

# Effects of land-use change on community diversity and composition are highly variable among functional groups

STUART I. GRAHAM,<sup>1,6,7</sup> MARGARET F. KINNAIRD,<sup>2</sup> TIMOTHY G. O'BRIEN,<sup>3</sup> TOR-G VÅGEN,<sup>4</sup> LEIGH A. WINOWIECKI,<sup>4</sup> TRUMAN P. YOUNG,<sup>5</sup> AND HILLARY S. YOUNG<sup>1</sup>

<sup>1</sup>Department of Ecology, Evolution and Marine Biology and the Marine Science Institute, University of California, Santa Barbara, California 93106 USA

<sup>2</sup>World Wide Fund for Nature International, P.O. Box 62440-00200, Nairobi, Kenya

<sup>3</sup>Wildlife Conservation Society, 2300 Southern Blvd, Bronx, New York 10460 USA

<sup>4</sup>World Agroforestry Centre (ICRAF), P.O. Box 30677, Nairobi, Kenya

<sup>5</sup>Department of Plant Sciences, University of California, Davis, California 95616 USA

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*Abstract.* In order to understand how the effects of land-use change vary among taxa and environmental contexts, we investigate how three types of land-use change have influenced phylogenetic diversity (PD) and species composition of three functionally distinct communities: plants, small mammals, and large mammals. We found large mammal communities were by far the most heavily impacted by land-use change, with areas of attempted large wildlife exclusion and intense livestock grazing, respectively, containing 164 and 165 million fewer years of evolutionary history than conserved areas (~40% declines). The effects of land-use change on PD varied substantially across taxa, type of land-use change, and, for most groups, also across abiotic conditions. This highlights the need for taxa-specific or multi-taxa evaluations, for managers interested in conserving specific groups or whole communities, respectively. It also suggests that efforts to conserve and restore PD may be most successful if they focus on areas of particular land-use types and abiotic conditions. Importantly, we also describe the substantial species turnover and compositional changes that cannot be detected by alpha diversity metrics, emphasizing that neither PD nor other taxonomic diversity metrics are sufficient proxies for ecological integrity. Finally, our results provide further support for the emerging consensus that conserved landscapes are critical to support intact assemblages of some lineages such as large mammals, but that mosaics of disturbed land-uses, including both agricultural and pastoral land, do provide important habitats for a diverse array of plants and small mammals.

*Key words:* Africa; alpha diversity; community composition; disturbance; ecosystem function; land-use change; mammal; phylogenetic diversity; plant; savanna; species richness; turnover.

## INTRODUCTION

The conversion of wildland to anthropogenic use is a major driver of contemporary biodiversity loss (Newbold et al. 2015, 2016). Humanity has now directly modified more than 50% of Earth's land cover (Millennium Ecosystem Assessment 2005), and land-use change is considered a major component of extinction risk for 46% of all IUCN Red Listed species (IUCN 2017). Although the impacts of land-use change on local-scale species diversity are often negative (Newbold et al.

2016), the nature of these impacts appears to differ among taxonomic groups and across ecological contexts (Allan et al. 2014, Gossner et al. 2016). Understanding which taxonomic groups, in which contexts, are most affected by land-use change is critical to help managers target conservation or restoration efforts based on local conditions, the particular taxa of interest, and the types of land-use change occurring.

A first methodological challenge to understanding the effects of land-use change on ecological communities is the choice of which metrics to use to describe any changes. The metrics that are most commonly used to quantify community responses to land-use change, species richness and species diversity, may not be the most appropriate for achieving management goals. These types of taxonomic diversity metrics are highly appealing in a management context because they require data

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<sup>6</sup> Present address: Department of Biology, University of Washington, Seattle, Washington 98195 USA.

<sup>7</sup> E-mail: sgraham3@uw.edu

that are often readily available. However, these metrics are frequently observed to remain stable or decline only modestly despite large changes in community composition and, critically, ecological function (Spaak et al. 2017, Hillebrand et al. 2018). The monitoring of taxonomic diversity metrics is therefore insufficient to evaluate whether protected areas support vital ecosystem services (Jarzyna and Jetz 2016). Consequently, there is increasing pressure on managers and decision makers to use alternative metrics of community composition that better capture the functional impacts of community compositional change.

Phylogenetic diversity (PD), traditionally measured as the sum of all branch lengths in the phylogeny of a community (Faith 1992), is increasingly being used to document evolutionarily and ecologically meaningful changes in community composition (Grab et al. 2019). The justification for using PD to infer ecological function lies in the phylogenetic conservation of traits. A community containing only closely related taxa, and therefore possessing low PD, is expected to have a low diversity of functional traits. Moreover, PD has been proposed as a potentially valuable proxy for functional diversity (FD) because it is objective, easily compared across even highly disparate taxa, and requires data that are readily available (Cavender-Bares et al. 2009, Srivastava et al. 2012; but see Winter et al. 2013 for a counter argument). In any case, as the evolutionary legacy of a community, PD should be positively correlated with evolutionary potential (Faith 1992) and the potential to adapt and persist through rapid environmental change (Forest et al. 2007, Sgrò et al. 2011, Mouquet et al. 2012). Notably, PD and taxonomic diversity often diverge in important ways. Of particular importance to our questions, multiple taxa have shown significantly more dramatic declines in PD than in species richness following anthropogenic disturbance (fish [D'Agata et al. 2014], birds [Edwards et al. 2015], zooplankton [Helmus et al. 2010], and trees [Ribeiro et al. 2016]; although the opposite pattern has been seen in frogs [Nowakowski et al. 2018]), suggesting that this metric may capture aspects of compositional change that taxonomic diversity metrics do not. For all these reasons, we thus focus our analyses on the effects of land use change on PD.

Surprisingly, we still have a very limited understanding of how the effects of land-use change on PD vary among taxonomic groups and ecological contexts. To our knowledge, there have been no previous studies that compare PD responses to land-use change across multiple taxonomic groups in the same system. This is an important knowledge gap given that taxonomic diversity responses have been observed to differ greatly among taxa (Allan et al. 2014, Gossner et al. 2016). We might expect PD responses to land-use change to show similar variation among taxonomic groups given that some (e.g., large mammals; Young et al. 2013, Ripple et al. 2015) tend to be disproportionately vulnerable to

anthropogenic pressures. In addition, the type of land-use change is likely to influence PD, as it does species diversity (Isaac and Cowlishaw 2004, Young et al. 2015, Vellend et al. 2017), due to the inherent taxonomic biases of certain land-use practices (e.g., hunting, weeding). Community PD responses may also depend on abiotic conditions, as was observed in a meta-analysis of species diversity responses where declines in species diversity following disturbance were largest in areas of high temperature and low precipitation (Mantyka-pringle et al. 2012). Divergent responses across coexisting species groups and across ecological contexts within a system would have many important implications for management. For example, this would suggest that managers cannot generalize across taxa or systems, and thus, high resolution taxa- and context-specific studies would be required to predict the benefits of restoration efforts. It would also suggest high potential for the disruption of the many fundamental ecological interactions that occur between taxonomic groups (e.g., predation, parasitism, pollination), with potential implications for ecosystem functionality. For example, declines in avian PD (Frishkoff et al. 2014, Cosset and Edwards 2017) following land-use change may indirectly disrupt seed dispersal or pollination services.

