Climatic stress mediates the impacts of herbivory on plant population structure and components of individual fitness

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Summary

1. 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.

2. 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.

3. 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.

4. 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.

5. *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.

Key-words: aridity, climate change, plant distributions, plant–herbivore interactions, population dynamics, savannas, stress gradients

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.

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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, Ritchie & McNaughton 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, Ritchie & McNaughton 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, Manion & Faber-Langendoen 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 large-scale herbivore exclusion experiment (Ungulate Herbivory Under Rainfall Uncertainty: 'UHURU') established in September 2008 (Goheen *et al.* 2013). One of four treatments in UHURU is applied

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. S1 in Supporting Information). Total rainfall increases > 45% from the Arid to Mesic site (440 mm year^{-1} at the Arid site, 580 mm year^{-1} at the Intermediate site and 640 mm year^{-1} 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 ×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, Testsuto & Makino 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 S1 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 × 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 2000). 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 $\chi_2^2 = 13.46$, $P = 0.001$).

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, $D_{96,59} = 0.3054$,
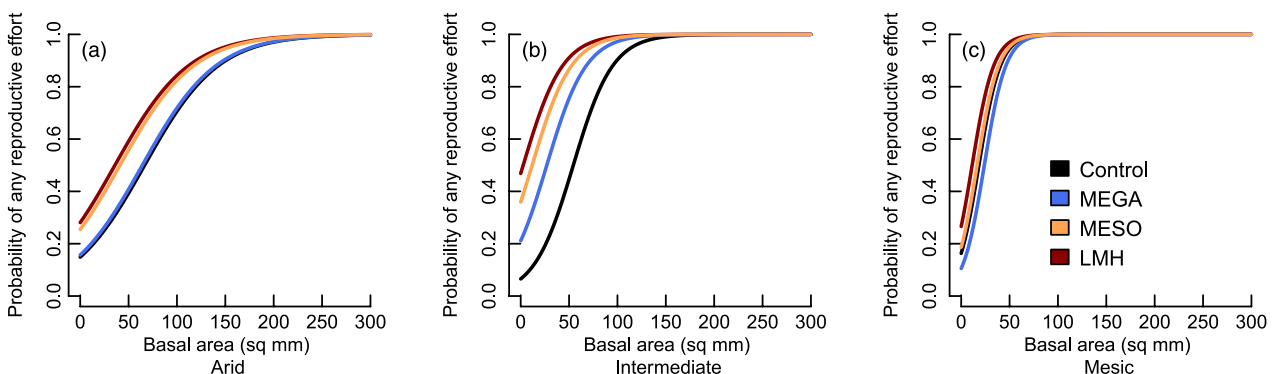

