Opposing spatial gradients in the abundance and diversity of woody plants and large herbivores in a semi-arid African savanna

By

Patrick T. Freeman

B.S. Stanford University, 2014

M.Sc. Stanford University, 2015

Thesis

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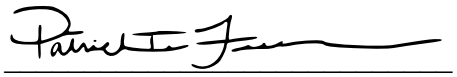
Date 4/30/2020 

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Date _____ _____

Dr. Tyler R. Kartzinel, Assistant Professor,

Department of Ecology and Evolutionary Biology

Date _____ _____

Dr. David M. Rand, Chair,

Department of Ecology and Evolutionary Biology

Approved by the Graduate Council

Date _____ _____

Andrew G. Campbell, Ph.D.
Dean of the Graduate School Professor of Medical Science Department of Molecular Microbiology and Immunology

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Abstract of "Opposing spatial gradients in the abundance and diversity of woody plants and large herbivores in a semi-arid African savanna"

by

Patrick T. Freeman, Degree Sc.M.

Brown University

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The resource specialization hypothesis posits that all consumers exhibit some degree of specialization and thus more diverse plant communities should support a greater diversity of herbivores. This has been largely borne out in communities of phytophagous insects, but the extent to which is applies to larger-bodied and highly mobile mammalian herbivores with generalized feeding systems has received less attention. We hypothesized that local plant community abundance and diversity (10s-100s of meters) is positively correlated with the abundance and diversity of large mammalian herbivores. We performed phylogenetically controlled analyses of spatial associations between plant and large mammalian herbivore community diversity at Mpala Research Centre's ForestGEO plot in Kenya. The analysis was based on a 1.2-km2 fine-grained map of tree stems and a grid of camera traps collected in conjunction with fine-scale topographic measurements. Local plant taxonomic and phylogenetic diversity were found to be weak predictors of local large-herbivore diversity, and contrary to prevailing theory, more often negatively correlated with one another. However, we did find that woody plant and large-mammal community turnover were strongly correlated, reflecting the strong segregation of both plant and animal community types across spatially adjacent but edaphically and topographically distinct habitat classes. Opposing gradients in plant and

herbivore abundance and diversity in response to underlying abiotic conditions highlight their important role in the structure and function of savanna ecosystems.

Introduction

A common expectation is that the diversity of plants and animals in an ecosystem should be positively correlated, both across latitudes and locally within communities (Castagneyrol & Jactel, 2012; Hutchins
on, 1959; Loreau et al., 2001; R. H. MacArthur & MacArthur, 1961; Mittelbach et al., 2007). Across scales, covariation in plant and consumer diversity often emerge as a result of similar responses to abiotic gradients (Clarke & Gaston, 2006; Mittelbach et al., 2007), disturbance regimes (Wootton, 1998), and biotic interactions (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009; Zhang et al., 2018). For example, access to energy or other environmental resources can generate concordant gradients in the diversity of both plants and animals between biomes (e.g., tundra vs. tropical rainforest) as well as within ecosystems (e.g., mesic vs. xeric microhabitats; Báldi, 2008; J. P. G. M. Cromsigt, Prins, & Olff, 2009; Jetz, Kreft, Ceballos, & Mutke, 2009; Jiménez-Alfaro, Chytrý, Mucina, Grace, & Rejmánek, 2016). Elucidating ecological factors that generate and maintain the biodiversity of plants and animals—across trophic levels—is critical for improving our predictions of how organisms, communities, and ecosystems may respond to human-driven environmental changes that can ultimately feedback on the delivery of critical ecosystem services (Díaz et al., 2015; Ehleringer, Cerling, & Dearing, 2002).

