

Climatic variation modulates the indirect effects of large herbivores on small-mammal habitat use

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Summary

1. Large mammalian herbivores (LMH) strongly shape the composition and architecture of plant communities. A growing literature shows that negative direct effects of LMH on vegetation frequently propagate to suppress the abundance of smaller consumers. Indirect effects of LMH on the behaviour of these consumers, however, have received comparatively little attention despite their potential ecological significance.

2. We sought to understand (i) how LMH indirectly shape small-mammal habitat use by altering the density and distribution of understorey plants; (ii) how these effects vary with climatic context (here, seasonality in rainfall); and (iii) the extent to which behavioural responses of small mammals are contingent upon small-mammal density.

3. We tested the effects of a diverse LMH community on small-mammal habitat use using 4 years of spatially explicit small-mammal trapping and vegetation data from the UHURU Experiment, a replicated set of LMH exclosures in semi-arid Kenyan savanna.

4. Small-mammal habitat use was positively associated with tree density and negatively associated with bare (unvegetated) patches in all plots and seasons. In the presence of LMH, and especially during the dry season, small mammals consistently selected tree cover and avoided bare patches. In contrast, when LMH were excluded, small mammals were weakly associated with tree cover and did not avoid bare patches as strongly. These behavioural responses of small mammals were largely unaffected by changes in small-mammal density associated with LMH exclusion.

5. Our results show that LMH indirectly affect small-mammal behaviour, and that these effects are influenced by climate and can arise via density-independent mechanisms. This raises the possibility that anthropogenic LMH declines might interact with changing patterns of rainfall to alter small-mammal distribution and behaviour, independent of numerical responses by small mammals to these perturbations. For example, increased rainfall in East Africa (as predicted in many recent climate-model simulations) may relax constraints on small-mammal distribution where LMH are rare or absent, whereas increased aridity and/or drought frequency may tighten them.

Key-words: African savannas, climate change, context dependence, contingency, ecosystem engineering, habitat use, herbivory, trait-mediated indirect interactions (TMII), ungulates and elephants, zoonotic disease risk

Introduction

Large mammalian herbivores (LMH) have variously been described as keystone species, ecosystem engineers and strong interactors, reflecting their diverse effects on communities and ecosystem functioning (Knapp *et al.* 1999;

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Paine 2000; Côté *et al.* 2004; Coverdale *et al.* 2016; Pringle *et al.* 2016). For example, at low-to-moderate densities, LMH can increase rates of nutrient cycling and plant productivity (McNaughton 1976; Hobbs 1996; Kielland, Bryant & Ruess 1997), whereas at higher densities, LMH often reduce both primary productivity and plant diversity via consumption and trampling (Olf & Ritchie 1998; Côté *et al.* 2004; Vellend 2004). Further, such direct effects of LMH on plants often propagate across multiple trophic levels to indirectly affect sympatric consumer populations. The role of LMH in structuring communities and ecosystems can, therefore, be substantial (e.g., Augustine & McNaughton 1998; Smit *et al.* 2001; Young *et al.* 2013; Daskin, Stalmans & Pringle 2016).

The magnitude of LMH impacts on ecological properties and processes, however, is variable in space and time, and the factors contributing to this contingency remain incompletely understood (Pringle *et al.* 2007, 2015; Goheen *et al.* 2013; Louthan *et al.* 2013; Foster, Barton & Lindenmayer 2014; Pellegrini *et al.* 2017). With wild LMH populations declining (Craigie *et al.* 2010; Di Marco *et al.* 2014) and climatic regimes changing in many parts of the globe (IPCC 2013), it is important to understand the ways in which abiotic context alters the effects of LMH on co-occurring faunal assemblages (Daskin & Pringle 2016). Although individual species' responses may vary, experimental exclusion studies have consistently revealed that total small-mammal abundance increases where LMH are absent (Keasing 1998, 2000; Hagenah, Prins & Olf 2009; Goheen *et al.* 2010; Parsons, Maron & Martin 2013). Large-scale 'real-world' LMH declines due to agricultural development have produced similar effects (Young *et al.* 2015).

Behaviourally or 'trait-mediated' indirect interactions often are at least as important as 'density-mediated' indirect interactions in governing ecological processes (Werner & Peacor 2003; Schmitz, Krivan & Ovidia 2004; Preisser, Bolnick & Benard 2005; Pearson 2010), although large-scale experiments aimed at understanding the relative importance of each type of interaction are rare (but see e.g., Maron & Pearson 2011; Ford *et al.* 2014, 2015). Most of this research has focused on predator → herbivore → producer pathways (i.e., trophic cascades), whereby predators indirectly affect the density of plants by altering density or behaviour of the prey they consume (Pearson 2010; see also Peckarsky *et al.* 2008; Schmitz *et al.* 2008). Other interaction pathways in which the initiator species are herbivores and the transmitter species are plants (i.e., exploitation competition, ecosystem engineering) have received far less attention (Pearson 2010). Moreover, whereas considerable attention has been directed towards the relative importance of density vs. behaviour in mediating indirect effects on the *densities* of receiver populations (e.g., Griffin & Thaler 2006; Abrams 2008), few studies have evaluated behaviour itself as an endpoint of interaction pathways.

