depend critically on herbivore density. Our results suggest that for intact communities of large mammalian herbivores, the effects of plant apparency are stronger than the competitive– facilitative effects of stress reduction. Our study further suggests that relatively low herbivore densities can effect a switch from support for stress reduction to support for plant apparency: our results show that a switch from net competition to net facilitation in mesic areas occurs at around half of average herbivore activity levels (Fig. 2).

Effects of neighbours on lifetime fitness are complicated by vital rate- or life stage-specific neighbour effects (Goldberg et al. 1999, Miriti 2006), and investigators rarely quantify all of these stage-specific effects, limiting our understanding of the sum effect of neighbours on plant fitness (Malkinson & Tielbörger 2010). Consistent with previous studies, our work shows that neighbour effects vary for different vital rates. In contrast to strong effects on growth, neighbours' effects on reproduction and survival in *H. meyeri* were weak; instead, the direct effects of aridity and herbivory were most important (Table 1 and Appendix Fig. 5). Surprisingly, aridity has a positive effect on cumulative probability of reproduction and fruit number, but these effects are likely mitigated by fewer reproductive events (Louthan et al. 2013). Our integration of multiple vital rates into a summed fitness metric shows that, in this system, the overall effect of neighbours on fitness is inconsistent with the predictions of the stress-reduction literature, likely because the effect of growth rate is diluted by effects of aridity and herbivores on reproduction and survival (Fig. 1c). Our results are consistent with those of the only other experimental study of which we are aware that has synthesized neighbours' effect on lifetime fitness in different stress environments (Stanton-Geddes et al. 2012). Because quantifying the total effect of neighbours on fitness is critical to assessing whether neighbours and aridity exert biologically relevant effects on population dynamics, additional studies along these lines would be valuable.

We assumed identical seed germination rates across all of our demographic projections, largely because we lack the requisite data to quantify germination rates under field conditions; however, our results on 5-year (approx. lifetime) fitness are robust to this (probably incorrect) assumption. First, seed germination rates are probably higher in mesic areas, increasing overall fitness in mesic areas to levels approaching those found in arid areas (Fig. 1c,d), but not changing the direction of the effect of neighbours. Second, neighbours probably increase 5-year fitness by increasing seedling germination rates (e.g. by providing safe sites or reducing seedling desiccation; Callaway 2007). It is possible that neighbours' facilitation of 5-year fitness via seedling facilitation is strong enough to counteract their observed competitive effects in the absence of herbivory (Fig. 1c). However, in the presence of herbivores, this effect will only serve to increase the facilitative effects of neighbours; thus, incorporating neighbours' facilitation of 5-year fitness would likely still show results consistent with plant apparency.

Most empirical tests of the stress-reduction literature have been conducted in places where large mammalian herbivores are either not present or have been functionally extirpated; as a result, we have a poor understanding of how large consumers might affect the competition–facilitation continuum arising from abiotic stress reduction. Determining how plant–plant interactions shape plant performance is a critical first step in assessing how these interactions shape community structure, but our results highlight that such interactions hinge critically on the top-down effects of herbivores. Considering the effects of plant–plant interactions in the context of higher trophic levels—particularly in ecosystems that harbour diverse, intact assemblages of large mammals—will provide a more complete picture of community dynamics.

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Data accessibility

Dataset will be uploaded onto the Dryad data repository 1 year following publication.

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CHAPTER 5

SPECIES INTERACTIONS MORE STRONGLY AFFECT POPULATION GROWTH RATE IN UNSTRESSFUL AREAS

Abstract

Understanding the forces that determine the origin and maintenance of species range limits is one of the central questions of ecology (Gaston 2003) with implications for both biodiversity of natural communities and climate change impacts on species distribution patterns (Parmesan 2006). Two broad classes of factors constrain species ranges: abiotic factors, such as temperature and precipitation, and species interactions such as predation and herbivory (Sexton et al. 2009). However, we lack a clear understanding of when and where each of these classes of factors operates most strongly. A hypothesis dating back to Darwin suggests that abiotic factors more often set limits in stressful areas, while species interactions dominate in more benign environments (Louthan et al. 2015). Despite the widespread assumption that this is a powerful generality, we have little empirical evidence that directly tests the idea. Here, we report strong support for this pattern from a series of experimental manipulations conducted across a sharp aridity gradient. We find stronger effects of herbivory, neighboring plants, and pollination limitation on estimated population growth rate of our focal plant species in mesic areas. We also show that larger effects of interactions in less stressful areas arise because of changes in the responsiveness of population growth to these effects with stress (Louthan et al. 2015), rather than higher densities or diversities of interactors in less stressful areas, commonly assumed to be the primary generating mechanism starting with Darwin (1859). Our results suggest that this pattern may occur across a wide variety of taxa with similar life histories and effects of species

interactions on vital rates. This work supports theoretical predictions concerning the factors setting range limits, provides new understanding about why these shifting effects occur, and has implications for understanding when and where we need to consider species interactions in both biodiversity studies and projections of species' ranges shifts.

Introduction

What sets and maintains species range limits is one of the fundamental questions of ecology and evolution (Gaston 2003), and also has profound implications for projections of the ecological effects of climate change (Parmesan 2006). While we know that abiotic conditions often set species range limits (Sexton et al. 2009), both long-standing theory (Darwin 1859) and a few empirical studies (reviewed in Sexton et al. 2009) show that species interactions, such as predation, competition, or parasitism, can also be important factors limiting population growth at species range limits. However, we lack a well-supported framework for predicting when and where each of these classes of factors might be most important. One long-standing but little-tested hypothesis predicts that abiotic stress should most often set range limits in apparently stressful environments, while species interactions should exert stronger effects in apparently benign environments (we refer to this idea, first proposed by Darwin (1859), as the Species Interactions-Abiotic Stress Hypothesis, SIASH; Louthan et al. 2015). Some small-scale studies have clearly supported this predicted pattern of effects (especially in intertidal systems; Connell 1961a,b), and correlational data suggest that it might exist across elevations (Ettinger et al. 2011) and latitudes (Sanford et al. 2003). Indeed, it has been cited as the main reason for lack of consistent, predicted shifts in the trailing edge of species range limits in recent climate change studies (Ettinger et al. 2011, Sunday et al. 2012). However, other studies have found contradictory evidence (Louthan et al. 2015) and to date we have few clear tests of the idea, particularly experimental tests, and none that quantify the importance of multiple species interactions on population performance or test for why such effects might arise.

The foundational assumption of SIASH asserts that species interactions exert stronger effects on population growth rate in unstressful areas, ultimately setting distributional limits by driving populations into decline. We tested this hypothesis for multiple species interactions across a rainfall gradient, using *Hibiscus meyeri,* a model plant species in East Africa that occurs across a substantial range of aridities (Louthan et al. 2013, Louthan et al. 2014). *Hibiscus meyeri* is a common subshrub in this acacia-dominated semi-arid savanna that experiences rainfall limitation (see Appendix), both competitive and facilitative effects from grasses and shrubs (Louthan et al. 2014), is browsed by a wide array of herbivores (Louthan et al. 2013), and appears to undergo delayed autonomous self-pollination that favors outcrossing while still ensuring self-pollination if outcross pollination does not occur (see Appendix; Ruiz-Guajardo 2008). Across three sites that span a substantial aridity gradient (22% higher rainfall in our Mesic than Arid Site), we collected demographic data on unmanipulated plants and plants within a nested set of experimental treatments including herbivore exclosures and neighbor removals (Goheen et al. 2013; Appendix). We used data collected over 4 years to estimate effects of multiple factors on survival, growth, and reproduction, and used these vital rate functions to construct demographic models that estimate population growth rate, λ, as a function of aridity (including both temporal and spatial variation), plant neighbors (we focus here on grass and herbaceous neighbors, which we experimentally manipulated, rather than trees and shrubs), mammalian herbivores, and pollinators (which were not manipulated in the field; see Appendix); this unified demographic approach allows us to both predict differences in population growth rate and dissect the mechanisms driving these changes.

Results and Discussion

In this system, SIASH predicts that species interactions exert stronger effects on population growth rate in mesic than in more arid areas. Consistent with this prediction, we find that all three species interactions (herbaceous neighbors, herbivores, and pollinators) exert stronger effects on λ in the Mesic Site (Fig. 1; woody plants were not considered here). The interacting effects of neighbors and herbivores are subadditive, such that neighbors exert some facilitative effects in the presence of herbivores (reducing the magnitude of their competitive effect), likely due to plant apparency effects (Fig. 1D; Louthan et al. 2014). However, the net effect of neighbors and herbivores together was still stronger in our Mesic Site. Similarly, pollinators increase λ substantially more in the Mesic Site; in combination with neighbors and herbivores these effects are also subadditive, such that adding pollinators to populations that have herbivores and neighbors has a weaker positive effect than adding pollinators to populations with no interactions. This subadditivity likely arises from negative effects of herbivores on reproduction (Fig. 2) and of neighbors on fruit-to-seedling transition (Appendix Table 11).

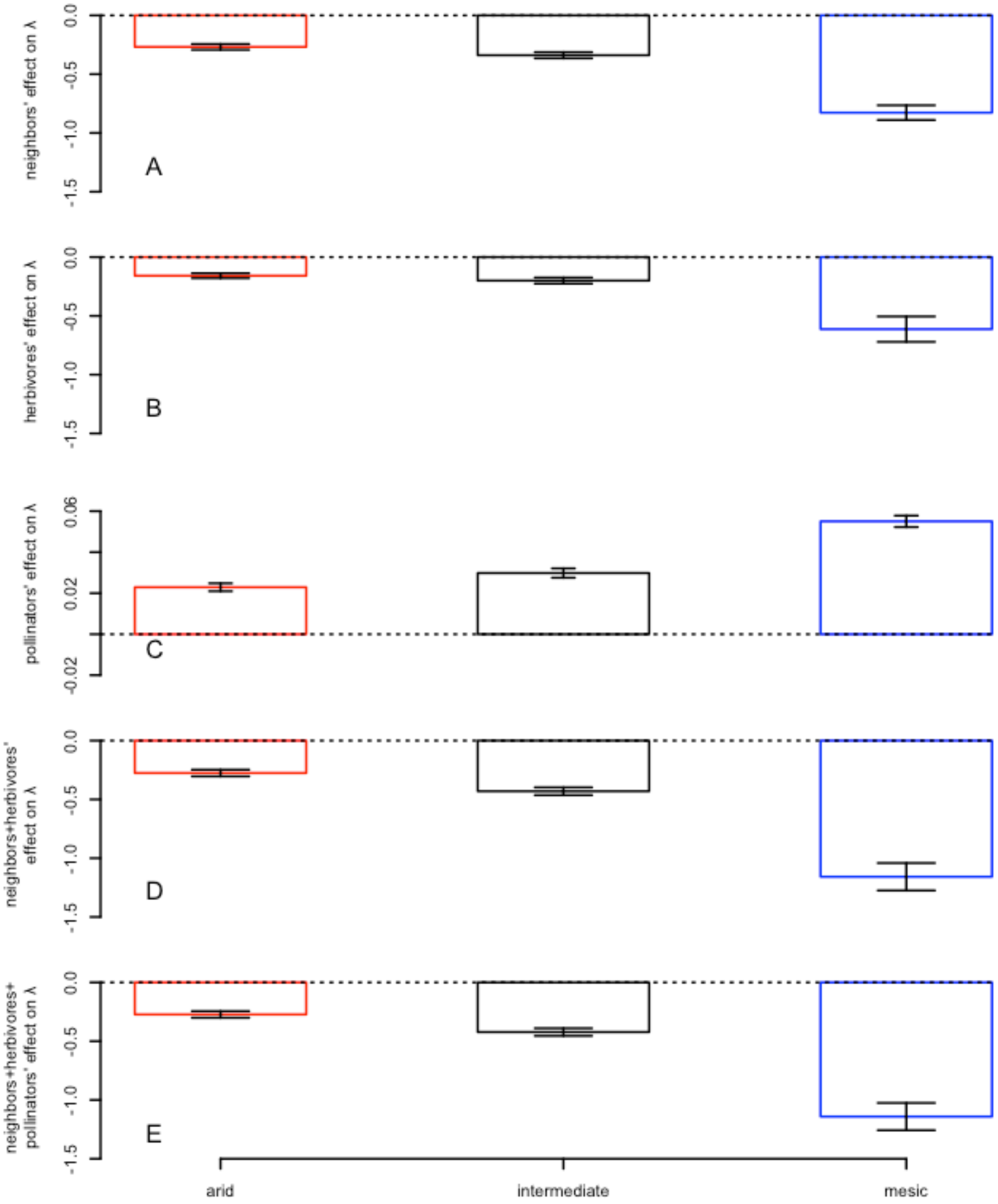

Figure 1. Species interactions exert stronger effects on population growth rate in the Mesic Site. Figures shows the change in lambda after adding in species interactions, both alone and in combination with one another: numbers <0 indicate the interaction(s) reduce fitness (compared to projections with no species interactions included), numbers > 0 indicate the interaction(s) increase fitness. Fractional changes (log(lambda with interaction(s)/lambda without interaction)) are averaged across 500 replications that incorporate uncertainty in the parameters for vital rates; bars represent 1 SD. Note the change in scale in (C). Mean field-observed lambda values are near one; see Appendix. These projections were constructed with best-fit models for vital rates (Appendix Table 11). Analogous values for predictions using global models (models that include all two-way interactions shown in Appendix Table 11) for vital rates are neighbors: Arid Site : -0.294 (SE: +/-0.0033), Intermediate: -0.372 (0.0328), Mesic: -1.07 (0.296), herbivores: -0.235

(0.0384), -0.276 (0.0423), -0.846 (0.3416), pollinators: 0.023 (0.0022), 0.031 (0.0025), 0.06 (0.0052), neighbors + herbivores: -0.305 (0.0382), -0.475 (0.0407), -1.378 (0.3366), neighbors+ herbivores+ pollinators: -0.302 (0.038), -0.424 (0.0298), -1.155 (0.1286). For comparison, see Appendix Fig. 7 for an analogous figure that includes only per-capita effects of species interactions (projections without block effects and with the same interactor densities at all rainfall levels).