Clarifying the biotic and abiotic factors that influence the diversity of plants and animals within communities can be complicated by a tendency for the abundance and diversity of organisms to covary. The Resource Specialization Hypothesis posits that locally diverse plant communities have the capacity to support locally diverse consumers, because species exhibit at least some degree of resource niche differentiation (Hutchinson, 1959; Pianka, 1966). In contrast, the More Individuals Hypothesis posits that more resource-rich environments support a greater

number of individual organisms, and thus are more likely to support a greater number of species (Hutchinson, 1959; Srivastava & Lawton, 1998; Wright, 1983). In communities of phytophagous insects, comparisons of these ecological hypotheses have found support for the resource specialization hypothesis. For example, Dinnage et al. (2012) determined that increases in herbivorous insect species richness was positively related to increases in the local taxonomic species richness and phylogenetic diversity of plant resources in a Minnesotan grassland ecosystem despite the lack of concordant increases in herbivore abundance associated with either resource diversity metric. Though they revealed similar positive relationships between plant and herbivorous insect diversity, several more recent studies in forested ecosystems in tropical China (Wang et al., 2019) and German temperate grasslands (Schuldt et al., 2019) have determined that many of these positive effects of plant diversity are mediated primarily through their simultaneous positive influence on consumer abundances. These results suggest that local site-based variation in conditions ranging from climate to shared eco-evolutionary history may play a role in affecting the degree to which biodiversity levels correspond locally across trophic levels.

Whereas plant-arthropod diversity relationships have been studied extensively, patterns of diversity in communities of larger-bodied, highly mobile, and more generalized herbivores like ungulates have been less studied. If there is any positive association between the diversity of plants and large animals, it is often assumed, it is a relationship that likely reflects predictions of the more individuals hypothesis since their generalist feeding ecology tends toward the reliance on higher-biomass and lower-quality food resources. However, because both biotic and abiotic drivers of community diversity operate in all ecosystems, casting the resource-specialization and more individuals hypotheses as alternative explanations for covariation in plant and animal diversity can be misleading. It is instead more productive to ask how biotic interactions modify

47 abiotic influences, and *vice versa*. For example, abiotic variables alone were sufficient for
48 predicting continental diversity gradients of vertebrates (Jetz et al., 2009). In contrast, however,
49 variation in vegetation diversity explained significant amounts of regional variation in the
50 diversity of six groups of vertebrates and invertebrates that was not accounted for by abiotic
51 variables alone (Jiménez-Alfaro et al., 2016). Large-scale resource gradients may thus set the
52 backdrop against which more localized mosaics of plant and animal diversity hotspots can be
53 established or maintained through biotic interactions. All else equal, the local diversity of plants
54 and herbivores may be more tightly linked than previously recognized (Kartzinel et al., 2015).
55 Testing the hypothesis that there is a link between the local diversity of plants and
56 animals due to resource specialization requires consideration of what it means to be a
57 'specialist'. Species richness is the most widely used index of diversity in studies on both
58 ecological communities and feeding specialization (Kartzinel & Pringle, 2020; Naeem et al.,
59 2016). In this dimension of diversity, the diversity of communities and the degree of specialism
60 both represent simple counts of species regardless of their compositional evenness, phylogenetic
61 relatedness, or functional characteristics (Funk et al., 2017; Reiss, Bridle, Montoya, &
62 Woodward, 2009). Yet counts of species richness may not adequately represent the diversity of
63 communities or degree of specialism, because a relatively small number of species can represent
64 a relatively broad diversity of evolutionary lineages, and *vice versa* (Cadotte, Cavender-Bares,
65 Tilman, & Oakley, 2009; Cavender-Bares, Kozak, Fine, & Kembel, 2009; Jones, Barber, &
66 Gibson, 2019). Within communities of large mammalian herbivores, for example, some species
67 may consume relatively few plant taxa (taxonomic specialists) from many plant lineages
68 (phylogenetic generalists) whereas others may consume many taxa from few lineages (Kartzinel
69 & Pringle, 2020). Therefore, even communities of 'generalized' large herbivores may develop

70 ‘hotspots’ of community diversity that spatially correspond to those of plant diversity—
71 consistent with the resource-specialization hypothesis—although this relationship may be
72 overlooked in favor of the more-individuals hypothesis in studies that only consider single
73 dimensions of specialization or large-scale biogeographic gradients.