Yet, although estimates of PD are likely more informative of community composition than species diversity estimates, we recognize that temporal stability in phylogenetic or even functional diversity does not necessarily reflect a parallel stability in community composition, nor does it guarantee the maintenance of pre-disturbance functioning. If land-use change results in high levels of turnover, the species that are gained could replace the phylogenetic diversity that was lost through extirpations despite representing entirely different lineages and ecological functions (Strauss et al. 2006, Sullivan et al. 2015, Weigel et al. 2016). Sobral et al. (2016) introduced a metric (called “false compensation”) that evaluates the degree to which community compositional change is influenced by species turnover that cannot be detected by alpha diversity metrics such as PD. This is a critical, but still understudied distinction, given that substantial functional changes can occur despite invariant species richness (Spaak et al. 2017) and we expect such false compensation may be commonly overlooked in analyses of PD responses. Given these recognized limitations of PD, we thus also examine the extent of compositional change undetected by PD, and the degree of phylogenetic signal in species' responses to land-use change.

In this study, we investigate patterns of PD and community composition for three co-occurring organismal groups (plants, small mammals, and large mammals) across four land-use types and a strong environmental gradient in East Africa. While these taxa have very distinct functional roles, they are also linked via multiple strong interaction types (herbivory, competition, and predation). We use these data to address four specific

questions regarding community responses to land-use change. First, we explore the effects of land-use change on PD by asking, (1) how does the effect of land-use change on PD vary across organismal groups? And (2) are PD responses dependent on the type of land-use change or other abiotic conditions? We then explore the aspects of community compositional change that would not be detected through the monitoring of alpha diversity metrics like PD by asking, (3) within organismal groups, are certain lineages disproportionately affected by land-use change? And (4) how large is the role of turnover in community responses to land-use change?

## METHODS

### *Study region*

This research was conducted in semiarid savanna-woodland ecosystems of Laikipia County, Kenya. This 9,770-km<sup>2</sup> region maintains high densities of free-ranging native mammals, including most of the largest taxa, for example elephant, lion, and giraffe (Kinnaird and O'Brien 2012). Laikipia covers a rainfall gradient ranging from approximately 400–750 mm/yr, driven largely by the rain shadow of Mt. Kenya. Soils are also variable, ranging from high clay content volcanic pelic vertisols (“black cotton”), to sandy clay loam metamorphic ferric and chromic luvisols (“red soils”).

We explored patterns of PD on four land-use types that occur in Laikipia: conserved, agriculture, fenced, and pastoral. Conserved land-use refers to managed conservancies that are highly accommodating of wildlife, with some actively managing for specific threatened species (rhinoceros) although many also support low to moderate intensity ranching of livestock (primarily cattle; 10–20 total livestock units (TLU) per km<sup>2</sup>; Kinnaird and O'Brien 2012). In addition, the conserved areas used for plant and small mammal sampling included the open access plots of two long-term exclosure experiments set within conservancies in the region. Areas of agriculture land use are used to grow planted crops, and most are small-scale subsistence, although some larger scale parcels do occur. The fenced land-use type refers to two slightly different land uses: long-term experimental exclosures and fenced commercial ranches. Experimental exclosures use fencing to exclude all large wildlife and livestock (Kenya Long-term Exclosure Experiment (KLEE) [Young et al. 1998], Ungulate Herbivory Under Rainfall Uncertainty experiment (UHURU) [Goheen et al. 2013]). Fenced commercial ranches maintain high densities of livestock (>25 TLU/km<sup>2</sup>), primarily cattle, and actively exclude large wildlife. We used experimentally fenced exclosures for plant and small mammal sampling, and fenced commercial ranches for large mammal sampling, but considered both to represent the same land-use type (fenced) due to their similar management priorities. The pastoral land-use type refers to group ranches, which are unfenced

parcels of generally poorer range condition owned by local pastoralist communities, with high stocking densities (>25 TLU/km<sup>2</sup>) consisting primarily of small stock (goats and sheep). Additional information on the management strategies of areas used for sampling is provided in Appendix S1: Table S1.

### *Collection of community data*

Between January and July of 2011, small mammal (<0.5 kg) and vascular plant community data were collected in parallel from 84 plots (Appendix S1: Fig S1) that represented specific land-use types: 13 agriculture, 12 fenced, 17 pastoral, and 42 conserved (details in Young et al. 2013, 2015). The plots were paired a priori, with each pair containing a conserved plot and a “disturbed” plot (agriculture, fenced, or pastoral) in close spatial proximity (<1 km apart). Each pair was separated from all other pairs by at least 2 km (typically 5–15 km). Small mammals were typically sampled in each plot on three consecutive nights using 100 Sherman traps across a 100 × 100 m grid, although for a subset of fenced plots we used 49 traps on a 50 × 50 m grid for four consecutive nights (details in Young et al. 2015). Each plot was sampled only one time, and paired conserved and disturbed plots were sampled simultaneously in order to minimize any effects of seasonality. Captured small mammals were identified to species, except cryptic *Crocodyrus* spp., which were aggregated at the genus level. Two rarely captured, diurnal species (*Paraxerus ochraceus*, *Xerus erythropus*) were excluded from analysis because nocturnal sampling could not accurately determine their presence or density. Abundance per species was calculated as catch per trap night. Using Schnabel estimates of actual population size, we estimate we captured 60% of all unique individuals per plot. Plant data were sampled using a grid sampling approach, with 250 points in each plot, sampled on 20 × 20 m grids directly overlaid on small mammal sampling grids (details in Young et al. 2013). Many plants could not be reliably identified to species when not in flower, and were aggregated at the genus level. While aerial cover (proportion of area covered with vegetation) and total cover (number of hits per pin) were tightly correlated, we used aerial cover per species in all presented analyses.

Large mammal communities were sampled contemporaneously but over a longer time period (May 2008–February 2012) using camera traps on eight properties (~10% of Laikipia county area) that represented three of our land-use types: conserved, fenced, and pastoral (Appendix S1: Fig S1, Table S1). Given the large home ranges of these animals, the small areas of agricultural land use were not sampled for this group. Camera trapping is widely used to characterize large mammal communities (Ahumada et al. 2011, Kinnaird and O'Brien 2012, Beaudrot et al. 2016). Camera trapping was conducted using Deercam film camera traps (Non-typical, Park Falls, Wisconsin, USA;  $n = 149$  camera trap

points) and Reconyx RM45 digital camera traps (Reconyx, Holmen, Wisconsin, USA;  $n = 585$  camera trap points) for a total of 548 sampling locations on conserved properties, 101 on fenced properties, and 85 on pastoral properties. Each trap was placed within 50 m of the center of a 1-km<sup>2</sup> (properties < 100 km<sup>2</sup> in area) or 2-km<sup>2</sup> (properties > 100 km<sup>2</sup> in area) sampling unit, usually on a game trail, and sampled 19–23 d during the dry season. All taxa were identified to species. For each site, we calculated a relative abundance index (RAI) per taxon using the number of independent photographic events per 100 trap days. To estimate animal abundance, we then calibrated RAI of independent photographs with independently derived abundance data (see Kinnaid and O'Brien 2012 and O'Brien et al. 2003 for details on these methods).

