

Synergistic effects of fire and elephants on arboreal animals in an African savanna

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Summary

1. Disturbance is a crucial determinant of animal abundance, distribution and community structure in many ecosystems, but the ways in which multiple disturbance types interact remain poorly understood. The effects of multiple-disturbance interactions can be additive, subadditive or super-additive (synergistic). Synergistic effects in particular can accelerate ecological change; thus, characterizing such synergies, the conditions under which they arise, and how long they persist has been identified as a major goal of ecology.

2. We factorially manipulated two principal sources of disturbance in African savannas, fire and elephants, and measured their independent and interactive effects on the numerically dominant vertebrate (the arboreal gekkonid lizard *Lygodactylus keniensis*) and invertebrate (a guild of symbiotic *Acacia* ants) animal species in a semi-arid Kenyan savanna.

3. Elephant exclusion alone (minus fire) had negligible effects on gecko density. Fire alone (minus elephants) had negligible effects on gecko density after 4 months, but increased gecko density twofold after 16 months, likely because the decay of fire-damaged woody biomass created refuges and nest sites for geckos. In the presence of elephants, fire increased gecko density nearly threefold within 4 months of the experimental burn; this occurred because fire increased the incidence of elephant damage to trees, which in turn improved microhabitat quality for geckos. However, this synergistic positive effect of fire and elephants attenuated over the ensuing year, such that only the main effect of fire was evident after 16 months.

4. Fire also altered the structure of symbiotic plant-ant assemblages occupying the dominant tree species (*Acacia drepanolobium*); this influenced gecko habitat selection but did not explain the synergistic effect of fire and elephants. However, fire-driven shifts in plant-ant occupancy may have indirectly mediated this effect by increasing trees' susceptibility to elephant damage.

5. Our findings confirm the importance of fire × elephant interactions in structuring arboreal wildlife populations. Where habitat modification by megaherbivores facilitates co-occurring species, fire may amplify these effects in the short term by increasing the frequency or intensity of herbivory, leading to synergy. In the longer term, tree mortality due to both top kill by fire and toppling by large herbivores may reduce overall microhabitat availability, eliminating the synergy.

Key-words: browsing megaherbivores, compounded disturbances, context-dependent responses, contingency, controlled burning, ecosystem engineers, habitat facilitation, keystone species, large mammalian herbivores, transiently synergistic indirect effects

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Introduction

A large and long-standing literature documents the crucial role of disturbance in shaping population dynamics and distributional patterns (Sousa 1984). Yet although the independent impacts of many types of disturbance are increasingly well characterized, the interaction of multiple disturbance types remains poorly understood and has been identified as 'a key general challenge in contemporary ecology' (Turner 2010). Specifically, 'there remains a paucity of empirical information about whether and when a disturbance will amplify or attenuate the effects of another, or change the probability of its occurrence' (Turner 2010), in part because many types of disturbance are difficult to experimentally manipulate or simulate.

One crucial question is whether the effects of multiple disturbance drivers are additive, and thus predictable from the effects of each driver independently, or non-additive, and therefore not predictable from the results of single-factor studies or simple additive models (Paine, Tegner & Johnson 1998). Furthermore, non-additive interactions may be either synergistic (super-additive) or antagonistic (subadditive) (terminology *sensu* Folt *et al.* 1999; see also Crain, Kroeker & Halpern 2008; Darling & Côté 2008). Identifying synergistic effects, and the conditions under which they arise, is particularly important: whereas antagonistic interactions will tend to dampen systems' responses to perturbations, synergistic interactions will amplify the impacts of disturbance (Darling & Côté 2008).

This study addresses the independent and interactive effects of two principal drivers of disturbance in African savannas, fire and elephants, both of which are powerful determinants of vegetation structure and other ecosystem properties (Bond 2008). These drivers are linked via feedback loops, and their biotic effects can interact in several ways. For example, fire can shape the distribution and foraging behaviour of large herbivores at spatial grains ranging from thousands of hectares (Archibald *et al.* 2005; Fuhlendorf *et al.* 2009; Sensenig, Demment & Laca 2010) to individual trees (Shannon *et al.* 2011). Conversely, grazing and browsing can alter the extent and intensity of fire by affecting fuel load and composition (Van Langevelde *et al.* 2003; Holdo, Holt & Fryxell 2009). In addition, each factor can modulate the other's subsequent impacts: trees debarked or toppled by elephants are more likely to die by fire, whereas previously burned trees may sustain more frequent or severe elephant damage due to changes in forage quantity or quality, structural robustness, etc. (Moncrieff, Kruger & Midgley 2008; Shannon *et al.* 2011).