74 We evaluated the extent to which the abundance and diversity of plants and large
75 mammalian herbivores are locally correlated across a fine-scale gradient in plant diversity and
76 productivity within a semi-arid Kenyan savanna. The savannas of East Africa comprise a mosaic
77 of habitats, diverse plant lineages, and the greatest extant density and diversity of large mammals
78 (Coverdale et al., 2016; Goheen et al., 2018; Kartzinel et al., 2014; H. S. Young et al., 2013; T.
79 P. Young, Okello, Kinyua, & Palmer, 1997). Although large mammalian herbivores can range
80 widely, many exhibit habitat preferences or associations that reflect differential needs for access
81 to water (Rubenstein, 2010; Thouless, 1995), behaviorally mediated predator avoidance (Ford et
82 al., 2014; Riginos, 2015), or foraging requirements that may include specific food-plant species
83 (Owen-Smith, Roux, & Macandza, 2013; Yoganand & Owen-Smith, 2014). In order to evaluate
84 local-scale (10s to 100s of meters) covariation in the taxonomic and phylogenetic diversity of
85 woody plants and large herbivores, we combined camera-trap data with fine-scale vegetation
86 data from the 1.2-km^2 Forest Global Earth Observatory (ForestGEO) plot at Mpala Research
87 Centre in Kenya (Anderson-Teixeira et al., 2015; Mutuku & Kenfack, 2019). The Mpala
88 ForestGEO plot spans an underlying soil and topographic gradient, making it possible to evaluate
89 support for the more-individuals and resource-specialization hypotheses both within and between
90 ecosystems that differ markedly in woody plant abundance while minimizing potentially
91 confounding effects of climatic and biogeographic variables. We tested three hypotheses: (*i*) the
92 diversity of woody plants and large herbivores is significantly different between ecosystems,

such that red soil habitats with greater woody plant biomass support greater taxonomic and phylogenetic diversity of both plants and animals compared to the black-cotton soils with lower woody plant biomass; (*ii*) local herbivore diversity is strongly and positively correlated with local plant diversity, both within and between ecosystems that support different baseline levels of resource availability, consistent with the resource-specialization hypothesis; and (*iii*) that spatially colocalized variation in the diversity and composition of plant and herbivore communities reflect the common influence of underlying topographic and edaphic gradients such that fine-scale topographic heterogeneity generates mosaic hotspots of both plant and animal diversity.

Materials and methods

Study system

The study took place in the 120-ha Forest Global Earth Observation (ForestGEO) plot at Mpala Research Centre and Conservancy in Kenya (0°17′ N, 36°53′ E, 1668.51–1792.23 m asl elevation) (Anderson-Teixeira et al., 2015; Mutuku & Kenfack, 2019). The plot is located in a semi-arid (~600 mm mean annual rainfall) savanna ecosystem and includes at least 62 woody plant species (Mutuku & Kenfack, 2019) out of at least 460 woody and herbaceous plant species from the region (Gill et al., 2019), 17 wild large mammalian herbivore species (here defined as >5 kg), 8 large carnivore species, and 5 species of domestic livestock that are herded in a quasi-pastoralist fashion typical of the region (cattle, camel, goats, sheep, and donkeys; Kinnaird & O'brien, 2012). The habitat is dominated by acacia trees and spans three soil types that are characteristic of the Laikipia Highlands of central Kenya: (*i*) the 'high plateau' habitat comprising poorly drained, clay- and nutrient-rich vertisols (black-cotton soil; elevation range:

116 1,775 m – 1,792 m asl); (*ii*) the 'low plain' habitat comprising well-drained, nutrient-poor, red
117 sandy loams (red sands soil; elevation range: 1,669-1,779 m asl); and (iii) the rocky 'slope'
118 escarpment habitat comprising transitional soil between the high plateau and low plain (range
119 1,679-1,779 m asl; Ahn & Geiger, 1987; T. P. Young et al., 1997). The woody plant community
120 of the high plateau is dominated by an acacia tree, *Vachellia drepanolobium*, that is able to
121 tolerate the stressful conditions required for growth in poorly-drained and clay-rich soils by
122 suppressing herbivory through an ant-plant mutualism, which it is able to invest in maintaining
123 on these nutrient rich black-cotton soils (Pringle, Prior, Palmer, Young, & Goheen, 2016). In
124 contrast, a more diverse array of relatively poorly defended acacias and other tree species
125 cooccur under the less stressful edaphic conditions typified by well-drained, nutrient-poor sandy
126 loams in the low plain habitat.
127
128 *Camera-trap grid*
129 In order to characterize the distribution of wildlife in the plot, we established a camera trap grid
130 in April of 2018. Motion-triggered cameras (Bushnell® Trophy Cam HD Aggressor Low glow,
131 Model #11-9874C) were deployed at regular locations at 100-m intervals throughout the plot,
132 with 14 grid points occurring in grid cells classified as high plateau, 3 in the slope habitat, and 16
133 in the low plain (Fig. 1a). For each remotely triggered photograph we recorded date, time, and
134 species using Wild-ID software (Bolger, Vance, Morrison, & Farid, 2011). Photos were initially
135 filtered of humans, domestic livestock (cattle, goats, sheep, and camels), birds, primates, small
136 mammals (<5 kg), large and small carnivores and insectivores, as well as false triggers caused by
137 wind, vegetation movement, or camera malfunctions. Remaining photos of large herbivore
138 species were temporally filtered to reduce the impacts of temporal autocorrelation such that