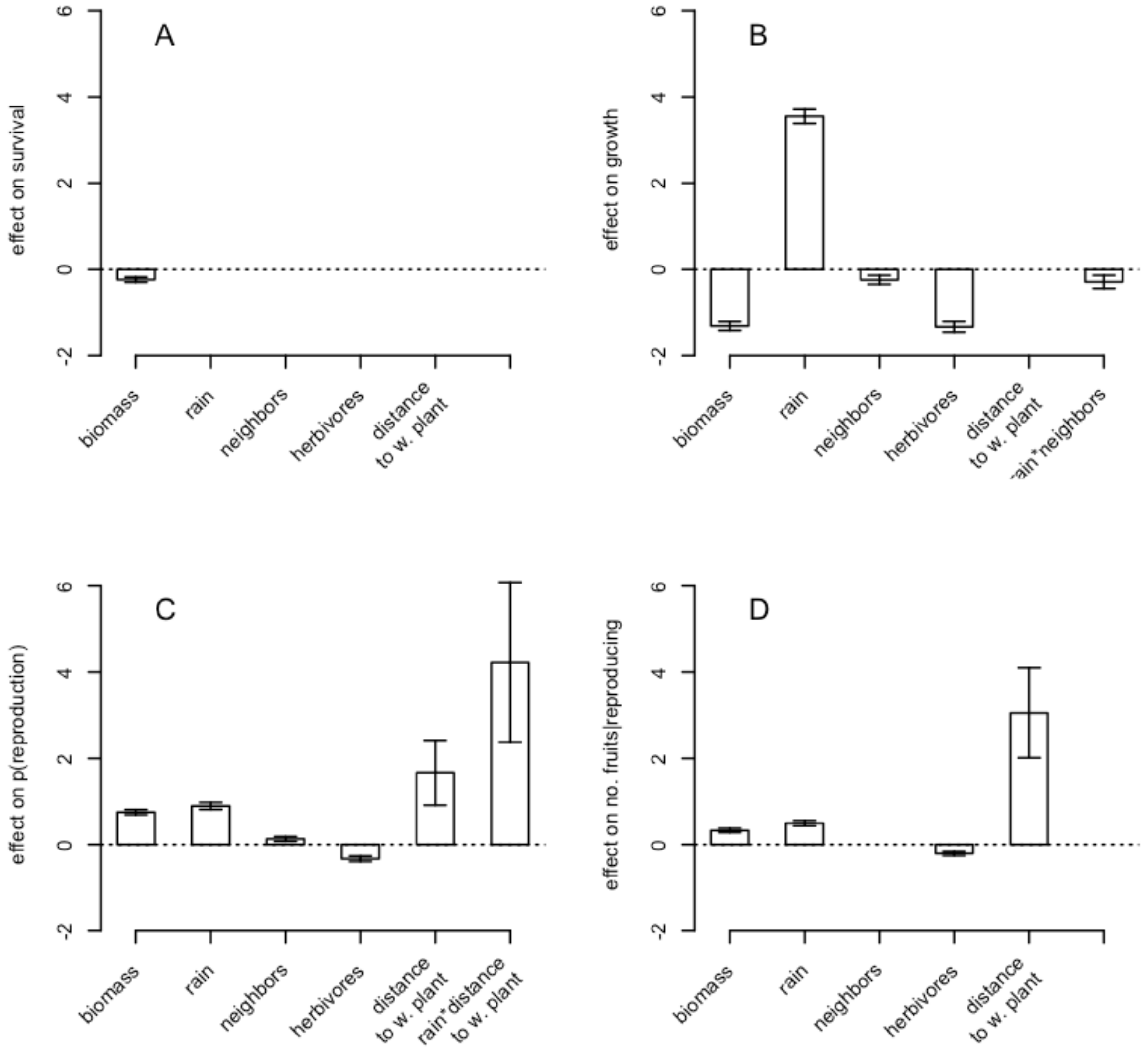

Figure 2. Effects of rain and species interactions on vital rates are reasonable. Figure shows the direction of fixed effect coefficients (initial biomass, rainfall, neighbor density, herbivore activity, and distance to woody plant; woody plants here are acacia and *Euphorbia nyikae*; see Appendix) for best-fit models of each vital rate (interactions, if present in the best-fit model, are shown in right-most bar; see Appendix Table 11). See Appendix Table 11 for fixed-effect estimates for variance in growth. Absence of bars indicates that fixed effect was not present in the best-supported model. Bars indicate standard error of coefficients. All coefficients are from models fit with standardized predictor variables, so magnitude of values reflects relative effect

size. Effects on variance in growth and fruit to seedling transition are shown in Appendix Table 11.

Several different mechanisms could explain the pattern of greater species interaction effects in more mesic areas. First, there may be higher density and diversity of interactors (e.g., herbivores, plant neighbors) in mesic areas: many of the earliest and most well-known advocates of the SIASH pattern suggest that this is the main driver of stronger effects on population growth rate in more benign environments (Darwin 1859; MacArthur 1972; we refer to these as "density effects"). Second, each interactor might exert stronger effects on individual vital rates in benign areas ("per capita demographic impact"; note that our vital rate functions show per interactor or interaction effects); for example, an herbivore could consume more *H. meyeri* in mesic areas, perhaps due to higher plant palatability, or due to patchier populations with higher local population densities, making plants easier to find. Finally, stress might change the life history of a species such that the same effects of interactors on vital rates would have stronger population-level effects in mesic areas ("life history effects"). For example, if sensitivity of populations in mesic areas to size-specific survival is higher than in arid areas, then herbivores' reduction of survival will have more substantial effects on λ in the Mesic Site. We decomposed these different effects by estimating changes in lambda that would result from these separate aspects of species interactions, quantifying the relative contribution of each effect (see Appendix). This decomposition shows that for all interactions, by far the most important driver of stronger effects of species interactions in the Mesic Site is life history effects (Fig. 3A-C). Only for neighbors is there any effect of density in generating this pattern, and in the case of herbivory, density effects actually result in stronger effects in Arid Sites (our system has higher herbivore densities in arid areas, the opposite of most systems; McNaughton et al. 1989, Salazar & Marquis 2012). This result is in direct contrast to the oft-cited density effects that researchers assume drive most of the SIASH pattern (Louthan et al. 2015).

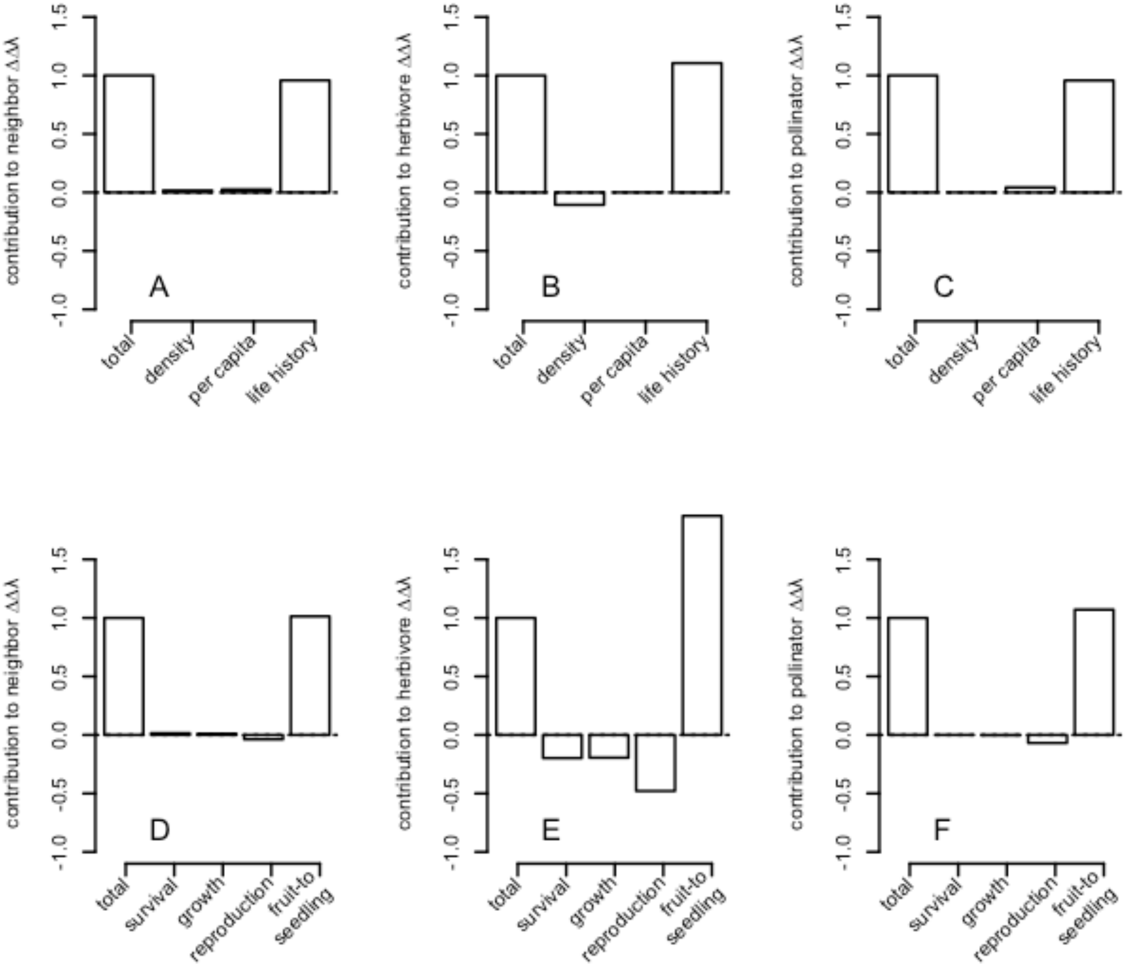

Figure 3. The life history mechanism drives support for the SIASH, with the majority of the effect generated by fruit-to-seedling transition rates. Figure shows the decomposition of the factors creating greater effects of species interactions on population growth rates (λ) in the Mesic v. Arid Site. The response variable in all panels, $\Delta\Delta\lambda$, is the difference between estimated lambda without and with each species interaction in the Mesic Site, minus the same difference for the Arid Site, and then rescaled to equal 1 for the observed full effect on lambda. A-C) The contribution of density effects, per-capita demographic effects, and life history effects to the total SIASH pattern seen in neighbor, herbivore, and pollination interactions. D-F) The contributions of individual vital rates (where reproduction includes both probability of reproduction and the number of fruits produced| reproduction) to generation of the SIASH pattern. “Total” bars serve as a reference for the total net effect of an interaction. Negative numbers indicate effects that contradict the main effect; for example, life history effects in neighbors weaken the net negative effects of neighbors in the Mesic Site. Numbers >1 indicate that some of that effect’s interaction

is negated by contrasting effect of other mechanisms. See Appendix Table 14 for the contribution of variance in growth, and Appendix Fig. 8 for sensitivities of lambda to individual vital rates.

A second, orthogonal approach to decomposing effects on population growth is to dissect how the effect of a species interaction on each vital rate influences overall differences in interaction strengths in Arid vs. Mesic Sites. Individually, the effects of each factor on different vital rates were consistent with our expectations: rainfall increased several aspects of *H. meyeri* performance (growth, and two components of reproduction; Fig. 2); herbivores had negative effects on these three vital rates (Fig. 2); neighbors decreased growth rates (Fig. 2) and fruit-to-seedling transition rates (Appendix Table 11); and distance to woody plants increased reproduction (Fig. 2). Despite these diverse effects, for all species interactions, effects on the fruit to seedling transition generate the majority of stronger effects of species interactions in the Mesic Site (Fig. 3D-F), likely due to *H. meyeri* population growth being sensitive to this vital rate (Appendix Fig. 8). These results suggest that the population-level effect of species interactions can in some cases be distilled to effects on one vital rate (making future studies of species interactions simpler, if researchers can identify that key vital rate).

It is not clear how commonly life history will generate stronger effects of species interactions in unstressful places, simply because we have limited data on how sensitivities of populations vary with stress, and sensitivity patterns can vary with life history strategy. Further, if species interactions do not happen to affect the vital rates to which populations are sensitive, we would likely see little support for SIASH. For example, in the case of herbivory, predation or parasitism, these interactions might exert no or weak effects on vital rates in unstressful areas, because unstressed victims are able to compensate for damage (as we may be seeing here in the case of herbivory; Maschinski & Whitman 1989), are less susceptible to attack, or more able to combat infection (Nelson & Demas 1996, Wirsing et al. 2002). Although it is difficult to generalize about the importance of the life history mechanisms generating the SIASH across species (particularly since this effect arises largely due to sensitivity to just one vital rate), our consistent results on multiple species interactions suggest that life history effects may be universally important.

