

Context-dependent effects of large-wildlife declines on small-mammal communities in central Kenya

HILLARY S. YOUNG,^{1,2,3,4,12} DOUGLAS J. MCCAULEY,¹ RODOLFO DIRZO,⁴ JACOB R. GOHEEN,^{3,5} BERNARD AGWANDA,⁶ CARA BROOK,⁷ ERIK OTÁROLA-CASTILLO,⁸ ADAM W. FERGUSON,⁹ STEPHEN N. KINYUA,³ MOLLY M. McDONOUGH,^{2,9} TODD M. PALMER,^{3,10} ROBERT M. PRINGLE,^{3,7} TRUMAN P. YOUNG,^{3,11} AND KRISTOFER M. HELGEN²

¹Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA

²Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013 USA

³Mpala Research Centre, Box 555, Nanyuki, Kenya

⁴Department of Biology, Stanford University, Stanford, California 94305 USA

⁵Department of Zoology and Physiology and Department of Botany, University of Wyoming, Laramie, Wyoming 82071 USA

⁶Mammal Section, National Museums of Kenya, Nairobi, Kenya

⁷Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA

⁸Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138 USA

⁹Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409 USA

¹⁰Department of Biology, University of Florida, Gainesville, Florida 32611 USA

¹¹Department of Plant Sciences, University of California, Davis, California 95616 USA

Abstract. Many species of large wildlife have declined drastically worldwide. These reductions often lead to profound shifts in the ecology of entire communities and ecosystems. However, the effects of these large-wildlife declines on other taxa likely hinge upon both underlying abiotic properties of these systems and on the types of secondary anthropogenic changes associated with wildlife loss, making impacts difficult to predict. To better understand how these important contextual factors determine the consequences of large-wildlife declines on other animals in a community, we examined the effects of three common forms of large-wildlife loss (removal without replacement [using fences], removal followed by replacement with domestic stock, and removal accompanied by crop agricultural use) on small-mammal abundance, diversity, and community composition, in landscapes that varied in several abiotic attributes (rainfall, soil fertility, land-use intensity) in central Kenya. We found that small-mammal communities were indeed heavily impacted by all forms of large-wildlife decline, showing, on average: (1) higher densities, (2) lower species richness per site, and (3) different species assemblages in sites from which large wildlife were removed. However, the nature and magnitude of these effects were strongly context dependent. Rainfall, type of land-use change, and the interaction of these two factors were key predictors of both the magnitude and type of responses of small mammals. The strongest effects, particularly abundance responses, tended to be observed in low-rainfall areas. Whereas isolated wildlife removal primarily led to increased small-mammal abundance, wildlife removal associated with secondary uses (agriculture, domestic stock) had much more variable effects on abundance and stronger impacts on diversity and composition. Collectively, these results (1) highlight the importance of context in determining the impacts of large-wildlife decline on small-mammal communities, (2) emphasize the challenges in extrapolating results from controlled experimental studies to predict the effects of wildlife declines that are accompanied by secondary land-uses, and (3) suggest that, because of the context-dependent nature of the responses to large-wildlife decline, large-wildlife status alone cannot be reliably used to predict small-mammal community changes.

Key words: community structure; defaunation; diversity; East Africa; environmental gradients; exclosure experiment; land-use change; species richness.

INTRODUCTION

Humans are causing large-scale declines in wildlife populations across the globe, often with disproportionate effects on animals with large body size (Cardillo et

al. 2008, Schipper et al. 2008, Collen et al. 2009, Craigie et al. 2010, Wilkie et al. 2011, Dirzo et al. 2014). The loss of large wildlife, or defaunation, is known to cause marked changes in community structure, composition, and ecosystem functioning (Estes et al. 2011). However, the actual effects of large-wildlife decline are challenging to predict because their magnitude and direction vary strongly across studies and systems, even when similar response metrics are used (Bakker et al. 2006, Pringle et

Manuscript received 25 May 2014; revised 3 July 2014; accepted 17 July 2014; final version received 8 August 2014.
Corresponding Editor: T. G. O'Brien.

¹² E-mail: hillary.young@lifesci.ucsb.edu

al. 2007, Young et al. 2013). Although there have been strong suggestions that community level responses to large-wildlife decline may be influenced by underlying environmental contexts (Pringle et al. 2007, Hopcraft et al. 2010, Porensky et al. 2013), experimental evidence documenting this phenomenon is limited, particularly for vertebrate communities. Given the rapid pace of wildlife decline, understanding the variation in effects of large-wildlife decline across environmental gradients will be essential to mitigating the impacts of wildlife declines on environmental services.

In this study, we explore the effects of multiple forms of decline in large wildlife (here, animals with body mass >15 kg) on small-mammal (<1 kg) communities across rainfall and soil gradients in central Kenya. East Africa is a center of mammalian diversity (Ceballos and Ehrlich 2006) that is currently undergoing rapid rates of wildlife decline and secondary land-use change, in part due to increasing human populations and a shift in these populations from migratory to more sedentary lifestyles, with strong associated impacts on land conversion (Prins 1992, Lamprey and Reid 2004, Ogotu et al. 2009). Wildlife in Africa has been lost through direct exploitation, disease, and land conversion (Fratkin 2001, Homewood 2004). Here, we examine the effects of three widespread types of wildlife decline: (1) isolated loss of large wildlife (defaunation, simulated through experimental exclosures), (2) replacement of wildlife with domestic stock (pastoral), and (3) decline in wildlife associated with conversion to crop agriculture, on the abundance, richness, diversity, and community composition of small mammals. Small mammals, including rodents, shrews, and elephant shrews, are particularly appropriate subjects for addressing these broader questions about the context dependence of environmental change. Owing to their small size and rapid reproductive rates they are, as a group, less vulnerable to decline from human disturbances compared to larger mammals, and often appear to actually benefit from large-wildlife decline and other forms of human modification of ecosystems both in East Africa and in other sites around the world (Keesing 2000, Smit et al. 2001, Gardner et al. 2007). However, many small-mammal species are also known to be highly vulnerable to anthropogenic change, both in the region and globally (Swihart et al. 2003, Amori et al. 2008, 2012, Cardillo et al. 2008, Fritz et al. 2009). Conversely, any disturbance-induced changes that may occur in small-mammal communities are likely to be important both ecologically and economically. Small mammals often are dominant herbivores and seed predators, capable of transforming diversity, composition, and structure of plant communities (Keesing 2000, Howe et al. 2002, Maclean et al. 2011). They are important food items themselves, constituting a prey base for many other vertebrates. From a human perspective, this group is particularly important as a reservoir of zoonotic diseases (Ostfeld and Holt 2004, Luis et al. 2013) and crop

predators (Leirs 2003, Stenseth et al. 2003). Due to their small home range sizes, high abundance and diversity, and relative ease of sampling, it is possible to quantify meaningful changes in community properties of small mammals within relatively small geographic areas (e.g., experimental plots) over short time scales.

Using multiyear data sets from experimental exclosures and replicated observations across landscapes in Kenya, where large wildlife have declined, often in association with secondary human uses, we asked three main questions about the impacts of large-wildlife decline on small-mammal communities: (1) How do various forms of large-wildlife decline affect small-mammal abundance, diversity, and community composition? (2) Do environmental gradients related to productivity (e.g., rainfall, soil fertility) mediate these responses in predictable ways? And (3) what are the proximate mechanisms (e.g., vegetation cover, predator activity) by which these environmental gradients may mediate small-mammal responses to wildlife decline? We then explore the implications of these results for land managers attempting to anticipate changes in ecosystem processes that could result from large-wildlife declines. Understanding where effects are likely to be strongest may ultimately help managers prioritize sites for large-wildlife conservation, and also enable managers to be proactive in addressing impacts of changes in small-mammal communities in areas where impacts are likely to be strongest.

