Aridity weakens population-level effects of multiple species interactions on *Hibiscus meyeri*

Allison M. Louthan[a,b,c,1], Robert M. Pringle[b,d], Jacob R. Goheen[b,e], Todd M. Palmer[b,f], William F. Morris[a], and Daniel F. Doak[b,c]

[a]Department of Biology, Duke University, Durham, NC 27708; [b]Mpala Research Centre, Nanyuki 10400, Kenya; [c]Environmental Studies Program, University of Colorado, Boulder, CO 80309; [d]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544; [e]Program in Ecology, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071; and [f]Department of Biology, University of Florida, Gainesville, FL 32611

Edited by Hugh P. Possingham, University of Queensland, St. Lucia, QLD, Australia, and approved November 14, 2017 (received for review May 22, 2017)

Predicting how species' abundances and ranges will shift in response to climate change requires a mechanistic understanding of how multiple factors interact to limit population growth. Both abiotic stress and species interactions can limit populations and potentially set range boundaries, but we have a poor understanding of when and where each is most critical. A commonly cited hypothesis, first proposed by Darwin, posits that abiotic factors (e.g., temperature, precipitation) are stronger determinants of range boundaries in apparently abiotically stressful areas ("stress" indicates abiotic factors that reduce population growth), including desert, polar, or high-elevation environments, whereas species interactions (e.g., herbivory, competition) play a stronger role in apparently less stressful environments. We tested a core tenet of this hypothesis—that population growth rate is more strongly affected by species interactions in less stressful areas—using experimental manipulations of species interactions affecting a common herbaceous plant, *Hibiscus meyeri* (Malvaceae), across an aridity gradient in a semiarid African savanna. Population growth was more strongly affected by four distinct species interactions (competition with herbaceous and shrubby neighbors, herbivory, and pollination) in less stressful mesic areas than in more stressful arid sites. However, contrary to common assumptions, this effect did not arise because of greater density or diversity of interacting species in less stressful areas, but rather because aridity reduced sensitivity of population growth to these interactions. Our work supports classic predictions about the relative strength of factors regulating population growth across stress gradients, but suggests that this pattern results from a previously unappreciated mechanism that may apply to many species worldwide.

abiotic stress | climate change | population growth | range boundaries | species interactions

Understanding the relative strength of the factors that regulate population growth and abundance is a fundamental goal of ecology. In the era of anthropogenic climate change, it is particularly important to understand what factors allow populations to persist and set species' range boundaries (1–4). Although we know that climate and other abiotic factors can constrain geographic ranges (2), theoretical and empirical studies show that predation, competition, and other species interactions can also limit population growth substantially enough to set range boundaries (5–8). One long-standing hypothesis, first proposed by Darwin (5), predicts that abiotic factors should set range boundaries in areas that are cold, dry, or both (hereafter "stressful environments"), whereas species interactions should set boundaries in less stressful environments. We refer to this idea, which has been discussed by multiple authors since Darwin (6–8) but never clearly named, as the species interactions–abiotic stress hypothesis (SIASH). Here, we use changes in estimated population growth rate as a metric of species interactions' effect size ("intensity" sensu ref. 9), and, as in previous work (8), we define "stress" as any abiotic condition, including but not limited to resource limitation, that reduces mean fitness or population growth rate. There are numerous experimental tests of this idea, but most focus on single interactions (e.g., refs. 10 and 11) and on small-scale gradients; most notably, antagonistic interactions across intertidal depths have generally supported the hypothesis (12, 13). Correlative data, such as abundance records (ref. 14, although see refs. 15 and 16) and studies of species distribution models (17) suggest that it might manifest across broader spatial scales (18, 19); patterns of cosympatry also provide mixed support (20, 21).

Nonetheless, we still require large-scale experimental tests of the generality of SIASH, tests of the mechanisms generating differential effects of species interactions across stress gradients, and simultaneous consideration of multiple types of species interactions (8). Opposing effects of different species interactions, multiple interacting stress gradients, or range boundaries caused by other factors (such as dispersal limitation, lack of genetic variability in peripheral populations, or other nondemographic constraints) could all limit the generality of Darwin's conjecture. In fact, the stress gradient hypothesis, which enjoys considerable empirical support, predicts that the intensity of positive vs. negative effects (but not necessarily net effect size) of species interactions should vary systematically with stress (22). While there is some evidence that both negative and positive interactions should set similar range limits (23), Darwin predicted only how the strength of antagonistic interactions varies across stress gradients (5). Despite this mixed empirical and theoretical support,

Significance

Predicting the impacts of global change on biodiversity requires understanding the factors that regulate population growth and set species' range boundaries. Darwin proposed that abiotic factors limit population growth in stressful areas, whereas species interactions dominate in less stressful environments because of an increased density and diversity of enemies (consumers, parasites, pathogens). We present experimental support for this hypothesized shift in the strength of species interactions with climate, but we also show that this pattern does not arise from Darwin's proposed mechanism. Our work implies that effects of species interactions on population growth rate decrease with stress, with implications for how different range boundaries are likely to respond to climatic change.

Author contributions: A.M.L. and D.F.D. designed research; A.M.L., R.M.P., J.R.G., T.M.P., W.F.M., and D.F.D. performed research; A.M.L. analyzed data; and A.M.L., R.M.P., J.R.G., T.M.P., W.F.M., and D.F.D. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

Data deposition: The data used to construct integral projection models and project population growth rates, as well as the data used in the *Supporting Information*, have been deposited in figshare (https://doi.org/10.6084/m9.figshare.5660608.v2).