#### *Environmental data*

Mean annual rainfall was interpolated for each plot and camera location by ordinary kriging (spherical model) applied to data from long-term rain gauges at 75 locations (Franz et al. 2010). Soil properties were obtained using the Land Degradation Surveillance Framework (LDSF); a systematic field survey that assesses multiple indicators of ecosystem health at georeferenced locations across landscapes in Sub-Saharan Africa, to produce maps using remote sensing imagery (Vågen et al. 2013, 2016). Specifically, maps were produced of soil organic carbon (SOC), pH, percent sand content, erosion, and probability of root-depth restrictions at 30 m resolution across the study area (for details, see Appendix S2). Values of these soil properties were extracted for each plot and camera location, and a principal components analysis was applied to the combined data to construct metrics of soil quality. PC1 showed a strong positive correlation with sand, pH, and erosion and a negative correlation with SOC, and therefore represents a measure of soil degradation. Given the high percentage (48%) of total variance explained by PC1 (hereafter, soil degradation) and conceptual links between soil degradation and site productivity, we used soil degradation as the sole soil parameter in our analyses.

#### *Evaluating phylogenetic diversity*

We evaluated PD for each organismal group in each sampling location, resulting in a total of 902 PD values (plants = 84, small mammals = 84, large mammals = 734). We used the Faith's Index metric of PD, calculated as the sum of all branch lengths in the phylogeny containing only the sampled taxa (Faith 1992). The 902 dated phylogenies used for PD evaluation were created by removing branches from one of three larger regional phylogenies (one for each organismal group). The taxa included in each regional phylogeny were the entire set of sampled species from the respective organismal group.

The plant regional phylogeny was created using the online tool Phylomatic v3 (Webb and Donoghue 2005), which removes branches from a pre-loaded phylogeny until only taxa contained in a user-provided data set remain.<sup>8</sup> We used the pre-loaded phylogeny R20120829 (APG III 2009). The internal nodes on the resulting phylogeny were dated using Phylocom 4.2 (Webb et al. 2008), replacing the default Wikstrom ages file (Wikstrom et al. 2001) with the file produced by Gastauer and Meira-Neto (2013) to avoid inaccuracies in tree calibration resulting from syntax inconsistencies between APG III and Wikstrom. The small and large mammal phylogenies were created by pruning a published, dated "supertree" of mammals (best estimates version; Bininda-Emonds et al. 2007). Each sampled taxon absent from the supertree was reclassified as one of its congeners for phylogeny construction.

#### *Statistical analysis*

*PD responses to land-use change.*—To explore whether PD responses to land-use change differed among organismal groups (question 1) and ecological contexts (question 2), we created three full linear mixed effects models (one for each organismal group) and performed model selection following the top-down strategy described by Zuur et al. (2009:121–122). The raw PD values from each sampling location formed the dependent variable in each of these models (plants  $n = 84$ , small mammals  $n = 84$ , large mammals  $n = 734$ ). The fixed effects in these models were as follows: land-use type, annual rainfall, soil degradation, and the interactions between land-use type and each of the environmental variables. We elected not to include the three-way interaction or the interaction between annual rainfall and soil degradation because preliminary model fitting suggested they did not improve model fit. We then selected the optimal random effects structure for our models by comparing models with this same complex fixed effects structure but different random effects structures using the Akaike information criterion corrected for sample size (AIC<sub>c</sub>; Appendix S1: Table S2). For all organismal groups, this resulted in a random intercepts model with plot pair (plants and small mammals) or ranch (large mammals) as the random effect. Next, we confirmed that the small amount of spatial autocorrelation in the large mammal data was sufficiently accounted for by model covariates (Appendix S1: Fig S2). We also confirmed the absence of strong multicollinearity among fixed effects according to variance inflation factors < 3 (Zuur et al. 2009). We then conducted model selection on our fixed effects structures using AIC<sub>c</sub> (Appendix S1: Table S3). When multiple nested models for the same organismal group had similar AIC<sub>c</sub> scores, we used likelihood ratio tests to confirm our model selection. This process resulted in a single final model for each organismal group that was

<sup>8</sup> <http://phylodiversity.net/phyloomatic/>

used for interpretation. We validated the assumptions of final models using residual plots.

*Community composition responses to land-use change.*—To determine whether certain lineages were disproportionately affected by land-use change (question 3), we quantified the association of each taxon with each land-use type as the proportion of its observations that occurred on that land-use type. We then tested for phylogenetic signal in these land-use associations, separately for each organismal group and each land-use type, using the Blomberg's  $K$  metric (Blomberg et al. 2003). We reshuffled taxa among tips of the phylogenies 1,000 times, recalculating phylogenetic signal for each iteration to build a distribution of  $K$  values under the null model of no phylogenetic signal. We concluded that the level of association with a particular land-use type exhibited significant phylogenetic signal in an organismal group if the observed  $K$  value was larger than the 95th percentile value of the corresponding null distribution. To further explore how associations with specific land-use types were distributed among taxa, we tested each individual taxon for significant “aversions” or “affinities” to each of the land-use types using a resampling approach (Appendix S3).

We asked how prevalent species turnover was in community responses to land-use change (question 4) using the methods described in Sobral et al. (2016). Specifically, for each plot pair used for plant and small mammal community sampling we calculated the Unifrac Index (Lozupone and Knight 2005) of phylogenetic beta diversity between the conserved land-use plot and the disturbed land-use plot. The Unifrac Index ranges from 0 (identical communities) to 1 (totally different communities). Using the functions provided by Leprieur et al. (2012), we decomposed total beta diversity values into two components: (1) nestedness, caused by plot differences in alpha diversity, and (2) turnover, caused by plot differences in species composition. The size of the turnover component relative to total beta diversity is indicative of the importance of species turnover for land-use change-mediated composition changes. This analysis was not conducted on the large mammal data because there was no meaningful way to break these data down into pairs for which beta diversity could be calculated.

All statistical analyses were conducted in R version 3.5.1 (R Core Team 2018) and all code and data used in analyses can be downloaded (see *Data Availability*).

## RESULTS

A total of 226 taxa were identified in our community surveys (148 plants, 22 small mammals, 56 large mammals; Appendix S1: Table S4).