METHODS

We conducted our study in the open, wooded savannas of Laikipia County in central Kenya (0°17' N, 36°52' E). Laikipia, predominantly under private ownership, still maintains communities of free-ranging large wildlife, including elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), zebra (*Equus quagga* and *Equus grevyi*), buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), leopard (*Panthera pardus*), lion (*Panthera leo*), among other large species. However, wildlife conservation is just one of multiple land management goals for the properties in the ~10 000-km² region of Laikipia. As a result, the area has a diverse mosaic of land-uses with strong variation in wildlife abundances. In many parts of East Africa, declines of large wildlife intensify with agricultural and pastoral activities (Western et al. 2009, Ogotu et al. 2011, Kinnaird and O'Brien 2012). However, these wildlife declines also frequently occur in East Africa in the absence of such forms of secondary human use (e.g., through poaching or disease [Prins and van der Jeugd 1993, Reid et al. 1997, Ogotu and Owen-Smith 2003]). In Laikipia, the isolated effects of loss of large wildlife have been examined through the use of two exclosure experiments (KLEE and UHURU, see *Survey sites and experimental design*). Both of these experiments have multiple treatments, including those that simulate the isolated loss of all large wildlife (>15 kg).

Ecosystem primary productivity in Laikipia is driven largely by a combination of rainfall and soil properties. Our study area encompassed gradients in both annual rainfall and soil type. Rainfall in the area is weakly trimodal (typically with three wet and three dry seasons per year, although with strong interannual variation) and ranges from ~400 to ~900 mm/yr in the area studied. The region consists of two major soil types that differ in their physical properties and productivity potential: black cotton, with low sand:silt ratios (high clay) and higher productivity; and red soils, with high sand:silt ratios and lower productivity (Augustine and McNaughton 2006). To characterize underlying soils, we measured their sand:silt ratio (ranging from ~0.2 to ~4.8) and used this as a continuous metric to quantify each site's position on the gradient between the region's two major soil types.

Survey sites and experimental design

We surveyed 98 sites within an area of ~3000 km² in Laikipia County. Of these, 24 sites were part of the aforementioned enclosure experiments on Mpala Research Centre, and 74 occurred in the surrounding landscape. Each site was 1 ha in size (100 × 100 m). To control for environmental heterogeneity, we used a matched-pair design in which all sites were paired (49 total site pairs) to include (1) one "low-wildlife" site that either excluded large wildlife experimentally (defaunated sites) or supported reduced large-wildlife populations as a result of anthropogenic landscape changes (e.g., pastoral or agricultural use), and (2) one "high-wildlife" site that also had low livestock densities (see *Wildlife and livestock activity*). The two paired sites were separated from one another by fences or rivers, but were always <1 km from each other, and thus had similar climatic conditions and soil types. Sites within a given pair were sampled simultaneously. This paired design allowed us to control for effects of seasonality and abiotic variables when examining effects of wildlife decline across each site pair. A priori assessments of wildlife abundance and secondary human use for each site (based on interviews with local land managers) were independently confirmed via direct surveys of wildlife and livestock (see *Wildlife and livestock activity*). Vegetation and wildlife (including predator) communities were also surveyed at each site. Site pairs were never closer than 2 km from one another (among pairs), and were more typically between 5 and 15 km apart (with the exception of site pairs in experimental blocks, as described in *Small-mammal sampling*). The exact location of site pairs within stratified treatments (land-use type), was haphazard, primarily determined by the following logistical constraints: (1) the sites within a pair had a strong barrier to wildlife and domestic stock movement (such as fence or river) that was still crossable by researchers, (2) landowners were willing to allow access to the disturbed portion of the river, (3) "high-wildlife" sites directly

abutted "low-wildlife" sites, and (4) there were no major anthropogenic structures in either of the site pairs.

Experimentally defaunated sites consisted of sites from one of two long-term enclosure experiments intended to simulate the isolated effects of wildlife loss on ecological communities: the Kenya Long-term Enclosure Experiment (KLEE; details in Young et al. [1997]) and the Ungulate Herbivory Under Rainfall Uncertainty experiment (UHURU; details in Goheen et al. [2013]). Both experiments employ a stratified randomized block design and both include multiple treatments with different combinations of size classes of wild and/or domestic animals excluded; however, in this study, we used only the total wildlife enclosure and the open access (control) plots as sites. There are three replicate plots of each treatment in both experiments; in KLEE each plot is 4 ha in size (this study sampled from the inner 1 ha), while in UHURU each plot is 1 ha in size (this study sampled from the inner 0.36 ha). (See Appendix A for justification of plot sizes based on long-term animal movement data.)

Small-mammal sampling

Small-mammal abundance was surveyed by setting a grid of 100 Sherman traps (7.6 × 8.9 × 22.3 cm) over each 1-ha site (10 × 10 m grid spacing between traps, baited with peanut butter and oats) for three nights per trapping session (300 trap nights per site). Traps were typically closed between 06:00 and 08:00 and opened between 16:30 and 18:30. While trapping success increased slightly with each night of trapping, the proportion of new captures decreased strongly with each night of capture. Thus with only three nights of trapping, we estimate a capture rate of >60% of all animals (calculated as the number of unique animals per site over the number of animals estimated based on Schnabel estimates of actual population size (Krebs 1999)). Captured small mammals were identified to species using external morphological characteristics, and marked. Hair (for isotopic analysis) and blood (for genetic identification) samples were collected, and each individual's mass, sex, and sexual condition recorded.

Since small-mammal species are often taxonomically cryptic, with multiple closely related species occurring in the same landscape, we sacrificed a subset of animals for voucher specimens on the final day of trapping at a given site. (Specimens are currently deposited in the mammal collections at National Museums Kenya, Nairobi, Kenya, and the Smithsonian's National Museum of Natural History, Washington, D.C., USA; USNM catalog numbers 599501–599651). Identities of voucher specimens were confirmed via cranial morphology; DNA barcodes of each species were then submitted to the Barcode of Life Project. When species-level identification was difficult to determine in the field, the identity of any individuals in question that were not lethally sampled was confirmed by comparing blood samples from these individuals to the reference DNA

barcodes from specimen vouchers. To further ensure that cryptic species were not missed in the field, blood spots from a random subset of the animals not sacrificed for voucher specimens (~10% of total catch per species) were used to confirm species identity using DNA barcodes.

There were two major exceptions to the protocols described above. First, in the UHURU experiment, due to the size of experimental sites, in order to avoid edge effects we only placed 49 traps per night in the central 0.36 ha (total 147 trap nights per site; Appendix A). Second, a small number of *Crocidura* spp. and *Mus* spp. specimens could not be successfully barcoded; when possible we used field characteristics to assign these individuals to species. However when we were unable to assign species identities based on field or genetic characteristics, they were excluded from diversity and richness analyses (but still included in abundance analyses).

Due to low capture and recapture rates at some sites, we assessed abundance of small mammals per site simply as the minimum number of animals known alive (Nichols and Pollock 1983), based on the number of unique individual small mammals captured per site. This was standardized by trapping effort (trap nights) to allow for comparison of UHURU to other trapping efforts. Three primarily diurnal species (*Dasymys incomtus*, *Paraxerus ochraceus*, *Xerus erythropus*) were captured only incidentally (<5 captures each) and were excluded from all analyses because trapping was unlikely to sample them adequately and representatively across sites.

Abiotic gradients

Sites of each of the three types of wildlife decline were distributed across both rainfall and soil gradients. Annual rainfall for each site was interpolated from long-term rain gauge data in the region (Franz et al. 2010). Sites were normally distributed across the rainfall gradient. Small-mammal sampling took place in two periods spread over 18 months (March 2010–May 2010 and November 2010–July 2011). Our paired sampling approach was designed to control for most seasonal variability in animal abundance. However, in all unpaired analyses we also included a “recent rainfall” metric in our analyses, assessed as mean rainfall over the three months prior to sampling. A three-month time period was selected because it was roughly consistent with time lags (3–4 months) observed for increases in rodent abundance following precipitation in other studies (Keesing 1998a, Dickman et al. 1999, Ernest et al. 2000, Sluydts et al. 2007). It is also slightly above the median age of sexual maturity for the most common genera captured in this study (Tacutu et al. 2013). Finally, to further control for seasonal variation, site pairs with different types of wildlife decline were distributed across seasons, such that there was no significant difference in the amount of recent rainfall

received among treatments (ANOVA, $F = 1.69$, $P = 0.20$).