[1]To whom correspondence should be addressed. Email: allisonmlouthan@gmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1708436115/-/DCSupplemental.

Downloaded from https://www.pnas.org by 70.185.125.9 on November 11, 2026 from IP address 70.185.125.9.

SIASH has recently been invoked to explain broad-scale patterns in species' abundance and distribution, including discrepancies between trailing and leading range boundary dynamics (19, 24).

The central premise of SIASH is that species interactions strongly limit population growth rate in less stressful areas, ultimately driving populations into decline, but have little effect on population growth rate in more stressful areas (8). Darwin originally proposed—and it is still commonly assumed—that higher densities or diversities of interacting species in less stressful areas generate stronger population-level effects of species interactions (5, 7, 25); we call this the "density mechanism." However, at least two other mechanisms could also generate this pattern. The "per capita impact mechanism" predicts that each individual interactor exerts stronger effects on vital rates (e.g., survival, growth, and reproduction) in less stressful areas. For example, an herbivore could consume more plant tissue in mesic areas because plants are more palatable or occur at higher densities, making them easier to find. The "life history mechanism" could operate if stress alters species' demographic patterns such that the same per capita effects and interactor densities generate stronger effects on population growth in less stressful areas. For example, if offspring establishment is higher in less stressful areas, then population growth may be more sensitive to herbivore-induced reductions in plant reproductive output in these areas than in more stressful sites.

Here, we experimentally test how multiple types of species interactions impact population growth rate across an abiotic stress gradient, and how differences in interaction strengths arise. We quantified the effects of four species interactions, including both positive and negative interaction types, on vital rates and population growth rates of a common African plant, *Hibiscus meyeri* (Malvaceae), across an aridity gradient in central Kenya. *H. meyeri* occurs in semiarid savannas, where plants experience (*i*) water limitation; (*ii*) both competitive and facilitative effects from neighboring shrubby and herbaceous plants (26); (*iii*) browsing by a diverse array of large mammals (27); and (*iv*) variability in insect-mediated outcross pollination (*Supporting Information*).

Results

At three sites across the stress gradient (Arid, Intermediate, and Mesic, collectively spanning a 22% increase in mean annual precipitation; ref. 28), we collected demographic data over 4 y on *H. meyeri* plants that varied in their distance to woody plants ("shrubs"), and that were subjected to factorial manipulation of (*i*) mammalian herbivores (27) (Fig. S1) and (*ii*) neighboring (<30-cm) herbaceous vegetation. We estimated effects of rainfall in the year before measurement, neighboring herbaceous plant cover ("herbs"), distance to nearest shrub, and herbivory ("herbivores," as estimated by the amount of mammalian herbivore dung) on five classes of vital rates (size-specific survival, growth, probability of fruiting, number of fruits given fruiting, and fruit-to-seedling transition rate), using mixed models with block as a random effect (Fig. S1). To simulate the positive effects of pollinator presence, we increased predicted values of seeds per fruit and fruits per plant (the two vital rates affected by inbreeding depression in a congener; ref. 29 and *Supporting Information*), as pollinators alleviate the inbreeding depression associated with facultative self-pollination (30), the most common type of pollination for *H. meyeri*. Species interactions and aridity influenced multiple vital rates, with the strongest aridity effects on fruit-to-seedling transition rate and strongest species interaction effects on decrease in reproduction due to shrub proximity and herbivore presence (Fig. S2 and Table S1).

We combined vital rate estimates to estimate stochastic population growth rate (λ_s) as functions of both stress (i.e., temporal and spatial variation in rainfall) and each type of species interaction using integral projection models (IPMs) (31), which, like other demographic models, use size- or other stage-specific estimates of different vital rates to generate estimates of population growth. We then simulated removal of herbs, shrubs, or mammalian herbivores (by reducing interactor densities to approximately zero in our mixed models and recalculating λ_s; *Supporting Information*) or addition of pollinators (by increasing predicted values of seeds per fruit and fruits per plant, as described above; hereafter, "simulated pollinators") to quantify the effect of each interaction on λ_s at each site. We then asked whether the strength of these effects differed consistently from the Mesic to Arid site (Fig. 1 and Fig. S3).

Effects of aridity and species interactions on population growth rate were all in the predicted directions: Arid λ_s was lower than Mesic λ_s, and the removal of consumptive or net competitive effects (i.e., herbs, shrubs, and herbivores) or addition of positive interactions (simulated pollinators), increased λ_s at all three sites (Fig. 1). The magnitudes of effects of all four species interactions were also consistent with SIASH's predictions: effects of each interaction on λ_s increased from the Arid to the Mesic site (Fig. 1). This consistent effect was observed even for simulated pollinators, a positive species interaction, and even when a species interaction had positive effects on one vital rate(s) and negative effects on others (e.g., removing shrubs reduced survival but increased number of fruits among plants that fruited; Fig. S2 and Table S1). Support for SIASH was also robust to model and parameter uncertainty, which we quantified by estimating a relative interaction effect (RIE) index, the difference between ln[(λ_s with herb, shrub, or herbivore removal, or simulated pollinator addition)/(λ_s under field conditions)] at the Mesic vs. Arid site for 1,000 sets of random vital rate models and parameter values (Fig. 2 and Fig. S3). RIE values, which compare the effect of a species interaction on λ_s between our two climatically extreme sites, were consistently greater than zero, conforming to SIASH predictions.