Our findings add experimental support for a foundational assumption of a long-held but poorly-tested hypothesis concerning the forces governing range limits, and suggest that clear and consistent patterns in the control of population growth rate and hence range limits may exist. Concomitant with the lack of abiotic control over some warm-edge limits (Ettinger et al. 2011, Sunday et al. 2012), our results suggest that species interactions could be driving many trailing-edge or tropical range limits, even without gradients in interactor density (Darwin 1859, MacArthur 1972) or interaction frequency (Schemske et al. 2009). In particular, our results caution against ignoring or minimizing effects of species interactions in setting range limits (Afkhami et al. 2014, Tingley et al. 2014) or in predicting future distribution patterns (Van der Putten et al. 2010, Blois et al. 2013, Raffa et al. 2013, Wisz et al. 2013), but we also provide a heuristic framework for when and where species interactions might be most important within a species range, and where they might be less important.

Materials and Methods

We worked at the Mpala Research Centre in central Kenya, in a semi-arid acacia-dominated savanna just off the equator, with little variation in temperature and a relatively intact, diverse herbivore community (see Appendix). We used a large-scale herbivore-exclusion experiment arrayed across a pronounced rainfall gradient (UHURU; Ungulate Herbivory Under Rainfall Uncertainty; Goheen et al. 2013); UHURU is comprised of an open control with three highly effective exclosures (see Appendix) that exclude different sized- guilds of herbivores, replicated three times ("blocks") at each of three sites across this rainfall gradient. Total rainfall increases 22% from the Arid to Mesic Site (Appendix Table 12), and soil characteristics do not vary substantially across this gradient (Goheen et al. 2013). We used rain gauges to get rainfall values, and we used quarterly herbivore dung counts (see Goheen et al. 2003) as a proxy for herbivore activity (see Appendix). Herbivore community composition is similar across sites, with elephant (*Loxodonta africana*), impala (*Aepyceros melampus*) and dik-dik (*Madoqua guentheri*) dominating (Louthan et al. 2014). In this ecosystem, *Hibiscus meyeri* is a common, apparently moderately palatable subshrub with no known chemical or physical defenses, which exhibits moderate compensatory regrowth following herbivory events. It is heavily browsed by many different herbivore species and experiences water limitation (Appendix). Flowers in *H. meyeri* present their style for insect-mediated outcross pollination, but also have a mechanism to touch their style to their anthers (presumably self-pollinating themselves) if no insects visit (A. Louthan, pers. obs). Self pollination is very common, but bouts of outcrossing can also occur (see Appendix), suggesting inbreeding depression is likely.

To quantify the importance of rainfall and herbivory on plant vital rates, between June 24- August 5 2011 we exhaustively searched randomly selected areas in all Sites and exclosure treatments (controlling for plant phenology; Louthan et al. 2013), as well as in transects outside of the UHURU experiment (coded as a separate block in our analyses) and marked and mapped all *H. meyeri* individuals, measuring size, reproduction, and neighbor cover in a 30 cm radius (see sample sizes in Appendix Table 13). Until 2014, we returned annually to remeasure these plants, also noting survival and distance to nearest woody plant (acacia, *Vachellia* sp and *Senegalia* sp, as well as *Euphorbia nyikae, Croton* sp, *Grewia* sp, *Balanities* sp, or *Boscia* sp) >

30 cm tall. We marked new plants in the same area to replace those that died, measuring 1719 unique individuals throughout the experiment.

To quantify the effect of neighbors on plant vital rates, we marked and measured haphazardly chosen plants in the full exclosures and open controls at all levels (see Louthan et al. 2014), as well as on transects outside of the UHURU experiment, randomly assigned 1/3 of them to a neighbor removal treatment, and cut down all biomass within a 30 cm radius, carefully painting the cut stalks with Roundup®. We removed this biomass every 6 months, and remeasured both unmanipulated and neighbor-removed plants annually, replacing dead or missing plants as necessary, resulting in 1504 individuals total (Appendix Table 13).

We used work on a congeneric species with a similar floral phenotype (*Hibiscus trionum;* Seed, Vaughton, and Ramsey 2006; see Appendix) to simulate a release from inbreeding depression caused by increased pollinator visitation rates. Our pollinator treatments, which assume that all fruits we observed in the field were selfed, represents a shift from no outcross pollination to all outcross pollination (both likely outcomes; field observed per-plant pollination rates are usually either none or all of flowers; see Appendix). Thus, our results represent the maximum possible effect pollinators could exert in this system.

Finally, we obtained fruit to seedling transition rates by counting all seedlings in a 2m radius around 118 highly fecund individuals arrayed across rainfall levels and herbivore exclosure combinations, once just after the dry season and once after the wet season. Seedlings entered the population with a height of 5.44 cm & a basal area of 0.96, the mean of all *H. meyeri* with height< 10 & a basal diameter of 2 (the upper limits for seedlings in the field; A. Louthan pers. obs).

We used a model selection framework to select best-fit mixed models for survival, growth, variance in growth, probability of reproduction, and number of fruits produced given reproduction. We found the best model from all subsets of a global model with initial biomass and all two-way interactions between rain (measured as site-and year-specific rainfall totals), herbivore activity, neighbor cover, and distance to nearest woody plant as fixed effects. Block and plant-measurer (of initial plant size) were random effects (see Appendix). We provide estimates of change in λ using global models in the figure legends. We first ensured that each subset of our data (unmanipulated plants, unmanipulated haphazardly selected plants, and unmanipulated plants within and outside of the UHURU experiment; Appendix) did not unduly change the parameter estimates of the global model. To obtain fruit to seedling transition rates, we divided seedling number by fruit number, and used a similar mixed model selection approach to select the best model for log-transformed seedlings per fruit, comparing all subsets of a global model with all interactions among rain, herbivore activity, and neighbor cover as fixed effects, and with block as a random effect (all the measurements were done by the same measurer). *Hibiscus meyeri* fruits have a maximum of 15 seeds (A. Louthan, pers. obs.), so we fixed the maximum seedlings per fruit at 15.

We used the model with the highest AIC weight for each vital rate to construct deterministic demographic matrices for 6 combinations of species interactions (none, + neighbors, + herbivory, + pollination, + herbivory & neighbors, + herbivory & neighbors & pollination) at each aridity level. We incorporated parameter uncertainty by sampling from the multivariate distribution of fixed effect parameter estimates (Appendix Table 11) and calculating each of the 6 above matrices for each set of parameter values. We show projections that include block effects and rainfall level x herbivore exclosure –specific predictor values (herbivore activity, neighbor cover, and distance to woody plant) in the main text. We show projections without block effects and with non- specific predictor values in the supplemental information; these include no effects of density nor unmeasured differences across levels (Appendix Fig. 7; effects in the Mesic Site are greater than effects in the Arid Site).

To understand whether per-capita demographic rates, sensitivities, or densities effect larger changes in λ in mesic areas, we decomposed the change in λ in Mesic v. Arid Sites into each of these three components. For each species interaction, we calculated $\Delta\lambda$ ($\lambda_{presence\ of\ species\ interaction}$-$\lambda_{absence\ of\ species\ interaction}$) for both Mesic ($\Delta\lambda_M$) and Arid ($\Delta\lambda_A$) Sites to obtain $\Delta\Delta\lambda = \Delta\lambda_M - \Delta\lambda_A$. For each interaction, we then estimated both the total value for $\Delta\Delta\lambda$ and the value for $\Delta\Delta\lambda$ when two types of effects were removed from the calculation (Appendix Table 14). We calculated three $\Delta\Delta\lambda$'s that set different effects to mean values:

1. focal species interactor densities
2. rain terms in rain* focal species interaction terms
3. block effects and rainfall in all other terms

Letting (1) vary represents varying interactor density with rainfall, (2) represents the variation in per-capita demographic rates, and (3) represents the variation in life history effects. For this calculation, we used the mean of the Mesic and Arid Site values of other predictor variables (besides rainfall and the focal species interaction; e.g., for the contribution of neighbors, we set herbivore and distance to woody plant to their mean value in Mesic and Arid Sites' full herbivore exclosure treatments, and pollinators to zero) to isolate the effect of rainfall and the species interaction of interest.

Finally, to assess which vital rates contributed most to $\Delta\Delta\lambda$, we used a similar approach, setting block effects and the rainfall terms for individual vital rates to the mean value to obtain the fractional contribution of each vital rate to the sum $\Delta\Delta\lambda$.

CHAPTER 6

CONCLUSION

In the study system that was my focus in this work, species interactions exert stronger effects on population growth rate in less stressful areas. Neighbors and herbivores exert stronger negative effects in mesic areas, and pollinators exert stronger positive effects in these same more mesic habitats. However, predicting population growth rates of *Hibiscus meyeri* subjected to multiple species interactions is not as straightforward: for example, herbivores modify the effect of neighbors, such that neighbors exert some positive effects in the presence of herbivores due to plant apparency. Further, these effects appear to be most often mediated by changes in the sensitivity to population growth rate to different vital rates with changing rainfall, such that small differences in the effect of species interactions on vital rates are amplified by large sensitivities to those vital rates in mesic areas, resulting in a strong net effect on population vital rate. These results have important implications for our understanding of species range limits, as well as for our predictions of shifts in species range limits.

Several added complexities were also revealed in my work regarding patterns in the strength of species interactions across stress gradients. For example, my third chapter shows that while herbivores exert stronger levels on population-level performance (e.g., abundance) in mesic areas, they exert weaker effects on individual performance (e.g., the reduction herbviores have on individual plants' growth rate). My fifth chapter shows similar effects; though we see stronger effects of herbivores on population growth rate in mesic areas, for at least some vital rates (e.g., growth) we see stronger effects of herbivores in arid, not mesic, areas. This discrepancy arises due to changes in the sensitivity of population growth rate to growth in mesic

v. arid areas. These findings suggest that studies of individual-level plant response to herbivores do not necessarily translate up to responses of plants at the population or abundance level. Thus, studies that look at changes in plant abundance or community composition should address multiple levels of plant performance.

Herbivores and neighbors also interact in complex ways that modify the importance of species interactions across stress gradients. Neighbors exert competitive effects on *H. meyeri,* but also appear to confer protection from herbivores due to plant apparency effects. Thus, the effect of neighbors on *H. meyeri* is different in the presence v. absence of herbivores, and relatively low herbivore densities (only half of what we see in the field) alter the net effect of neighbors on *H. meyeri* performance. Interestingly, predictions of the recent ecological literature (that neighbors exert facilitate effects in arid areas, but competitive effects in mesic areas) enjoy little support in our system, particularly for components of fitness.

In spite of these complications, using all the data I collected during my dissertation to parameterize demographic models that include multiple effects on population growth, I find that herbivores, neighbors, and pollinators (all of the species interactions I studied in my dissertation) have stronger effects in mesic areas. These results provide strong support for the predictions of the species interactions-abiotic stress hypothesis (SIASH; see Chapter 2): neighbors, herbivores and pollinators exert stronger effects on populations in mesic areas than in arid areas. Neighbors exert the strongest effect (competitive, but with some facilitative effects in the presence of herbivores), herbivores an intermediate, negative effect, and pollinators the weakest, positive effect. Higher densities of interactors in mesic areas are not the primary driver of this pattern. Instead, changes in the sensitivity of population growth rate to vital rates result in stronger effects of species interactions in mesic areas.

This work provides support for a broad, long-standing, but relatively untested, hypothesis concerning the origin of and persistence of species range limits. There is still a dearth of empirical evidence testing this idea, despite the fact that it is often assumed to be a strong generality. In particular, there are four non-independent mechanisms that may govern the strength of species interactions and could result in the SIASH-predicted pattern, both at the level of plant response and at the community level. However, these mechanisms do not necessarily lead to SIASH-like patterns in nature. In trying to address these questions, my work is particularly novel in its synthetic approach that includes data on multiple types of species interactions, its focus on aridity as a stressor, and the relatively well-preserved ecosystem that still has many species interactions intact. Further work on this system will try to dissect the role of different size-guilds of herbivores as a function of abiotic stress, using the UHURU experimental setup, as well as expand on the implications for species distribution models by recommending locations where these models should include species interactions.

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APPENDIX

Chapter 2 Appendix

Glossary

Deterministic growth rate: population growth rate assuming no temporal variation in growth rate.

Geographic range: the geographic area where a species is extant. In this work, we are primarily concerned with coarse-grained species ranges (e.g., at the continental scale) rather than distributions at a fine-grain scale (e.g., east- versus west-facing slopes of the same mountain).

Low density stochastic growth rate ($\lambda_{L.D.}$): stochastic population growth rate at low densities, such as when a new population is establishing or a current one is on the verge of extinction, both of which will drive range limits. Population growth at higher densities might be strongly affected by negative density dependence and density-dependent species interactions, and thus might provide a biased assessment of the factors driving range limits. *Range limit*: the geographic area where a species transitions from being present to being absent. Here we are primarily concerned with coarse-grained species ranges (see 'geographic range').

Sensitivity of population growth rate: how responsive population growth rate is to perturbations from current values of a factor of interest. For example, high sensitivity to pollination indicates that changing pollination rates would substantially change population growth rate; low sensitivity to pollination indicates that changing pollination rates would have minimal effect on population growth rate.

Species Interactions–Abiotic Stress Hypothesis (SIASH): the hypothesis that range limits in stressful areas are more often set by stress tolerance, but range limits in nonstressful areas are more often set by species interactions.

Species interactions: interactions with other organisms that have some effect on individual or population performance, including both positive and negative effects.

Stochastic growth rate: population growth rate including temporal variation in growth rate.

Stress: any number of abiotic conditions that reduce population performance (even if populations are well adapted to 'stressful' conditions), including factors that lead to low average or high variability in population performance or reduced colonization and increased extinction. This definition includes the effects of chronic physical stress, low resource availability, or high disturbance frequency and severity; these are often difficult to disentangle (but see Rex et al. 2000). Different species might find different ends of an abiotic gradient 'stressful.' Note that we do not include biotic stressors under this definition; although many biotic factors can reduce individual and population performance, others, for example, mutualisms, can increase performance. While some biotic interactions are also 'stressful', for our presentation we restrict use of this term to abiotic conditions.