We sampled soil parameters at each site using pooled soil samples (3–5 locations per site, 0–20 cm depth). Soil samples were dried and sieved prior to analysis of the percentage of sand, silt, and clay (Brookside Laboratories, New Knoxville, Ohio, USA). Sites showed a clear bimodal distribution along the sand:silt content parameter.

Vegetation surveys

Vegetation at each site was surveyed at 50 sampling stations per site, placed on a 20 × 20 m grid that overlaid the 100 sampling locations of the 10 × 10 m mammal sampling grid. At each station we dropped five survey pins perpendicular to the grid line, with each pin 1 m apart from the previous pin (thus sampling a total of 4 m). At each of these total 250 pin drops per site we recorded all species that contacted the pin or were immediately above the pin, and the number of contacts per pin. For each site we then calculated vegetation cover (number of contacts of vegetation per survey pin), and species richness (number of species hitting at least one pin). Agricultural intensity was quantified by the percentage of agricultural crops in all pin drops; low-wildlife agricultural sites all had >10% cover of agricultural crop and lower than median levels of wildlife activity (detailed in *Wildlife and livestock activity*). Details of vegetation sampling are provided in Young et al. (2013).

Wildlife and livestock activity

To estimate the relative activity of wildlife and livestock at each site we surveyed the percentage of dung, categorized as either “domestic” or “wildlife.” These dung counts are not intended as a metric of actual abundance of animals, but only as a metric of relative activity levels of wildlife and livestock between and among site pairs (see Staver et al. [2012]). We also used these data to confirm a priori classifications of sites as high wildlife or low wildlife and classifications of low-wildlife sites as either pastoral or agricultural. To be considered in paired analysis, the high-wildlife site had to have higher than median levels of wildlife dung cover (0.76% overall cover) and, for low-wildlife pastoral sites, the percentage of livestock to wildlife dung had to be at least 50% higher in the low-wildlife as compared to the high-wildlife site (mean difference was 150%). Only two putative low-wildlife sites did not meet either these criteria, or criteria for low-wildlife agricultural sites, and were excluded from the analysis. To complement dung surveys, we used camera traps simultaneously. Camera traps provided both an index of activity for putative predators of small mammals and confirmed the general accuracy of dung surveys in estimating relative abundance of wildlife and livestock (details in Appendix B).



PLATE 1. There were 29 species of small mammals captured in the course of this study, including, pictured here, the grey climbing mouse, *Dendromus melanotis*. Photo credit: Lauren Helgen.

Statistical analyses

We calculated an effect size of land-use change on responses of small mammals (abundance, richness, and diversity) across each site pair as $\log_{10}[(\text{small-mammal response}_{\text{low}} - \text{small-mammal response}_{\text{high}})/(\text{small-mammal response}_{\text{high}} + 1)]$. The subscripts “low” and “high” refer to low-wildlife and high-wildlife sites. A value of zero thus indicated no change, while positive values indicated an increase in the response in managed habitats, and negative values indicated a decrease in the response in managed habitats. Data were log-transformed in order to normalize the responses. To compare effect sizes across land-use types and to examine the role that core environmental factors had upon these effect sizes, we used analysis of covariance (ANCOVA) tests. We included all of the following factors in the models: type of wildlife decline (defaunation only, or accompanied by pastoral or agricultural use) in the site pair, average annual rainfall at each site pair, average sand : silt ratio at each pair, and activity of wildlife (based on dung surveys) at the site in the pair. Results were found to be similar if percentage change in wildlife activity across the pair was used instead of activity on conserved site only. Wildlife dung cover was log-transformed prior to analysis. We also included interactions between type of wildlife decline and the two regionally important abiotic factors (soil, rainfall) examined.

To examine the proximate drivers of variation in small-mammal abundance, richness, and diversity across all sites we conducted a second set of ANCOVA analyses. These analyses included the following factors: form of wildlife decline, vegetation cover, vegetation

species richness, activity of wildlife (log-transformed dung cover), predator activity, recent rainfall, annual rainfall, soil sand : silt ratio, and the interaction of soil and annual rainfall with form of wildlife decline. Prior to conducting tests we confirmed a lack of strong multicollinearity among predictors; using a variance inflation factor (VIF) analysis all covariates had VIFs < 4.0 (a level above which concern of collinearity is merited). For land-use type, which is of particular concern given our underlying questions, the VIF was below 1.3 for all models, indicating no substantial collinearity with other variables. Sites, rather than site pairs, were the unit of replication in this analysis. Small-mammal abundance was log-transformed to meet assumptions of normality for the abundance analysis.

To understand changes in small-mammal community composition across wildlife and environment gradients we conducted nonmetric multidimensional scaling (NMDS). To compare species similarity across communities we conducted analyses of similarity (ANOSIM) among land-use types (Clarke 1993). We examined the role of environmental gradients and other site factors (Appendix C) on composition using nonparametric multivariate ANOVAs (McArdle and Anderson 2001), calculating P values using general permutation procedures (Manly 2007). To identify the species driving these relationships we conducted an indicator species analysis using the labdsv package in R (Dufrêne and Legendre 1997). This uses a hierarchical clustering approach to identify species characteristic of a given habitat or type of land-use through the relative specificity and fidelity of each species in each type of land-use. A good indicator in this analysis will include species that are both

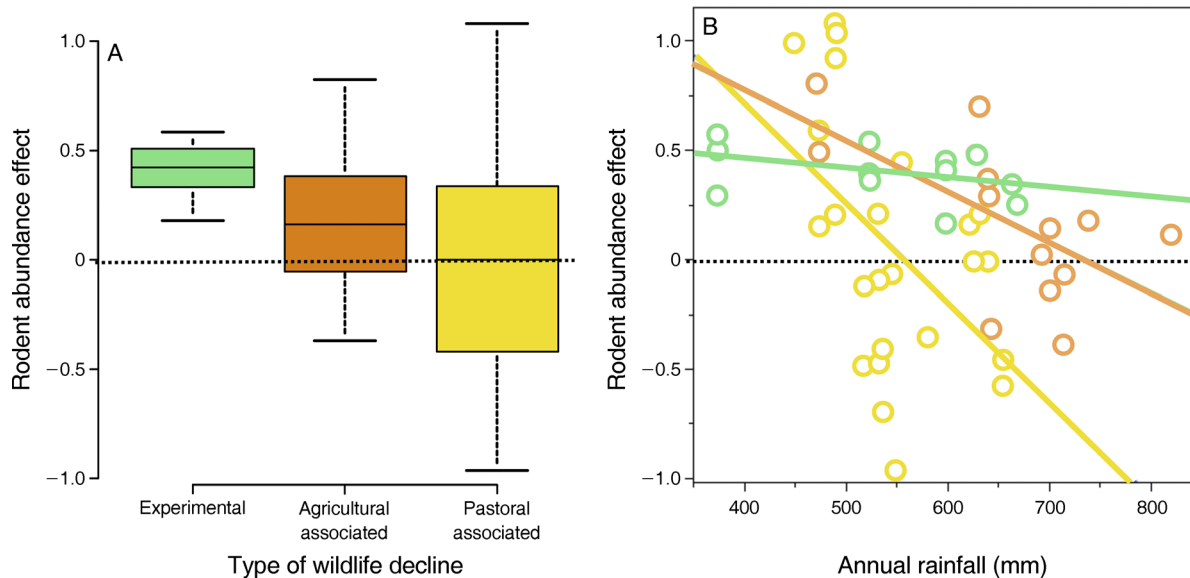


FIG. 1. Effects of wildlife declines on small-mammal abundance, comparing high-wildlife to low-wildlife sites under different situations of wildlife decline (A). Values above the zero line indicate increases in low-wildlife landscapes. The high variation in the effect is strongly correlated with annual rainfall, but there is a rainfall \times site type interaction (B).

abundant in that land-use type, and found predominantly only in that land-use type. To compare species richness among forms of wildlife decline we calculated rarefied richness estimates using a bootstrap approach (using raref2 function in R rich package) for each form of wildlife decline to compare across forms of wildlife decline with different sampling intensities (with site being the unit of replication); we then performed a randomization test (using the c2cv function) to examine the differences in species richness across site types (Rossi 2011). Shannon diversity per site was estimated using individual rarefaction estimates using the program EstimateS 9.1.0 (Colwell 2013). Except as otherwise noted, all analyses were conducted in R 2.12.1 (R Development Core Team 2005).