To test how the density, per capita impact, and life history mechanisms each contributed to stronger effects of species interactions on population growth under less stressful conditions, we decomposed RIE values into the relative contribution of each mechanism by reestimating RIE while holding the various parameters controlling nontarget mechanisms constant in the underlying vital rate functions (*Materials and Methods*). For shrubs, herbivores, and simulated pollinators, the life history mechanism almost entirely accounted for stronger effects in the Mesic site (Fig. 3). For *H. meyeri*'s interaction with herbs, the density mechanism also contributed substantially to stronger effects in the Mesic site. For herbivory, the density mechanism actually reduced RIE values due to higher herbivore activity at the Arid site during our study (28) (*Supporting Information*).

The strong support for the life history mechanism means that population growth was more sensitive at the Mesic than the Arid site to changes in one or more vital rates that were influenced by each species interaction. To isolate the contribution of each vital rate's variation with aridity to the difference in effects of species interactions across sites, we adopted a similar approach to that described for our first decomposition. In these RIE calculations, λ_s estimates were generated using site-specific values of the target species interaction on all vital rates, but values of only the target vital rate included site-specific rainfall and block effects (*Materials and Methods*), isolating the effects of aridity-driven vital rate differences.

For each species interaction, changes across sites in a single vital rate generated the majority of the SIASH pattern. For interactions with herbs, shrubs, and simulated pollinators, changes in the fruit-to-seedling transition rate (Fig. S2) generated essentially the entire pattern of stronger effects of species interactions at the Mesic site (Fig. 4). For herbs and simulated pollinators, these effects were at least partially direct, as these species interactions affected fruit-to-seedling transition rate (Fig. S2 and Table S1). By contrast, for shrubs, these effects were entirely indirect: shrubs did not directly affect fruit-to-seedling transition rate (Fig. S2 and Table

Downloaded from https://www.pnas.org by 70.185.125.9 on November 11, 2026 from IP address 70.185.125.9.

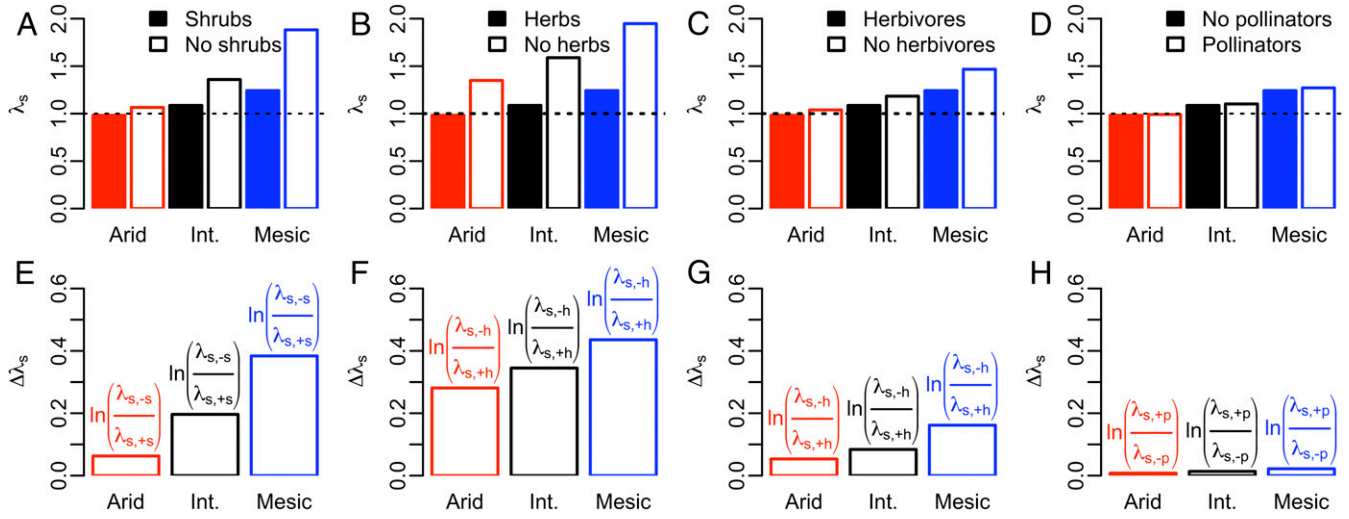


Fig. 1. Aridity and all four species interactions affected *H. meyeri* population growth rate (λ_s). We calculated λ_s with natural levels of the species interactions (filled bars) and with modified levels of the species interactions (open bars) at each site (*A–D*) and calculated the mean log ratio of each λ_s pair ($\Delta\lambda_s$; *E–H*) across 1,000 replicates incorporating model and parameter uncertainty. For antagonistic interactions, we estimated effects on λ_s using the ratio of growth in the absence of the interaction (indicated by −s and −h) to that under natural levels of the interaction (*A–C* and *E–G*, indicated by +s and +h); for simulated pollinators, to preserve the same scaling, we used the opposite ratio (*D* and *H*; +p indicates the presence of simulated pollinators, and −p indicates the absence of simulated pollinators). Int., Intermediate site.

S1), but the much higher Mesic site fruit-to-seedling transition rate means that the effects of shrubs on reproductive rates generated much larger increases in λ_s at the Mesic than Arid site. For herbivores, aridity-driven differences in reproduction (combined probabilities of fruiting and number of fruits among plants that fruited) directly generated the majority of the SIASH pattern (Fig. 4*C*, Fig. S2, and Table S1), although survival and mean growth also contributed (and fruit-to-seedling transition rate countered the net effect). In sum, at the Mesic site, the life history of *H. meyeri* was altered such that λ_s was far more sensitive to the effects of all four species interactions on vital rates, especially those that altered reproduction or recruitment (Fig. S4).