### *PD responses to land-use change*

Land-use type had a significant influence on PD of all three organismal groups, but the land-use types

associated with highest PD differed among groups (Fig. 1, Table 1). Plant and small mammal communities showed similar patterns, with both groups having highest PD in fenced areas, second-highest in conserved areas, and lowest in agricultural and pastoral areas. Large mammal communities had highest PD in conserved areas, with fenced and pastoral areas harboring around 40% fewer years of evolutionary history.

The influence of environmental variables on PD also varied among organismal groups (Fig. 2, Table 1). Plant PD was unaffected by annual rainfall or soil degradation, with neither variable being included in the final plant model. The interaction between annual rainfall and land-use type was included in both the small mammal and large mammal final models. Among small mammal communities, there was a positive relationship between PD and annual rainfall in conserved and fenced areas, but this relationship was absent in agricultural and pastoral areas (Fig. 2a). For large mammal communities, the relationship between PD and annual rainfall was positive in pastoral areas, negative in fenced areas, and absent in conserved areas (Fig. 2b). Soil degradation was included in only the large mammal model, where it had an interactive effect with land-use type. The relationship between large mammal community PD and soil degradation was positive in conserved areas, but mostly absent in fenced and pastoral areas (Appendix S1: Fig. S3).

### *Community composition responses to land-use change*

We found no evidence of phylogenetic signal in associations to land-use types in plants, small mammals, or large mammals (Table 2). Instead, even closely related taxa varied widely in their affinities and aversions to the different land uses (Appendix S1: Table S4). Many taxa did show affinities for anthropogenic land uses; among small mammals, affinities to anthropogenic land uses

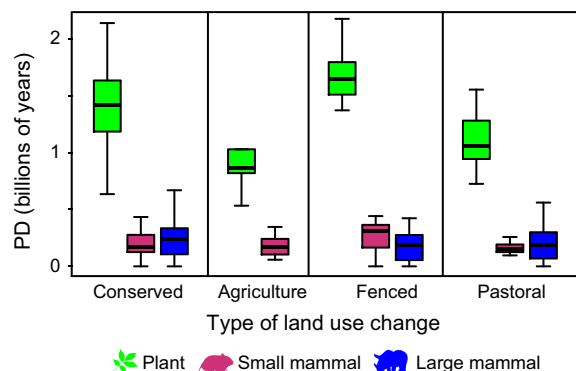


FIG 1. Phylogenetic diversity (PD) of plant, small mammal, and large mammal communities in areas of differing land use. Thick horizontal lines indicate median values. The top and bottom of each box indicates the upper and lower quartile, respectively. Whiskers extend to the highest and lowest observed values that lie within 1.5 times the interquartile distance of the upper and lower quartiles, respectively.

TABLE 1. Effects of land-use type and environmental variables on phylogenetic diversity of plant, small mammal, and large mammal communities.

Fixed effect	Plants		Small mammals		Large mammals	
	$\beta$	SE	$\beta$	SE	$\beta$	SE
Intercept	1470.54***	55.63	-176.91†	104.84	491.19***	123.78
Agriculture	-580.24***	88.54	485.84*	224.23		
Fenced	297.56**	91.85	-3.58	297.50	547.32	311.62
Pastoral	-342.09***	78.45	338.72†	189.92	-2210.94*	784.96
Annual rainfall			0.64**	0.18	-0.21	0.22
Soil degradation					20.24**	7.75
Agriculture $\times$ annual rainfall			-0.84*	0.35		
Fenced $\times$ annual rainfall			0.20	0.56	-1.10*	0.49
Pastoral $\times$ annual rainfall			-0.64†	0.34	4.63**	1.76
Agriculture $\times$ soil degradation						
Fenced $\times$ soil degradation					-48.59†	25.40
Pastoral $\times$ soil degradation					-28.60†	15.85

Notes: Regression coefficients ( $\beta$ ), standard errors (SE), and statistical significance for each fixed effect contained in the final model for each organismal group are presented. Blank cells indicate that the variable was not included in the final model for that group. The intercept value represents the conserved land-use type. Large mammal communities were not surveyed in the agriculture land-use type.

†  $0.1 < P < 0.05$ ; \*  $0.01 < P < 0.05$ ; \*\*  $0.001 < P < 0.01$ ; \*\*\*  $P < 0.001$ .

were more common than aversions, but the opposite was true for plant and large mammal taxa (Appendix S1: Table S5). Among plant taxa, aversions to agricultural and pastoral areas were particularly prevalent in the families Acanthaceae, Fabaceae, and Malvaceae (Fig. 3). The grass family (Poaceae), the most speciose in our sampling, showed some affinities to agriculture (Fig. 3), but aversions to agriculture and pastoral were more common. Aversions to anthropogenic land uses were less common among small mammals, with many taxa (e.g., *Mus minutoides*, *Mastomys natalensis*) showing significant affinities for agriculture (Fig. 4; Appendix S1: Table S5). Among large mammals, the larger carnivores (e.g., *Panthera spp.*), non-domestic grazers (e.g., Bovidae, Equidae), and browsers (e.g., Elephantidae, Giraffidae) showed aversions to fenced and pastoral land uses (Fig. 5). However, some bovids (e.g., bushbuck, steinbuck, waterbuck), smaller herbivores (e.g., duiker, hare), and smaller carnivores (e.g., serval, jackal) showed affinities to fenced and/or pastoral areas.

Changes in plant and small mammal community composition following land-use change involved considerable species turnover (Fig. 6; Appendix S1: Table S6). Conversion to agriculture led to the largest changes in community composition for both plants and small mammals, but turnover was a more important component of community change for plants than small mammals.

## DISCUSSION

### PD responses to land-use change

The effects of land-use change on local PD varied considerably between the organismal groups surveyed (Fig. 1). Not surprisingly, given the nature of the

disturbances, large mammals showed the most negative PD responses to anthropogenic land-uses, with fenced and pastoral communities, respectively, containing 165 and 164 Myr less evolutionary history than conserved communities (~40% declines). These dramatic PD declines are similar in magnitude to those observed in birds (Frishkoff et al. 2014) and fish (D'Agata et al. 2014) in disturbed habitats. Notably, our results show that high-intensity pastoral land-use substantially alters large mammal communities, even without strong direct hunting (prohibited in this region) or fencing. As would be expected, the types of large mammals that were most negatively impacted were (1) large carnivores, which are frequently (largely illegally) removed from pastoral settings (Ripple et al. 2014) and (2) large and mega-ungulates, presumably impacted by competition with domestic stock for forage, as well as perhaps by intentional removal (Ogutu et al. 2014, Kartzinzel et al. 2015). Medium to small herbivores (e.g., duikers, hares) and smaller predators (e.g., servals and jackals), as well as all domestic species, instead showed affinities to disturbed habitats. These findings are consistent with the globally pervasive pattern of size-selective defaunation, particularly in the tropics (Fritz et al. 2009, Young et al. 2016), and may have implications for continued ecosystem structure and function due to the myriad of services that large mammals often disproportionately provide (Estes et al. 2011, Dirzo et al. 2014). For example, the megafauna in this system (e.g., elephant and giraffe) that were strongly impacted have unique roles in ecosystems that are not fulfilled by smaller taxa (Pringle 2008, Waldram et al. 2008).