Chapter 3 Appendix

Site	Control	LMH	transect plants
Arid	229	100	108
Intermediate	203	73	NA
Mesic	242	78	111

Table 1. Number of plants selected haphazardly in Control and LMH treatments, as well as the number of plants from transects outside of UHURU.

response variable	site	intercept	basal area	treatment: LMH	treatment: MEGA	treatment: MESO	Block
binary all rep (logistic link)	Arid	-1.743527	0.026201	0.802487	0.060697	0.669783	0.27942
		< 2e-16	< 2e-16	0.000168	0.844560	0.030484	
	Intermediate	-2.659528	0.048903	2.533327	1.340211	2.081860	0.78444
		2.68e-07	4.82e-16	< 2e-16	0.000449	2.62e-08	
	Mesic	-1.634529	0.089482	0.619715	-0.504881	0.161095	0.20196
		< 2e-16	< 2e-16	0.00861	0.10011	0.61329	

Table 2. Estimates of fitted coefficients of mixed models predicting the probability of floral initiation within all treatments at each of the three sites. Coefficients for each treatment are shown, with their corresponding p-value underneath; standard errors for block effects are also shown.

response variable	site	treatment	D-statistic	p-value	d.f.
basal area	Arid	MEGA	0.1495	0.427	74,64
basal area	Arid	MESO	0.29	0.004721	74,70
basal area	Arid	LMH	0.1241	0.6924	74,59
basal area	Intermediate	MEGA	0.1303	0.6623	58,68
basal area	Intermediate	MESO	0.2529	0.04603	58,60
basal area	Intermediate	LMH	0.2638	0.02988	58,53
basal area	Mesic	MEGA	0.1807	0.1568	77,79
basal area	Mesic	MESO	0.208	0.108	77,60
basal area	Mesic	LMH	0.3966	2.898e-06	77,96
height	Arid	MEGA	0.1441	0.4793	74,63
height	Arid	MESO	0.4131	9.296e-06	74,70
height	Arid	LMH	0.3032	0.00453	74,60
height	Intermediate	MEGA	0.2796	0.01449	58,69
height	Intermediate	MESO	0.4103	9.721e-05	58,60
height	Intermediate	LMH	0.6466	1.792e-11	58,64
height	Mesic	MEGA	0.2052	0.0703	80.79
height	Mesic	MESO	0.1833	0.1994	80,60
height	Mesic	LMH	0.4125	7.108e-07	80,96

Table 3. Results from Kolmogorov-Smirnov tests on size distributions in Control vs. all exclosure treatments at both sites.

			height			*joint height-basal area*
Site	Treat-ment	CV	skewness	kurtosis	STVI	STVI
Arid	CONT	89.01268	1.409963	4.36802	0.9188904	0.526797728
Arid	LMH	98.2377	1.120872	3.273084	0.9876112	0.256634908
Arid	MEGA	97.56361	1.115245	3.027976	0.9999957	0.407108423
Arid	MESO	86.49621	1.031359	3.131429	0.998718	0.368129063
Intermediate	CONT	98.65973	3.242656	16.001666	0.591381	0.139163372
Intermediate	LMH	85.4513	1.134612	3.801393	0.9023573	0.375042334
Intermediate	MEGA	98.30278	2.292	9.103383	0.7027178	0.468369039
Intermediate	MESO	87.07172	1.231257	4.265006	0.8833367	0.325172276
Mesic	CONT	72.23705	1.441591	5.114709	0.8116973	0.265150908
Mesic	LMH	97.08433	1.519864	5.652084	0.8494241	0.248853522
Mesic	MEGA	111.1401	1.929374	6.831015	0.7838742	0.359167808
Mesic	MESO	86.90101	1.29439	3.851703	0.9210721	0.247030879
			basal area			
Site	Treat-ment	CV	skewness	kurtosis	STVI	
Arid	CONT	149.4658	1.89925	5.763306	0.9002467	
Arid	LMH	263.612	5.598039	37.559571	0.4731567	
Arid	MEGA	136.5649	2.537322	11.897877	0.6532568	
Arid	MESO	162.1599	2.658441	10.181062	0.8065785	
Intermediate	CONT	288.39065	5.584459	36.174573	0.4907375	
Intermediate	LMH	121.65298	1.725768	5.700031	0.8905998	
Intermediate	MEGA	122.35641	2.144546	8.305461	0.7573571	
Intermediate	MESO	99.39288	1.43649	5.270606	0.846519	
Mesic	CONT	126.82806	1.7213898	5.457257	0.8738231	
Mesic	LMH	150.36312	3.1148174	14.714525	0.5980563	
Mesic	MEGA	133.22152	2.3479213	10.204692	0.6589857	
Mesic	MESO	122.86712	1.5933317	4.913646	0.9229467	

Table 4. The effect of exclosures on the STVI, coefficient of variation (CV), skewness, and kurtosis of height and basal area size distributions. Note that the CV, STVI, and Gini coefficient are non-independent, and that the joint STVI is not independent from the height STVI or the basal STVI; thus results should be interpreted with caution.

coefficients	response variables			
	H:BA ratio (1/4 root transformed)		fruits per biomass (log transformed)	
Intercept	1.47	54.9	-0.9	-6.5
basal area	0.004	-26.43		
treatment:LMH	0.248	8.05	0.216	1.27
treatment: MEGA	0.0515	1.22	0.319	1.253
treatment: MESO	-0.0198	-0.47	0.292	1.362
site: Arid	-0.02	-0.47	-0.16	-0.97
site: Mesic	0.139	4.03	0.438	2.804
LMH* Arid	-0.0396	-0.94	-0.0669	-0.293
MEGA* Arid	-0.0541	-0.93	-0.652	-1.866
MESO* Arid	0.177	3.05	-0.026	-0.088
LMH* Mesic	-0.248	-5.92	-0.083	-0.395
MEGA* Mesic	-0.0344	-0.62	-0.671	-2.088
MESO* Mesic	0.095	1.63	-0.692	2.408
block (std dev)	0.031		0	
residual (std dev)	0.312		1.008	

Table 5. Estimates of fitted coefficients of mixed models predicting number of fruits per biomass and height: basal area ratio as a function of site and treatment. Coefficients for each treatment are shown, with their corresponding t-value to the right; standard error for block effects and residuals are also shown.

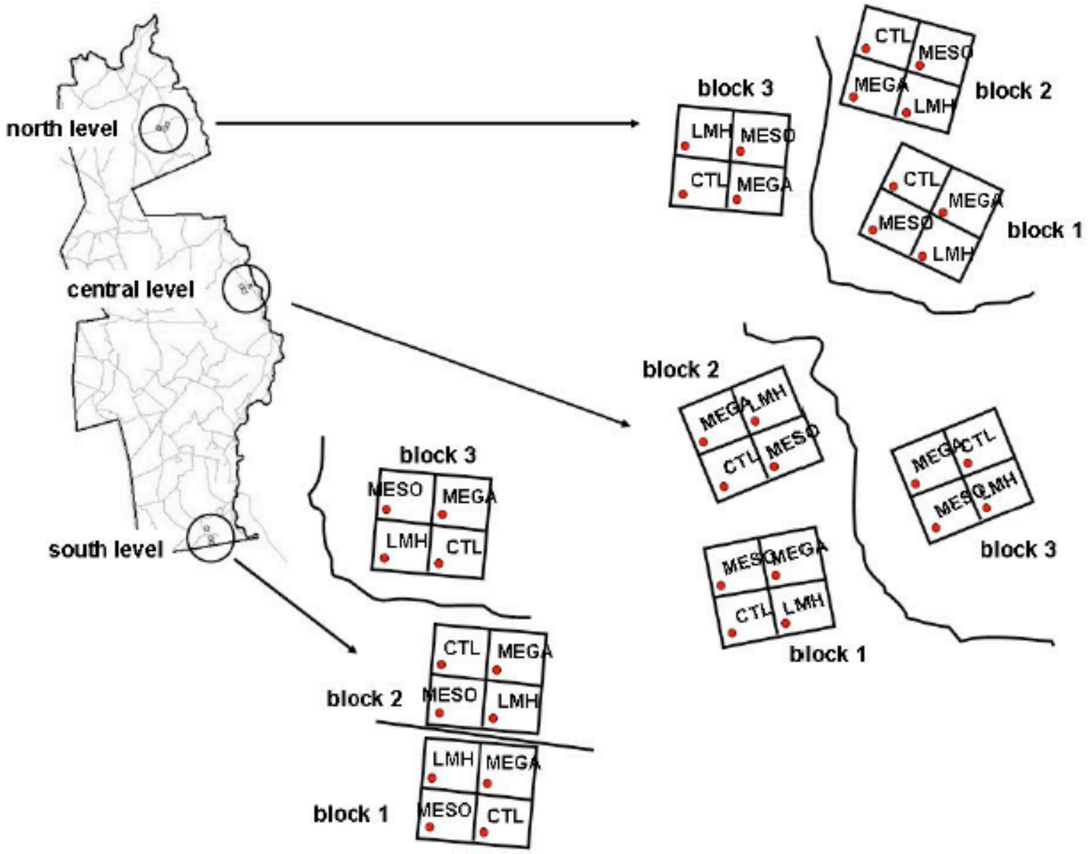

Figure 1. Figure of UHURU schematic. Blocks with 4 treatments are replicated three times, in a completely randomized block design, at each of three sites across an aridity gradient. Rainfall greatest in the Mesic, least in the Arid. See text for details.

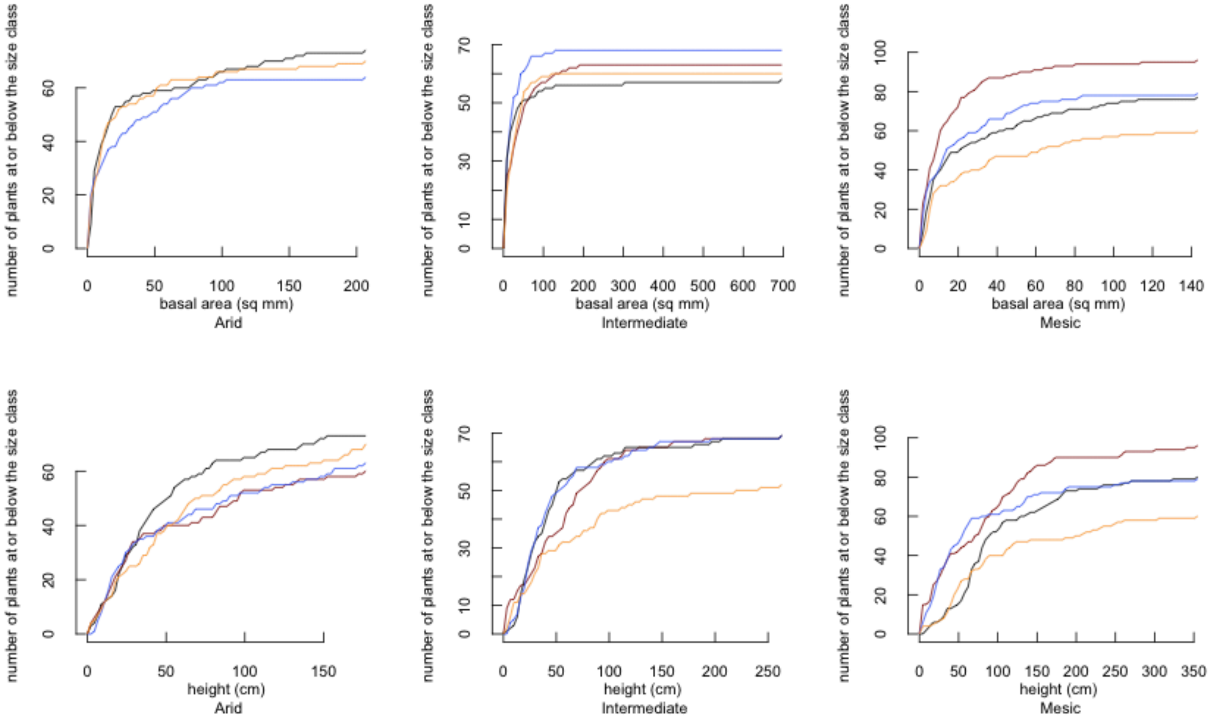

Figure 2. Empirical CDFS constructed with raw numbers rather than proportion of the population, for both basal area and height CDFs in all site- treatment combinations. Colours as in previous figures.