RESULTS

Small-mammal abundance

A total of 29 species and 1710 individuals were caught over 26 646 trap nights. Overall, large-wildlife activity was correlated to a significant decrease in total small-mammal abundance. These effects, however, were variable depending on the forms of wildlife decline investigated (Fig. 1A; $F = 3.2$, $df = 2$, 39 , $P = 0.05$). Experimental wildlife removal led to large and consistent increases in small-mammal abundance; wildlife decline associated with agriculture caused smaller and nonsignificant increases in small-mammal abundance; replacement with domestic stock had no overall effect on small-mammal abundance and showed the largest variability among site pairs (Fig. 1A). Much of the remaining variation observed in small-mammal response to type of wildlife decline was driven by variation in

annual rainfall among site pairs ($F = 11.4$, $df = 1$, 39 , $P = 0.002$; Fig. 1B), with increases in small-mammal abundance in low-rainfall environments, and decreases in high-rainfall environments. There was also a significant interaction between rainfall and type of defaunation ($F = 3.6$, $df = 2$, 39 , $P = 0.04$), with the rainfall effect being strongest in sites with secondary pastoral use, moderate in sites with agricultural secondary use, and absent in wildlife exclosure site pairs (Fig. 1B). Soil characteristics and large-wildlife activity in high-wildlife sites were not significantly correlated with small-mammal abundance, nor was the interaction of land-use and soil significantly correlated with small-mammal abundance.

Among all sites, the proximate drivers of abundance were rainfall ($F = 5.3$, $df = 1$, 48 , $P = 0.03$; Appendix D), and vegetation cover ($F = 10.1$, $df = 1$, 48 , $P < 0.01$), both of which had a positive relationship with small-mammal abundance. Neither predator activity, plant species richness, soil properties, activity of wildlife, nor recent rainfall had a significant relationship with small-mammal abundance. As in pairwise analysis, rainfall also had a significant interaction with type of wildlife decline in this site-by-site analysis ($F = 3.05$, $df = 1$, 48 , $P = 0.04$); soil properties did not interact significantly with type of wildlife decline in explaining small-mammal abundance.

Community composition

The community composition of small mammals responded differently to each land-use type (ANOSIM $R = 0.152$, $P = 0.001$; Fig. 2A). Pairwise comparisons showed that the community composition of small mammals on each land-use type was significantly

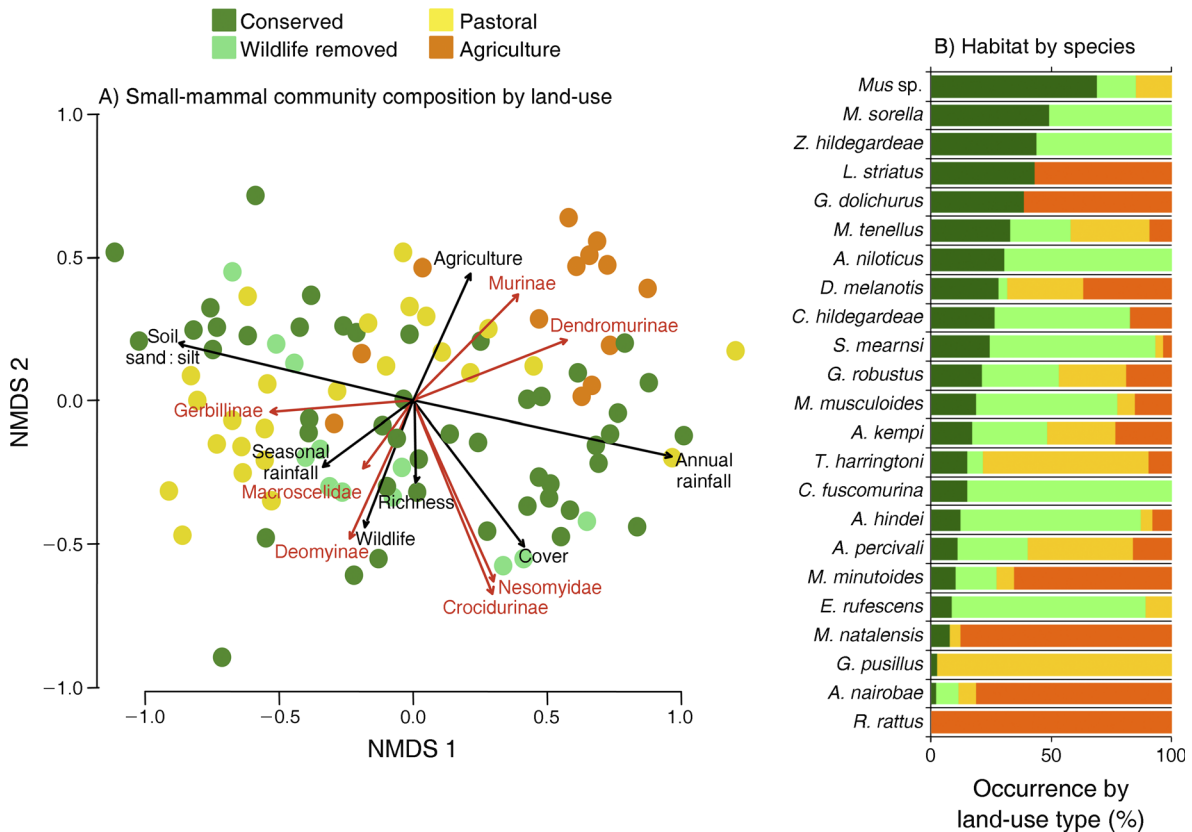


FIG. 2. (A) Variation in community composition of small mammals is shown in an NMDS plot (based on number of new animals per species per trap night) across all survey sites. There is strong clustering of communities by site type, with novel communities (occupying unique composition space) created in sites with secondary agricultural and, to a lesser extent, in pastoral uses. Each circle represents a site, color-coded by site type. Black arrows show correlations of biotic and abiotic features to community composition. Red arrows depict subfamilies of small mammals driving the variation in composition. The length of arrows corresponds to the strength of the correlation (only significant correlations shown). (B) Variation in community composition across habitats is driven by strong habitat preferences by species. Only 23 species are shown (taxa with fewer than 10 total captures are not shown). Habitat preferences are standardized by number of trap nights per habitat.

different from those on any other land-use type, with the exception that community composition in experimental control sites did not differ from that in wildlife enclosure sites (Table 1). Consistent with this observation, both the proportional representation of agricultural plants (any food species) per site and the activity of wildlife in a site were significant predictors of community composi-

tion; annual rainfall and soil properties were also important factors (Appendix C). The changes in composition were apparently driven by strong land-use preferences among species (Fig. 2B). Indicator species analyses show that agricultural sites were dominated by murine rodents (species classified in the subfamily Murinae, particularly *Mastomys natalensis*, *Arvicanthis*

TABLE 1. Similarity comparisons and richness estimates among site types.