Theoretical models incorporating fire–browser interactions have predicted synergistic effects on savanna vegetation structure (Dublin, Sinclair & McGlade 1990; Van Langevelde *et al.* 2003; Holdo 2007; Holdo, Holt & Fryxell 2009), and empirical studies have documented interactive effects of fire and browsing on woody plants

(Moncrieff, Kruger & Midgley 2008; Holdo *et al.* 2009; Staver *et al.* 2009; Shannon *et al.* 2011). However, the attribution of these browsing effects to elephants specifically remains challenging, given that 'most studies have little success in separating elephant impacts from those caused by other herbivores and events such as fire, soil characteristics and drought' (Guldmond & van Aarde 2008). This suggests the need for factorial manipulations, but 'unfortunately, there are almost no experiments that have controlled for the impact of fire and herbivory, as well as the interaction between them' in savannas (Midgley, Lawes & Chamaille-Jammes 2010).

Even less well resolved are the indirect ramifications of fire- and elephant-driven shifts in vegetation structure for wildlife populations. Although the importance of disturbance propagation in shaping savanna food webs has long been recognized (McNaughton 1992), quantification of these indirect effects has lagged until recently (reviewed in Parr & Chown 2003; Keesing & Young 2014). As management priorities of savannas and rangelands world-wide increasingly expand to encompass biodiversity conservation, there is a corresponding need to characterize the effects of fire, large herbivores and their interaction on non-mammalian wildlife (Fuhlendorf *et al.* 2012). Although it is predictable that the processes affecting woody vegetation structure will also affect arboreal fauna, the direction and magnitude of these effects is not obvious *a priori*. For example, elephants have been shown both to decrease bird abundance and richness by reducing availability of arboreal perches (Ogada *et al.* 2008), and to increase the abundance and richness of herpetofauna by increasing structural habitat complexity, which creates refuges from predation risk and climatic stress that are otherwise scarce in savannas (Pringle 2008; Nasser, McBrayer & Schulte 2011). Fire can likewise have variable indirect effects on arboreal vertebrates, mediated by shifts in habitat structure and prey availability (Gregory, Sensenig & Wilcove 2010; Nkwabi *et al.* 2010). Yet we are unaware of prior studies evaluating indirect effects of fire, elephants and their interaction on other animal populations.

We experimentally quantified the indirect effects of fire and elephants on arboreal vertebrates and invertebrates in a simple and well-studied semi-arid savanna in central Kenya, using replicated factorial combinations of controlled burns and megaherbivore (i.e. elephant and giraffe) exclosures. We focused on the responses of the numerically dominant arboreal vertebrate and invertebrate guilds: insectivorous lizards and symbiotic plant-ants. The ant guild comprises four species that are obligate inhabitants of the mono-dominant whistling-thorn tree (*Acacia drepanolobium* Harms ex Sjöstedt), which covers >95% of the habitat (Palmer *et al.* 2008, 2013; Tarnita, Palmer & Pringle 2014). Because of the effective antiherbivore defence provided by these ants, *A. drepanolobium* trees are rarely browsed by elephants under baseline conditions (Goheen & Palmer 2010). The lizard guild comprises three species, of which the diurnal Kenya dwarf gecko

Lygodactylus keniensis Parker accounts for >99% of individuals; in fact, *L. keniensis* has the highest population density of any vertebrate species in this system (>1000 ha⁻¹ in places) and a biomass density rivalling that of a common antelope, Grant's gazelle (Pringle *et al.* 2007). Prior mechanistic experiments have shown that these highly arboreal lizards preferentially occupy elephant-damaged trees, because the splintering of woody stems by elephants creates cracks and crevices that geckos use as refuges and nest sites (Pringle 2008) (Fig. S1, Supporting information).

We predicted (a) that elephant exclusion alone would have weak indirect effects on gecko density, but (b) that fire would reduce ant abundance (plant defence) and thus (c) increase the frequency of elephant damage (Shannon *et al.* 2011), leading to (d) a synergistic positive effect on gecko density where the two disturbance types were present together. To explore the mechanisms underlying these predicted effects on geckos, we further quantified likely determinants of gecko habitat selection, including prey availability and occupancy patterns of plant-ant species that are more or less aggressive towards insects and geckos cohabiting the same trees.

Materials and methods

STUDY SYSTEM

Work was conducted at the Mpala Research Centre in Laikipia, Kenya (36°52' E, 0°17' N, 1800 m elevation). Rainfall at this site averages 550–600 mm/year, in a weakly trimodal annual pattern with a dry season from January to March. Fires are infrequent in this system (Okello *et al.* 2007) due to a combination of the short dry season, fire suppression by landowners (Sankaran, Augustine & Ratnam 2013), discontinuous understory cover in many parts of the region (Augustine 2003) and an extensive network of roads that act as firebreaks. Our study site had not burned for 20 years prior to this study. Large mammalian herbivores include elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), buffalo (*Syncerus caffer*), zebra (*Equus quagga* and *E. grevyi*), hartebeest (*Alcelaphus buselaphus*), Grant's gazelle (*Nanger granti*) and domestic cattle.