Discussion

Population growth of *H. meyeri* was more sensitive to species interactions in abiotically less stressful areas, supporting the fundamental pattern hypothesized by SIASH (8). This finding accords with prior experimental and correlative studies, including Connell's (12, 13) experimental studies on predation and herbivory in intertidal ecosystems and work describing broad-scale patterns in species distributions (14, 17, 19, 21, 24, 25). Our findings of weaker net competitive effects of herbs and shrubs in the Arid site are also consistent with the predictions of the stress gradient hypothesis (22), although we do not see evidence of net facilitative effects on population growth under any conditions in our study.

Variation in plant life history across the aridity gradient was integral to generating the SIASH pattern: aridity sharply decreased fruit-to-seedling transition rate, which in turn reduced the sensitivity of population growth to both this vital rate itself, as well as, less substantially, to other vital rates associated with offspring production (Fig. S4). Low sensitivities to these vital rates in the Arid site resulted in weak population-level effects of species interactions that affected offspring production. This finding differs from the common assumption that the SIASH pattern arises due to higher densities or diversities of interacting species in less stressful areas (5, 7, 25). This life history mechanism could generate the SIASH pattern in many systems and should operate whenever (*i*) one or more proportional sensitivities to λ_s decrease with stress and (*ii*) species interactions have similar proportional effects on vital rates across a stress gradient. One other full demographic study provides evidence that the proportional sensitivity of λ to vital rates might differ systematically across environmental gradients in just this way (32). However, we also note that the life history mechanism could also generate the opposite of the SIASH pattern if proportional sensitivities to λ_s increase with stress.

The strong effects of aridity on vital rate sensitivities associated with offspring production and survival that we see here seem likely to be present for many plant populations that occur across stress gradients. Stress, specifically aridity, tends to have the strongest negative impacts on younger and more vulnerable life stages, such that seed establishment and seedling survival are strongly impacted (33–36). These negative impacts will tend to decrease the relative effect of species interactions that affect offspring production on population growth, leading to the exact SIASH pattern we document here.

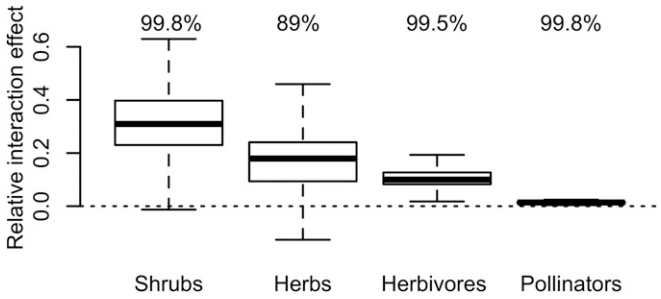


Fig. 2. Species interactions exerted stronger effects on λ_s in less stressful areas. The difference between Mesic and Arid $\Delta\lambda_s$ (Fig. 1) represents the relative interaction effect (RIE), with RIE > 0 indicating stronger effects of manipulating species interactions at the Mesic site than the Arid site. Boxplots show predictions incorporating model and parameter uncertainty, and numbers above boxes indicate the percentage of 1,000 replicates where RIE > 0. For antagonistic interactions, we estimated effects on λ_s using the ratio of λ_s with a species interaction removed to that with the natural levels of the species interaction; for simulated pollinators, to preserve the same scaling, we used the opposite ratio.

Downloaded from https://www.pnas.org by 70.185.125.9 on November 11, 2026 from IP address 70.185.125.9.

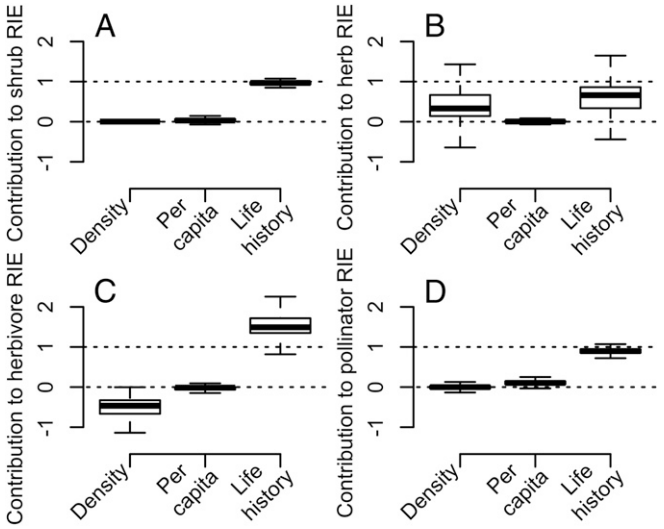


Fig. 3. The SIASH pattern arose primarily from the life history mechanism. Boxplots show RIE values, incorporating model and parameter uncertainty of 1,000 replicates, decomposing the mechanisms creating greater effects of species interactions on λ_s in the Mesic vs. Arid site, for shrubs (*A*), herbs (*B*), herbivores (*C*), and simulated pollinators (*D*). Values are standardized by dividing by the total RIE from a replicate, so that with strict additivity the three values would sum to 1. Positive numbers indicate that the mechanism contributed to the expected SIASH pattern; negative numbers indicate mechanisms opposing the net pattern (e.g., the density mechanism for herbivory, *C*, contributed to stronger effects of herbivores in the Arid site, opposing the net SIASH pattern).