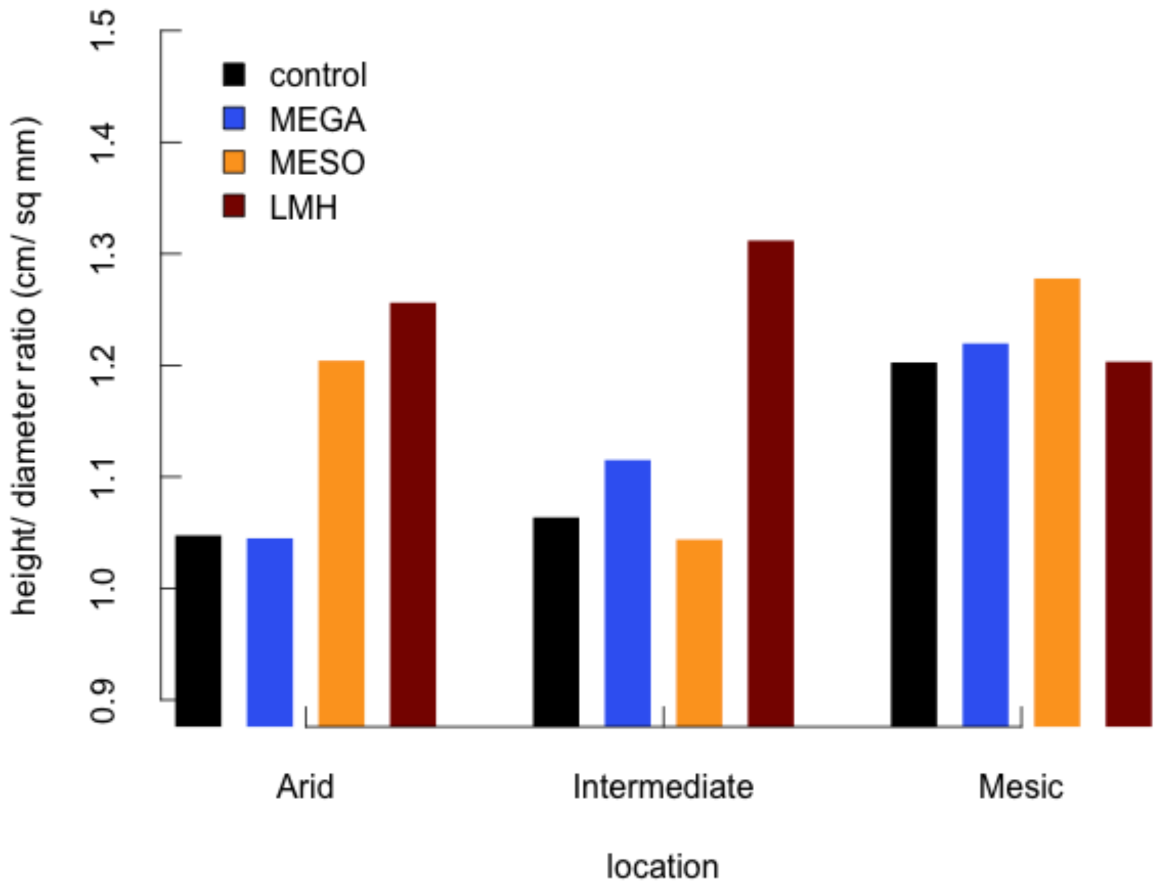

Figure 3. Predicted height: basal area ratio across sites and treatments. Basal area, site, treatment, and site*treatment are significant (basal area: $\chi_1^2 = 601.89$, $P < 2.2e\text{-}16$, treatment: $\chi_3^2 = 75.252$, $P = 3.199e\text{-}16$, site: $\chi_2^2 = 8.9654$, $P = 0.0113$, site*treatment $\chi_6^2 = 58.969$, $P = 7.289e\text{-}11$; ratio is ¼-root transformed; see Table 5). A two-way ANOVA indicates that site, treatment, and their interaction are all significant at $p<0.0003$.

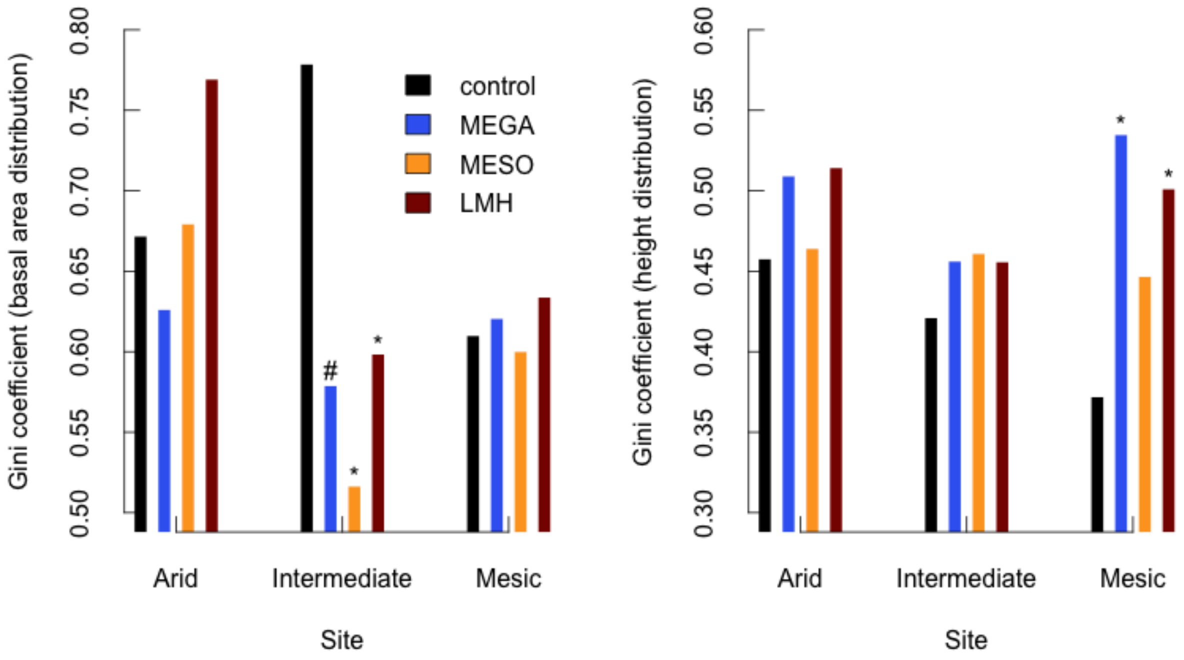

Figure 4. Gini coefficients for all sites and treatments. Significant differences between Control and each exclosure treatments calculated using a pooled bootstrapping technique (see text); # indicates marginally significant differences (p<0.10), * indicates p<=0.05.

Hibiscus meyeri densities

Densities do not differ in a systematic way across UHURU (Table 6). We estimate stem density by calculating the number of plants found per total area searched in each quarter-block (negative binomial general linear model, with densities multiplied by 100 and then rounded up to the nearest whole number; site: $F_{2,139}$= 4.3374, P = 0.013; treatment: $F_{3,136}$ = 4.9475 , P = 0.001956, site*treatment interaction: $F_{6,130}$= 1.9109, P = .0750, Block: $F_{6,124}$ = 3.1994, , P = 0.003845 ; see Table 6). In this analysis, the Arid*LMH interaction term significantly decreased the density of *H. meyeri* (z-value= -2.09512, p-value= 0.01176), but the Mesic *LMH interaction term was not significant, suggesting that herbivores have less of a negative effect on *H. meyeri* densities in the Arid site than in Intermediate or Mesic sites.

	CONT	LMH	MEGA	MESO
Arid	0.844	0.359	0.335	0.194
Intermediate	0.1328	0.4542	0.066	0.078
Mesic	0.254	0.584	0.140	0.349

Table 6. Means of raw densities, calculated as the number of plants found per area searched. .

Statistical routines

We used general linear models with a negative binomial error to assess how insect herbivory and densities varied across sites and treatments, using the anova function to assess significance of these effects. We used mixed models (lmer function in the lme4 package in R, with an identity link and Gaussian errors), to analyze the effect of site and treatment (fixed effects) and block (random effect) on ¼ transformed height:basal area ratios and log-transformed reproductive effort per biomass (basal area*height). To determine the probability of floral initiation as a function of initial plant basal area, we used the same lmer function in R, assuming binomial errors, to generate coefficients for each site and treatment combination. We used the lm function in R to generate predictions of empirical CDF functions, using first, second and third order values of basal area as predictor variables, and logit transformed proportions (scale was 0.25 to 1.25) as a response variable. Finally, we used the anova function, wilcox.test function, and ks.test function for anovas, Wilcoxon signed-rank tests, and Kolmogorov-Smirnov tests, respectively.

Insect damage

While we find no differences in percent of leaves suffering insect damage in Control areas across the UHURU experiment, but we found a significant site* treatment interaction when using data from all sites (negative binomial general linear model; Table 7). Arid LMH plants exhibit significantly higher rates of insect damage than Arid Control plants, and Mesic MESO plants suffer significantly less damage than Mesic Control plants.

Predictor variable	df	deviance	residual df	p-value
height	1	10.141	2009	0.00145
site	2	15.094	2007	0.00053
treatment	3	19.26	2004	0.00024
site*treatment	6	24.922	1998	0.00035
block	8	11.973	1990	0.15244

Table 7. Results from a negative binomial general linear model of percent of leaves suffering insect damage, using all site and treatment combinations

Chapter 4 Appendix

		height (cm)			basal area (cm^2)		
		small	medium	large	small	medium	large
aridity level	exclosure						
arid	control	18.23 (0.21)	38.13(0.40)	84.53(0.65)	4.68(0.57)	17.90(0.30)	53.24(0.79)
arid	total exclosure	25.40 (0.82)	60.68(1.11)	105.80(3.20)	3.63(0.21)	16.86(1.03)	38.98(2.20)
mesic	control	21.95 (0.18)	46.03(0.26)	73.86(0.71)	5.30(0.14)	14.14(0.28)	32.43(0.51)
mesic	total exclosure	28.68 (2.38)	83.86(1.55)	157.03(3.50)	2.95(0.14)	21.28(0.28)	105.16(0.51)

Table 8. Mean basal area and height sizes for small, medium, and large size classes, with standard errors in parentheses.

response variables	predictor variables										residual variance	support	
	fixed effects									random effects			
	intercept	*initial height*	*herbivore activity*	*aridity*	*neighbors*	*herbivore activity x aridity*	*herbivore activity x neighbors*	*neighbors x aridity*	*herbivore activity x aridity x neighbors*	*block*		*AICc*	*AIC weight*
height after annual growth	77.216 (15.120)	0.902 (0.074)	-0.240 (0.426)	Mesic: 30.007 (24.880)	No neighbors: -9.983 (17.908)	Dung* Mesic: -1.604 (1.134)	Dung*No neighbors: 67.550 (29.639)	Mesic* No neighbors: 67.550 (29.639)	Dung* Mesic*No neighbors: -3.741 (1.421)	101.6	2523.4	3252.3	0.341
height after annual growth	72.760 (12.390)	0.890 (0.075)	-0.196 (0.312)	Mesic: 67.400 (19.221)		Dung* Mesic: -3.657 (0.842)				116.47	2594.30	3252.5	0.297
height after annual growth	75.981 (12.871)	0.889 (0.075)	-0.203 (0.312)	Mesic: 68.022 (19.363)	No neighbors: -5.909 (5.868)	Dung* Mesic: -3.704 (0.843)				124.77	2583.04	3253.7	0.171
height after annual	70.500 (13.951)	0.889 (0.0743)	0.034 (0.394)	Mesic: 67.817 (19.248)	No neighbors: 4.298	Dung* Mesic: -3.682	Dung*No neighbors: -0.445			120.11	2576.30	3254.8	0.094

growth					(12.026)	(0.841)	(0.458)						
annual survival	2.850 (0.249)									0	1	135.9	0.15
annual survival	2.619 (0.312)				No neighbors: 0.552 (0.521)					0	1	136.8	0.097
annual survival	1.964 (0.807)		0.016 (0.027)	Mesic: -2.590 (1.472)	No neighbors: 1.574 (1.586)	Dung* Mesic: 0.293 (0.140)	Dung*No neighbors: -0.026 (0.0480)	Mesic* No neighbors: 5.027 (3.324)	Dung* Mesic*No neighbors: -0.429 (0.188)	0	1	137	0.087
annual p(fruit)	0.774 (0.327)	0.018 (0.005)		Mesic: -0.852 (0.357)						0.056	1	292.1	0.263
annual p(fruit)	1.288 (0.593)	0.017 (0.005)	-0.016 (0.016)	Mesic: -1.036 (0.380)						0.029	1	-141.438	293.1
annual p(fruit)	0.843 (0.356)	0.018 (0.005)		Mesic: -0.855 (0.355)	No neighbors: -0.147 (0.295)					0.054	1	-141.843	293.9
annual p(fruit)	0.380 (0.324)	0.018 (0.005)								0.226	1	-143.987	294.1
annual number of fruits | fruiting	1.702 (0.242)	0.010 (0.002)	-0.017 (0.006)	Mesic: -0.544 (0.161)						0	1.466	904.3	0.187
annual number of fruits | fruiting	1.443 (0.285)	0.010 (0.002)	-0.008 (0.009)	Mesic: -0.534 (0.161)	No neighbors: 0.504 (0.299)		Dung * no neighbors: -0.018 (0.011)			3.33E-12	1.450e+00	-444.527	905.6
annual number of fruits | fruiting	1.661 (0.252)	0.010 (0.002)	-0.017 (0.006)	Mesic: -0.542 (0.161)	No neighbors: 0.085 (0.146)					0	1.4637	-445.811	906.0
annual number of fruits | fruiting	1.271 (0.314)	0.010 (0.002)	-0.004 (0.009)	Mesic: -0.332 (0.224)	No neighbors: 0.863 (0.408)		Dung* no neighbors: -0.025 (0.013)	Mesic *no neighbors: -0.413 (0.321)		6.1974e-13	1.4416e+00	-443.705	906.1
annual number of fruits | fruiting	1.698 (0.245)	0.010 (0.002)	-0.017 (0.007)	Mesic: -0.507 (0.390)		Dung * Mesic: -0.002 (0.019)				0	1.4655	-445.976	906.4

Table 9. Best-fit models (AIC weight >0.08) of vital rates as a function of height, herbivore presence, aridity, and neighbor presence. Parameter estimates for coefficients for main effects are shown, with standard errors in parentheses and MCMC estimates of *p*-values in italics; for categorical or interaction effects, each parameter estimate is shown separately. Variance of random effects and residual variance are also shown; for binomial mixed models, residual variance is fixed at 1. We do not present significance values for individual parameters, as their interpretation for mixed models is not straightforward (Golderg et al. 1999).

effect	**Df**	**F**	**p**
aridity	1	72.5333	*< 2.2e-16*
herbivore presence	1	48.811	*5.98E-12*
neighbor presence	1	4.4636	*0.03494*
aridity*herbivore presence	1	0.0018	0.96645
aridity*neighbor presence	1	0.2362	0.62709
herbivore presence*neighbor presence	1	4.3209	*0.03797*
aridity*herbivore presence*neighbor presence	1	0.0001	0.99169

Table 10. Results of a three-way ANOVA conducted on simulated plant 5-year fitness, with neighbor presence, herbivore presence,and aridity, as well as all potential interactions, as predictor variables. Significant p-values ($p \leq 0.05$) show in italics.