While large mammal PD was consistently lower on both types of anthropogenic land use, plant and small mammal PD varied greatly among these land-use types (Fig. 1). Both groups' PD was higher in fenced areas

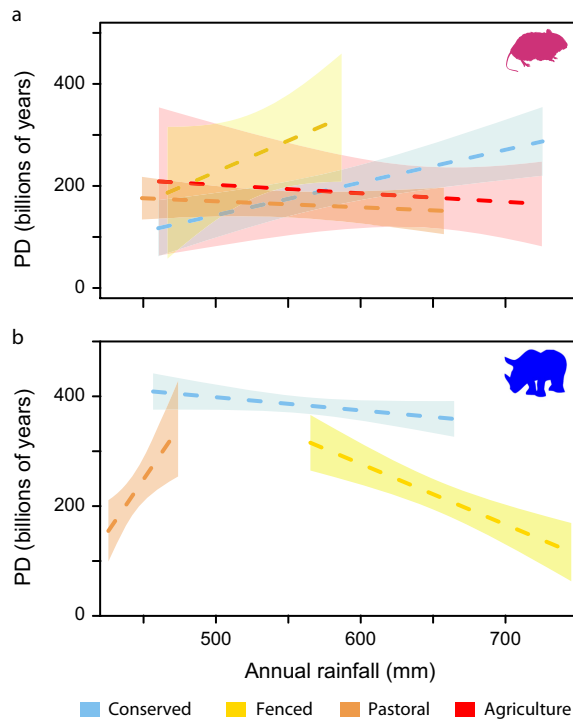


FIG 2. Relationship between phylogenetic diversity (PD) and annual rainfall for (a) small mammal and (b) large mammal communities based on land-use type. Dashed lines represent linear models of PD predicted by annual rainfall within a given land-use type. Shaded regions represent confidence intervals of these models. Colors represent different land-use types as indicated in the legend. Note that small and large mammal communities were not sampled in the same sites (see *Methods* for details).

than conserved areas, perhaps mechanistically driven by the reduced presence of large mammals in these same site types. Where they occur, large mammals often dominate competitive interactions such that their loss would allow the release of grazing-sensitive plants and competing herbivorous small mammals (Keesing and Young 2014, Veblen et al. 2016). Interestingly, the increase in plant PD in fenced plots despite a concurrent increase in herbivorous small mammal PD (and abundance; Young et al. 2015) suggests that small mammals are relatively ineffective at controlling plant diversity. This is consistent with studies on species-level diversity and biomass from this region, which show incomplete control of plants (only partial compensation) and changed community composition, despite dramatic increases in small mammal biomass after large animal removal (Porensky et al. 2013, Young et al. 2013, Riginos et al. 2018). The lack of evidence for increases in plant or small mammal PD in pastoral areas, which had similarly low large mammal PD, may be attributed to the addition of livestock, which appear to have similar ecological effects on plant and small mammal communities as do large wildlife (Veblen et al. 2016). Moderate and large plant PD decreases in

TABLE 2. Evaluation of phylogenetic signal in land-use type associations.

Organismal group and land-use type	<i>K</i>	<i>K</i> null	<i>P</i>
<b>Plants</b>			
Conserved	0.13	0.15 (0.05)	0.67
Agriculture	0.14	0.14 (0.04)	0.53
Fenced	0.11	0.15 (0.04)	0.79
Pastoral	0.13	0.15 (0.05)	0.68
<b>Small mammals</b>			
Conserved	0.27	0.40 (0.19)	0.82
Agriculture	0.24	0.40 (0.18)	0.88
Fenced	0.34	0.41 (0.18)	0.67
Pastoral	0.26	0.41 (0.19)	0.84
<b>Large mammals</b>			
Conserved	0.32	0.28 (0.07)	0.29
Fenced	0.26	0.28 (0.11)	0.57
Pastoral	0.36	0.29 (0.14)	0.25

*Notes:* Blomberg's *K* values (*K*) are presented for the degree of association with each land-use type (proportion of total observations occurring on that land-use type) separately for each organismal group. Although Blomberg's *K* assumes a continuous unbounded trait, results did not differ qualitatively when abundance proportions were logit-transformed, and analysis of untransformed proportions is presented. For each estimate, Blomberg's *K* values for that same parameter calculated from 1,000 simulated communities under the null model of no phylogenetic signal are presented (*K* null; median (SD)). The proportion of null model values greater than the observed value is also presented to evaluate whether observed *K* values are significantly larger than expected under the null (*P*).

pastoral and agricultural areas, respectively, align well with the intentional strong management for specific plants (e.g., weed control, fuelwood extraction) in these land uses. However, these results contrast with a meta-analysis that found plant functional diversity to be unaffected by agricultural intensification (Flynn et al. 2009).

One interesting note is that the PD of plant and small mammal communities appears to respond similarly to the types of land-use change surveyed in this study. The proportional declines in PD for these two groups were strikingly similar even though plant species richness was much higher across sampling plots (plants, 23.7% ± 1.0%; small mammals, 4.4% ± 0.2%; mean ± SE). It may be that plant taxa depend on direct or indirect interactions with specific small mammal taxa or vice versa. Alternatively, they may also be responding similarly to changed large mammal communities (e.g., release from predation and competition pressure, respectively), showing strong responses where all large mammals are removed, and relatively minimal effects when wild mammals are ecologically replaced with surrogate domestic herbivores. While this suggests that managers may be able to generalize findings of changes in plant PD to small mammal PD (necessitating the survey of only one group), this finding notably does not apply to large mammals, highlighting the need for taxa specific studies to inform management when considering a broad group of taxa (Allan et al. 2014, Gossner et al. 2016).