Understanding the mechanisms by which herbivore-initiated interaction pathways induce changes in small-

mammal behaviour and activity patterns may help us understand how small mammals influence ecosystem processes (Keasing & Crawford 2001; Johnston & Anthony 2008). Release of small-mammal abundance from competition with LMH has been shown to increase ectoparasite abundance and zoonotic disease risk (Ostfeld *et al.* 2006; Young *et al.* 2017), as well as seed-predation pressure (Pringle *et al.* 2014). Yet, changes in the spatial distribution, activity patterns and other behaviours of small mammals—irrespective of any increase in abundance—can also affect seed dispersal (Hirsch *et al.* 2012; Steele *et al.* 2014), disease transmission (Page, Swihart & Kazacos 2001) and agricultural damage (Schauber *et al.* 2009). In other words, the ultimate consequences of LMH decline or exclusion may hinge in part on density-independent behavioural shifts by small mammals.

Rainfall has strong effects on small-mammal density and behaviour (Ernest, Brown & Parmenter 2000; Kelt *et al.* 2004; Previtali *et al.* 2009; Edelman 2014). For example, rainfall alters the effects of LMH on rodent abundance in Kenya (Young *et al.* 2015). Prior work in African savannas has demonstrated that the density and spatial arrangement of understorey vegetation is often suppressed by LMH (Augustine & McNaughton 1998; Van Langevelde *et al.* 2003; Veblen & Young 2010; Pringle *et al.* 2011), and that understorey plants typically are water-limited during the dry season (Scholes & Archer 1997 and references therein). We therefore hypothesized that LMH would alter the spatial distribution and activity patterns of small mammals through effects on the patch structure and connectivity of understorey plants (Bergstrom 2013), and that the strength of these effects would vary with seasonal shifts in rainfall.

We used data from a network of long-term large herbivore exclusion plots in a semi-arid central Kenyan savanna (Pringle 2012; Goheen *et al.* 2013; Kartzinel *et al.* 2014) to study this interaction pathway (Fig. 1). Specifically, we sought to understand: (i) how LMH indirectly shape small-mammal habitat use by altering the density and distribution of understorey plants; (ii) how these effects vary with rainfall; and (iii) the extent to which behavioural responses of small mammals are contingent upon small-mammal density (Fig. 1; Pearson 2010).

We predicted that the strength of small-mammal habitat associations would diminish when wet conditions, LMH exclusion, or both led to denser, more homogeneously distributed understorey vegetation. Specifically, we predicted that small-mammal utilization of woody cover (and avoidance of bare ground) would be strongest during dry seasons in plots with LMH present (i.e., when and where vegetation density in the understorey is lowest), weakest during wet seasons when LMH were excluded (i.e., when and where vegetation density in the understorey is highest), and intermediate in the other two treatment × season combinations. Further, we predicted that small-mammal habitat utilization would be largely density

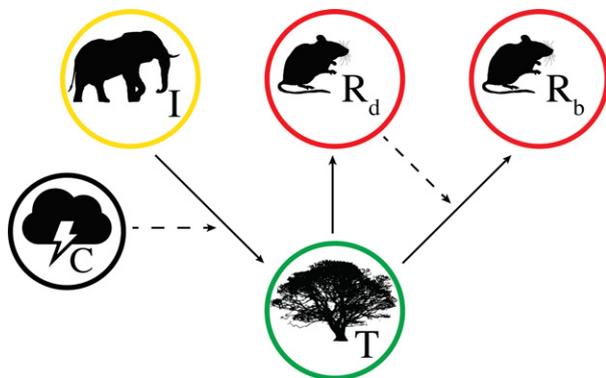


Fig. 1. Conceptual model illustrating the hypothesized indirect interaction pathway investigated in this study. Initiator taxa (I, large mammalian herbivores) reduce density of transmitter taxa (T, understory vegetation), which in turn influences both the density (R_d) and behaviour (R_b) of receiver taxa (small mammals). Climate (C) modifies the I→T interaction, while R_d potentially modifies the T→ R_b interaction (i.e., effects of the transmitter taxa on behaviour of the receiver taxa might be modified by density, or might instead be density-independent). Solid arrows, direct interactions; dashed arrows, interaction modifications (following Wootton 1994). [Colour figure can be viewed at wileyonlinelibrary.com]

independent, because individuals are capable of rapidly adjusting their behaviour in response to changes in the distribution or density of understory vegetation that subsequently influence access to forage and risk of predation. Thus, in statistical models of habitat use by small mammals, the interactive effects of small-mammal density and understory vegetation density on behaviour should be weaker than direct effects of vegetation density on behaviour (based on comparisons of standardized parameter estimates). Alternatively, if habitat use were density-dependent, we would instead expect the interactive effects of small-mammal density and vegetation density on behaviour to outweigh the direct effects of vegetation alone.

Materials and methods

STUDY AREA

We conducted our study at the Mpala Research Centre, a 20 000-ha conservancy in the Laikipia highlands of central Kenya (0°17' N, 37°52' E). Mpala's vegetation consists of a discontinuous understory of grasses and forbs (Augustine 2003) and an overstorey dominated by three species of Acacia (*A. etbaica*, *A. brevispica*, and *A. mellifera*; Goheen *et al.* 2013). At least 22 species of wild LMH occur at Mpala, spanning three orders of magnitude in body size ranging from dik-dik (*Madoqua guentheri*; 5 kg) to elephant (*Loxodonta africana*; 5000 kg; Augustine 2010).

