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Mechanisms of plant–plant interactions: concealment from herbivores is more important than abiotic-stress mediation in an African savannah

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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.

1. 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 [1]. Amelioration of abiotic stress in harsh environments is a well-supported mechanism of facilitation in many communities [2–5]. 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 ([6], see [7] 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 ([1], but see [4,8,9]).

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 [2]: 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. [3]), some revisions to the SGH predict slightly different patterns (e.g. hump-shaped [10]). Hence, here we refer to the original monotonic relationship as facilitation via stress reduction. Studies conducted across a variety of gradients—including altitudinal [3], aridity [11,12] and nutrient gradients [13]—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 [1,6,8,14]. Consistent with plant apparency, a variety of studies have shown that facilitation is more common or intense when herbivore pressure is greater [15–17].

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 [1]. Consistent with this prediction, Bulleri *et al.* [9] 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 [18] 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 [19]) 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 [20]. 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 [7].

2. Material and methods

(a) Study site and experimental design

All fieldwork was conducted 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 [21]. 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, [21]). 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 [21]. 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 [22]). 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 ($\pm$9.8 s.e.) in mesic and 73.2 ($\pm$19.8) in arid areas, averaged across seven surveys of nine 2×60 m transects in each aridity level between 2009 and 2011 [21]. Impala dung counts are significantly higher in the arid site [21]. Perhaps most importantly, regular dung counts [21] suggest that dik-dik, which appear to exert the strongest influences on *H. meyeri* performance in this system [19], 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 [21]).

Hibiscus meyeri is a short-lived, common, perennial subshrub, frequently occurring near or beneath trees. Little is known about its chemical defences [19], 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 [19]. *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 [19]. Herbivores do exert strong effects on *H. meyeri* population size structure, with significant increases in plant recruitment in the absence of herbivores [19]. 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 [3]), 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).

(b) 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 $4.7 \, cm^2 \pm 0.06$ s.e., mean height $21.4 \, cm \pm 0.10$ s.e.); medium ($16.8 \, cm^2 \pm 0.11$ s.e., $50.6 \, cm \pm 0.17$ s.e.); and large ($50.9 \, cm^2 \pm 0.35$ s.e., $91.6 \, cm \pm 0.35$ s.e.; see the electronic supplementary material, table S1). 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 [24].

(c) 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 [25]. 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 [21], 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 [21].

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 [26] 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 [25]. 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 [26]). 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.

3. 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

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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 [23], 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 the electronic supplementary material, table S2.

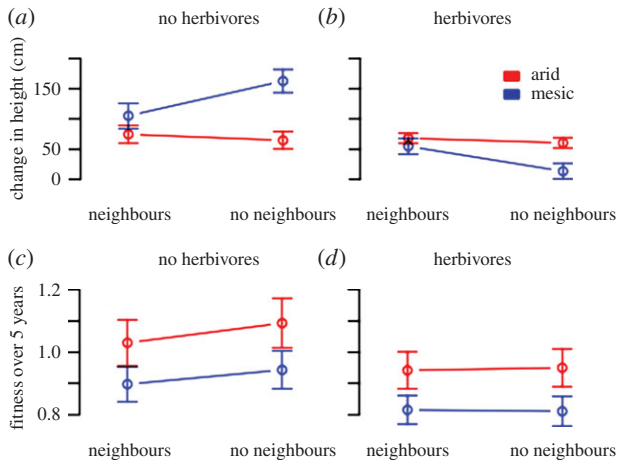| | predictor variables | | | | | | | | random effects | support | |
| | fixed effects | | | | | | | | | | |
response variables	initial height	herbivore activity	aridity	neighbours	herbivore activity × aridity	herbivore activity × neighbours	aridity × neighbours	herbivore activity × aridity × neighbours	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

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 electronic supplementary material, figure S2 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 ($p \leq 0.05$; electronic supplementary material, table S3). 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 [19]), but we assume similar seed set per fruit and germination rates in all matrices.

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 electronic supplementary material, figure S2 for an alternate presentation showing raw data.

and aridity on growth (indicated by support for a three-way interaction among aridity, neighbours and herbivore activity; table 1 and electronic supplementary material, table S2), suggesting that concealment by neighbours may be more important than stress-mediation as a mechanism of facilitation in this large-herbivore-dominated system.

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 (figure 1c,d; electronic supplementary material, table S3). In the absence of large herbivores, neighbours reduced projected fitness at both arid and mesic sites (figure 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
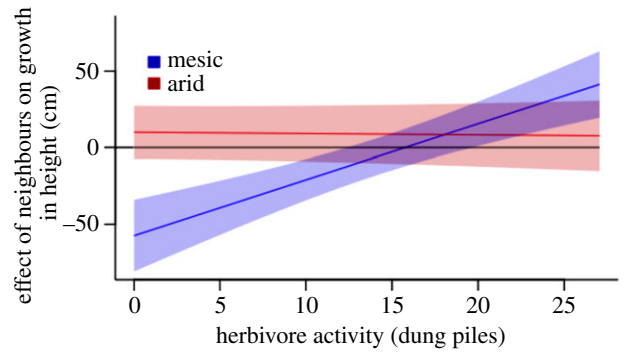
herbivore exclosures (figure 1d; significant interaction between neighbour presence and herbivore activity $F = 4.3209$, $p = 0.038$; electronic supplementary material, table S3). This result supports the prediction from plant-apparency theory that neighbours should exert facilitative effects in the 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; figure 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 (figure 2).

4. 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 (figure 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 [7,27,28]. 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 [7,29–31]. 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 (figure 1b), and herbivores alleviated the competitive effects of neighbours on fitness (figure 1c,d). Our work is consistent with the suggestion of Graff et al. [8] 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 [1]. 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 [8,32,33]. In a salt marsh community, Crain [18] 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. [9] 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 (figure 2).

Effects of neighbours on lifetime fitness are complicated by vital rate- or life stage-specific neighbour effects [34,35], and investigators rarely quantify all of these stage-specific effects, limiting our understanding of the sum effect of neighbours on plant fitness [20]. 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 electronic supplementary material, figure S1). Surprisingly, aridity has a positive effect on cumulative probability of reproduction and fruit number, but these effects are likely mitigated by fewer reproductive events [19]. 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 (figure 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 [36]. 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 (figure 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 [7]). 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 (figure 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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