In our study, per capita effects of species interactions and density of interactors were largely unchanged with stress (Fig. S2). In other species or other species interactions, per capita effects on vital rates might differ with stress, such that we would not see the same level of support for SIASH that we observe in this study. For example, antagonistic interactions such as herbivory, predation, or parasitism might exert negligible effects on vital rates in less stressful areas because individuals are better able to compensate for damage (37) or deter attack (38, 39), resulting in weaker support for SIASH. Alternatively, if interactor density decreases with stress, then we might see stronger support for SIASH, as well as stronger effects of the density mechanism in generating the SIASH pattern (as we found for effects of herbs on *H. meyeri*). The density mechanism might play a crucial role over larger spatial scales, such as latitudinal gradients, that can exhibit strong variation in interactor diversity and density (40). Although our results were consistent across a multitude of species interactions and suggested a strong role for the life history mechanism, further demonstrating the generality of the pattern will require attention to a broader range of taxa and stress gradients. In the case of multiple uncorrelated abiotic stressors, support for SIASH will depend on patterns of interactor density and diversity, per capita impacts of interactors, and life history of the focal organism across the combined stress gradients; the latter two in particular are poorly understood for most species, even across a single axis of one type of stress.

Our results suggest that species interactions may be the strongest force setting *H. meyeri* range boundaries in less stressful areas by limiting population growth and ultimately driving $\lambda_s < 1$. We did not see direct evidence for population decline due to species interactions, likely because our experiment was not near the species' mesic range boundary; while precipitation in our experiment spans an appreciable fraction (8%) of the range of annual precipitation levels experienced by *H. meyeri* across its range, the conditions at our study sites were on the arid end of the species' climate envelope (*Supporting Information*). For species interactions to set the mesic range boundary would require that impacts of species interactions on population growth continue to increase with rainfall and offset any positive, direct effects of increasing moisture. Confirmation of this hypothesis would require transplant experiments beyond the species' climatic range boundaries combined with manipulations of species interactions, as well as tests of other potential range boundary drivers.

Collectively, our data show that the effects of species interactions on population growth rate vary as a function of stress, a crucial step in distinguishing abiotic vs. biotic controls of both population growth and range boundaries. Consistent with the apparent lack of abiotic control over some warm-edge range boundaries (19, 24), our results suggest that species interactions could constrain many trailing edge boundaries (24) while having relatively weak effects on leading edge boundaries. Furthermore, we show that this pattern results from a hitherto-largely overlooked mechanism, changes in the sensitivity patterns of population growth with decreasing stress. These results caution against ignoring or minimizing effects of species interactions when predicting future distributions (4, 41–46).

Materials and Methods

We worked at the Mpala Conservancy in central Kenya, a semiarid acacia savanna (0°17′N, 37°52′E), with little spatial temperature variation and a diverse assemblage of large mammalian herbivores (*Supporting Information*). We used a replicated large-scale exclusion experiment arrayed across a pronounced rainfall gradient [Ungulate Herbivory Under Rainfall Uncertainty (UHURU) (28)] to manipulate mammalian herbivores. UHURU comprises 36 1-ha plots, including unfenced controls and three size-selective exclosure treatments; each treatment is replicated three times in blocks at each of three sites across the rainfall gradient (Fig. S1). Total average rainfall increases 22% from the Arid to Mesic site, and soil characteristics do not vary

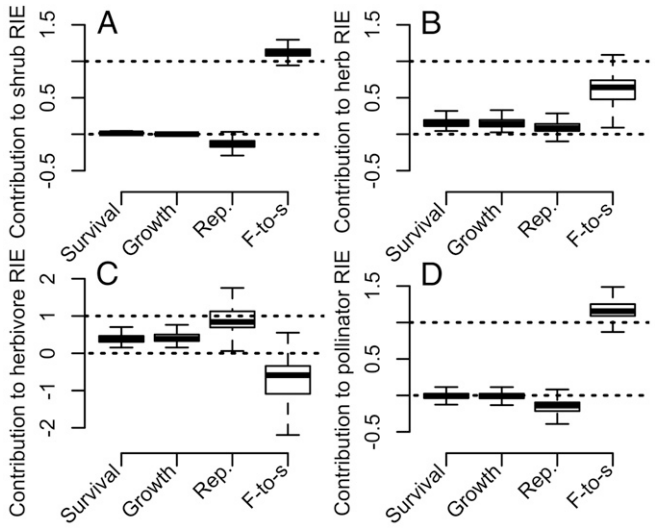


Fig. 4. The difference between fruit-to-seedling transition rate between Arid and Mesic sites was the primary vital rate difference generating the SIASH pattern. Boxplots show contributions of each vital rate to total RIE value for 1,000 replicates incorporating model and parameter uncertainty of decompositions of the vital rates, analogous to Fig. 3, for shrubs (*A*), herbs (*B*), herbivores (*C*), and simulated pollinators (*D*). Values are standardized by dividing by the total RIE from a replicate, so that with strict additivity the four values would sum to 1. Positive numbers indicate that aridity-driven differences in a vital rate contributed to the expected SIASH pattern; negative numbers indicate effects opposing the net pattern [e.g., for herbivores (*C*), fruit-to-seedling transition rate contributed to stronger effects of herbivores in the Arid site, opposing the SIASH pattern]. Note difference in scale in *D*. F-to-s, fruit-to-seedling transition rate; Rep., reproduction (probability of fruiting and number of fruits given fruiting).

Downloaded from https://www.pnas.org by 70.185.125.9 on November 11, 2026 from IP address 70.185.125.9.

substantially across this gradient (28). We used rain gauges to measure precipitation and quarterly herbivore dung counts (28) as a proxy for herbivore density (*Supporting Information*). We collected data from all herbivore exclosure treatments and used it to parameterize vital rate models, but our herbivore presence/absence contrast compares results from unfenced plots and the total-exclosure treatment, which reduces densities of all large mammal herbivores to zero.