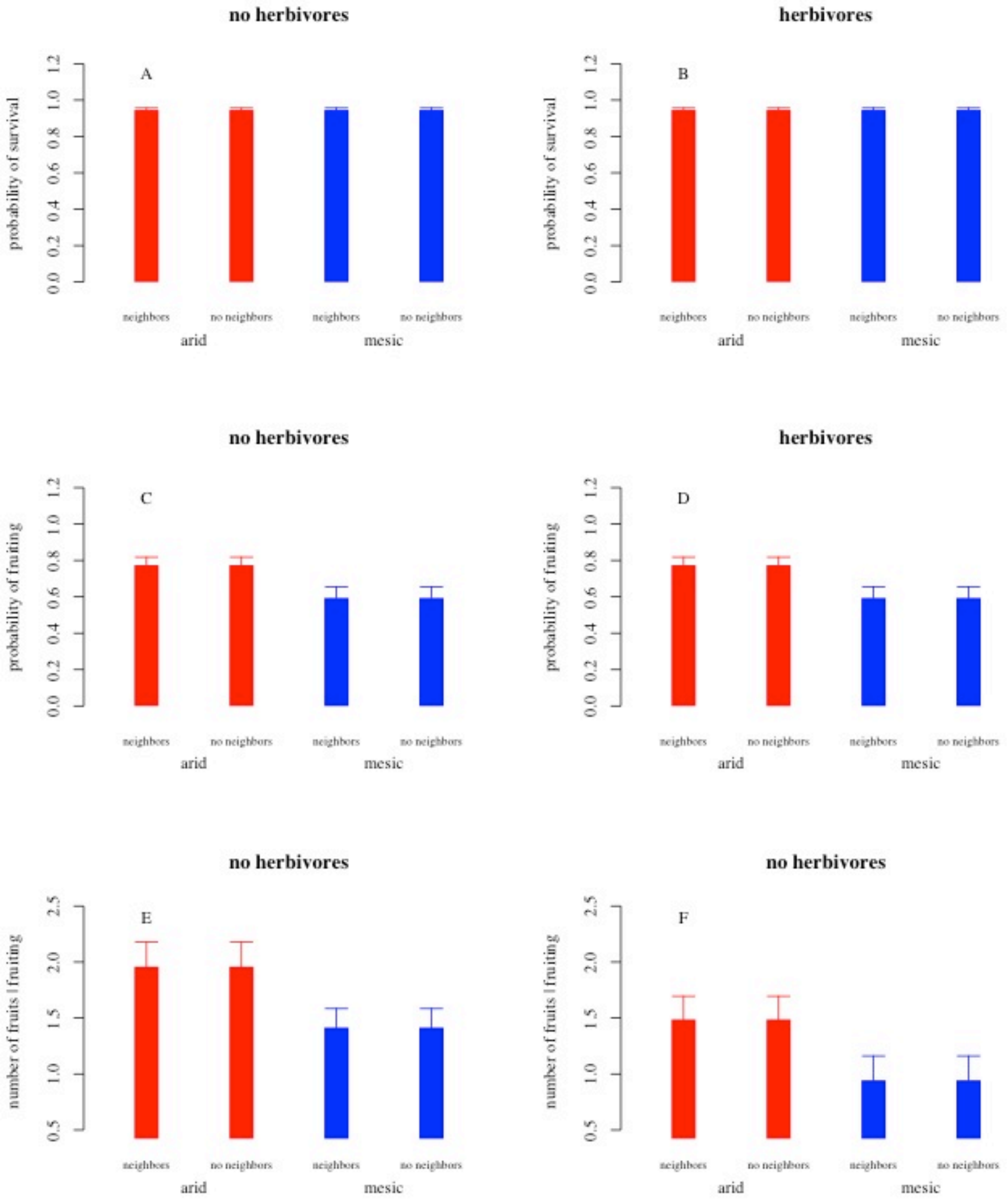

Figure 5. Best fit mixed-model predictions of survival, probability of fruiting, and number of fruits given fruiting, as a function of neighbor presence, aridity, and herbivore presence (zero herbivore activity, A, C, E, and average herbivore activity across control treatments, B, D, F). Bars represent standard error of fixed-effect parameter estimates.

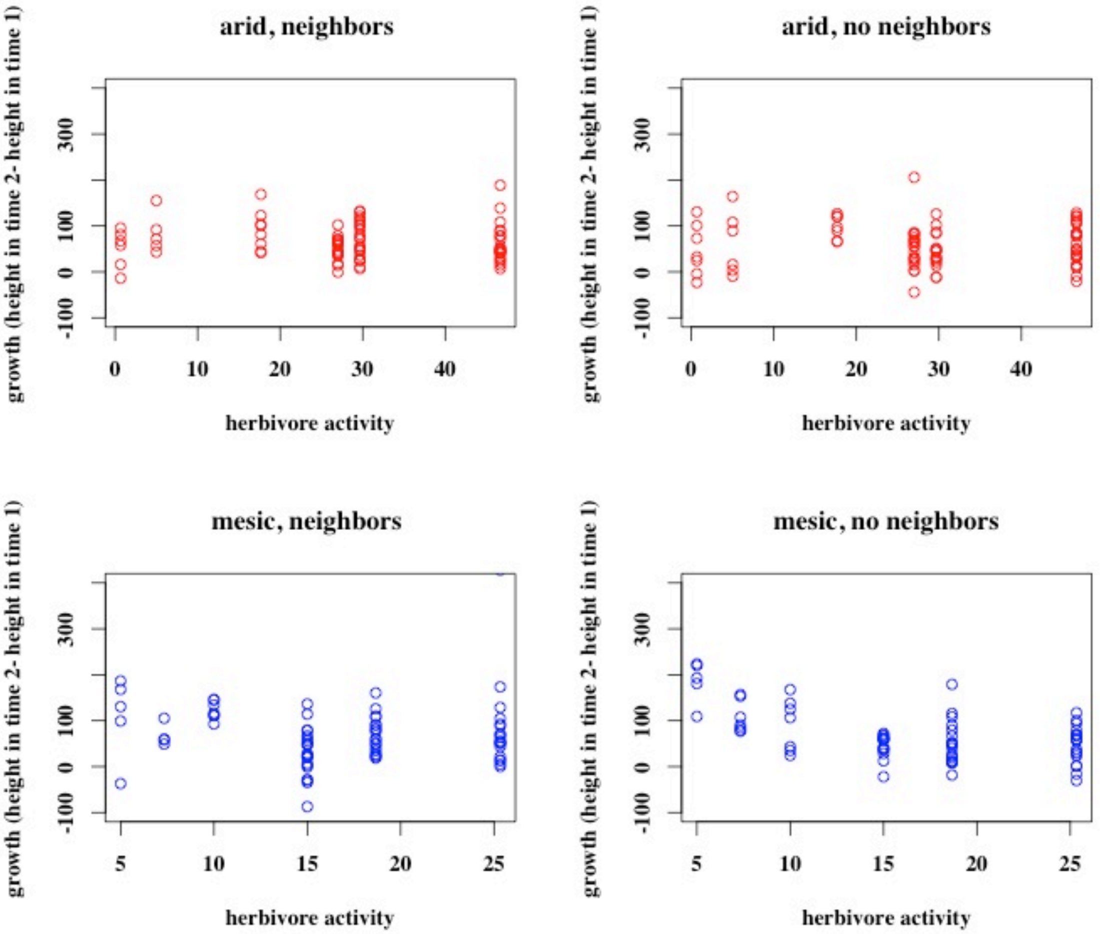

Figure 6. Graph of growth as a function of herbivore activity (dung counts), for both arid (red) and mesic (blue) environments. Negative growth rates can occur if a plant is eaten by herbivores and does not compensate for damage.

Chapter 5 Appendix

		vital rate					
		survival	growth	var(growth)	p(reproduction)	no. fruits| reproduction	fruit to seedling
fixed effects	(Intercept)	2.3323 (< 2e-16)	0.8537 (0.0423)	24.0303 (5.02e-08)	-0.8517 (8.92e-07)	1.5327 (< 2e-16)	-0.59363 (0.7103)
	biomass	-0.2365 (7.81e-05)	-1.3154 (< 2e-16)	17.9336 (< 2e-16)	0.7485 (< 2e-16)	0.3275 (7.63e-12)	
	rain		3.5505 (3.14e-13)	16.5695 (1.13e-12)	0.8928 (< 2e-16)	0.4947 (< 2e-16)	
	herbivore activity		-1.334 (< 2e-16)	2.1937 (0.20771)	-0.3292 (2.79e-07)	-0.2064 (3.14e-05)	
	distance to woody plant			74.8974 (0.11863)	1.6633 (0.0272)	3.0551 (0.00334)	
	neighbor cover		-0.241 (0.0210)	-6.1631 (7.42e-05)	0.1317 (0.0156)		-0.04949 (0.0309)
	rain*herbivore activity			-0.2461 (0.91057)			
	rain*distance to woody plant			182.8682 (0.00241)	4.2276 (0.0226)		
	rain*neighbor cover		-0.2882 (0.0585)	-2.2826 (0.30095)			
	herbivore activity* distance to woody plant			-9.9359 (0.76741)			
	herbivore activity*neighbor cover			-3.9247 (0.01520)			
	distance to woody plant*neighbor cover			-49.8704 (0.15110)			
SD's of random effects	block	0.2303	1.252	6.49	0.5794	3.60E-01	2.992
	measurer	0.1702	0.1315	0	0	6.22E-07	NA
	residual	NA	4.8782	69.88	NA	NA	2.349

Appendix Table 11. Fixed-effect parameter estimates for survival, growth, variance in growth, p(reproduction), number of fruits| reproduction, and fruit to seedling transition, with each fixed effects' *p*-values in parentheses (obtained using anova() in lmerTest), and standard deviation of random effects. We fit survival and probability of reproduction with a binomial error term, growth and variance in growth with a normal, and number of fruits |reproduction with a negative binomial (which was a better fit than a Poisson for both best-fit and global models, according to a log likelihood test). Note that binomial and negative binomial models (survival, p(reproduction), and number of fruits| reproducing) have fixed residual variance, so we do not show these values, and that predictor variables are scaled for all the vital rates besides fruit to seedling transition.

Mesic	Intermediate	Arid	year
369.4	235.4	200.6	2009
707.43	703.98	630.72	2010
717.22	773.62	474.615	2011
727.131	785.3153333	662.8686667	2012
597.185	585.1366667	520.54	2013
444.295	380.69	429.3516667	2014

Table 12. Cumulative annual rainfall in mm for 2009-2014 at each of the three UHURU rainfall levels.

Sites	herbivore exclosure	unmanipulated non-experimental plants	unmanipulated experimental plants	experimental plants subject to neighbor removals	plants subject to additional water
Intermediate	open control	53	134	69	NA
Intermediate	LMH	49	30	27	19
Intermediate	Mega	44	NA	NA	NA
Intermediate	Meso	31	NA	NA	NA
Mesic	open control	86	161	80	NA
Mesic	LMH	102	33	24	21
Mesic	Mega	88	NA	NA	NA
Mesic	Meso	68	NA	NA	NA
Arid	open control	83	150	79	NA
Arid	LMH	68	60	24	20
Arid	Mega	74	NA	NA	NA
Arid	Meso	70	NA	NA	NA
Mesic	open transects	49	35	22	NA
Arid	open transects	37	44	22	NA

Table 13. Initial sample sizes (number of individual *H. meyeri* marked and followed) for data collection in 2011 in each rainfall level*herbivore exclosures treatment combination; open controls are open to all herbivores, LMH excludes all herbivores larger than hares, Mega

excludes mega-herbivores and larger, and Meso excludes meso-herbivores and larger. At each census, we replaced plants as necessary to maintain consistent sample sizes; plants were lost due to mortality or inability to relocate plants. For our experimental work, we tagged more plants in control plots than we did in herbivore exclosure plots (due to a desire to leave some plants in herbivore exclosures unmanipulated for future experiments). Further, in LMH plots, experimental plants were 1/3 control, 1/3 neighbor removal, and 1/3 supplemental water, while in control plots, experimental plants were 1/3 neighbor removal plants and 2/3 control, with no supplemental watering (a pilot experiment indicated that elephants preferentially consume supplementally watered plants, so we did not conduct this experiment in the open control).