This site is underlain by heavy clay 'black-cotton' vertisols, and the biotic community is representative of those on similar soils throughout East Africa. The ant-associated *A. drepanolobium* accounts for >95% of woody cover, with >90% of trees < 4 m tall. In the absence of fire, nearly all of these trees are occupied by one of four species of symbiotic plant-ants (*Crematogaster mimosae*, *C. sjostedti*, *C. nigriceps* and *Tetraoponera penzigi*; (Young, Stubblefield & Isbell 1997). Although these four ant species differ in their aggressiveness towards herbivores (Palmer *et al.* 2010), they are collectively effective in deterring elephant browsing (Goheen & Palmer 2010).

Diurnal *Lygodactylus* geckos are widespread and locally common throughout Africa. Our focal species *L. keniensis* preys on aerial and arboreal insects up to 30 mm long (Pringle & Fox-Dobbs 2008). Individual trees constitute microhabitat, with up to one male and several females and subadults per tree. Previous studies at our site have experimentally identified several

correlates of gecko microhabitat selection, including elephant damage, tree size and prey abundance (Pringle *et al.* 2010; Donihue *et al.* 2013). Other lizards at this site include the side-striped chameleon *Chamaeleo (Trioceros) bitaeniatus* and the tree agama *Acanthocercus atricollis*. Although we recorded these two species in our surveys, they accounted for <<1% of individuals and were too infrequent for us to estimate their population sizes; we therefore focus on the dominant *L. keniensis* throughout.

HERBIVORE-EXCLUSION AND CONTROLLED-BURN EXPERIMENTS

The Kenya Long-term Exclusion Experiment (KLEE), established in 1995, independently manipulates the presence and absence of megaherbivores (elephants and giraffes), wild ungulates and cattle in a series of 4-ha plots (Young *et al.* 1998). One replicate of each herbivory treatment is present within each of three randomized blocks (north, central and south). In this study, we isolated the effects of megaherbivores using just two treatments: fenced megaherbivore-exclusion plots ('exlosures') and 'unfenced' control plots allowing all species. All plots used in this study are periodically grazed by cattle as well as wild ungulates. The megaherbivore-exclusion treatment uses wires at heights of 2 m (electrified) and 2.3 m (ground) to block access by elephants and giraffes only; this treatment is accessible to all other herbivores and carnivores (see photograph in Fig. S2, and see Young *et al.* 1998 for full details of the experimental design). As will become apparent, our results are clearly attributable to elephants and not giraffes; we therefore refer throughout the paper to the effects of elephants and of elephant exclusion rather than the generic 'megaherbivores'.

In February–March 2013, one 900-m² area (henceforth 'patch') was burned within each of the 4-ha plots. Complete details of the burning protocol are reported by Kimuyu *et al.* (2014). Patches were selected with an attempt to control for variation across treatments and blocks in tree density, to avoid potentially confounding differences in fire temperature, herbivore utilization, etc. For comparison with burned patches, we selected an unburned patch in each plot (using the same criteria), yielding a fully factorial split-plot design: 900-m² patches (burned vs. unburned) were nested within 4-ha plots (megaherbivores present vs. absent), which were nested within randomized blocks, with three replicates of each treatment combination (12 total patches).

All trees in the six burned patches (but not in the corresponding unburned patches) were individually tagged for long-term monitoring. In July 2013 (coinciding with the first of three lizard censuses), we recorded basal circumference, height, resident ant species, and the presence of severe elephant damage (defined as breakage of the main stem or damage to >50% of the crown) for each of these trees; these data were later used to model gecko microhabitat selection.

LIZARD AND ANT SURVEYS

We censused geckos in July 2013 (continental rains, 4 months post-burn), March 2014 (dry season, 12 months post-burn) and July 2014 (16 months post-burn) using mark–resight methods originally developed for Caribbean *Anolis* lizards (Heckel & Roughgarden 1979; Schoener, Spiller & Losos 2004) and previously used for geckos in this system (Pringle *et al.* 2007). We vis-

ited each 900-m² patch on three consecutive days, searching every tree and marking each lizard with a visit-specific colour of diluted water-soluble paint, which was applied from a distance with a forester's tree-marking squirt gun. We estimated population density (scaled per ha) as the mean of the three possible pairwise Chapman estimates, a bias-corrected variant of the Lincoln index:

$$N = [(M + 1)(C + 1)/(R + 1)] - 1$$

where M and C are the numbers of individuals marked on the first and second (or first and third, or second and third) visits, respectively, and R is the number of individuals resighted on the second visit. The mean Chapman estimate in each patch was very highly correlated ($r = 0.98$) with estimates generated using a multivariate contingency-table approach (Heckel & Roughgarden 1979). However, the latter method is more difficult to compute and failed to significantly fit the data for one patch in each year; thus, for consistency, we used the mean Chapman estimate throughout (cf. Schoener, Spiller & Losos 2004).