139 species detections were only considered independent if taken greater than 30 minutes apart. For
140 each herbivore species, we calculated a relative abundance index (RAI) as the total number of
141 independent photographs over the course of the survey divided by the total number of working
142 camera trap days and multiplied by 100 to yield an index in units of detections per 100 working
143 camera days. Prior work on large-bodied animals using similar camera-trap designs has
144 demonstrated that this RAI-based approach yields relative abundance estimates that correlate
145 strongly with independent estimates of animal abundance (e.g., aerial surveys; Kinnaird &
146 O'brien, 2012; Palmer, Swanson, Kosmala, Arnold, & Packer, 2018; Rovero & Marshall, 2009),
147 even though RAI-based approaches do not incorporate information on species-level detection
148 probabilities common in more sophisticated occupancy modeling frameworks (Dorazio & Royle,
149 2005; MacKenzie et al., 2002; Sollmann, Mohamed, Samejima, & Wilting, 2013). The relative
150 abundance of all herbivores at a given grid point was calculated as the cumulative sum of RAI
151 values all species recorded at that grid point over the entire the survey period.
152
153 *Data sources*
154 We obtained data from the ForestGEO Network and from previously published plant and animal
155 phylogenies. The initial comprehensive ForestGEO survey began in 2010 by using a regular
156 spatial grid comprised of 400-m^2 quadrats (Mutuku & Kenfack, 2019). In each quadrat, stems of
157 all woody trees and shrubs > 0.5 m above ground level were geolocated, tagged, and measured
158 for diameter knee height (dkh). Tree species identifications were completed in the field by
159 experienced researchers from the East African Herbarium at the National Museum of Kenya. The
160 complete tree census dataset was downloaded from the Smithsonian ForestGEO data portal
161 (https://forestgeo.si.edu/). This dataset included 363,798 individual stems belonging to 139,078

individual trees and shrubs, comprising 67 morphospecies from 41 genera and 22 families (Mutuku & Kenfack, 2019). The main and auxiliary stems of each uniquely identified tree were mapped and measured. The dataset was filtered to include only living stems > 2 cm dkh and > 50 individuals in the plot to reduce the potentially outsized influence of rare species on downstream diversity calculations. The resulting dataset used for all community-level diversity analyses comprised 135,970 individuals and 354,863 stems. Individuals representing 40 morphospecies from 25 genera were identified only to the genus level, and these taxa represent approximately 8% (individual taxa range: 0.02 – 2.53%) of the remaining stems. Tree abundance was quantified as the total number of individually marked woody stems occurring within a 25-m circular polygon centered at each camera trap location. To evaluate phylogenetic diversity and relatedness among species in the plot, we utilized publicly available plant and animal phylogenies. We used a plant community phylogeny that was recently compiled for the flora of Mpala based on an extensive DNA barcode library (Gill et al., 2019; Kartzinel et al., 2015). This community phylogeny included 28 of the predominant woody plants in the community, accounting for 90.6% of all uniquely identified trees in the full ForestGEO dataset. The final plant dataset consisted of 126,088 individually identified and georeferenced woody plants (318,178 total stems) from 20 species in 14 genera (Fig. 1). To evaluate the phylogenetic relationships between mammals included in our analysis, we used a published mammalian megaphylogeny (Fritz, Bininda-Emonds, & Purvis, 2009), which included all large species included in our camera-trap analyses.