Our data were collected within the UHURU Experiment, which was established in 2008 (Goheen *et al.* 2013). UHURU comprises four size-selective herbivore-exclusion treatments, in which different subsets of LMH are excluded from 1-ha (10 000 m²) plots using electric fencing. Long-term small-mammal data have been collected within the two extreme treatments: total enclosures that prevent access by all species of LMH >5 kg,

and unfenced plots accessible to all species. In these two treatments, we have sampled small mammals every-other month since 2009, along with twice-yearly understory surveys and annual tree censuses (Kartzinel *et al.* 2014). The UHURU treatments are each replicated three times in randomized blocks across a rainfall gradient from north to south within Mpala, but we focus here on the southern (wettest) set of three enclosure-unfenced plot pairs, because this was the only location where small-mammal abundance was sufficiently high (see Goheen *et al.* 2013; their fig. 8). The fencing used to exclude LMH is permeable to snakes and appears to have little effect on small carnivores that consume small mammals; cumulative capture rates of slender mongoose (*Galerella sanguinea*), dwarf mongoose (*Helogale parvula*), genet (*Genetta genetta*) and zorilla (*Ictonyx striatus*) are comparable in exclusion plots (0.037 individuals/100 trap-nights ± 0.008 SEM) and unfenced plots (0.046 individuals/100 trap-nights ± 0.03 SEM; Wambua & Goheen unpublished data). Large cats gain access by climbing nearby trees and jumping over the 2-m tall fences (Goheen *et al.* 2013). It is therefore unlikely that our results were driven by predator exclusion.

SMALL-MAMMAL TRAPPING

We trapped small mammals in enclosure and unfenced plots beginning in May 2009. A central 60 × 60 m grid of 49 stakes in a 10 × 10 m lattice in each plot served as the basis for both small-mammal and understory-vegetation sampling. On each of four consecutive nights, a single Sherman live trap was placed at each of the 49 grid stakes, opened in the late afternoon, baited with peanut butter and oats, and checked and closed early the following morning. We recorded weight, sex, age and reproductive condition of each animal at the time of capture and marked them with Monel fingerling ear tags for subsequent identification. We used marked individuals to calculate the minimum number known alive (MNKA) for each species, scaled to an area of 1 ha, as an index of small-mammal density in each treatment, year and season (Previtali *et al.* 2009; Goheen *et al.* 2013) to serve as a predictor variable in models of small-mammal habitat use. Species identifications were based on diagnostic morphological traits and have been verified with DNA barcodes (Goheen *et al.* 2013).

Based on long-term rainfall patterns in southern Mpala from 1999 to 2015 (MAP = 660 mm), we classified trapping sessions in January and March as 'dry season' (monthly mean = 24 mm) and those in September and November as 'wet season' sessions (monthly mean = 62 mm). We analysed data from 2010 (the first full year of data collection, which began in May 2009) through 2013. Because three small-mammal species (*Aethomys hindoi*, *Gerbilliscus robustus* and *Saccostomus mearnsi*) accounted for >85% of captures during this interval, we restricted our analyses to those three species. All of our focal species are either herbivorous or omnivorous and rely on many of the same forage resources (e.g., seeds, grasses, roots, fruits and insects) that are utilized by LMH (Bergstrom 2013; cf. Kartzinel *et al.* 2015).

VEGETATION SAMPLING

We quantified spatial variation in four plant-community characteristics likely to influence small-mammal habitat use: (i) density of understory vegetation; (ii) cover of bare ground; (iii) percent tree canopy cover; and (iv) tree density (weighted by size class). Understorey vegetation was surveyed during February–March

(dry season) and again during September–October (wet season) of each year. To quantify understorey density in each survey, we placed a 10-pin point frame (Bonham 1989) adjacent to each of the 49 grid stakes (the same as in the trapping grid) in each plot and recorded the total number of ‘pin hits’ (i.e., intersections with vegetation). This measure is strongly and positively correlated with plant biomass (Augustine 2002). We also tallied the number of pins that touched bare soil without intersecting vegetation, to index the percent cover of unvegetated ground. Although vegetation data were collected for each plant species, we summed pin hits across plant species and used the total number of hits in each plot as an aggregate measure of understorey vegetation density and cover of bare soil in our analyses.

Tree canopy cover (%) was estimated in each 100-m² cell within the central 3600-m² lattice of grid stakes during July–August 2011 (Kartzinel *et al.* 2014). Data on canopy cover of the overstorey layer were collected as part of a broader habitat survey that took place only once during our study in 2011. However, there was relatively little temporal variation in tree canopy cover within each experimental treatment during the interval covered by our study, especially relative to the spatial variation observed throughout the UHURU experiment (range of 0–90% canopy cover across treatments and blocks), and it is unlikely that accounting for it would have qualitatively altered our results.