In the July 2013 and March 2014 surveys, we recorded height, basal circumference, ant inhabitant and presence of severe elephant damage (0/1, per the criteria above) for all trees in each patch. In burned patches, where all trees were individually tagged and monitored, we recorded the tag number of occupied trees, enabling us to compare attributes and ant inhabitants of occupied vs. unoccupied trees. Although corresponding individual-level tree-level data do not exist for the unburned patches in this study, the drivers of gecko habitat selection in unburned areas have been characterized previously (Pringle 2008; Pringle *et al.* 2010; Donihue *et al.* 2013).

PREY ABUNDANCE

We quantified prey availability in July of 2013 and 2014, using methods devised for other arboreal lizard populations (Schoener, Spiller & Losos 2002). In each year, three sticky traps (22 × 14 cm² clear plastic sheets with Tangle-Trap[®] adhesive coating on one side) were tied to vegetation *c.* 1.5 m above ground level, near the centre of each patch. We recorded the total number of arthropods captured after 72 h (*c.* 5200 total trap hours across the 2 years), identified each individual to order and measured its length (nearest mm). From these data, we generated two metrics of prey availability: number of individuals and total prey length per trap (averaged across the three traps in each patch). Aerial and arboreal Coleoptera, Diptera and Hemiptera collectively accounted for >75% of the 1090 arthropods captured (all ≤ 15 mm long), which corresponds well with the taxonomic distribution, size range and habitat stratum of these geckos' prey base (Greer 1967; Hardy & Crnkovic 2006; Pringle & Fox-Dobbs 2008).

DATA ANALYSIS

Descriptive statistics are given as means ± 1 SEM. Statistical analyses were conducted in R version 3.1.0 (R Development Core Team 2014). Because burned/unburned patches were nested within megaherbivore treatments, which in turn were nested within blocks, we analysed data using linear mixed-effects models (lme in the nlme library) to account for potential spatial non-independence. Fire (within plot) and megaherbivores (within

block) were specified as factorial fixed split-plot effects, with block as a random whole-plot effect. For gecko density, we conducted a separate analysis for each survey period (4, 12 and 16 months post-burn), to capture temporal variation in the strength of the experimental treatments and their interaction. We likewise analysed prey length and abundance separately for each year, but because these were unresponsive to the experimental treatments in both years, we averaged them to create time-integrated values for each patch and present analyses of only these mean values below. Because elephant damage was absent in megaherbivore-exclusion plots, we compared densities of elephant-damaged trees as a function of fire treatment (fixed) within block (random). We tested for correlations between gecko density and other patch-scale attributes using data from the July 2013 and March 2014 gecko censuses; we lacked patch-scale habitat data for July 2014.

To identify the factors driving gecko microhabitat selection at the scale of individual trees, we built a candidate set of 18 binomial generalized linear mixed models, with binary tree occupancy as the response variable (trees were 'occupied' if at least one gecko was present in any of the three 2013 census visits). The candidate set included a minimal model (intercept only) plus all combinations of the following three predictors and their first-order interactions: tree size (circumference, square-root transformed following prior work), binary elephant damage (0/1) and ant symbiont (categorical, with six levels corresponding to the four ant species, plus 'empty' trees, and 'other' for the 15 non-*A. drepanolobium* trees). We analysed all 559 trees with circumference ≥ 4 cm (the minimum viable size for gecko occupancy) within the six burned patches, using data from the 2013 gecko census. Models were specified using the glmer function in the lme4 library, with block and plot-within-block as random effects. We then ranked these models using the corrected Akaike Information Criterion (AIC_c; Burnham & Anderson 2002).

Results

PATCH-SCALE EFFECTS OF FIRE AND ELEPHANTS

In July 2013, neither fire nor elephants had pronounced main effects on gecko densities, but they had a strong synergistic interaction ($F_{1,4} = 16.48$, $P = 0.015$): gecko densities were 115–173% greater in patches with both disturbances present than in any other treatment combination (Fig. 1; Tables 1 and S1). We found no main effect of megaherbivore exclusion: in the absence of fire, gecko density remained roughly equivalent in the presence and absence of elephants for the 16-month duration of the study (Fig. 1, Table 1). In contrast, the main effect of fire grew stronger with time as densities in burned-exclosure patches increased: by July 2014, gecko densities were *c.* 100% greater in burned than in unburned patches, irrespective of elephant presence/absence (Fig. 1, Table 1). Correspondingly, the synergistic fire × elephant interaction progressively attenuated with time and was undetectable after 16 months (Fig. 1, Tables 1 and S1). In March 2014, the proportional representation of hatchlings and juveniles was significantly greater in burned than in unburned patches (0.35 ± 0.03 vs. 0.22 ± 0.03 ;