In this ecosystem, *H. meyeri* is a common water-limited subshrub (*Supporting Information*). It is heavily browsed by multiple mammal species, has no pronounced chemical or physical defenses, and exhibits moderate compensatory regrowth following herbivory (27). Its flowers present their styles for outcross pollination by insects but can also self-pollinate if no insects visit. Self-pollination is very common, but bouts of outcrossing also occur (*Supporting Information*). *H. meyeri* life history varies substantially across this gradient (time required by the population to increase by a factor of R_0, generation time, is 22.1 y in the Arid, 15.0 in the Intermediate, and 9.9 in the Mesic site; Fig. S2).

Data Collection. In July 2011, to assess effects of rainfall and herbivory on *H. meyeri* vital rates, we searched randomly selected areas in all UHURU sites and treatments (controlling for plant phenology; ref. 27), as well as four transects outside of the UHURU experiment (two at the Mesic and two at the Arid site, each coded as a separate block for analysis), and marked and mapped all *H. meyeri* individuals, measuring size, counting fruits, and estimating percent ground cover of all vegetation in a 30-cm radius (sample sizes in Table S2). Until 2014, we returned annually to remeasure these plants, also recording survival and distance to nearest woody or succulent shrub (acacia, *Vachellia* spp., and *Senegalia* spp., as well as *Euphorbia nyikae*, *Croton dichogamous*, *Grewia* spp., *Balanities* spp., or *Boscia* sp.) >30 cm tall. Throughout the study, we marked new plants in the same areas to replace dead individuals for a total of 1,719 unique individuals followed.

To quantify the effect of herbaceous neighbors on plant vital rates, we marked and measured haphazardly chosen plants (arrayed across the size spectrum) in the total-exclosure and unfenced control plots and transects at all sites (26), randomly assigned one-third to a neighbor removal treatment, and removed all herbaceous biomass within a 30-cm radius, carefully painting the cut stalks with herbicide (glyphosate) to prevent resprouting. We repeated this biomass removal procedure twice yearly and remeasured all plants annually, replacing dead or missing plants as necessary, for a total of 1,504 individuals (Table S2).

Unlike the experimental approach used for herbs and herbivores (which estimates the effect of experimentally reducing species interactions from their naturally occurring densities to zero) and the observational approach we used for shrubs (which quantifies the effect of shrubs at naturally occurring average vs. far distances), we used a simulation-based approach based on partial observational data to estimate the possible effects of pollinators. We used work on a congeneric species with a similar floral phenotype [*Hibiscus trionum* (29); *Supporting Information*] to simulate a release from inbreeding depression caused by increased pollinator visitation rate (which affected two vital rates, fruit-to-seedling transition rate and number of fruits given fruiting). Our pollinator simulations assume that all fruits we observed in the field were self-pollinated, and represent a shift from 0% outcross pollination to 100% outcross pollination (both plausible outcomes, as field observations indicated that per-plant outcross-pollination rates were usually either 0% or 100%; *Supporting Information*). Thus, our results reflect the maximum possible effect pollinators could exert in this system (but see *Supporting Information*), although we do not experimentally quantify their effect.

We obtained fruit-to-seedling transition rate data by counting all seedlings in a 2-m radius around fecund individuals arrayed across all site*exclosure-treatment combinations immediately after a wet season.

Statistical Analysis. We used corrected Akaike information criterion (AICc) to select best-fit mixed-effects models for survival, mean growth, variance in growth, probability of fruiting, number of fruits produced, and fruit-to-seedling transition rate. We identified the best models from all subsets of a global model with initial biomass and all two-way interactions between rainfall (measured as site- and year-specific rainfall totals), herbivore activity (estimated via dung counts in each herbivore exclosure treatment*block combination), neighboring herbaceous plant cover, and distance to nearest shrub as fixed effects (or all interactions among rainfall, herbivore activity, and neighboring biomass cover as fixed effects for fruit-to-seedling transition rate; *Supporting Information*). Using continuous predictor variables (e.g., dung counts rather than herbivore exclosure treatment, or rainfall rather than site) allowed us to capitalize on spatiotemporal variation in these predictor variables to improve our predictions of vital rate responses.

For each of the three sites, we constructed stochastic IPMs (31) for each of five kernels representing different combinations of species interactions: (*i*) field conditions: + herbs, + shrubs, + herbivores, − simulated pollinators; (*ii*) field conditions − shrubs; (*iii*) field conditions − herbs; (*iv*) field conditions − herbivores; (*v*) field conditions + simulated pollinators, using 5 y of rainfall data (*Supporting Information*).

We incorporated both model and parameter uncertainty into our estimates of λ_s values (and hence effects of species interactions on λ_s). To do so, for each vital rate, we first selected a model from among those with ΔAICc $\leq$ 2 and with a probability of selection proportional to the model's AICc weight, and then sampled from the multivariate distribution of fixed-effect parameter estimates for the selected model (Table S1) and calculated each of the five above kernels for each set of parameter values. We replicated this procedure 1,000 times. For each replicate and species interaction, we calculated $\Delta\lambda_s = \ln(\lambda_s$ with altered species interactions/λ_s under field conditions) for both Mesic ($\Delta\lambda_{s,M}$) and Arid ($\Delta\lambda_{s,A}$) sites to obtain an RIE value (RIE = $\Delta\lambda_{s,M} - \Delta\lambda_{s,A}$). We present a graphical illustration of our approach to calculate $\Delta\lambda_s$ in Fig. 1 and our approach to calculate RIE in Fig. S3. Effects of species interactions in the Intermediate site always fell between those at Mesic and Arid sites. Alternative methods of parameterizing IPMs yielded similar results (*Supporting Information*), and λ_s values were near unity (Fig. S5).