We censused woody overstorey vegetation in each 3600-m² trapping grid once per year by exhaustively searching each 100-m² grid cell and recording the occurrence of each canopy species that we observed. We assigned individual plants to one of five height classes (≤ 1 m, 1–2 m, 2–3 m, 3–4 m and ≥ 4 m) and calculated a weighted estimate of relative tree density by multiplying the number of trees in each height class by the rank order of the class (1 through 5 from shortest to tallest), summing the products, and then dividing by the 100-m² area of the grid cell. Although these data were collected annually, there were few differences in cell-specific density estimates among years in our study, and missing values were present for some grid cells in tree-census data from 2011 and 2013. Accordingly, we averaged cell-specific density estimates from 2010 and 2012 and used the resulting means as a time-invariant predictor variable in subsequent analyses of small-mammal distributions.

DATA ANALYSIS

Because we expected LMH (the ‘initiator’ taxa of the indirect effect) to influence the distribution of small mammals (the ‘receiver’ taxa) indirectly by altering the distribution and density of vegetation (the intermediary ‘transmitter’ taxa; Fig. 1), we used two-way ANOVA (Neter *et al.* 1996) to test for effects of LMH exclusion and season on understorey vegetation. We used the mean number of vegetation pin hits across all grid stakes in each plot as the response variable in our analysis, and thus plots ($n = 6$) were the unit of replication. We included treatment and season as main effects, a treatment \times season interaction term, and plot ID as a blocking factor. Statistical significance was assessed based on $\alpha \leq 0.05$.

We tallied the total number of small-mammal capture events that occurred during wet and dry season months, respectively, at all 49 grid stakes within each treatment, plot and year (2010–2013) as a spatially explicit measure of habitat use. We included recapture events in this count of total captures for two reasons: (1) distribution of small mammals was the focus of our analyses, rather than abundance; and (2) analysis restricted only to new

captures (i.e., with recapture events excluded) produced parameter estimates that were qualitatively similar to those with all captures and recaptures, but also less precise due to reduced sample size. We matched spatially explicit capture data with understorey data at two spatial scales, ‘local’ and ‘neighbourhood’. At the local scale, capture data from each grid stake were combined with the understorey data (vegetation density and bare soil) collected at that stake during the same season and year. At the neighbourhood scale, capture data were combined with mean values of the understorey variables estimated from all stakes immediately surrounding (and including) the capture site ($n = 4$ –9 stakes, area = 100–400 m², depending on the location of the stake in the grid). This approach allowed us to evaluate whether small-mammal distributions in enclosure vs. unfenced plots were influenced more strongly by the two understorey variables at each capture site, or instead within a larger neighbourhood surrounding each capture site. Overstorey data (canopy cover and relative woody-stem density) were combined with capture data in the same spatially explicit manner as the understorey data. These data, however, were from 10-m² grid cells rather than at individual stakes. Therefore, we only evaluated the influence of overstorey vegetation on small-mammal distribution at the neighbourhood scale.

We quantified the relationship between small-mammal habitat use (total capture events) and vegetation characteristics (understorey and overstorey), small-mammal density (MNKA) and interactions between these factors by fitting generalized linear mixed models with Poisson error distributions (Zuur *et al.* 2009) to the data from each treatment \times season combination. We were primarily interested in estimation of effects rather than prediction, so we standardized all predictor variables by subtracting the mean and dividing by the standard deviation to facilitate direct comparison of model coefficients (Neter *et al.* 1996). We included a random intercept with a nested grouping structure (plot nested within year) in each model so that conditional effects were estimated for each unique combination of plot and year (Zuur *et al.* 2009). We did not attempt to correct for overdispersion in our models, because dispersion parameters were ≤ 1.5 in all but one model (Zuur *et al.* 2009).

We used the marginal value of Akaike’s information criterion ($_m$ AIC; Vaida & Blanchard 2005; Bolker *et al.* 2009) for model selection (Burnham & Anderson 2002) with the following four goals in mind: (i) to determine which characteristics of the understorey (vegetation density or bare ground) and overstorey (canopy cover or relative tree density) most strongly influenced small-mammal distribution in each treatment and season (vegetation density and bare ground were negatively correlated, and canopy cover and relative tree density were positively correlated, both with $|r| > 0.90$, and thus only one variable from each category could be included in the same model); (ii) to identify the spatial scale (local or neighbourhood) at which relationships between small-mammal distribution and understorey characteristics manifested most clearly in each treatment \times season combination; (iii) to evaluate whether a nonlinear (square) transformation of understorey or overstorey variables improved model fit; and (iv) to test whether the inclusion of interactions between small-mammal density and vegetation characteristics improved model fit. Small-mammal density was included as a predictor variable at all stages of the modelling process to control for the effects of density through time on the number of capture events in each season and year.

We began the model selection process for each treatment \times season combination by fitting four ‘understorey’ models,

each representing a unique combination of understorey effect (either vegetation density or bare ground) and scale (either local or neighbourhood). We then used $mAIC$ to determine which combination of understorey effect and scale to bring forward to the next stage of the modelling process; we considered the model with the lowest $mAIC$ to have the most empirical support (Burnham & Anderson 2002). In the next stage of our analysis, we fit two additional models, each of which included the understorey variable from the previous stage, in combination with either tree canopy cover or relative tree density. Again, the model with the lowest value of $mAIC$ was selected to move forward to the next stage of analysis. In the third stage of our analysis, we sequentially replaced each linear term with its square and used $mAIC$ to determine whether transformation improved model fit. In the final stage, we added interactions between small-mammal density and the understorey and overstorey variables selected in prior stages and again used $mAIC$ to determine whether to retain one or both interaction terms in the model. We report P -values for all main effects and interaction terms included in the best model for each combination of season and treatment. We also used the method of Nakagawa & Schielzeth (2013) to calculate both the marginal R^2 (i.e., $R^2_{GLMM(m)}$; a measure of the variance explained by the fixed factors) and the conditional R^2 (i.e., $R^2_{GLMM(c)}$; a measure of the variance explained by both the fixed and random factors) of the best model in each set. We performed all analyses using the lme4 package in program R v3.0.2 (R Development Core Team 2013).