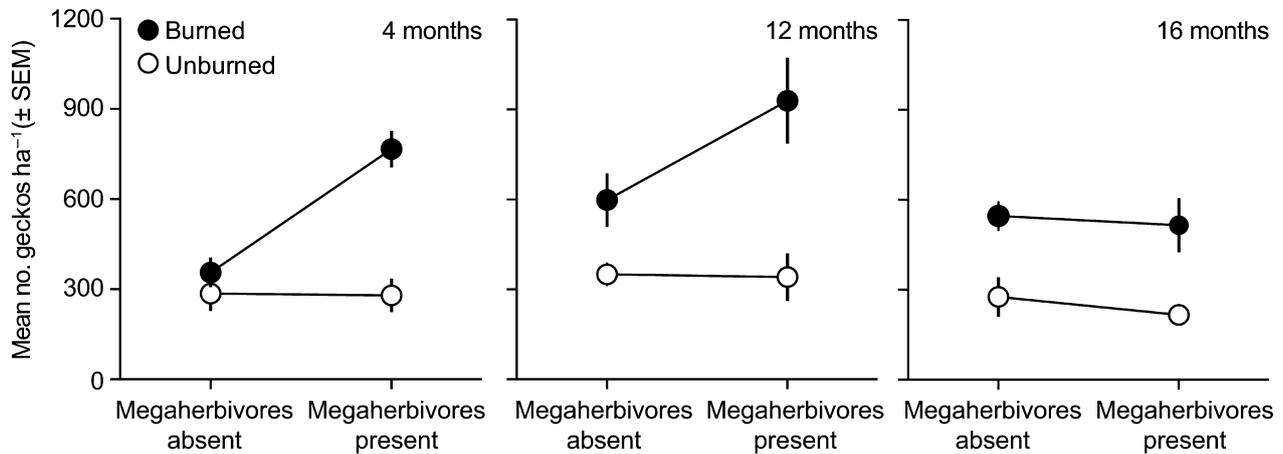


Fig. 1. Interaction plots of gecko density as a function of fire treatment and megaherbivore presence/absence in July 2013 (4 months post-burn), March 2014 (12 months post-burn) and July 2014 (16 months post-burn).

Table 1. Descriptive statistics for patch-level response variables in each treatment combination

Response	Means ± SEM for each treatment combination			
	–Mega –Fire	–Mega +Fire	+Mega –Fire	+Mega +Fire
Gecko density ha ⁻¹ (Jul. 2013)	286 ± 53	356 ± 44	280 ± 51	766 ± 56
Gecko density ha ⁻¹ (Mar. 2014)	350 ± 36	598 ± 84	341 ± 74	930 ± 138
Gecko density ha ⁻¹ (Jul. 2014)	276 ± 61	546 ± 47	216 ± 26	516 ± 47
Total tree density ha ⁻¹	1115 ± 144	1044 ± 76	819 ± 171	1026 ± 145
Mean tree circumference (cm)	19 ± 2	19 ± 1	18 ± 1	19 ± 1
Mean prey abundance trap ⁻¹	15.3 ± 1.8	12.8 ± 1.9	18.9 ± 3.2	13.6 ± 0.3
Mean prey length trap ⁻¹ (mm) [†]	56.0 ± 11.1	38.3 ± 3.1	61.1 ± 16.3	40.8 ± 0.7
No. <i>C. sjostedti</i> trees ha ⁻¹	396 ± 60	241 ± 77	215 ± 144	363 ± 71
No. <i>C. mimosae</i> trees ha ⁻¹	374 ± 82	404 ± 58	411 ± 128	374 ± 13
No. <i>C. nigriceps</i> trees ha ⁻¹	81 ± 37	85 ± 35	19 ± 10	56 ± 32
No. <i>T. penzigi</i> trees ha ⁻¹	233 ± 83	11 ± 6	74 ± 15	4 ± 4
No. unoccupied trees	22 ± 6	274 ± 26	26 ± 16	204 ± 47
No. elephant-damaged trees ha ⁻¹	0	0	44 ± 11	378 ± 46

See Table SI for statistical tests of the fixed effects megaherbivore exclusion, fire and their interaction.

[†]Prey metrics shown here are averages across two 72-h samples in July 2013 and July 2014.

main effect of fire $F_{1,4} = 13.03$, $P = 0.023$; other factors n.s.), possibly reflecting enhanced reproductive success.

The density of elephant-damaged trees (in plots with elephants present) was 8.5 times greater in burned than in unburned patches in July 2013 (Table 1; $F_{1,4} = 72.97$, $P = 0.013$ for main effect of fire; see photograph in Fig. S3) and changed little during the remainder of the study. However, there were no significant differences among the four treatment combinations in terms of total tree density, mean tree size, prey abundance or total prey length (Tables 1 and S1). Mean gecko density was highly correlated with density of elephant-damaged trees in July 2013 ($r = 0.92$, $F_{1,10} = 59.96$, $P < 0.0001$; Fig. 2) and March 2014 ($r = 0.81$, $F_{1,10} = 19.6$, $P = 0.001$), but was not significantly correlated at the patch scale with mean tree density, tree size, prey availability or the colony density of any symbiotic ant species in either year.