Characterizing the abiotic environment

In order to evaluate the influence of topographic habitat variables on plant and animal diversity and community composition, we determined fine-scale elevation, slope, and convexity based on elevation data recorded across the extent of the plot (Mutuku & Kenfack, 2019). We measured topography across a regular 5m x 5m grid. Gridded values were then assigned to the 20m x 20m quadrats that were used in the vegetation censuses as reported in the ForestGEO *fgeo.analyze* package (Lepore et al., 2019) in R (R Core Team, 2019). After standardizing measures of elevation, slope, and convexity to a mean of 0 and standard deviation of 1, the three variables were used to classify the 3,000 20-m x 20-m quadrats into the three major habitats identified *a priori* (high plateau, slope, and low plain) using Ward hierarchical clustering (Ward 1963, Figure 1). Finally, we calculated the topographic wetness index (TWI), which reflects the ability of a landscape to retain water and is a strong predictor of wildlife distributions in savanna ecosystems (Hopcraft, Anderson, Pérez-Vila, Mayemba, & Olff, 2012). We calculated TWI by integrating the total water catchment area and slope of each grid cell. Cells with high TWI values tend to be flat or concave and have large catchment areas. In order to calculate TWI, we used the *build.layers* function in the R package *dynatopmodel* (Metcalfe, Beven, & Freer, 2018).

Characterizing plant and animal communities

We compared the diversity of woody plants within 25-m radii (the approximate maximum detection distance of our camera trap model) surrounding each of the 33 camera traps and their corresponding diversity of large herbivores. We quantified species richness (the count of unique species) and two metrics of phylogenetic diversity and community structure using the R package *picante* v. 1.8 (Kembel et al., 2010). The phylogenetic diversity metrics included the standard

effect sizes of mean pairwise distance (*ses*MPD) and mean nearest taxon distance (*ses*MNTD). These measures use null model randomization procedures to determine whether observed communities are composed of taxa from phylogenetically clustered lineages or are more evenly distributed across the phylogeny than expected by chance assembly (in the case of *ses*MPD) and the degree to which closely related species tend to co-occur (in the case of *ses*MNTD; Webb, Ackerly, McPeek, & Donoghue, 2002). For each camera trap site, we randomly generated 999 communities that shuffled the names of taxa across the phylogeny while holding the richness of the community constant and compared observed MPD, and MNTD values to distributions derived from these randomizations to determine if they were significantly different than zero. We employ both metrics because MPD is more sensitive to the phylogenetic diversity of deep-branching lineages in the community phylogeny, whereas MNTD is more sensitive to the branching structure closer to the tips of the phylogeny (Mazel et al., 2016).

In order to characterize the compositional turnover of plant and animal communities across the plot's edaphic and topographic gradients, we evaluated pairwise taxonomic and phylogenetic dissimilarity for all sites. We decomposed overall community dissimilarity into both taxonomic and phylogenetic components using the phylogenetic community dissimilarity (PCD) metric based on the *pcd* function in the R package *picante* v. 1.8 (Ives & Helmus, 2010; Kembel et al., 2010). The PCD metric is partitioned into a non-phylogenetic component determined by the taxonomic similarity of two communities (i.e., which species the two communities share; *PCDc*) and a phylogenetic component that depends upon relationships between non-shared species (*PCDp*). Thus, *PCD* = *PCDc* x *PCDp*. If *PCD* = 1, two communities are no more or less similar than communities assembled from random selections from a regional species pool. If *PCDp*=1, then *PCD*=*PCDc*, and thus community differences only reflect

taxonomic compositional differences. However, if *PCDc*=1, then differences are due entirely to the phylogenetic distances between non-shared species (*PCDp*). If all non-shared species between two communities are phylogenetically closely related, phylogenetic dissimilarity will be low, while if the two communities have non-shared species that come from very different clades of the community phylogeny then phylogenetic dissimilarity between the two communities would be high. We calculated *PCD* for herbivores using species-specific RAI values at each camera trap and we calculated *PCD* for woody plants based on the circular sampling sites around each camera location.