To understand how the density, per capita impact, and life history mechanisms contributed to the patterns of RIE values, we decomposed the change in λ_s in Mesic vs. Arid sites attributable to each. For each species interaction, we estimated three modified RIEs; for each, we set two of the following three effects to mean values (mean pooled across Arid and Mesic sites) in our mixed-model vital rate functions, leaving site-specific values for Arid and Mesic vital rate functions for only one of the three effects: (*i*) density of focal interactors (e.g., herbivore activity level); (*ii*) rainfall terms in rainfall*focal species interaction terms (e.g., rainfall*herbivore activity level); (*iii*) block effects and rainfall in all other terms besides rainfall*focal species interaction terms. Retaining site-specific terms for (*i*) represents variation in interactor density with rainfall (density mechanism), (*ii*) represents variation in per capita vital rates (per capita impact mechanism), and (*iii*) represents the variation in life history effects (life history mechanism), assuming that block effects are entirely composed of effects of rainfall differences across sites (our results are robust to this assumption; *Supporting Information*). Field densities of pollinators do not vary between the Mesic vs. Arid site; thus, we could not vary (*i*) for simulated pollinators, and the rainfall terms in rainfall*focal species interaction (*ii*) comprises all rainfall terms in fruits per plant and fruit-to-seedling transition rate, the two vital rates affected by inbreeding depression. Block effects and rainfall values in all other vital rates comprise the life history mechanism. For example, to determine herbivore RIE attributable to the life history mechanism, we set Arid and Mesic site herbivore activity level equal to the mean herbivore activity level in Arid and Mesic sites (*i*) and did the same for rainfall values in rainfall*herbivore activity terms (*ii*), such that vital rate functions for Mesic vs. Arid sites differed only in block effects and rainfall values in other terms. To obtain a modified RIE, we followed the procedure described above, but using the modified vital rate functions just described. To quantify the contribution of each mechanism, we calculated a modified RIE and compared it to an unmodified RIE that used site-specific focal species interaction levels, rainfall values, and block effects.

To assess how aridity-driven differences in each type of vital rate contributed to RIE values, we used a similar approach. In these calculations, λ_s values were generated using site-specific values of the focal species interaction on all vital rates, but only the focal vital rate had site-specific rainfall and block effects. Values for all nonfocal species interactions, as well as rainfall and block values for nonfocal vital rates, were set to mean values across both sites. Note that variance in growth was always set to mean values. In this way, we isolated the effect of rainfall (assuming that block effects were driven by rainfall) and each focal species interaction on each focal vital rate, and then used the resulting λ_s values to calculate RIE. Comparing these modified RIE values to the unmodified RIE for an interaction gives the fractional contribution of each vital rate to the total RIE.

All data used to construct IPM projections are archived on figshare.

ACKNOWLEDGMENTS. We acknowledge funding from the Philanthropic Educational Organization Scholar Award; United Nations Educational, Scientific and Cultural Organization-L'Oréal International Fellowship; Wyoming National Aeronautics and Space Administration Space Grant; funds from the Universities of Colorado and Wyoming; National Science Foundation (NSF) Division of Environmental Biology (DEB) Grant 1311394 (with D.F.D.) (to A.M.L.); NSF Awards DEB-1355122, DEB-1457691, and IOS-1656527 (to R.M.P.); NSF DEB Early Concept Grants for Exploratory Research Grant 1547679, NSF DEB Grant

Downloaded from https://www.pnas.org by 70.185.125.9 on November 11, 2026 from IP address 70.185.125.9.

1556728, and awards from the University of Wyoming and the University of Wyoming Biodiversity Institute (to J.R.G.); NSF DEB Grant 1149980 (to T.M.P.); NSF DEB Grant 1242355 (to W.F.M. and D.F.D.); Strategic Environmental Research and Development Program Grant 15 RC01-096 (to W.F.M.); and NSF DEB Grant 1352781 (to D.F.D.). The UHURU experiment was built with a Natural Sciences and Engineering Council Research Tools and Instruments grant.