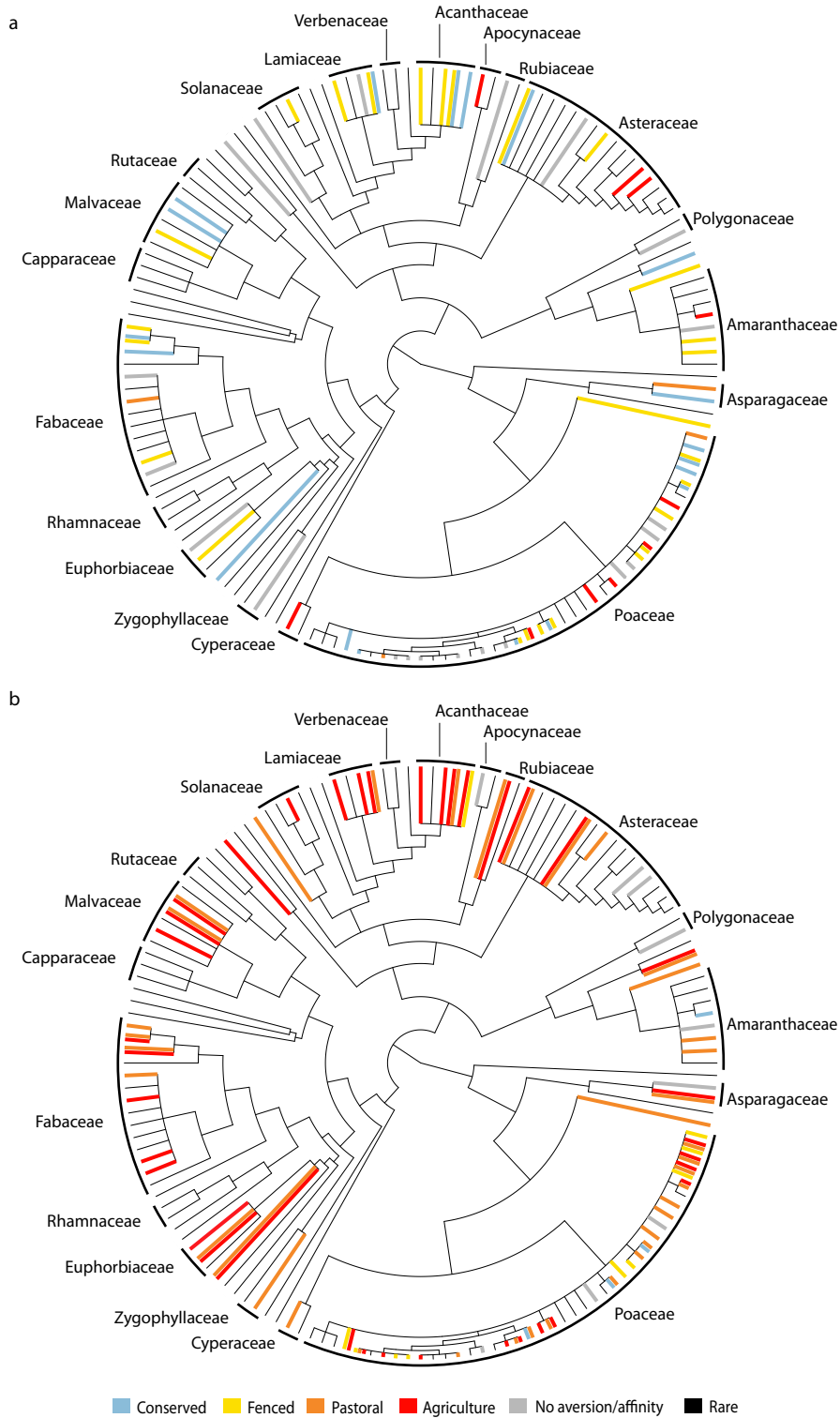
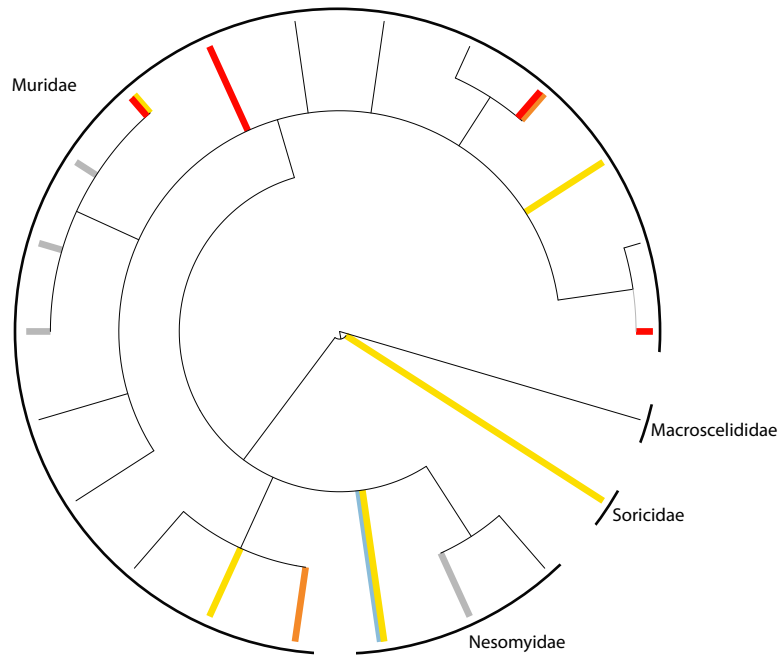


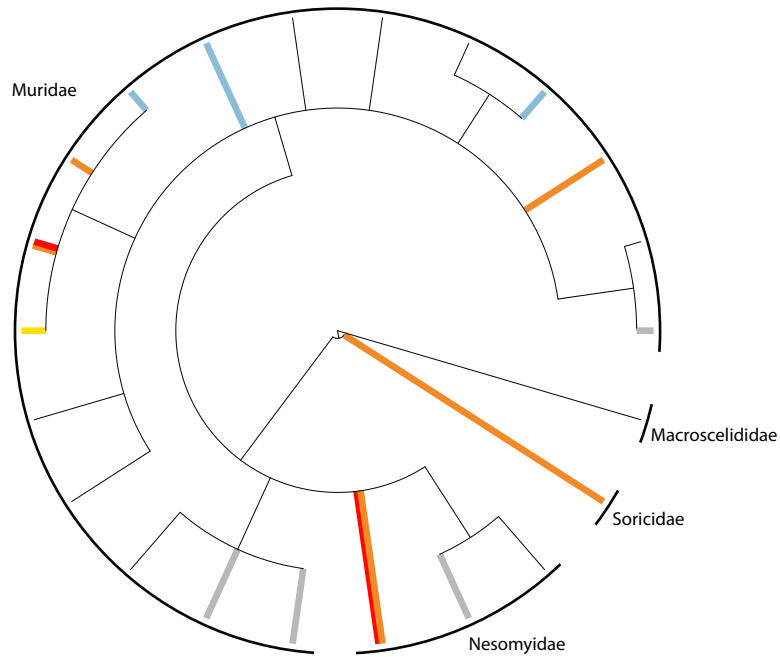
FIG 3. Phylogenies showing significant (a) affinities and (b) aversions to specified land-use types by plant taxa. Affinities and aversions were concluded from, respectively, higher and lower abundance in a given land use than expected under a null model (see Appendix S3). Colors of terminal branches represent the land-use type that each taxon had an affinity or aversion to (see inset legend). Land-use aversions were not calculated for rare species (thin black terminal branches). All taxonomic families except those represented by only a single taxon in our sample are labeled.



a



b



■ Conserved   
 ■ Fenced   
 ■ Pastoral   
 ■ Agriculture   
 ■ No aversion/affinity   
 ■ Rare

FIG 4. Phylogenies showing significant (a) affinities and (b) aversions to specified land-use types by small mammal taxa. Affinities and aversions were concluded from, respectively, higher and lower abundance in a given land use than expected under a null model (see Appendix S3). Colors of terminal branches represent the land-use type that each taxon had an affinity or aversion to (see inset legend). Land-use aversions were not calculated for rare species (thin black terminal branches). All taxonomic families are labeled.