Hypothesis testing

In order to test hypothesis *i*, that the diversity of both woody plants and large herbivores is related to ecosystem-level resource availability, we compared the average diversity of both communities across the 33 sampling sites. To compare plant and animal abundance between ecosystems, we used the number of plant stems in each 25-m radius plot and the cumulative RAI value for large herbivores as response variables in ANOVA. To compare diversity between ecosystems, we used each of the three diversity metrics—taxonomic richness, *ses*MPD, and *ses*MNTD—as response variables. Assumptions of normality in model residuals and homogeneity of variance across groups were assessed using Shapiro Wilk and Levene tests, respectively. ANOVA assumptions were not met when using raw abundance and taxonomic richness metrics and thus we log-transformed to improve normality in the distribution of residuals and homogeneity of variances across groups. Phylogenetic measures (*ses*MPD and *ses*MNTD) were not log-transformed due to their inclusion of values less than zero. To evaluate pairwise differences between groups, we used Tukey's Honest Significant Difference tests (alpha

252 = 0.05). Our hypothesis would be supported if plant and animal diversity are significantly greater
253 in low plain habitat where there are more woody plant individuals compared to the high plateau.
254 In order to determine the effect of unequal sampling across our three major habitat units, we also
255 performed sample-based interpolation and extrapolation using the Bernoulli product model
256 (Colwell et al., 2012). Interpolation and extrapolation curves derived from these analyses and
257 their interpretations are available in Fig. S2.

258 In order to test hypothesis *ii*, that local plant and herbivore diversities were strongly
259 positively correlated, we tested for correlations between each measure of abundance and
260 diversity for plants and animals at each of the sampling sites. To characterize plant-herbivore
261 abundance and diversity relationships both within and across habitat types, we performed
262 ANCOVAs. For this analysis, we combined sites in the low plain and slope habitats due to the
263 small number of sites available on the slope (N = 3) and the compositional similarity between
264 slope and low plain habitats (see Results for PCD analyses). We used herbivore community
265 characteristics as the dependent variables and corresponding vegetation characteristics as
266 independent variables, with the covariate being habitat type (high plateau vs. low plain/slope).
267 Our hypothesis that local herbivore diversity is positively correlated with local plant diversity,
268 regardless of ecosystem and consistent with the resource-specialization hypothesis, would be
269 supported if positive trends were apparent in both habitats; diversity values in the low plain/slope
270 habitats should be greater compared to the high plateau because ecosystems with more
271 individuals are expected to support greater levels of biodiversity in general.

272 We tested hypothesis *iii,* that environmental gradients would produce concordant
273 gradients in locally correlated plant and herbivore diversity, in two ways. First, we tested
274 whether phylogenetic and taxonomic compositional turnover was predictable based on

topographically defined habitat types (plateau and slope/low plain habitat classes) by performing permutational multivariate analyses of variance (perMANOVA) using the *adonis* function in *vegan* in R (Oksanen et al., 2019). Our hypothesis that spatial changes in community composition at both trophic levels reflects similar responses to underlying topographic and edaphic conditions would be supported if habitat type is a significant predictor of phylogenetic community dissimilarity. Secondly, we evaluated the degree to which spatial variation in the diversity and composition of plant and herbivore communities was correlated across the plot's environmental gradient. We tested for significant overall correlation between turnover in plant and animal communities using Mantel tests (Borcard, Legendre, & Drapeau, 1992) based on the PCD and PCDc metrics. In order to account for the possibility that spatial correspondence between communities is determined by the distance between sampling sites with respect to the habitat gradient, we used partial Mantel tests to evaluate correlations between plant and animal dissimilarity while accounting for the distance between camera trap locations (Borcard et al., 1992).