Site type similarity/richness data	High wildlife	Low wildlife + agriculture	Low wildlife experimental	Low wildlife + livestock
Similarity				
High wildlife (<i>P</i> , (<i>R</i>))		0.01 (0.31)	0.86 (−0.70)	0.02 (0.09)
Low wildlife + agriculture (<i>P</i> , (<i>R</i>))			0.001 (0.56)	0.001 (0.44)
Low-wildlife experimental (<i>P</i> , (<i>R</i>))				0.001 (0.31)
Species richness				
Richness (mean ± SE)	23.6 ± 0.7	16.1 ± 1.4	19.7 ± 0.7	15.7 ± 0.7
95% CI	22.3–25.0	13.3–18.8	18.4–21.0	14.3–17.1

Note: For the Site type, similarity values, the *P* value is given first, followed by the *R* value in parentheses.

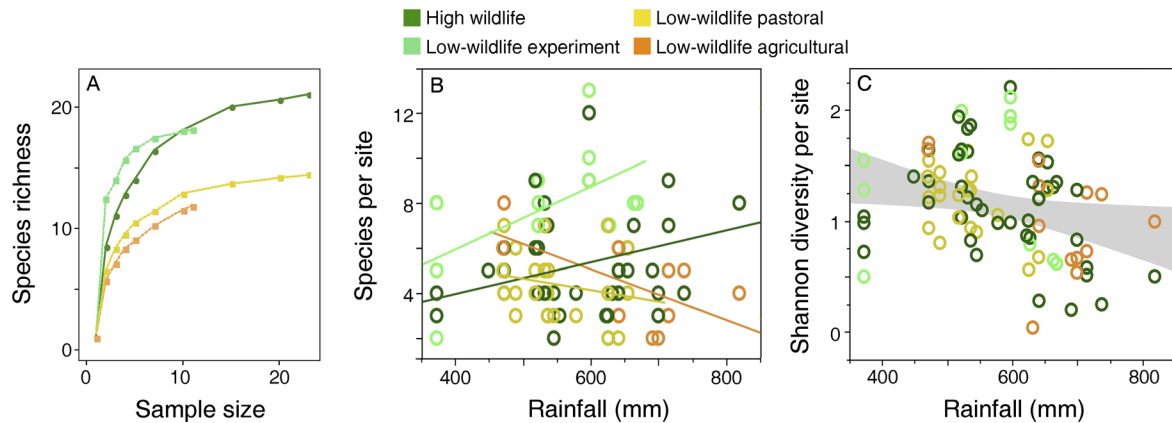


FIG. 3. (A) Rarefaction curves (with site as the unit of replication) for species richness for each site type show that higher overall diversity is found in high-wildlife and experimental low-wildlife than in low-wildlife sites with secondary anthropogenic change. Richness estimates generated are presented in Table 1. (B) On a per-site basis, species richness is significantly related to land-use type and the interaction between land-use and annual rainfall. (C) Defaunation has no significant effect on diversity (Shannon Diversity index), but rainfall is negatively correlated with diversity. The 95% confidence interval is shown in gray.

nairobae, and *Mus minutoides*), pastoral sites were dominated by gerbils (species classified in the subfamily Gerbillinae, particularly *Gerbillus pusillus* and *Taterillus harringtoni*). Wildlife enclosure and conserved sites had a broader range of species composition, and no significant differences in indicator species between these two habitats were identified. Environmental gradients and plant community characteristics also played a strong role in driving variation in community composition (Appendix C). Higher annual rainfall and increased vegetation cover were associated with increases in pouched mice (*Saccostomus mearnsi*) and shrews (*Crocidura* spp.), while greater sand:silt ratios were correlated with greater abundance of gerbils (Appendix C).

Species richness and diversity

Of the 29 small-mammal species captured in this study, all but one species, *Rattus rattus*, the sole introduced species captured in this system, occurred in high-wildlife sites (see Plate 1). In contrast, 10 species were not observed in each of the other site types converted for human use (Appendix E). The 95% confidence interval for small-mammal richness based on bootstrap randomization showed that richness was highest in high-wildlife and wildlife enclosure sites and lower in pastoral and agricultural sites (Table 1, Fig. 3A).

As species richness of small mammals at a site is unlikely to be completely captured in a single three-day sampling period, our best comparison of species richness across land-use types is as an aggregate across all sites. However, to understand the role that environmental context may have in mitigating effects of land-use change on species richness and diversity, and to identify the proximate drivers of these patterns, we also conducted analyses on a site pair and site basis. In pairwise ANCOVA comparisons, parallel to those

conducted for pairwise comparisons of small-mammal abundance, species richness was significantly lower in low-wildlife sites than in paired high-wildlife sites (95% CI of response ratio = -0.67 to -0.83). The decline in species richness varied by land-use and was stronger in agricultural and pastoral sites than in enclosure sites ($F = 10.62$, $df = 2, 39$, $P < 0.001$). There were no significant effects of rainfall, soil, total wildlife activity, or land-use \times rainfall or land-use \times soil interactions on species richness ($P > 0.1$ for all). There were no significant effects of site type or other measured factors on Shannon diversity indices ($P > 0.2$ for all).

To analyze possible proximate drivers of diversity change across all sites (rather than site pairs) we used the same ANCOVA factors employed in per site analyses of abundance changes of small mammals, namely: land-use type, vegetation cover, vegetation species richness, wildlife activity (log-transformed dung cover), predator activity, soil sand:silt ratio, annual rainfall, recent rainfall, and interactions between land-use and both annual rainfall and soil (Appendix F). We found that species richness varied significantly by site type ($P < 0.0001$, $F = 8.90$, $df = 3, 48$), with higher species richness in low-wildlife experimental enclosures than in any other site type. While there was no overall effect of rainfall on species richness, there was a significant interaction of site type \times rainfall ($P = 0.02$, $F = 3.71$, $df = 3, 48$), with species richness increasing with increased rainfall in enclosure and conserved sites, but negatively correlated with rainfall in agricultural sites and (nonsignificantly) in pastoral sites (Fig. 3B). Small-mammal species richness was also linearly correlated with plant species richness ($P = 0.04$, $F = 4.36$, $df = 1, 48$). The drivers of Shannon diversity were different from those of species richness. In this case annual rainfall was the best predictor of diversity with higher diversity at low-rainfall sites ($P = 0.03$, $F = 5.1$, $df = 1, 48$; Fig. 3C) and, consistent with results from pairwise analysis, there was

no significant effect of land-use or any other factor examined on diversity.

DISCUSSION

Effects of large-wildlife declines on small-mammal communities

Land-use change, when considered without reference to the specific type of change or to environmental context, generally caused decreases in small-mammal species richness, and shifts in composition, but had much more variable effects on abundance (although the overall effect was positive). In general, the magnitude and variation of effects differed strongly by the type of land-use change, with the effects of isolated wildlife loss via controlled manipulations (large-wildlife exclosures) being generally different from wildlife loss associated with pastoral or agricultural conversion. The effects on abundance were strongest (on average more than doubling of small-mammal abundance) in wildlife exclosure sites, consistent with multiple other studies documenting numerical compensation of small mammals following the loss of large mammals (Fig. 1A) (Keesing 1998b, 2000, Caro 2001, 2002, Smit et al. 2001, Saetnan and Skarpe 2006, Gardner et al. 2007, Goheen et al. 2010). The other two land-use changes were associated with relatively small net changes in small-mammal abundance and more rainfall-dependent variation in abundance changes that were observed across site pairs. In contrast, the effects on species richness and composition were generally much stronger in agricultural and pastoral sites and largely absent from wildlife exclosure sites. The highly disparate strength of small-mammal responses to isolated wildlife removal (using exclosures) as compared to other types of land conversion strongly suggest that caution should be used in extrapolating results from exclosures to other disturbed habitats that also include reduced wildlife. While isolated wildlife removal certainly does occur (e.g., extensive poaching, disease die-offs of large ungulates), this type of defaunation is not regionally common; in Laikipia, areas where large wildlife are absent typically also have extensive secondary human uses. Cumulatively, our results show that such secondary land-use changes do not simply exacerbate changes identified under wildlife removal alone, but rather cause a suite of changes in community composition that are distinct from those associated with wildlife loss and that vary by environmental context.