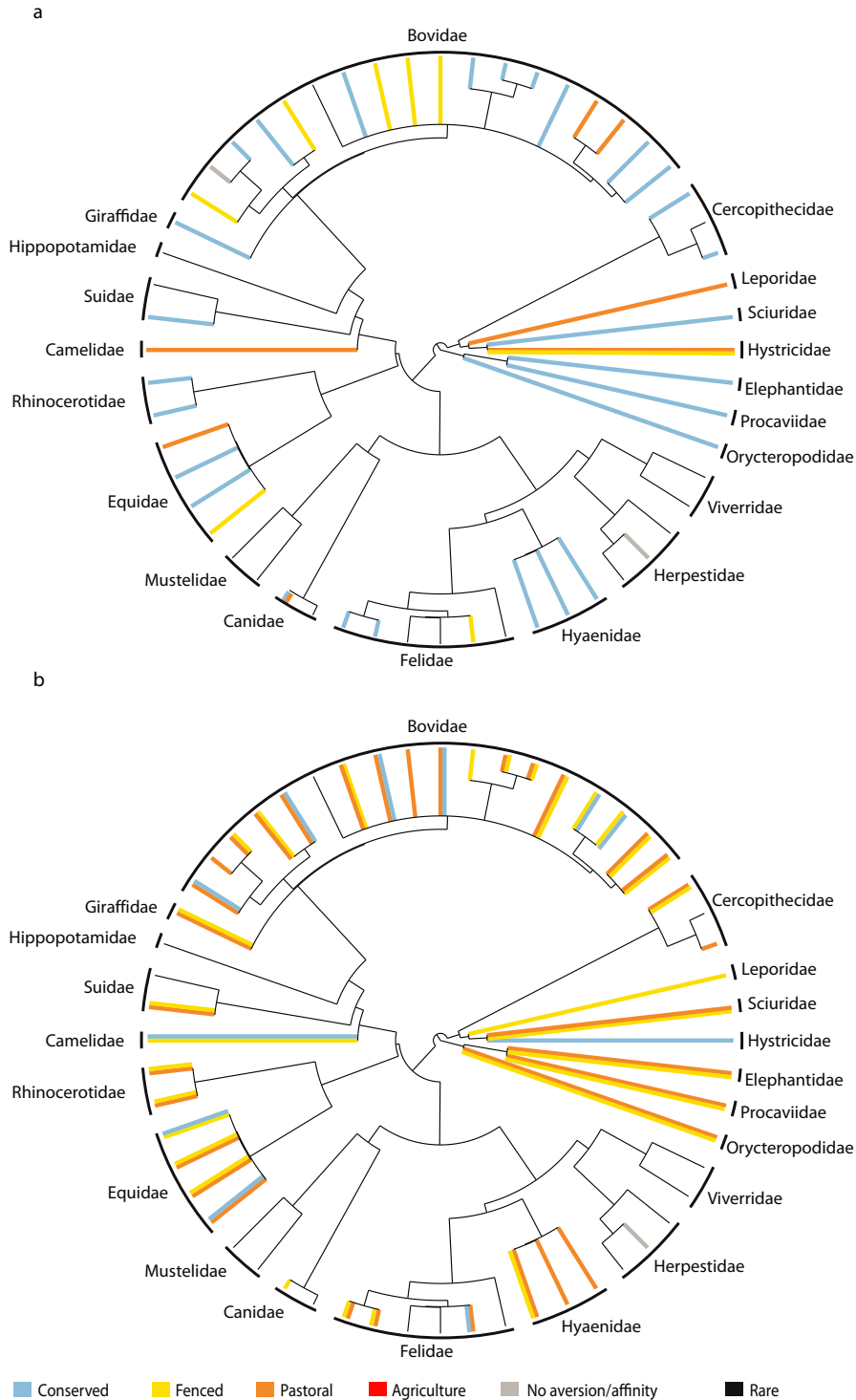


FIG 5. Phylogenies showing significant (a) affinities and (b) aversions to specified land-use types by large mammal taxa. Affinities and aversions were concluded from, respectively, higher and lower abundance in a given land use than expected under a null model (see Appendix S3). Colors of terminal branches represent the land-use type that each taxon had an affinity or aversion to (see inset legend). Land-use aversions were not calculated for rare species (thin black terminal branches). All taxonomic families are labeled.

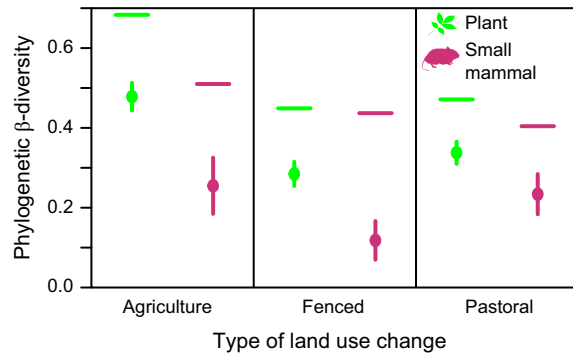


FIG 6. Changes in composition of plant and small mammal communities following land-use change involve considerable species turnover. Beta diversity was calculated for 42 plot pairs, each containing a conserved and an anthropogenic land-use plot (agriculture, 13; fenced, 12; pastoral, 17) in close spatial proximity. The average total  $\beta$ -diversity (horizontal lines) of plot pairs representing different types of land-use change, as well as the mean and SE of the fraction of these totals that resulted from species turnover (points and error bars), are shown.

Patterns of PD among small and large mammal communities (but not plant communities) were influenced by annual rainfall (Fig. 2; Appendix S1: Fig S3). We observed a positive relationship between PD and annual rainfall among small mammal communities on conserved and fenced land uses and among large mammal communities on pastoral land uses. Considered in isolation, these results align with a meta-analysis that showed species diversity responses to habitat disturbance to be less negative in areas of higher precipitation (Mantyka-pringle et al. 2012). However, we did not observe this relationship in most of the organismal group by land-use type combinations that we surveyed, and there was even a negative relationship between PD and annual rainfall in large mammal communities of fenced areas. In contrast to the relatively strong impacts of precipitation, we observed only a weak interactive effect of soil degradation, and only on large mammals, suggesting that managers may not need to consider soil properties in targeting management efforts (Appendix S1: Fig. S3). Although the mechanisms behind these examples of context dependence are not well understood, they are not surprising given that biodiversity patterns are typically a result of interacting environmental, geographic, and land-use patterns (Witman et al. 2004, D'Agata et al. 2014). More research on the environmental mediation of PD responses to land-use change is certainly needed, but these results suggest that information on rainfall and land-use type of disturbed areas may be useful for prioritizing conservation efforts (e.g., toward areas of low precipitation).