Interaction	Total $\Delta\Delta\lambda$	Density $\Delta\Delta\lambda$	Life history $\Delta\Delta\lambda$	Per capita $\Delta\Delta\lambda$	Total $\Delta\Delta\lambda$ (non-specific predictors)
neighbors	-1.725	-0.02110436	-1.203694	-0.0320246	-1.213367
herbivory	-1.461	0.08938248	-0.9333092	-0.0004559387	-0.7433832
pollination	0.1744	0	0.1151085	0.005195311	0.1247737

Interaction	Total $\Delta\Delta\lambda$	Survival $\Delta\Delta\lambda$	growth $\Delta\Delta\lambda$	Var (gr) $\Delta\Delta\lambda$	P(rep) $\Delta\Delta\lambda$	No seeds |reproduction $\Delta\Delta\lambda$	Fruit-to-seedling $\Delta\Delta\lambda$	Total $\Delta\Delta\lambda$ (non-specific predictors)
neighbors	-1.725	-0.02175857	-0.01452455	-0.03967284	0.01431554	0.04155432	-1.50182843	-1.213367
herbivory	-1.461	0.08815362	0.08646560	0.072363	0.08099107	0.1321458	-0.83239250	-0.7433832
pollination	0.1744	5.889145e-05	-3.546622e-04	0.001502456	-0.003962623	-0.006100006	1.559514e-01	0.1247737

Table 14. $\Delta\Delta\lambda$ values for each interaction and the contribution of each type of mechanism and vital rate to total $\Delta\Delta\lambda$. Note that the Total $\Delta\Delta\lambda$ (non-specific predictors) sets all other species interactions to the mean value between the Arid and Mesic Sites (e.g., for neighbors, herbivore activity is the mean herbivore activity in the Mesic and Arid Sites' full herbivore exclosures, pollinator density is zero, and distance to woody plant is the mean distance in the Mesic and Arid Sites' full exclosures; see Chapter 5), so is not the same as the Total $\Delta\Delta\lambda$, which uses Site-specific species interactions values, such that Arid Site values are different than Mesic Site values. "Total $\Delta\Delta\lambda$" is the value used in Chapter 5 Figure 1.

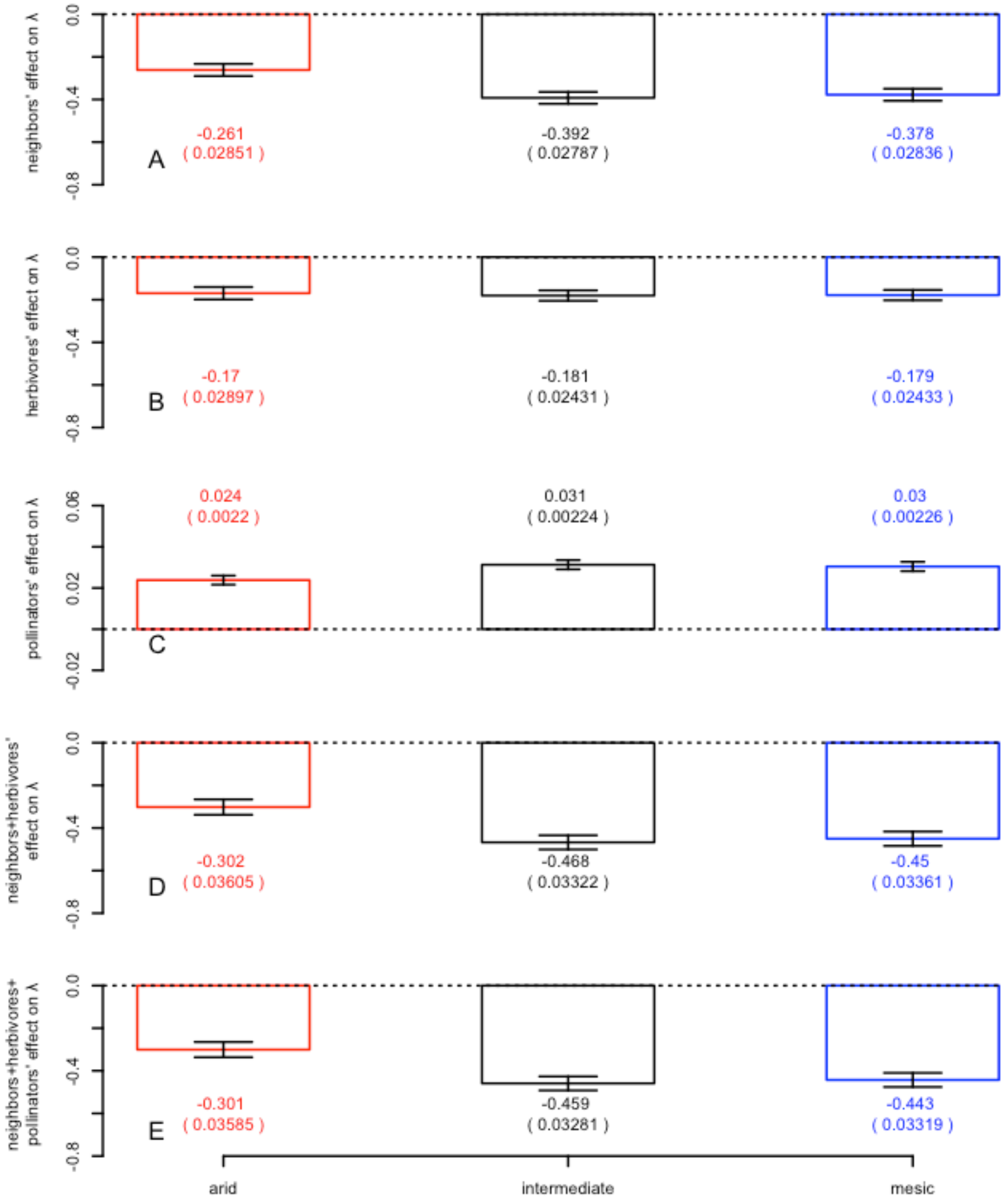

Figure 7. Change in lambda after adding in species interactions, both alone and in combination with one another, with non-specific predictors (the mean value of neighbor cover, distance to woody plant, and herbivore activity, across the corresponding herbivore exclosure in Arid, Intermediate, and Mesic Sites) and no block effects; numbers <0 indicate the interaction(s) reduce fitness, numbers > 0 indicate the interaction(s) increase fitness. Differences (log(lambda with interaction/lambda without interaction)) are averaged across 500 replications that incorporate uncertainty in parameters for vital rates. Bars represent 1 SD, and we indicate mean

change in lambda (with standard errors in parentheses) because differences are difficult to see. Note that the similarity between this figure and Chapter 5 Fig. 1 suggest that density exerts minimal effects on the overall magnitude of the change in lambda between Mesic and Arid Sites, as our main text analyses also indicate. Analogous values for predictions using global models for vital rates are neighbors: Arid Site: -0.288 (SE: 0.04), Intermediate: -0.432 (0.0405), Mesic: -0.417 (0.0409), herbivores: -0.244 (0.0427), -0.262 (0.0439), -0.26 (0.0435), pollinators: 0.025 (0.0028), 0.032 (0.0027), 0.031 (0.0028), neighbors + herbivores: -0.336 (0.0471), -0.521 (0.0467), -0.502 (0.0467), neighbors+ herbivores+ pollinators: -0.334 (0.047), -0.459 (0.0328), -0.443 (0.0332).

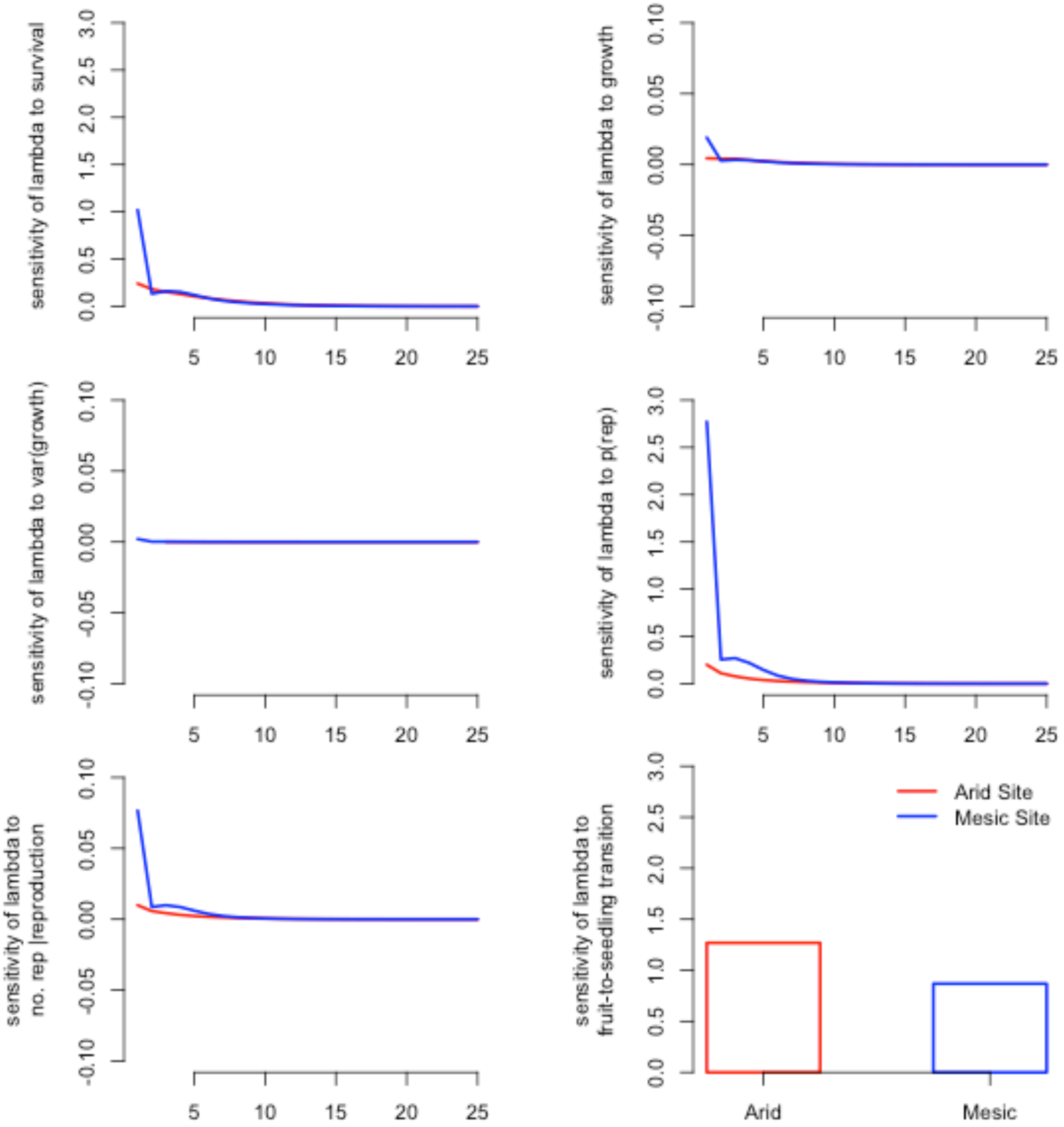

Figure 8. Sensitivities of lambda to size-specific vital rates at Arid and Mesic Sites. Results are shown for matrices with no species interactions and Site-specific values of distance to woody

plant (as in the reference matrix in Chapter 5, Fig. 1). Sensitivities were obtained via perturbation. Note the change in scale between growth, variance in growth, and number of fruits given reproduction.

Pollinator effects

Hibiscus meyeri has a floral phenotype that appears to favor outcrossing by an insect vector, but presumably assures self-fertilization in the absence of an effective pollination event. Similar to a well-studied *Hibiscus* in this same system (Ruiz-Guajardo 2008), *H. meyeri* displays flowers for only one day; stigmas remain exposed to outcross pollen until the afternoon, when, if they have not received outcross pollen, they bend back to touch their style to the anthers surrounding the style (presumably resulting in self-pollination; A. Louthan, pers. obs). *Hibiscus trionum*, a facultative selfer with a similar floral phenotype to *H. meyeri*, shows weak, delayed inbreeding depression, likely due to repeated incidences of self-fertilization. In *H. trionun,* performance of selfers compared to outcrosses was worst for maternal seeds per fruit (outcross to selfer performance ratio= 1.0526) and flowers per plant in the F1 generation (ratio=1.0989) (Seed, Vaughton, and Ramsey 2006).

We opportunistically collected data on fraction of self-pollinated flowers in 245 plants across all levels and treatments from 2010 to 2013. Fraction of self-pollinated flowers per plant in the field ranges from 0 to 1, but there is little variation among levels in per plant average selfing rate across flowers (Arid Site 0.99, Intermediate, 0.99, Mesic, 1.0); note that incorporating lower selfing rates in Arid Sites into our analysis would result in even weaker effects of pollinators in Arid Sites.

Most commonly, plants self-pollinate all their flowers, but some plants receive outcross pollen on all their flowers (Fig. 9). Thus, we assumed that all observed *H. meyeri* plants selfed in the field, and for our pollination treatment, we simulated outcrossing of all flowers by adding a fractional increase of 1.0526 in seeds per fruit and a fractional increase in 1.0989 in fruits per plant. Thus, our "pollinator" treatment represents the most optimistic gains possible in pollinator service: complete selfing to complete outcrossing, but these are both realistic possibilities in the field.

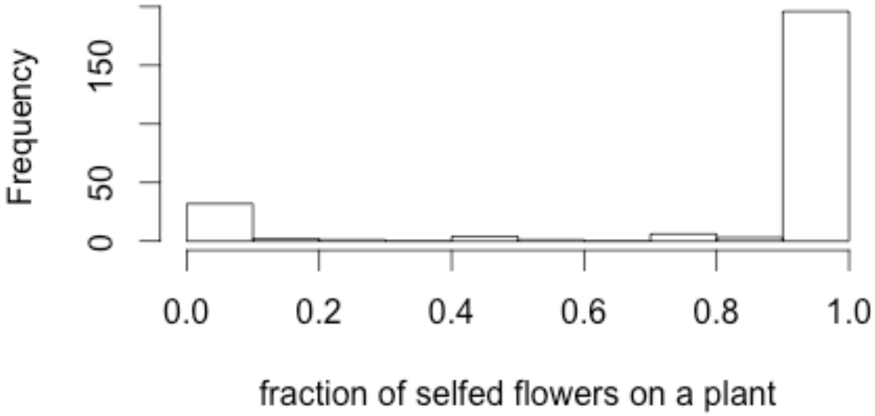

Figure 9. Fraction of selfed flowers on a plant (where a style recurved more than 90 degrees counted as a selfed flower) across all levels and treatments.