Fig 1. The effect of herbivore exclosures on the probability of initiating reproduction as a function of plant size (basal area), for all treatment and site combinations. Lines represent fitted probability distributions derived from mixed models with block as a random effect (Appendix Table S2). Likelihood ratio tests supported including treatment at all sites (Arid, $\chi^2 = 16.456$, $P = 0.0009$; Intermediate, $\chi^2 = 99.437$, $P < 2.2e-16$; Mesic, $\chi^2 = 11.984$, $P = 0.007$).
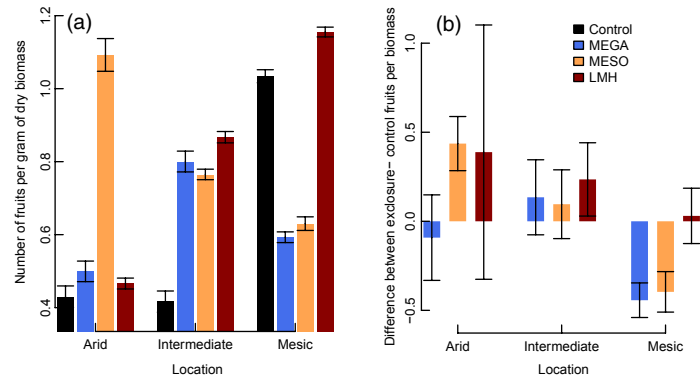
Fig 2. (a) The number of fruits per gram dry biomass (given that an individual produced fruits), as a function of site, treatment and their interaction (mixed model; site: $\chi_2^2 = 13.31$, $P = 0.0013$; treatment: $\chi_3^2 = 6.29$, $P = 0.098$; treatment*site: $\chi_6^2 = 12.57$, $P = 0.050$, with block as a random effect; table S5). (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.
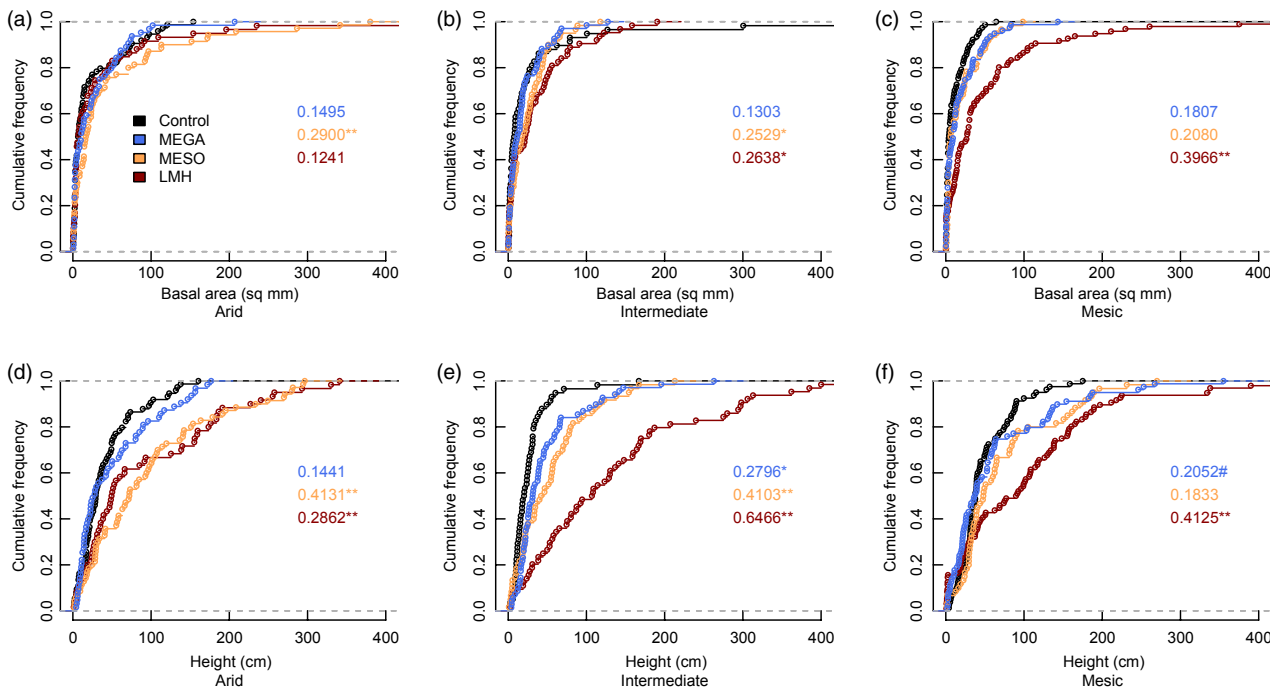
Fig 3. Cumulative probability distributions for size structures at the Arid, Intermediate and Mesic sites, measured for both height and basal area. Colours as in previous figures. D-statistics of Kolmogorov–Smirnov tests between exclosure and control treatments are shown in the colour corresponding to the exclosure treatment; # indicates marginally significant ($P < 0.10$), * indicates significant at the $P < 0.05$ level, ** indicates $P < 0.005$ (see Appendix, Table S3). We have conducted 3 Kolmogorov–Smirnov tests for each site–size metric combination; thus, individual reported P-values should be interpreted with caution. See Fig. S3 for alternative presentations of size distributions.

$P = 0.002$; Fig. 3; Appendix Fig. S2), suggesting that both recruitment and plant growth are greater in more mesic areas in the absence of mammalian herbivory.

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 S2), 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; Fig. S3).

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 S6), 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).

Size distributions of *H. meyeri* populations also differed sharply as a function of both site (rainfall) and treatment (Figs 3, 5 and Appendix Fig. S2), 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 S3). 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
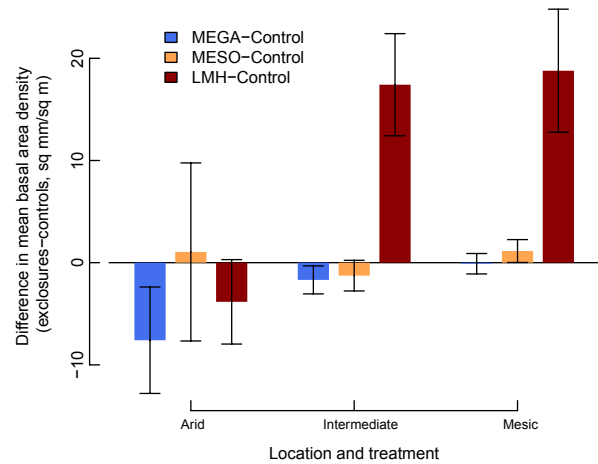
Fig 4. Difference in mean basal area density between exclosure and Control block pairs for all exclosure–Control comparisons (MEGA–Control, MESO–Control, LMH–Control) and sites. Error bars represent one SE calculated across blocks.