The number of trees inhabited by the plant-ant *Tetraponera penzigi* (8% of all trees) was significantly reduced in burned patches (Table 1), consistent with that species' disproportionately low survivorship immediately after the fire (Kimuyu *et al.* 2014). Conversely, the density of uninhabited *A. drepanolobium* trees was nearly ten-fold greater in burned (239 ± 29 ha⁻¹, c. 25% of all trees) than in unburned patches (24 ± 7 ha⁻¹, c. 2.5% of all trees), a legacy of the fire-induced colony mortality documented by Kimuyu *et al.* (2014). Empty trees were significantly smaller on average than trees with ant colonies (one-way ANOVA on square-root-transformed circumference, $F_{1,542} = 43.60$, $P < 0.0001$), likely because fire-induced colony mortality was greatest on smaller trees (< 50% survivorship on trees < 2 m tall: Kimuyu *et al.* 2014). The only other ant species whose abundance varied significantly among treatments was *Crematogaster sjostedti*, which was

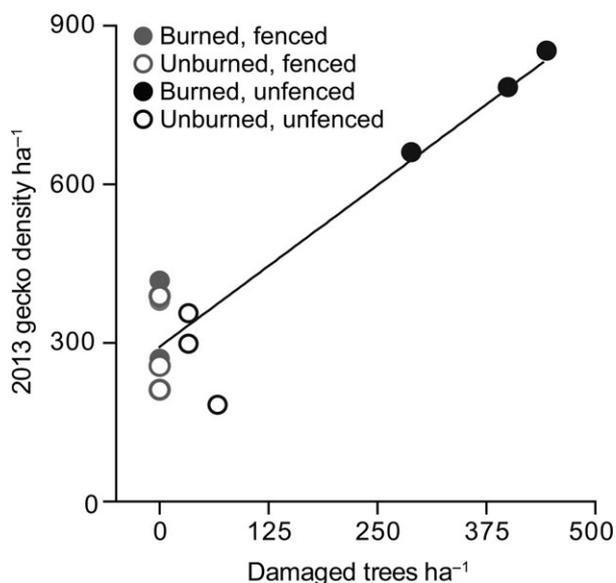


Fig. 2. Correlation between gecko density and the density of elephant-damaged trees in July 2013 (4 months post-burn). Each point represents one 900-m² patch ($n = 12$). A least-squares linear regression line is shown for all patches combined ($r = 0.92$); this trend is even stronger when patches within fenced elephant-exclusion plots are removed from the analysis ($r > 0.96$).

most abundant in the unburned–fenced and burned–unfenced plots (Tables 1 and S1).

TREE-SCALE DRIVERS OF GECKO MICROHABITAT SELECTION

The best-fitting model of per-tree gecko occupancy (Akaike weight $w_i = 0.43$) included all the three main effects (tree size, ant symbiont and elephant damage) with no interactions (Table 2). All three models with substantial empirical support ($\Delta_i < 2$; Burnham & Anderson 2002) contained all three main effects and differed only in the inclusion of interaction terms (combined $w_i = 0.78$). Parameter estimates from the best-fitting model showed that geckos selected for trees that were large, severely elephant damaged and inhabited by the non-aggressive ant symbiont *C. sjostedti*, whereas they selected against *A. drepanolobium* trees lacking ant colonies (Table S2).

Discussion

Four months after an experimental burn, the combined indirect impact of fire and megaherbivores on gecko density was synergistic (Folt *et al.* 1999): the effect of both factors combined was considerably stronger than the additive effect of the two factors independently (Fig. 1). Over the ensuing year, this synergy diminished and disappeared, resulting in a simple (but strong) main effect of fire persisting after 16 months. As noted above, we can think of no plausible mechanism by which giraffes could have contributed to this result, so we focus our discussion on elephants – the only other species excluded by our fences.

Table 2. Binomial generalized linear mixed models of gecko microhabitat selection in July 2013, ranked using AIC_C

Model rank	Model	AIC _C	K	Δ_i	w_i
1	Size + ED + Ant	543.00	10	0.00	0.43
2	Size + ED + Ant + (Size*ED)	544.68	11	1.68	0.18
3	Size + ED + Ant + (ED*Ant)	544.87	14	1.87	0.17
4	Size + ED + Ant + (Size*ED) + (ED*Ant)	545.98	15	2.98	0.10
5	Size + Ant	546.03	9	3.03	0.09
6	Size + ED + Ant + (Size*Ant) + (ED*Ant)	550.91	19	7.91	0.01
...					
18	Intercept only	661.14	3	118.1	0.00

Parameters of the best-fitting model are shown in Table S2. Sample size for all models is 559 trees. All models included block and plot-within-block as random effects to account for potential spatial autocorrelation. Notation follows Burnham & Anderson (2002): K is the number of parameters in the model; Δ_i is the difference in AIC_C between a given model i and the best model in the set; and w_i is the Akaike weight (i.e. the probability that model i is the best model in the set). Of the predictor variables, ‘Size’ is square-root-transformed tree size; ‘ED’ is presence/absence of elephant damage (0/1), and ‘Ant’ is ant symbiont species.