In addition to our modelling analyses, we visually examined relationships among small-mammal distribution, bare ground and relative tree density by overlaying spatially explicit capture data on heat maps of those variables for all combinations of treatment, plot, year and season. Although these representations cannot be analysed with quantitative precision, they are useful for interpreting and intuiting the quantitative results, and for illustrating year-to-year variability. We chose bare ground and tree density as the primary variables of interest based on results of our modelling analyses (see Results). We depicted spatial variation in the amount of bare ground by producing 10-m² rasters from understorey sampling data (i.e., pin hits) collected at the grid stakes in each plot, and then used bilinear interpolation (ArcGIS 10.2) to convert those rasters to heat maps of bare ground with a 1-m² resolution. Capture data from each grid stake were then overlaid on maps of bare ground, with the size of the point at each stake location representing the number of individuals captured at that site. For tree density, we used the approach described above to produce a single heat map of spatial variation in relative tree density for each combination of treatment and plot.

Results

Understorey vegetation density was 25% higher, on average, in enclosure plots than unfenced plots in both seasons (ANOVA, $F_{1,42} = 5.10$, $P = 0.029$; Fig. 2) and 46% higher during the wet season than the dry season across treatments ($F_{1,42} = 14.72$, $P < 0.001$; Fig. 2). Neither plot nor the treatment \times season interaction had significant effects in this analysis ($P > 0.64$).

Understorey density and bare ground coverage were more closely related to small-mammal distribution at the neighbourhood scale than the local scale in all treatments

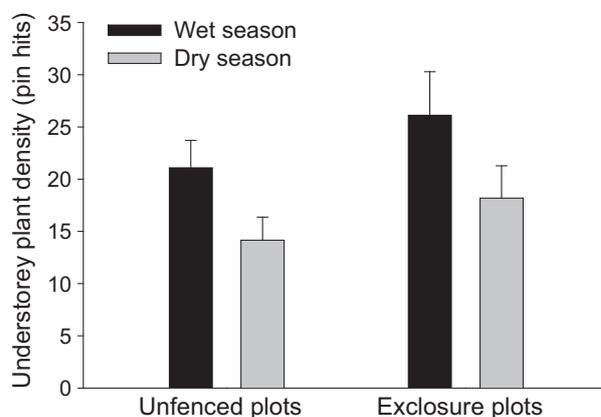


Fig. 2. Understorey vegetation density (mean number of vegetation hits per 10-pin point frame in each plot) with 90% confidence intervals in enclosure and unfenced plots during the wet (September/October) and dry (February/March) seasons of 2010–2013. Plots were the units of replication for means and confidence intervals.

and seasons ($\Delta mAIC > 2$ between best neighbourhood model and best local model; Table S1, Supporting Information), and bare ground was consistently a better predictor of small-mammal distribution than understorey density ($\Delta mAIC > 2$; Table S1). Likewise, relative tree density typically outperformed canopy cover as a predictor of small-mammal distribution across treatments and seasons, although the relative support for models containing one or the other of those variables was sometimes essentially equivalent ($\Delta mAIC \leq 2$; Table S1). Nonlinear transformations of bare ground cover and tree density never improved model fits (Table S1).

Small-mammal density was higher in enclosure plots than in unfenced plots in both seasons and was higher during the wet season than the dry season across treatments (Fig. 3). However, small-mammal density also increased markedly between 2010 and 2013 in all treatments and seasons (Fig. 3). The inclusion of interactions between density and our two main effects (bare ground cover and relative tree density at the neighbourhood scale) did not improve model fit (i.e., it increased $mAIC$) in two of the four treatment \times season combinations (enclosure plots during the wet season and unfenced plots during the dry season; Table S1), indicating that the influence of vegetation structure on small-mammal distribution was unaffected by small-mammal density in those combinations. In contrast, the best model of small-mammal spatial distribution in enclosure plots during the dry season included both interaction terms, and the best model for unfenced plots during the wet season included an interaction between small-mammal density and tree density (Table S1); this indicates that the effect of vegetation structure on small-mammal distribution was modulated by increasing density of small mammals in those two treatment \times season combinations. Nevertheless, standardized parameter estimates for significant interaction terms were always considerably less (usually by a half to a third)

than those of the main effects themselves (Table 1), indicating that direct effects of vegetation structure on small-mammal distribution were greater in magnitude than indirect effects that were modulated by small-mammal density.