#### *Community composition responses to land-use change*

Local diversity metrics are not intended to capture compositional changes, and yet, similar to umbrella

species, these metrics are often used by managers as a more tractable index of ecological integrity. While research has increasingly highlighted the fact that species richness may hold steady even while high species turnover erodes the ecological function of the system (Spaak et al. 2017), PD is often considered as a more valuable metric for management because of its frequent correlations to ecosystem function and direct measurement of evolutionary history (Grab et al. 2019). By comparing communities on a variety of land-use types in close spatial proximity, we provide a holistic view of the likely responses of three organismal groups to land-use change. These data allow us to describe the aspects of community change that may be missed by a monitoring strategy that relies solely on PD.

Interestingly, we found no evidence of significant phylogenetic signal in land-use type associations for any organismal group (Table 2). This suggests that, in this system and these organismal groups, there is not a set of lineages that are disproportionately affected by land-use change. Moreover, this implies that responses to land-use change can differ substantially among closely related taxa. If closely related taxa perform similar ecological functions, then all the taxa performing a given ecological function are unlikely to be lost following a particular land-use change. However, some functionally important traits (e.g., large body size in the large mammal group) are not particularly phylogenetically conserved in these communities and therefore the observed patterns of turnover could have substantial consequences for ecological functioning.

We did detect considerable species turnover in the responses of plant and small mammal communities to land-use change that was not detected by PD (Fig. 6). It is known that PD can remain stable during community change if the newly arriving species replace the PD that was lost through local extirpations and that this does not necessarily imply the maintenance of all ecological functions (Sobral et al. 2016). For example, a recent study found that lineages of late-season bees were replaced by lineages of spring-flying bees in areas of intense anthropogenic use, suggesting strong functional change despite invariant PD (Harrison et al. 2018). An example from this system of likely functional consequences is that although we observed plant PD to be only slightly lower under pastoral use (Fig. 1), many palatable grass species declined significantly (e.g., *Brachiaria lachmantha*, *Cynodon plectostachyus*, *Pennisetum stramineum*; Fig. 3). The extirpation of these preferred forage species could make this land-use less appealing to native herbivores and thereby have cascading effects across trophic levels despite only a moderate decline in plant PD. In this particular example, the strong decline of palatable grasses in pastoral landscapes may partially explain the dramatic declines of large mammals in this land-use type, which were of similar magnitude to declines in areas from which they were actively excluded (fenced). This example highlights the importance of

using a complement of metrics including both diversity and composition, particularly to identify changes in high value species.

It is not clear if the substantial compositional turnover seen in these systems is likely to reflect changes in ecosystem functioning. For example, there is substantial evidence that cattle can serve as functional proxies for large wildlife (Veblen et al. 2016), such that many functions may be maintained despite turnover. Turnover associated with land-use change will, however, tend to favor common, cosmopolitan and commensal species (in this case, cattle, goats, and the regionally pervasive *Mus minutoides* and *Mastomys natalensis*), with specific life history traits, and ecological functions (Concepción et al. 2017, Leitão et al. 2018). At a regional level, this homogenization will likely reduce landscape level functional diversity. It is beyond the scope of this study to suggest whether the changed functionality of these novel ecosystems will have net-positive or net-negative effects on ecosystem service provision to humans in this landscape. Certainly, some of these species will have positive human impacts (e.g., livestock) while others will have negative impacts (e.g., rodents *Mastomys natalensis* and *Mus minutoides* are major regional crop pests and zoonotic disease reservoirs). However, where the management goal is to preserve ecological integrity or predisturbance functionality, our data suggests that while PD may be preferable to taxonomic diversity metrics, it is still not a substitute for direct comparisons of species composition. We recommend a tractable management approach may be to combine PD monitoring with temporal measurements of beta diversity. Using the approach developed by Sobral et al. (2016) and employed in this study, temporal measures of beta diversity could be decomposed to highlight the amount of turnover that has occurred and therefore where compositional changes are greatest. In addition, the monitoring of specific ecosystem services (e.g., pollination) that relate to management goals may be a tractable way to estimate the maintenance of ecological functioning.

#### CONCLUSION

Overall, our study found highly variable effects of land-use change on PD across taxa and ecological contexts. This finding supports the growing consensus that, despite the often dramatic declines in taxonomic diversity and PD following anthropogenic land-use change, some types of disturbed land-use can still provide conservation value for some taxa. For example, although pastoral land-use types have greatly reduced levels of PD in plant and large mammal communities, they still provide valuable habitat for small mammal diversity. However, these same results also highlight the complex variation in responses to land-use change among organismal groups, and across abiotic and anthropogenic contexts. Consequently, managers cannot assume that results about the value of a particular disturbed land-use

type for a particular taxa can be generalized to other taxa or other types of disturbed land-use. This also means that there are no simple recommendations for particular land-use types that best preserve evolutionary history or functionality across a wide suite of taxa in all environmental conditions. Instead, managers that aim to maintain evolutionary history of multiple taxa in anthropogenically disturbed landscapes will likely need to maintain a diversified matrix of land-use types rather than promoting a single “best” land-use type for non-conserved landscapes. More promisingly, our results suggest that collating and using regional environmental data can allow managers to identify specific areas where particular forms of land-use change are likely to be most detrimental, potentially allowing managers to prioritize conservation activities to areas where they will have the strongest benefits for preserving evolutionary history and ecosystem functionality. Importantly, even the relatively simple and easily gathered metric of annual rainfall can apparently provide important additional insight on where diversity gains of conservation may be highest for specific taxa. Notably, soil data, which are much more intensive in both time and resources to collect and analyze, offer relatively little additional information.

While our results do support the value of PD in reflecting community change following disturbance, our results also emphasize that even this metric may not be a sufficient proxy for ecological integrity. In many cases moderate PD changes belied high levels of species turnover that involved the invasion of species phylogenetically distinct from those that were extirpated. To the extent that functional change parallels phylogenetic change, this suggests that most organismal groups are likely to experience substantial functional changes (Harrison et al. 2018). We thus expect that land-use change will likely drive strong changes, although not necessarily net reductions, in the types of functions and services provided in these ecosystems as particular functional groups such as large herbivores fall out (Keesing and Young 2014, Smith et al. 2016). This evidence of strong compositional turnover, combined with likely mismatches in ecological interactions from differential responses across taxonomic groups, emphasizes the large potential changes in ecosystem functioning that may occur if we fail to maintain conserved communities with intact networks of interactions and functions in a landscape mosaic.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1973/full>

#### DATA AVAILABILITY

All data and code used in the analyses presented can be downloaded from Zenodo at <https://doi.org/10.5281/zenodo.3246811>