We propose the following interpretation of these results, based on both the data and analyses presented above and on prior work in this system. Ant colonies effectively defended trees in unburned–unfenced patches (Goheen & Palmer 2010), such that few trees were damaged and no significant main effect of elephant exclusion occurred for any response variable (Table S1). In contrast, fire killed a substantial proportion of ant colonies (Kimuyu *et al.* 2014) and increased trees’ susceptibility to elephant damage in burned–unfenced patches, leading to a rapid increase in the incidence of severely damaged trees (Table 1, Fig. S3). Because elephant-damaged tree stems and branches provide refuges and nest sites and are thus preferred microhabitat for geckos (Pringle 2008), gecko density increased rapidly via local immigration into burned–unfenced patches (Fig. 2), augmented by recruitment of hatchlings from eggs laid in elephant-created crevices (Fig. S1). After 16 months however, the crowns of many elephant-toppled trees had separated from the stem base and fallen on the ground (Fig. S4); this reduced overall habitat availability in burned–unfenced patches, prompting emigration of geckos and attenuation of the synergistic fire \times elephant interaction (although densities remained elevated relative to unburned–unfenced patches).

Meanwhile, the main effect of fire was muted in the first 4 months post-fire, but grew stronger as top-killed woody biomass slowly disintegrated, creating structural refugia functionally similar to those produced immediately by elephant damage. We repeatedly observed geckos sheltering underneath bark that had partially sloughed off

the stems of fire-damaged trees. Termites and wood-boring insects might also have contributed to the emergence of these microhabitat features over time. In short, fire enhanced local gecko densities via the same mechanism – creation of otherwise limiting refuges and nest sites – in both the presence and absence of elephants, but these effects emerged and attenuated at different rates. We expect that the main effect of fire will also eventually attenuate, and for the same reason: namely, mortality of the large trees most preferred as gecko microhabitat. Indeed, Okello *et al.* (2007) found that although *c.* 100% of *A. drepanolobium* trees survived for 9 months after a fire, the density of large trees declined by 64% after 8 years. Thus, the decadal-scale net effect of fire on local gecko density is likely to be negative. We consider several key components of this interpretation in greater detail below.

First, elephant damage was the only factor significantly correlated with gecko density at the patch scale and is the only factor that can explain the short-term synergistic effect of fire and megaherbivores. The factors driving gecko habitat selection at the scale of individual trees within burned patches (Table 2) were consistent with those from previous studies in unburned areas (Pringle 2008; Pringle *et al.* 2010; Donihue *et al.* 2013), suggesting that gecko microhabitat selection is independent of recent fire history. Elephant damage was the only one of these tree-scale factors that responded to the combination of fire and elephants in the same way as gecko density. Mean tree size did not differ across treatments. Colony density of the non-aggressive ant *C. sjostedti* was as great in the unburned–fenced treatment (where gecko density was lowest) as in the burned-unfenced treatment (Table 1). Trees lacking symbiotic ants of any species were avoided by geckos (Table S2), likely because these empty trees tended to be small, yet empty trees were (like geckos) most abundant in burned plots (Tables 1, S1). Prey availability, which has previously been shown to increase gecko microhabitat preference (Pringle *et al.* 2010), was if anything greater in *unburned* patches where gecko densities were lowest (Table 1), suggesting that our treatment effects were not driven by shifts in food availability.

Multiple non-exclusive mechanisms could account for the observed increase in elephant-damaged trees within burned patches. We hypothesize that a major contributor to this effect was reduction in the abundance of symbiotic ants, which have previously been shown to govern elephants' forage preferences: elephants readily ate *A. drepanolobium* branches from which ants had been removed, and avoided branches of otherwise favoured *Acacia* species to which ants had been added (Goheen & Palmer 2010). However, elephants may also preferentially utilize previously burned trees due to improved forage quality (Shannon *et al.* 2011), which can occur via increased nutritive value and/or decreased physical and chemical defences of foliage in the post-fire flush (Carlson *et al.* 1993; Schindler, Fulbright & Forbes 2004; Skidmore *et al.* 2010). In addition, the severity of damage induced by one type of disturbance may be greater for trees previously impacted by

another type of disturbance (Holdo 2007; Moncrieff, Kruger & Midgley 2008): structural damage caused by fire could weaken woody stems, increasing their likelihood of being snapped by browsing elephants. In our system, stem-boring cerambycid beetles are an important source of structural damage, which has been shown to increase following experimental removal of the aggressive plant-ants *C. mimosae* and *C. nigriceps* (Palmer *et al.* 2008); thus, fire may have indirectly increased beetle damage by eliminating ant colonies, thereby weakening trees. Additional research is currently underway to disentangle the mechanism(s) by which fire increased trees' susceptibility to elephant damage in this experiment.