Small-mammal spatial distributions were positively associated with relative tree density and negatively associated with bare ground in all plots and seasons (Table 1; Fig. 4); however, these habitat associations were stronger during the dry season and/or when LMH were present and were strongest when those factors were combined

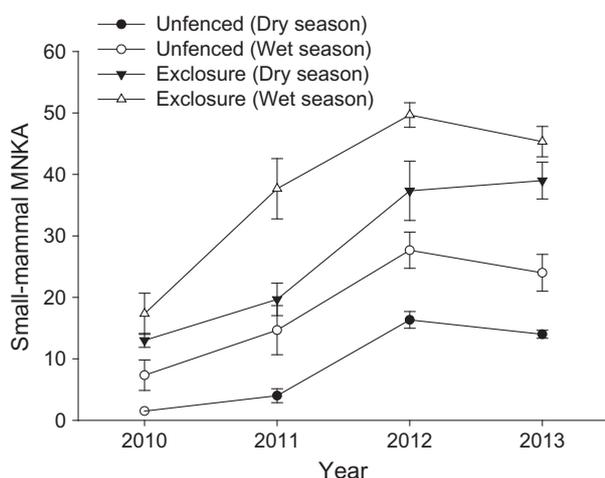


Fig. 3. Minimum number known alive (MNKA) of three species of small mammals in enclosure and unfenced plots during the wet (September/October) and dry (February/March) seasons of 2010–2013. Plots were the units of replication for means and confidence intervals.

(i.e., in unfenced plots during the dry season; Table 1; Fig. 4). Where LMH were present, small-mammal distributions were positively associated with tree density and negatively associated with bare ground during both wet and dry seasons (Figs 4 and 5). In addition, avoidance of bare ground during the dry season was stronger in the presence of LMH than in enclosure plots (Table 1; Fig. 4). Where LMH were excluded, small mammals were more evenly distributed during the wet season than during the dry season, when both understorey-vegetation density and relative tree density structured the distribution of small mammals (Figs 4 and 5). Indeed, the positive association between small-mammal captures and tree density in enclosure plots diminished nearly five-fold during the wet season relative to the dry season, and avoidance of bare ground was also less pronounced (Table 1; Fig. 4).

Discussion

Our results show that LMH indirectly influenced spatial patterns of activity and habitat use by small mammals, and that these indirect effects were contingent on rainfall. Association with tree cover and avoidance of bare ground by small mammals was greater (i) during the dry season and (ii) where LMH were present. Conversely, habitat associations were weakest in LMH-exclusion plots during the wet season. Moreover, although our results provided some support for density-dependent shifts in habitat use (Morris 1992, 2002), the effect of vegetation structure on small-mammal behaviour ($T \rightarrow R_b$ in Fig. 1) was consistently stronger than the interactive effect of vegetation structure and small-mammal density on behaviour ($R_d \rightarrow [T \rightarrow R_b]$ in Fig. 1) across all treatments and seasons; this

Table 1. Standardized parameter estimates, confidence intervals (CI) and *P*-values from generalized linear mixed models of factors affecting the distribution of small-mammal captures at Mpala Research Centre, Kenya, 2010–2013. Results are shown for the best model in each combination of treatment (Exclosure or Unfenced) and season (Wet or Dry) based on marginal Akaike's information criterion (Table S1). Marginal ($R^2_{GLMM(m)}$) and conditional ($R^2_{GLMM(c)}$) R^2 for each model were calculated using the equations of Nakagawa & Schielzeth (2013). MNKA, minimum number known alive

Model	Parameter	Estimate	90% CI		<i>P</i>	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$
			Lower	Upper			
Exclosure – Wet	Bare ground	–0.310	–0.382	–0.238	<0.001	0.40	0.41
	Tree density	0.061	0.015	0.107	0.031		
	MNKA	0.362	0.355	0.369	<0.001		
Exclosure – Dry	Bare ground	–0.425	–0.529	–0.321	<0.001	0.45	0.46
	Tree density	0.250	0.188	0.312	<0.001		
	MNKA	0.449	0.337	0.561	<0.001		
	MNKA × bare ground	0.181	0.066	0.296	0.010		
	MNKA × tree density	–0.140	–0.201	–0.079	<0.001		
Unfenced – Wet	Bare ground	–0.398	–0.499	–0.297	<0.001	0.42	0.42
	Tree density	0.376	0.299	0.453	<0.001		
	MNKA	0.673	0.579	0.767	<0.001		
	MNKA × tree density	–0.117	–0.189	–0.045	0.007		
Unfenced – Dry	Bare ground	–0.670	–0.849	–0.491	<0.001	0.36	0.37
	Tree density	0.293	0.195	0.391	<0.001		
	MNKA	0.746	0.481	1.011	<0.001		