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 S3).

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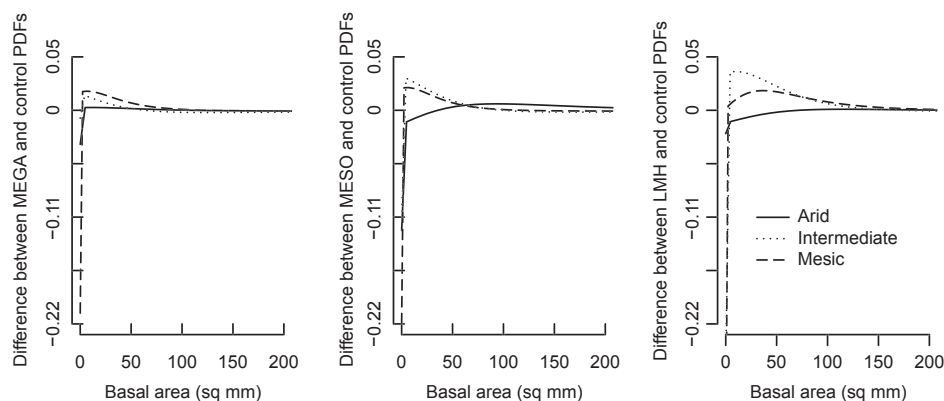
Fig 5. Differences in smoothed size distributions between Control and exclosure treatments, shown using an anti-logged *y*-axis for clarity. Positive values indicate that the exclosure treatment has a higher fraction of individuals in that size class than does the Control treatment.

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. S4), 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. S4).

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

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: $CV_{basal\ area}$ & $skewness_{basal\ area}$: 0.97; $CV_{basal\ area}$ & $kurtosis_{height}$: 0.519; $CV_{basal\ area}$ & $kurtosis_{basal\ area}$: 0.962; $skewness_{height}$ & $kurtosis_{height}$: 0.989; $skewness_{height}$ & $STVI_{joint}$: 0.523; $skewness_{basal\ area}$ & $kurtosis_{basal\ area}$: 0.994; $skewness_{basal\ area}$ & $STVI_{joint}$: 0.541; $kurtosis_{height}$ & $STVI_{joint}$: 0.547; $kurtosis_{basal\ area}$ & $STVI_{joint}$: 0.564; $Gini_{height}$ & CV_{height}: 0.989; $Gini_{basal\ area}$ & $kurtosis_{basal\ area}$: 0.857; $Gini_{basal\ area}$ & $CV_{basal\ area}$: 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 S4 for values from all treatments

	Arid			Intermediate			Mesic		
	Control	LMH	Difference (LMH-Control)	Control	LMH	Difference (LMH-Control)	Control	LMH	Difference (LMH-Control)
height									
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

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, Ash & Groves 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. S4). 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 UH-URU 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, Girard & Brown 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 meso-herbivores (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 (Gómez & 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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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Information on *Hibiscus meyeri* densities, statistical routines and insect damage.

Table S1. Number of plants selected haphazardly in Control and LMH treatments, as well as the number of plants from transects outside of UHURU.

Table S2. Estimates of fitted coefficients of mixed models predicting the probability of floral initiation.

Table S3. Results from Kolmogorov–Smirnov tests on size distributions in Control vs. all exclosure treatments.

Table S4. The effect of exclosures on the STVI, coefficient of variation (CV), skewness and kurtosis of height and basal area size distributions.

Table S5. Estimates of fitted coefficients of mixed models predicting number of fruits per biomass as a function of site and treatment.

Table S6. Means of raw densities, calculated as the number of plants found per area searched.

Table S7. Results from a negative binomial general linear model of per cent of leaves suffering insect damage, using all site and treatment combinations.

Fig. S1. Figure of UHURU schematic.

Fig. S2. Empirical CDFS constructed with raw numbers rather than proportion of the population.

Fig. S3. Predicted height/basal area ratio across sites and treatments.

Fig. S4. Gini coefficients for all site and treatment combinations.