These results may also provide some insight into variable findings on compositional and diversity effects from other studies that include only small-scale experimental manipulations of large wildlife (Keesing and Young 2014) or only large-scale landscape observations (Caro 2001, 2002) on small-mammal communities in East Africa. However, although our results from exclosures closely mirrored those of other exclosure systems (Keesing and Young 2014), including strong increases in abundance and little effect on diversity or

composition, we saw very different results from those of Caro (2001, 2002), who at the landscape scale observed consistently higher abundance and diversity of small mammals in anthropogenic habitats as compared to conserved habitats. It may be that the strong heterogeneity in habitat (including closed forest) in Caro's (2001, 2002) studies drives these differences in results. Regardless, different conclusions across these studies suggest that large-wildlife activity alone is not a reliable indicator of the status of small-mammal communities, and that environmental and human context must be considered.

In a broader context, our work reinforces findings from other studies that suggest that it is difficult to extrapolate from carefully controlled, experimental contexts into broader ecosystems (Carpenter 1996, Skelly 2002, Schmitz 2004, Lunde et al. 2012, Young et al. 2013). While experimental manipulations are invaluable in identifying mechanisms of change and pinpointing causality, they can fail to approximate real-world effects for multiple reasons, including scale, environmental context, and multiple secondary effects not included in manipulations. Although the experimental manipulations used here are relatively large in scale, and expansive in the environmental context they cover, by design, they emphasize the effect of the treatments in the absence of any other possible sources of "experimental noise" and hence do not include varied types of secondary land transformation. Wildlife exclosures do tell us a great deal about the function of large wildlife in a landscape. However, their ability to approximate the effects of wildlife loss is thus more limited in a broader anthropogenic landscape where secondary land-use change is common. Yet, the comparison of experimental to nonexperimental systems also creates limitations on the inferences that can be made, and particularly limits our ability to identify specific drivers of differences among land-uses. Further experimental work is needed to identify the mechanisms that underlie these patterns, and if they are experimental artifacts, or unaccounted-for variables.

Effects of abiotic context on small-mammal responses

Although this study took place within one broad habitat type (wooded savanna) over a moderately constrained geographic area (~3000 km²), there were strong effects of environmental gradients on small-mammal communities. Annual rainfall was a particularly strong and consistent predictor of small-mammal abundance, diversity, and community composition, often subsuming the overall effect of wildlife decline across all sites. Notably, environmental gradients also strongly mediated the responses of land-use change, and explained a large amount of variation in abundance and richness responses within a land-use type. For example, the strong variation in abundance of animals following a particular form of wildlife decline was largely explained by variation in rainfall gradients. High-rainfall sites

tended toward decreases in small-mammal abundance following land-use change, while low-rainfall sites tended toward increases in small-mammal abundance following wildlife loss and secondary land-use change. This could potentially be due to relatively weaker bottom-up control in more productive systems. Differences in interactions between abundance and rainfall across various forms of wildlife decline and land-use may be due to differences in life history traits of the species that are most prevalent in each land-use type.

Species richness responses within a land-use type also varied significantly by land-use type, but the magnitude and even direction of rainfall effects varied by land-use. The importance of such abiotic gradients is consistent with previous studies (Pringle et al. 2007) and may explain the divergent results on land-use change and disturbance observed in other studies of African small mammals (Eccard et al. 2000, Keesing 2000). By identifying the drivers of the variability in community response to land-use change, we should ultimately be able to better model trade-offs between protection of managed lands and conservation of intact habitats (Pereira and Daily 2006, Mendenhall et al. 2011).

Mechanisms driving change

Of the multiple factors examined here as possible indicators of change in small-mammal communities, land-use type, vegetation cover, and rainfall were the most important. The relatively large observed variation in soils was poorly correlated with most response variables, although it was strongly associated with variation in community composition of small mammals (as is the case with the community composition of vegetation [Goheen et al. 2013]). Other predictors that we considered, including large-wildlife activity, predator activity, and recent rainfall, were either of minor or no importance in predicting community responses. This is somewhat surprising, because all of these factors are known to cause changes in small-mammal abundance in other systems (Keesing 2000, Hanski et al. 2001, Brown and Ernest 2002) and because our data show that isolated reductions of large wildlife do cause changes in small-mammal abundance. However, given the context-dependent nature of large-wildlife responses observed, and given that changes in wildlife abundance likely mechanistically impact small mammals through changes in vegetation, it is not surprising that vegetation cover should be a better predictor of small-mammal responses (Keesing 2000, Smit et al. 2001). Furthermore, large domestic herbivores may at least partially compensate for the role of large, wild herbivores in pastoral landscapes (Keesing and Young 2014), and direct subsidies from agriculture may overpower any effect of large-wildlife loss on food abundance.

The lack of correlations between small-mammal abundance or composition and predator activity may indicate a lack of strong direct control by mammalian predators on small mammals. Vegetation cover, which

provides protection from all predators, may thus be more relevant to predator avoidance (Orrock et al. 2004). Notably, the methods used here only surveyed mammalian predators, and thus these data are not indicators of total predator activity (e.g., snakes, raptors, and others not surveyed). However, it seems unlikely that raptor abundance will vary on the small spatial scale of site pairs, and other work has shown that snake abundance appears to increase in sites where small mammals are more abundant, suggesting they are responding to, not driving, small-mammal abundance changes (McCauley et al. 2006).

For land and wildlife managers, the identification of simple environmental indicators such as vegetation cover and rainfall levels, without regard to wildlife activity, as an indicator of small-mammal community characteristics, provides the potential for easy and practical metrics by which to locate and target high-value small-mammal habitats. This provides promising opportunities to identify these high-priority sites quickly and even remotely, for example, using Landsat, IKONOS, or Quickbird imagery to classify local-scale vegetation indices relevant for small-mammal communities.

Synthesis

Given the ubiquity of declines of large wildlife in East Africa, and around the world, land and wildlife managers need clear guidance on how to anticipate the cascading implications of these declines on broader ecological communities. In our examination of the responses of ecologically and economically significant small mammals to large-mammal declines, both the magnitude and the type of impacts (e.g., abundance vs. diversity and composition) of large-wildlife loss on small mammals were contingent both upon the abiotic and anthropogenic contexts in which these declines occur.

Understanding the differential effects of land-use change on abundance and composition of small mammals will be important for predicting effects on ecosystem function and the services (and other environmental impacts) provided by these animals. As just one example, small mammals are considered a reservoir of great importance for human zoonotic diseases (Mills and Childs 1998). When systematic changes in the abundance of small mammals occur following wildlife decline (as observed following experimental defaunation), this may cause increases in the risk of many rodent-borne diseases (Ostfeld and Holt 2004, Young et al. 2014). Conversely, for zoonotic diseases that have high host specificity, and are primarily frequency dependent, changes in community composition and species richness observed under more intensive types of land-use conversion, particularly in agricultural sites, will likely have more profound impacts than any changes in density (Venesky et al. 2013, Lacroix et al. 2014). For example, several species that appear to thrive in agricultural land-uses (e.g., *M. natalensis*, *A. nairobae*)

are known to be excellent hosts for several regionally important human pathogens (Oguge et al. 1997), and thus agricultural landscapes will likely increase prevalence of pathogens primarily hosted by these species. However, the relationship between host competence for a pathogen and resilience to a given type of disturbance is likely to vary across pathogens, and it is critical to understand the details of changes in host community composition, host density, and host competence for a given pathogen in order to understand likely effects of disturbance on zoonotic disease risk. Similarly complex results may be expected in the cases of other functional roles of small mammals, as both identity and abundance of small mammals will affect functions such as seed dispersal, and crop and seed predation.