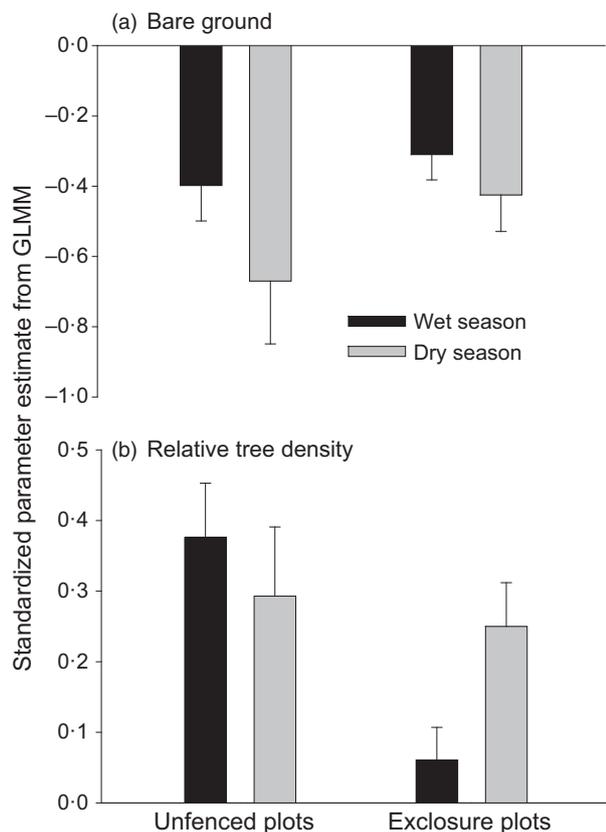


Fig. 4. Standardized parameter estimates (with 90% confidence intervals) from generalized linear mixed models (GLMMs) of small-mammal distribution during the wet (September/October) and dry (February/March) seasons of 2010–2013. Parameter estimates indicate direction and magnitude of the effects of (a) bare ground and (b) relative tree density on distribution of small mammal captures in enclosure and unfenced plots.

suggests that the observed behavioural responses were not solely a function of intensified competition due to increased small-mammal densities in enclosure plots.

The contingency of the effects of LMH exclusion on small-mammal behaviour may stem from variation in forage availability, perceived or actual risk of predation, or a combination of the two. In African savannas, small mammals compete with LMH for food (Keesing 1998; Hagenah, Prins & Olf 2009), and exclusion of LMH typically increases understorey vegetation density. As vegetation senesces during the dry season, facilitative shading or physical protection of understorey plants by woody trees and shrubs, as well as the woody plants themselves (e.g., via seed production; Pringle *et al.* 2014), may produce islands of high-quality forage that attract small mammals to those patches whether or not large herbivores are present (e.g., Long *et al.* 2008; Riginos *et al.* 2009; Louthan *et al.* 2014). Likewise, contraction and reduced connectivity of understorey patches in the dry season reduces protection from predators, which might reduce individuals' willingness to venture farther across the landscape.

We hypothesize that contraction of understorey vegetation during dry seasons, droughts, or in the presence of

heavy grazing dissects the landscape with 'rivers' of bare soil that small mammals are reluctant to cross, leaving them confined to 'islands' of woody vegetation and remnant understorey patches (which themselves are facilitated by woody cover); subsequent expansion of understorey vegetation during wet seasons and/or when herbivory is reduced creates a more homogeneously crossable landscape, relaxing the habitat specificity of small mammals. We recommend future experimental work aimed at explicitly testing this hypothesis, and the intriguing possibility that particular spatial patterns or configurations of vegetation lead to emergent effects on small-mammal behaviour and distribution that cannot be predicted from understorey density or tree-canopy cover alone (Pringle *et al.* 2010; Pringle & Tarnita 2017).

We also hypothesize that the patterns we observed may be linked in part to the behaviour of elephants. By toppling and smashing thorny trees and shrubs, elephants create refuge habitats that are inaccessible to other species of large herbivores and therefore support dense understorey vegetation (Coverdale *et al.* 2016), and that also provide refuge for small animals (Pringle 2008; Pringle *et al.* 2015). This protected and comparatively low-risk forage base is likely attractive to small mammals, which might strengthen the positive association between small-mammal activity and tree canopies in the presence of elephants and other LMH; when high-quality forage is abundant and more evenly distributed (i.e., during the wet season and in the absence of LMH; Fig. 2), small mammals likely become less dependent on these refugia for food and cover. Experimental tests of this hypothesis—and of the relative importance of exploitation competition and ecosystem engineering pathways in the interaction chain shown in Fig. 1—would be useful.

Although grazing can increase the exposure of small mammals to predators (as alluded in the discussion above; see also Birney, Grant & Baird 1976; Edge, Wolff & Carey 1995; Peles & Barrett 1996), two lines of evidence suggest that this was not the primary mechanism underpinning the habitat-use responses we observed. First, previous work in our study system found no detectable differences in vulnerability of small mammals to predators between plots with and without large herbivores (Keesing 1998). Second, various predators of small mammals such as snakes and birds also increase in abundance and/or exhibit higher activity levels when LMH are excluded (McCauley *et al.* 2006; Ogada *et al.* 2008); these trends could offset any effects stemming from increased exposure due to reduced vegetation density.

Populations of LMH are declining throughout Africa at unprecedented rates (du Toit & Cumming 1999; Craigie *et al.* 2010), and climate models predict substantial increases in precipitation in many areas of the world, including East Africa (particularly during the dry season, although precipitation forecasts remain highly uncertain, and decreased precipitation is also possible; IPCC 2013). Our results indicate that this combination of factors