Another possible complication to our way of simulating pollination effects is that effects of inbreeding depression are usually more severe in stressful environments (Armbruster & Reed 2005). Thus, a change from 0 to 100% outcross pollination may have more substantial impacts in our Arid Site than in our Mesic Site. When incorporating a 69% increase in the magnitude of inbreeding depression in the Arid Site compared to the Mesic Site (species-wide average of increase in inbreeding depression in stressful v. benign sites, according to a recent review, Armbruster & Reed 2005), we see stronger effects of pollinators in our Arid Site (completely contrary to SIASH). It is possible that this percentage is an overestimation of the magnitude of effects of inbreeding depression in the Arid Site in *H. meyeri,* for three reasons: (i) while some of the “benign” sites in this review were greenhouse conditions, watering *H. meyeri* in our Mesic Site still increases performance, indicating our Mesic Site is clearly still stressful; (ii) lineages within an inbred population often exhibit very different relationships between stress and inbreeding depression, suggesting inconsistent responses (Armbruster & Reed 2005); and (iii) 24% of species show no change at all in inbreeding depression with stress (Armbruster & Reed 2005).

Random effects are unimportant

We conducted replicate measurements by different measurers at the same time (or within ~2 days) to get an estimate of measurer effects on our measurement of size. Our two metrics of size, basal area and height, were strongly correlated across multiple measurers. We assumed that measurements by A. Louthan (who performed measurements consistently throughout the duration of this study) were “true” measurements. Average fractional deviation from Louthan’s measurements [(alternate measurer’s measurements- Louthan’s measurements)/Louthan’s measurements] was small (0.14 for basal area and 0.12 for height), and the r-squared of log-transformed basal area*height (we use basal area*height in our biomass estimation; see below) of a linear regression between the alternate measurer’s measurements and Louthan’s measurements was 0.93 (see Fig. 10). Further, the random effect of measurer only explained a small fraction of total variance of the model (see Table 15).

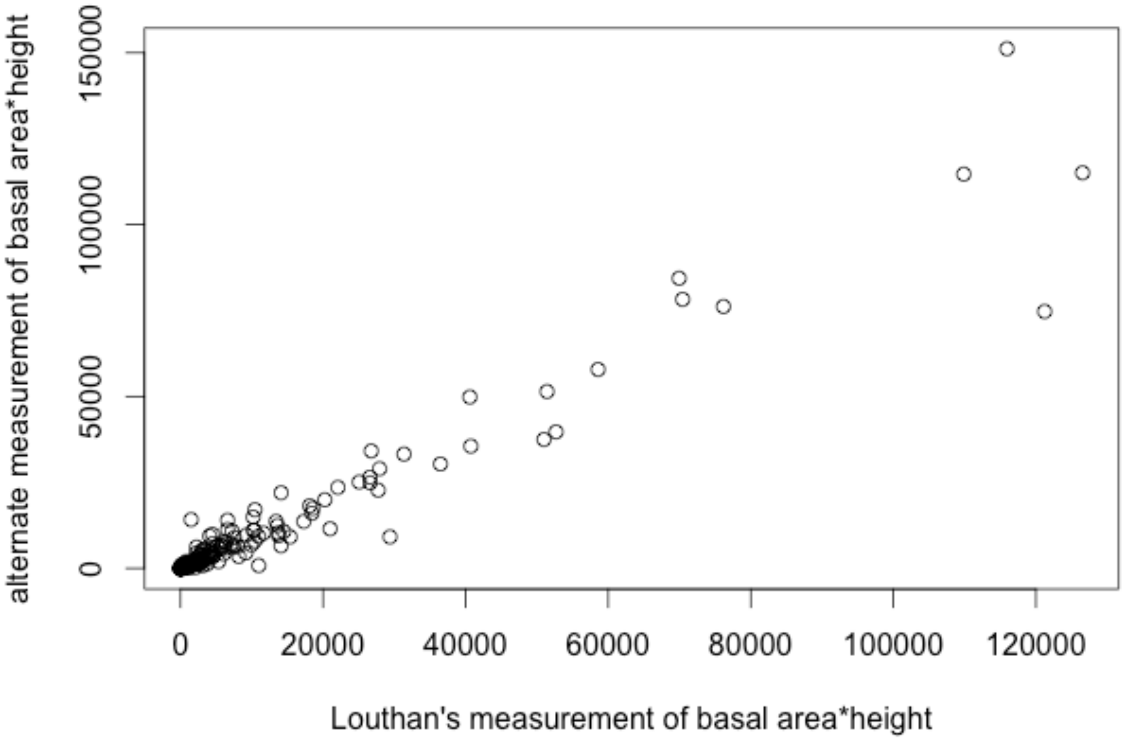

Figure 10. Louthan's measurement v. alternate measurers' measurement of basal area*height. We expect to see more substantial variation at larger sizes, as larger plants are likely measured with more error.

vital rate model	fraction variance explained by block	fraction variance explained by measurer
survival, best fit	4.90E-02	2.68E-02
growth, best fit	6.18E-02	6.81E-04
variance in growth, best fit	8.55E-03	0.00E+00
p(reproduction), best fit	2.51E-01	0.00E+00
number of fruits|reproduction, best fit	1.15E-01	3.43E-13
survival, global	4.02E-02	2.18E-02
growth, global	5.98E-02	8.79E-04
variance in growth, global	7.52E-03	1.85E-16
p(reproduction), global	2.47E-01	0.00E+00
number of fruits|reproduction, global	1.09E-01	0.00E+00

Table 15. Fraction of total variance (residual variance + variance explained by block + variance explained by measurer) attributed to each random effect, for both best-fit and global vital rates.

Getting biomass

To generate a unified metric of size, we measured and harvested above-ground biomass of 30 plants arrayed equally across the three rainfall levels, drying to a constant weight and then regressing log-transformed dry biomass on log-transformed basal area *height. This gave us biomass= exp(0.3338488 * log(basal area*height)), which had an r-squared of 0.88.

Plants subject to neighbor removal treatments show a different relationship between basal area and height (increased basal area growth relative to height, perhaps due to alleviation of light limitation; A. Louthan personal observation). To generate a separate biomass regression for plants without neighbors, in July 2012 we also conducted neighbor removals on 19 plants using the same protocols as neighbor removals in the main text (7 at the Intermediate site, 3 at the Arid Site, 9 at the Mesic Site; sample sizes are unequal due to mortality after establishment of these treatments, and for each site, we had roughly equal numbers of plants in both the full exclosures and areas open to herbivores). In June 2014, we measured and harvested them, drying to a constant weight and then regressing log-transformed dry biomass on log-transformed basal area *height. This gave us biomass= exp(0.3593906 * log(basal area*height)), which had an r-squared of 0.90. We used these two equations to get estimates of biomass for both unmanipulated plants and plants subject to neighbor removal treatments.

Rainfall is a stressor

We know that water is a limiting resource. First, we observed the highest lambda values in the Mesic Site in the absence of any of our three measured species interactions (Table 16). Also, we conducted a watering experiment within the full exclosures at each of three levels, watering 19-21 plants at each level (see Table 9 for sample sizes) with 7.5 L every month for 10 months (March 2014-Feburary 2015) and comparing them to the growth of unmanipulated control plants (of the neighbor removal experiment) over this same interval. This level of rainfall approximated ½ the long-term average of rain in the Mesic Site (2009-2012, when we initiated the experiment). We compared all putative subsets of growth as a function of the interaction between level and treatment, with block as a random effect. Due to small sample size, the best-supported model indicates constant growth rates regardless of rainfall level or watering treatment (AIC weight = 0.486), but the second-best supported model indicates a positive effect of additional water on plant growth (AIC weight = 0.239).

Site	no neighbors no herbivores no pollinators	neighbors no herbivores no pollinators	no neighbors herbivores no pollinators	no neighbors no herbivores pollinators	neighbors herbivores no pollinators	neighbors herbivores pollinators
Arid	1.230 (0.0360)	0.9370 (0.0167)	1.048 (0.0244)	1.259 (0.0387)	0.9317 (0.127)	0.9341 (0.0127)
Intermediate	1.545 (0.0570)	1.0945 (0.0220)	1.262 (0.0377)	1.593 (0.0615)	0.9985 (0.145)	1.007 (0.0151)
Mesic	3.618 (0.492)	1.5548 (0.117)	1.925 (0.126)	3.826 (0.530)	1.101 (0.0300)	1.124 (0.0318)

Table 16. Lambda values as a function of rainfall amount and presence of species interactions, with standard deviation shown in parentheses (standard deviations are calculated across 500 replicates that assume parameter uncertainty in the best-fit models for vital rates). Field-observed lambda values (naturally occurring lambda values) are highlighted in red.

Rainfall

Average annual rainfall from 2009-2014 (the records available at submission time) is 486.4 mm/year in the Arid Site, 577.4 mm/year in the Intermediate Site, and 593.8 mm/ year in the Mesic Site (Table 12). Rainfall data before June 2010 come from manual rain gauges (1 at each of the three rainfall levels), and after from automatic rain gauges (2-3 at each of the three rainfall levels) in the full exclosure treatments.

Calculation of rain & interactor density values

We used cumulative rainfall (the average of 2-3 automatic rain gauges at each rainfall level) between the midpoint of the first *H. meyeri* remeasurement period (this period was usually 2-3 months long) and the midpoint of the second *H. meyeri* remeasurement period as a predictor variable. Specifically, we used rainfall between each of our *H. meyeri* remeasurement periods as a predictor variable for survival and growth during that same interval, as well as reproduction at the end of that interval.

Similarly, we used dung counts (a proxy for herbivore activity) during the interval as a predictor of survival and growth during that interval and reproduction at the end of that interval. For each dung survey*rainfall level*block*treatment combination, we summed total dung counts collected along 3 transects to get an estimate of herbivore activity per survey (Goheen et al. 2013). To obtain an estimate of average herbivore activity in each rainfall level*block*treatment during the intervals between *H. meyeri* measurements, we averaged the data from the dung counts conducted between the midpoint of the first *H. meyeri* remeasurement period and the midpoint of the second *H. meyeri* remeasurement period. We used the midpoint of the dates over which the dung survey was conducted as the date of the dung survey in this analysis. For our initial measurements, we averaged the data from the dung counts collected over the previous year. We discarded dung counts for hippo, which are only counted in 1 survey (only 1 dung pile was found), as well as for all predators. For survey 9, the Intermediate Site blocks 1 & 2 were not labeled, so we discarded these dung counts. For survey 8, there were missing data for a few species (new camel dung, old waterbuck dung, baboon), so we replaced these missing data with zeros, as average dung counts across all transects for these species were 0.004, 0.004, 0.005, respectively.

For our transects outside of the UHURU plots, for which we had neither rainfall data nor herbivore dung counts, we used the average of all that rainfall levels' blocks' data for a given time period. Transects were ~200 m from the plots, and thus likely experience similar herbivore densities and rainfall levels.

For our main results, presented in Figs. 1 and 2 of Chapter 5, we used the average of observed rainfall values between our *H. meyeri* remeasurement periods to get rainfall level-specific values of rainfall, and we averaged across all blocks' observed herbivore activity values between our *H. meyeri* remeasurement periods to get rainfall level* herbivore exclosure treatment-specific herbivore activity predictor variables. For neighbor cover and distance to woody plant, we averaged all non-manipulated plants' observed values in each rainfall level* herbivore exclosure plot to get a mean value for each rainfall level* herbivore exclosure. For our results with non-specific predictor variables, for rainfall we used the average of observed rainfall values between our *H. meyeri* remeasurement periods to get rainfall level-specific values of rainfall (as above). For dung counts, we averaged across all blocks' observed herbivore activity values between our *H. meyeri* remeasurement periods to get herbivore exclosure treatment-specific herbivore activity predictor variables. Finally, for neighbor cover and distance to woody plant, we averaged all non-manipulated plants' observed values to get a universal mean value.

For our calculations of sensitivities, we used a matrix with no neighbors, herbivores, or pollinators, and the mean distance to woody plant (across Arid, Intermediate, and Mesic Sites) in the absence of herbviores. We assumed that herbivore activity in full exclosures was "no herbivory" and that a neighbor cover of 0 was "no neighbors."

Densities of herbivores across herbivore exclosures & rainfall levels

Herbivore exclosures are highly effective and herbivore densities are higher in our Arid Site. We used dung count data from the 19 dung count surveys used in this study, conducted between July 2010 and May 2015, to test for differences in herbivore activity. We summed total dung found in each rainfall level*treatment*block* survey combination, then averaged across blocks for each survey. We found a significant effect of rainfall level on log-transformed dung counts in control areas open to herbivores (ANOVA, F= 5.69 p= 0.006), with higher herbivore activity in the Arid Site than in the Mesic Site (Tukey's HSD, p= 0.004); mean dung counts values in open controls are Arid Site: 23.6, Intermediate: 21.5, and Mesic: 13.4. Herbivore exclosure had significant effects on total dung: a two-way ANOVA revealed nonsignifincant effects of level and level*treatment, but significant effects of treatment (F=94.7488 p=<2e-16). Control, MEGA, and MESO had greater amounts of total dung than LMH (Tukey's HSD, p<<0.05).

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