We propose that the differences in gecko density among treatments were initiated by local migration and preferential selection of trees with greater refuge and nest-site availability and subsequently maintained by some combination of greater reproductive success and survivorship on trees with favourable structural attributes. Suggestive in this last respect is the significantly greater proportional abundance of juvenile geckos in burned patches in March 2014, which suggests greater reproductive output and/or hatchling survival in these areas. Indeed, during the 2014 censuses, we observed multiple sets of eggs within stems damaged by fire and/or elephants. These observations suggest that our results reflect the interplay of both behavioural (habitat selection) and numerical (demographic) responses of geckos to disturbance.

We conclude by addressing several caveats associated with our experimental approach and its specific combination of spatial and temporal scales. First, we controlled for tree density when selecting burned and unburned patches, which was necessary to minimize potentially confounding variation in fire intensity, herbivore utilization, etc. (Kimuyu *et al.* 2014). In so doing, however, we risked failing to detect chronic effects arising from megaherbivores' reduction of tree cover. Gecko density increases linearly with the density of trees >1 m tall, with slope ≈ 0.5 (Pringle *et al.* 2007). Thus, the net indirect effect of elephants on geckos should comprise both short-term positive impacts driven by increased microhabitat quality and longer-term negative impacts driven by decreased microhabitat quantity. However, total tree density within the larger 4-ha KLEE plots at the time of the study was only *c.* 37% greater inside vs. outside megaherbivore exclosures, which would predict only *c.* 19% greater gecko density within exclosures if we had selected patches randomly with respect to tree density. To the contrary, mean gecko density in unfenced-burned plots across all three surveys was 47% and 143% greater, respectively, than in burned and unburned exclusion plots. Thus, our main finding of transiently synergistic positive effects of fire and elephants on gecko density seems robust to the baseline effect of megaherbivores on tree density after nearly 20 years of experimental exclusion.

A second consideration is the potential contingency of our results on the spatial scale of our manipulations. Our

900-m² burns were large relative to the size of gecko territories (individual trees), but small relative to the typical extent of fire. Because fire also killed the ant colonies on many trees (in addition to other possible effects on palatability and stem structure), the burns created islands of susceptible trees in a sea of less-susceptible forage. This might have led to the concentration of elephant damage in these small patches and consequently to more pronounced indirect effects on gecko densities than would have occurred following a larger fire. However, a previous experiment at our site, in which 1-, 9- and 81-ha plots were burned in both continuous and patchy configurations (Sensenig, Demment & Laca 2010), found elevated numbers of elephant-topped trees in burned plots of all sizes; indeed, the highest rates of toppling occurred in 81-ha continuous burn and in 1-ha patchy burns (in which burned patches were 30 × 30 m, as in the present study; RLS, unpublished data). Thus, we believe that our conclusions are unlikely to be an artefact of the spatial scale of our manipulations, although future experimental tests of this conjecture would be informative.

Finally, with respect to temporal scale and the broader disturbance regime, we note that our results reflect a pulse of fire in a landscape in which fires are rare. In the absence of additional fires, we expect the effects of fire on gecko density and ant community structure to persist as a legacy effect for at least several more years, because woody biomass decays slowly in this semi-arid system. The consequences of increasing fire frequency are harder to predict. On the one hand, geckos strongly select larger trees, which are more likely to survive fires, and frequent fires would prevent fuel accumulation, reducing the likelihood of high-intensity fires that might kill large trees. On the other hand, a 40-year fire manipulation in South Africa showed that although return interval had surprisingly little effect on tree density, frequent fires decreased tree size (Higgins *et al.* 2007), which would negatively affect geckos.

These considerations underscore the challenges inherent in efforts to understand the effects of multiple disturbance interactions (Turner 2010) and point to the need for future research on the spatial and temporal dynamics and contingencies of these effects (especially in the context of broader disturbance regimes), which are difficult or impossible to assess using conventional experimental approaches (Fuhlendorf *et al.* 2009). Nonetheless, our study clearly shows that after controlling for potentially confounding factors and feedbacks, (a) the combined effects of fire and elephants on arboreal animals were considerably greater than the sum of each factor in isolation within the first 4–12 months post-fire and (b) these effects were temporally dynamic, and the synergy transient, such that only the main effect of fire was detectable after 16 months. These findings represent some of the only experimental evidence to date about how fire and elephants interactively shape small-animal assemblages, which are the key components of savanna biodiversity. They further suggest that studies of multiple disturbances

should measure responses at several intervals, because different disturbance types have legacies of variable duration, leading to shifts in the nature and of strength of the interaction term over time.

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Data accessibility

The data sets supporting this article are available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.bt21d> (Pringle *et al.* 2015).

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Supporting Information

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

Figure S1. Photographs of Kenya dwarf gecko and close-up of elephant-damaged tree.

Figure S2. Photograph of a burned plot within megaherbivore-exclusion treatment.

Figure S3. Photograph of an unfenced burned plot 4 months post-burn.

Figure S4. Photograph of an unfenced burned plot 16 months post-burn.

Table S1. Fixed-effect tests from linear mixed-model analysis.

Table S2. Parameters of the best-fitting binomial model of per-tree gecko occupancy.