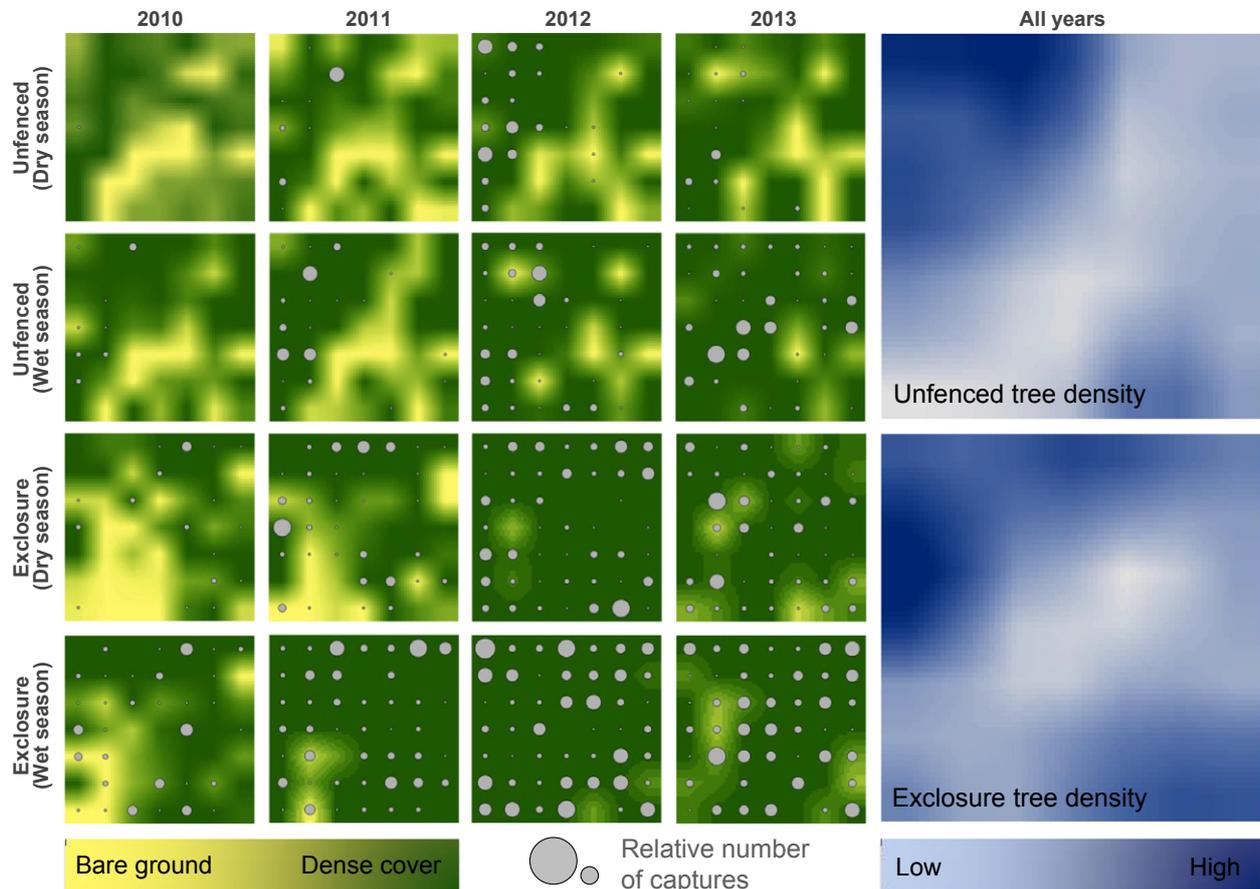


Fig. 5. Illustration showing distribution of small-mammal captures (blue circles) relative to cover of bare ground and tree density in unfenced and enclosure plots in one of three experimental blocks. Traps were placed 10-m apart in a 60×60 m grid. Size of circles is proportional to total number of small mammals (of all species) captured at each location in the grid during the wet (September and November) and dry (January and March) seasons of 2010–2013. [Correction added after online publication on 4 May: Figure 5 replaced with correct revised figure]. [Colour figure can be viewed at wileyonlinelibrary.com]

would likely relax habitat specificity among small mammals, in addition to increasing small-mammal densities. Because even moderate densities of small mammals can exert strong effects on savanna vegetation (Keesing 1998), this combination of increased abundance and relaxed habitat specificity could reshape savanna plant assemblages. In addition, increased use of grasslands by small mammals in the absence of large herbivores may degrade the nutritional quality of understorey vegetation over time (as suggested by Keesing 1998), which could make it more difficult for some species of large herbivores to re-establish. Finally, the responses of small mammals to LMH exclusion observed in our study have potential to increase the frequency of interactions, both direct and indirect, between small mammals and humans. Small mammals serve as zoonotic disease reservoirs in our system and elsewhere (Howe, Brown & Zorn-Arnold 2002; Ostfeld *et al.* 2006; Young *et al.* 2017) and can be major agricultural pests (Leirs *et al.* 1996; Stenseth *et al.* 2003). Negative effects of small mammals on human livelihoods may, therefore, be a non-trivial unanticipated consequence of LMH declines in a changing climate (du Toit & Cumming 1999).

Authors' contributions

J.R.G., R.M.P., R.A.L. and T.M.P. conceived and designed the study; A.W., J.R.G. and R.M.P. conducted field work; R.A.L. analysed the data; R.A.L. and R.M.P. wrote the manuscript; other authors made significant contributions to the draft and approved it for publication.

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Data accessibility

All raw data included in our analyses are available in Dryad Digital Repository <https://doi.org/10.5061/dryad.p112b> (Long *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Tabular results of generalized linear mixed models used to evaluate the influence of vegetation characteristics and small-mammal density on the spatial distribution of total small-mammal capture events at Mpala Research Centre, Kenya.