1. Gaston KJ (2003) *The Structure and Dynamics of Geographic Ranges* (Oxford Univ Press, New York).
2. Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. *Annu Rev Ecol Evol Syst* 40:415–436.
3. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669.
4. Alexander JM, Diez JM, Hart SP, Levine JM (2016) When climate reshuffles competitors: A call for experimental macroecology. *Trends Ecol Evol* 31:831–841.
5. Darwin C (1859) *On the Origin of Species by Means of Natural Selection* (J. Murray, London).
6. Dobzhansky T (1950) Evolution in the tropics. *Am Sci* 38:209–221.
7. MacArthur RH (1972) *Geographical Ecology: Patterns in the Distribution of Species* (Harper and Row, Princeton).
8. Louthan AM, Doak DF, Angert AL (2015) Where and when do species interactions set range limits? *Trends Ecol Evol* 30:780–792.
9. Brooker R, et al. (2005) The importance of importance. *Oikos* 109:63–70.
10. Miller TEX, Louda SM, Rose KA, Eckherg JO (2009) Impacts of insect herbivory on cactus population dynamics: Experimental demography across an environmental gradient. *Ecol Monogr* 79:155–172.
11. Matassa CM, Trussell GC (2015) Effects of predation risk across a latitudinal temperature gradient. *Oecologia* 177:775–784.
12. Connell JH (1961) Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol Monogr* 31:61–104.
13. Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.
14. Newsome TM, et al. (2017) Top predators constrain mesopredator distributions. *Nat Commun* 8:15469.
15. Fourcade Y, Öckinger E (2016) Host plant density and patch isolation drive occupancy and abundance at a butterfly's northern range margin. *Ecol Evol* 7:331–345.
16. Gutierrez D, Vila R, Wilson RJ (2016) Asymmetric constraints on limits to species range influence consumer-resource richness over an environmental gradient. *Glob Ecol Biogeogr* 25:1477–1488.
17. Peers MJL, Thornton DH, Murray DL (2013) Evidence for large-scale effects of competition: Niche displacement in Canada lynx and bobcat. *Proc Biol Sci* 280:20132495.
18. Sanford E, Roth MS, Johns GC, Wares JP, Somero GN (2003) Local selection and latitudinal variation in a marine predator-prey interaction. *Science* 300:1135–1137.
19. Ettinger AK, Ford KR, HilleRisLambers J (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* 92:1323–1331.
20. Jankowski JE, Robinson SK, Levey DJ (2010) Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* 91:1877–1884.
21. Pasch B, Bolker BM, Phelps SM (2013) Interspecific dominance via vocal interactions mediates altitudinal zonation in neotropical singing mice. *Am Nat* 182:E161–E173.
22. Brooker RW, Callaghan TV (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: A model. *Oikos* 81: 196–207.
23. Godsoe W, et al. (2016) Interspecific interactions and range limits: Contrasts among interaction types. *Theor Ecol* 10:167–179.
24. Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. *Nat Clim Chang* 2:686–690.
25. Hargreaves AL, Samis KE, Eckert CG (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am Nat* 183: 157–173.
26. 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 Biol Sci* 281:20132647.
27. 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. *J Ecol* 101:1074–1083.
28. Goheen JR, et al. (2013) Piecewise disassembly of a large-herbivore community across a rainfall gradient: The UHURU experiment. *PLoS One* 8:e55192.
29. Seed L, Vaughton G, Ramsey M (2006) Delayed autonomous selfing and inbreeding depression in the Australian annual *Hibiscus trionum* var. *vesicarius* (Malvaceae). *Aust J Bot* 54:27–34.
30. Ruiz-Guajardo JC (2008) Community plant–pollinator interactions in a Kenyan savannah. PhD dissertation (University of Edinburgh, Edinburgh).
31. Ellner SP, Childs DZ, Rees M (2016) *Data-Driven Modelling of Structured Populations* (Springer, Berlin).
32. Angert AL (2006) Demography of central and marginal populations of monkeyflowers (*Mimulus cardinalis* and *M. lewisii*). *Ecology* 87:2014–2025.
33. Moles AT, Westoby M (2004) Seedling survival and seed size: A synthesis of the literature. *J Ecol* 92:372–383.
34. Evans MEK, Ferrière R, Kane MJ, Venable DL (2007) Bet hedging via seed banking in desert evening primroses (*Oenothera,* Onagraceae): Demographic evidence from natural populations. *Am Nat* 169:184–194.
35. McDowell N, et al. (2008) Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol* 178: 719–739.
36. Eckhart VM, et al. (2011) The geography of demography: Long-term demographic studies and species distribution models reveal a species border limited by adaptation. *Am Nat* 178(Suppl 1):S26–S43.
37. Maschinski J, Whitham TG (1989) The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. *Am Nat* 134:1–19.
38. Nelson RJ, Demas GE (1996) Seasonal changes in immune function. *Q Rev Biol* 71: 511–548.
39. Wirsing AJ, Steury TD, Murray DL (2002) Relationship between body condition and vulnerability to predation in red squirrels and snowshoe hares. *J Mammal* 83:707–715.
40. Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annu Rev Ecol Evol Syst* 40:245–269.
41. Afkhami ME, McIntyre PJ, Strauss SY (2014) Mutualist-mediated effects on species' range limits across large geographic scales. *Ecol Lett* 17:1265–1273.
42. Tingley R, Vallinoto M, Sequeira F, Kearney MR (2014) Realized niche shift during a global biological invasion. *Proc Natl Acad Sci USA* 111:10233–10238.
43. Van der Putten WH, Macel M, Visser ME (2010) Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. *Philos Trans R Soc Lond B Biol Sci* 365:2025–2034.
44. Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013) Climate change and the past, present, and future of biotic interactions. *Science* 341:499–504.
45. Raffa KF, Powell EN, Townsend PA (2013) Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proc Natl Acad Sci USA* 110:2193–2198.
46. Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Glob Ecol Biogeogr* 16:743–753.
47. Armbruster P, Reed DH (2005) Inbreeding depression in benign and stressful environments. *Heredity (Edinb)* 95:235–242.
48. Sandner TM, Matthies D (2016) The effects of stress intensity and stress type on inbreeding depression in *Silene vulgaris*. *Evolution* 70:1225–1238.
49. Polhill D (1988) *Flora of Tropical East Africa: Index of Collecting Localities* (Royal Botanic Gardens, Kew, UK).
50. Hijmans R, van Etten J (2016) Raster: Geographic Data Analysis and Modeling. R Package, Version 2.5-8. Available at https://CRAN.R-project.org/package=raster. Accessed March 17, 2017.
51. Wang HH, et al. (2015) Species distribution modelling for conservation of an endangered endemic orchid. *AoB Plants* 7:plv039.
52. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978.
53. Caylor K, Gitonga J, Martins D (2016) *Mpala Research Center Meteorological and Hydrological Dataset* (Mpala Research Center, Laikipia, Kenya).

Downloaded from https://www.pnas.org by 70.185.125.9 on November 11, 2026 from IP address 70.185.125.9.