While the interactions we observed are complex, based on our cumulative observations we highlight three patterns that we believe may better empower managers to predict some of these effects. (1) While the effects of defaunation on small mammals were highly variable, productivity (in this context mediated by rainfall) was critical to predicting this variation. In general responses were stronger, particularly for abundance changes, in low-productivity sites. While more work in other systems and with other taxa will be useful to assess the generality of this pattern, these data suggest that managers should target lower-productivity sites for large-wildlife conservation and management actions, as cascading impacts to other ecological constituents seem to be higher in these sites. (2) The effects of defaunation on small mammals depended strongly on what land-use changes were associated with wildlife loss. Isolated (experimental) defaunation resulted primarily in increased abundance of small mammals, while defaunation associated with secondary anthropogenic land-use change resulted primarily in compositional changes. The impacts on ecosystem functions and services provided by small mammals under these different types of defaunation are thus likely to be quite different, and managers will need to be careful in extrapolating results from experimental defaunation, or any single form of defaunation, more broadly. (3) Likely because of the complex, context-dependent nature of the effects of defaunation, large-wildlife activity was itself a poor overall predictor of small-mammal community abundance, diversity, or composition. Managers specifically interested in identifying or conserving particular small-mammal communities can focus on simple habitat parameters (particularly vegetation cover and rainfall) without needing to directly examine the more complex metric of large-wildlife activity. Considering all these issues will better empower us to effectively understand and confront the often complex responses of ecosystems to the rapidly proceeding declines in large wildlife that are occurring in many parts of the world. This should allow managers to better prioritize large-wildlife conservation in sites where reverberating effects of defaunation and secondary land transformation may be

strongest. It will also allow managers to proactively approach the management of ecological functions or services (e.g., disease control and monitoring) that will likely be strongly impacted by changes in small-mammal communities.

ACKNOWLEDGMENTS

We thank Jack Silanje, Peter Lokeny, Evelyn Ndinda, Stephen Nyaga, Frederick Erii, Margaret Kinnaird, John Lochikuya, Matthew Namoni, Jackson Ekadeli, Abdikadir Ali Hassan, Simon Lima, Patrick Etelej, Anne Adelson, and Pasha Feinberg for their assistance throughout this project. We also thank the Kenyan Government, Kenya Wildlife Service, National Museums Kenya, Mpala Research Centre, Ol Jogi Ranch, Ol Pejeta Ranch, Segera Ranch, Ol Misor Ranch, and the Lekiji, Il Motiok, Koiya, Lododo, Narok, Il Polei, Thome, Marura, and Kimugandura communities for their assistance in facilitating this research. Financial support for this project came from the James Smithson Fund of the Smithsonian Institution, the National Geographic Society (Grants 4691-91, 8846-10, 9106-12), National Science Foundation (LTREB BSR-97-07477, 03-16402, 08-16453, DEB-09-09670), Natural Sciences and Engineering Council of Canada, African Elephant Program of the U.S. Fish and Wildlife Service (98210-0-G563), Woods Institute for the Environment, Smithsonian Barcoding Network Grant, and Smithsonian Institution Women's Committee (SWC No. 22 and No. 44). We also thank the National Sciences and Engineering Research Council of Canada, the University of Wyoming, the University of Florida, the Princeton Environmental Institute's Grand Challenges Initiative, and the National Geographic Society (9291-13). We thank Tim Caro, Tim O'Brien, and two anonymous reviewers for their thoughtful comments on earlier versions of the manuscript. All small-mammal trapping and sampling was undertaken in accordance with institutional animal care and use permits (Smithsonian Institution IACUC permit No. 2009-04) and the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). We thank S. Miller, L. Helgen, C. France, A. Driskell, D. Lunde, J. Ososky, L. Cattaneo, A. Hintz, and H. Kafka for assistance at the Smithsonian.

LITERATURE CITED

- Amori, G., S. Gippoliti, and K. M. Helgen. 2008. Diversity, distribution, and conservation of endemic island rodents. *Quaternary International* 182:6–15.
- Amori, G., S. Masciola, J. Saarto, S. Gippoliti, C. Rondinini, F. Chiozza, and L. Luiselli. 2012. Spatial turnover and knowledge gap of African small mammals: using country checklists as a conservation tool. *Biodiversity and Conservation* 21:1755–1793.
- Augustine, D. J., and S. J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* 9:1242–1256.
- Bakker, E. S., M. E. Ritchie, H. Olf, D. G. Milchunas, and J. M. Knops. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9:780–788.
- Brown, J., and S. Ernest. 2002. Rain and rodents: complex dynamics of desert consumers. *BioScience* 52:979–987.
- Cardillo, M., G. Mace, J. L. Gittleman, K. E. Jones, J. Bielby, and A. Purvis. 2008. The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B* 275:1441–1448.
- Caro, T. M. 2001. Species richness and abundance of small mammals inside and outside an African national park. *Biological Conservation* 98:251–257.

- Caro, T. M. 2002. Factors affecting the small-mammal community inside and outside Katavi National Park, Tanzania. *Biotropica* 34:310–318.
- Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77:677–680.
- Ceballos, G., and P. R. Ehrlich. 2006. Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences USA* 103:19374–19379.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Collen, B., J. Loh, S. Whitmee, L. McRae, R. Amin, and J. E. Baillie. 2009. Monitoring change in vertebrate abundance: the Living Planet Index. *Conservation Biology* 23:317–327.
- Colwell, R. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and Application. <http://purl.oclc.org/estimates>
- Craigie, I. D., J. E. M. Baillie, A. Balmford, C. Carbone, B. Collen, R. E. Green, and J. M. Hutton. 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation* 143:2221–2228.
- Dickman, C., P. Mahon, P. Masters, and D. Gibson. 1999. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research* 26:389–403.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345:401–406.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Eccard, J. A., R. B. Walther, and S. J. Milton. 2000. How livestock grazing affects vegetation structures and small-mammal distribution in the semi-arid Karoo. *Journal of Arid Environments* 46:103–106.
- Ernest, S., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88:470–482.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, and J. B. Jackson. 2011. Trophic downgrading of planet earth. *Science* 333:301–306.
- Franz, T. E., K. K. Caylor, J. M. Nordbotten, I. Rodríguez-Iturbe, and M. A. Celia. 2010. An ecohydrological approach to predicting regional woody species distribution patterns in dryland ecosystems. *Advances in Water Resources* 33:215–230.
- Fratkin, E. 2001. East African pastoralism in transition: Maasai, Boran, and Rendille cases. *African Studies Review* 44:1–25.
- Fritz, S., O. Bininda-Emonds, and A. Purvis. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters* 12:538–549.
- Gardner, G. A., T. M. Caro, E. B. Fitzherbert, T. Banda, and P. Lalbhai. 2007. Conservation value of multiple-use areas in East Africa. *Conservation Biology* 21:1516–1525.
- Goheen, J. R., T. M. Palmer, G. K. Charles, K. M. Helgen, S. N. Kinyua, J. E. Maclean, B. L. Turner, H. S. Young, and R. M. Pringle. 2013. Piecewise disassembly of a large-herbivore community across a rainfall gradient: the UHURU experiment. *PLoS ONE* 8:e55192.
- Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. *Journal of Animal Ecology* 79:372–382.
- Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Small-rodent dynamics and predation. *Ecology* 82:1505–1520.
- Homewood, K. M. 2004. Policy, environment and development in African rangelands. *Environmental Science and Policy* 7:125–143.
- Hopcraft, J. G. C., H. Olf, and A. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution* 25:119–128.
- Howe, H., J. Brown, and B. Zorn-Arnold. 2002. A rodent plague on prairie diversity. *Ecology Letters* 5:30–36.
- Keesing, F. 1998a. Ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. *Journal of Mammalogy* 79:919–931.
- Keesing, F. 1998b. Impacts of ungulates on the demography and diversity of small mammals in central Kenya. *Oecologia* 116:381–389.
- Keesing, F. 2000. Cryptic consumers and the ecology of an African savanna. *BioScience* 50:205–215.
- Keesing, F., and T. P. Young. 2014. Cascading consequences of the loss of large mammals in an African savanna. *BioScience* 64:487–495.
- Kinnaird, M. F., and T. G. O'Brien. 2012. The role of private lands, livestock management and human tolerance on diversity, distribution and abundance of large wildlife. *Conservation Biology* 26:1026–1039.
- Krebs, C. J. 1999. *Ecological methodology*. Second edition. Benjamin/Cummings, Menlo Park, California, USA.
- Lacroix, C., A. Jolles, E. W. Seabloom, A. G. Power, C. E. Mitchell, and E. T. Borer. 2014. Non-random biodiversity loss underlies predictable increases in viral disease prevalence. *Journal of the Royal Society Interface* 11:20130947.
- Lamprey, R. H., and R. S. Reid. 2004. Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *Journal of Biogeography* 31:997–1032.
- Leirs, H. 2003. Management of rodents in crops: the Pied Piper and his orchestra. *ACIAR Monograph Series* 96:183–190.
- Luis, A. D., D. T. Hayman, T. J. O'Shea, P. M. Cryan, A. T. Gilbert, J. R. Pulliam, J. N. Mills, M. E. Timonin, C. K. Willis, and A. A. Cunningham. 2013. A comparison of bats and rodents as reservoirs of zoonotic viruses: Are bats special? *Proceedings of the Royal Society B* 280:20122753.
- Lunde, K. B., V. H. Resh, and P. T. Johnson. 2012. Using an ecosystem-level manipulation to understand host-parasite interactions and how they vary with study venue. *Ecosphere* 3:art84.
- Maclean, J. E., J. R. Goheen, D. F. Doak, T. M. Palmer, and T. P. Young. 2011. Cryptic herbivores mediate the strength and form of ungulate impacts on a long-lived savanna tree. *Ecology* 92:1626–1636.
- Manly, B. F. 2007. *Randomization, bootstrap and Monte Carlo methods in biology*. CRC Press, Boca Raton, Florida, USA.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297.
- McCauley, D. J., F. Keesing, T. P. Young, B. F. Allen, and R. M. Pringle. 2006. Indirect effects of large herbivores on snakes in an African savanna. *Ecology* 87:2657–2663.
- Mendenhall, C., C. Sekercioglu, F. Oviedo Brenes, P. Ehrlich, and G. Daily. 2011. Predictive model for sustaining biodiversity in tropical countryside. *Proceedings of the National Academy of Sciences USA* 108:16313–16316.
- Mills, J. N., and J. E. Childs. 1998. Ecologic studies of rodent reservoirs: their relevance for human health. *Emerging Infectious Diseases* 4:529.
- Nichols, J. D., and K. H. Pollock. 1983. Estimation methodology in contemporary small-mammal capture-recapture studies. *Journal of Mammalogy* 64:253–260.

- Oguge, N., M. Rarieya, and P. Ondiaka. 1997. A preliminary survey of macroparasite communities of rodents of Kahawa, Central Kenya. *Belgian Journal of Zoology* 127:113–118.
- Ogutu, J., H. P. Piepho, H. Dublin, N. Bhola, and R. Reid. 2009. Dynamics of Mara–Serengeti ungulates in relation to land use changes. *Journal of Zoology (London)* 278:1–14.
- Ogutu, J. O., and N. Owen-Smith. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters* 6:412–419.
- Ogutu, J. O., N. Owen-Smith, H. P. Piepho, and M. Y. Said. 2011. Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. *Journal of Zoology (London)* 285:99–109.
- Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behavioral Ecology* 15:433–437.
- Ostfeld, R. S., and R. D. Holt. 2004. Are predators good for your health? Evaluating evidence for top down regulation of zoonotic disease reservoirs. *Frontiers in Ecology and the Environment* 2:13–20.
- Pereira, H. M., and G. C. Daily. 2006. Modeling biodiversity dynamics in countryside landscapes. *Ecology* 87:1877–1885.
- Porensky, L. M., S. E. Wittman, C. Riginos, and T. P. Young. 2013. Herbivory and drought interact to enhance diversity and spatial patterning in a savanna understory. *Oecologia* 173:591–602.
- Pringle, R. M., T. P. Young, D. I. Rubenstein, and D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences USA* 104:193–197.
- Prins, H. H. 1992. The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19:117–123.
- Prins, H. H., and H. P. van der Jeugd. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology* 81:305–314.
- R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reid, R. S., C. J. Wilson, R. L. Kruska, and W. Mulatu. 1997. Impacts of tsetse control and land-use on vegetative structure and tree species composition in south-western Ethiopia. *Journal of Applied Ecology* 34:731–747.
- Rossi, J.-P. 2011. rich: an R package to analyse species richness. *Diversity* 3:112–120.
- Saetnan, E. R., and C. Skarpe. 2006. The effect of ungulate grazing on a small-mammal community in southeastern Botswana. *African Zoology* 41:9–16.
- Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, A. S. Rodrigues, S. N. Stuart, and H. J. Temple. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322:225–230.
- Schmitz, O. 2004. From mesocosms to the field: the role and value of cage experiments in understanding top-down effects in ecosystems. *Insects and ecosystem function*. Springer Series in Ecological Studies 173:277–302.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92.1:235–253.
- Skelly, D. K. 2002. Experimental venue and estimation of interaction strength. *Ecology* 83:2097–2101.
- Sluydts, V., L. Crespin, S. Davis, M. Lima, and H. Leirs. 2007. Survival and maturation rates of the African rodent, *Mastomys natalensis*: density-dependence and rainfall. *Integrative Zoology* 2:220–232.
- Smit, R., J. Bokdam, J. dem Ouden, H. Olf, H. Schot-Opschoor, and M. Schrijvers. 2001. Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology* 155:119–127.
- Staver, A. C., W. J. Bond, M. D. Cramer, and J. L. Wakeling. 2012. Top-down determinants of niche structure and adaptation among African acacias. *Ecology Letters* 15:673–679.
- Stenseth, N. C., et al. 2003. Mice and rats: the dynamics and bio-economics of agricultural rodents pests. *Frontiers in Ecology and the Environment* 1:367–375.
- Swihart, R. K., T. C. Atwood, J. R. Goheen, D. M. Scheiman, K. E. Munroe, and T. M. Gehring. 2003. Patch occupancy of North American mammals: Is patchiness in the eye of the beholder? *Journal of Biogeography* 30:1259–1279.
- Tacutu, R., T. Craig, A. Budovsky, D. Wuttke, G. Lehmann, D. Taranukha, J. Costa, V. E. Fraifeld, and J. P. de Magalhães. 2013. Human Ageing Genomic Resources: integrated databases and tools for the biology and genetics of ageing. *Nucleic Acids Research* 41:D1027–D1033.
- Venesky, M. D., X. Liu, E. L. Sauer, and J. R. Rohr. 2013. Linking manipulative experiments to field data to test the dilution effect. *Journal of Animal Ecology* 83:557–565.
- Western, D., S. Russell, and I. Cuthill. 2009. The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS ONE* 4:e6140.
- Wilkie, D. S., E. L. Bennett, C. A. Peres, and A. A. Cunningham. 2011. The empty forest revisited. *Annals of the New York Academy of Sciences* 1223:120–128.
- Young, H. S., R. Dirzo, K. M. Helgen, D. J. McCauley, S. A. Billeter, M. Y. Kosoy, L. M. Osikowicz, D. J. Salkeld, T. P. Young, and K. Dittmar. 2014. Declines in large wildlife increase landscape-level prevalence of rodent-borne disease in Africa. *Proceedings of the National Academy of Sciences USA* 111:7036–7041.
- Young, H. S., D. J. McCauley, K. M. Helgen, J. R. Goheen, E. Otárola-Castillo, T. M. Palmer, R. M. Pringle, T. P. Young, and R. Dirzo. 2013. Effects of mammalian herbivore declines on plant communities: observations and experiments in an African savanna. *Journal of Ecology* 101:1030–1041.
- Young, T. P., B. Okello, D. Kinyua, and T. M. Palmer. 1997. KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science* 14:94–102.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–F are available online: <http://dx.doi.org/10.1890/14-0995.1.sm>

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.465ts>