Finally, in order to determine the degree of species-specific habitat associations at both trophic levels and their influence on taxonomic and phylogenetic differentiation between communities, we performed indicator species analyses. Specifically, we calculated the point biserial correlation coefficient, an abundance-based counterpart to Pearson's phi coefficient of association between species and each of the three habitats (plateau, escarpment, low plain), corrected for unequal sampling across habitat types using the *indicspecies* package in R (Cáceres & Legendre, 2009). Species abundances were relativized using the Hellinger transformation prior to indicator species analyses. Pearson's phi coefficient range from -1 to 1, indicating strong avoidance and preference, respectively (Chytrỳ, Tichỳ, Holt, & Botta-Dukát, 2002). We used

298 bootstrapping to produce 95% confidence intervals and evaluate whether species-habitat
299 associations significantly differ from zero.
300
301 **Results**
302 We generated three datasets suitable for testing hypotheses about the fine-scale correlation of
303 woody plant and large-herbivore diversity. We recorded 8,879 temporally independent
304 photographs of 17 wild herbivore species over 10,075 trap days (305.34 ± 89.34 s.d. working
305 days/camera) across N=33 sampling sites. Plant communities in the 25-m radii surrounding each
306 of these sampling sites cumulatively included a subset of 20 woody plant species out of 40 of the
307 morphospecies included in our final plot-wide dataset. The primary topographic axes of
308 microhabitat variation across the plot were slope and convexity (Fig. 1, Table 1). The high
309 plateau sites were flat and relatively topographically homogeneous whereas sites along the
310 escarpment and in the low plain habitats had significantly greater topographic heterogeneity:
311 elevation was greatest on the high plateau (mean = 1,787 m asl) and decreased through the slope
312 (1,754 m asl) into the low plain (1,692 m asl). Both slope and convexity were lowest in the high
313 plateau habitat, intermediate in the low plain, and greatest on the slope; TWI was greatest on the
314 high plateau where there are relatively flat surfaces that provide little opportunity for directional
315 run off and clay soils that inhibit infiltration, intermediate at low plain sites and least along the
316 slope (Fig. S1, Table 1).
317 Across habitat types, results were consistent with our first hypothesis that the low plain
318 and slope habitats that support more individual woody plants would be more taxonomically rich
319 and phylogenetically diverse for plants. Woody plant stem abundance differed significantly
320 across habitats ($F_{2,30} = 11.24$, $P < 0.001$), being lowest on the high plateau (mean 238

stems/site), peaking along the slope (1,604 stems/site), and being intermediate in the low plain (855 stems/site; Fig. 2a, Table 1). Plateau sites were significantly sparser in woody vegetation than either slope or low plain sites (Tukey $HSD_{plateau\text{-}slope}$ $P = 0.007$; Tukey $HSD_{plateau\text{-}low\ plain}$ $P < 0.001$), but slope and low plain sites did not differ significantly in their mean stem counts (Tukey HSD $P = 0.664$). In the case of woody plant species richness, log-transformations improved the normality of residuals compared to untransformed values but did not meet normality assumptions based on Shapiro-Wilk tests ($P = 0.271$). However, one-way ANOVA tests are considered to be robust to violations of the normality assumption (McDonald, 2009) and thus we proceeded with parametric post-hoc tests and interpretations noting that our conclusions should be viewed conservatively. Woody plant richness also differed significantly across habitats ($F_{2,30} = 21.40$, $P < 0.001$), with high plateau sites having two- to three-fold lower richness (mean = 4.4 species/site) than the slope (14.3 species/site, Tukey HSD $P < 0.001$) and low plain (9.6 species/site, Tukey HSD $P < 0.001$) habitats (Fig. 2b, Table 1). Slope and low plain sites did not differ significantly with regard to their species richness (Tukey HSD $P = 0.259$). Similar patterns were observed for *ses*MPD (one-way ANOVA, $F_{2,30} = 7.01$, $P = 0.003$) with the slope sites consistently exhibiting the greatest average phylogenetic diversity (compared to plateau and low plain Fig. 2c, Table 1). Slope habitat vegetation communities at camera trap sites contained taxa from significantly more deeply divergent lineages (mean *ses*MPD = 0.85) compared to those in the plateau (mean = -1.5; Tukey HSD $P = 0.032$) but did not differ statistically in their amount of phylogenetic diversity than the low plain camera trap sites (mean = -0.2, Tukey HSD $P = 0.374$). While no local sites in the plateau habitats showed significant phylogenetic clustering, two out of 16 traps in the low plain habitat did. At these two sites, acacia species *Senegalia mellifera*, *Senegalia brevispica*, *Vachellia etbaica*, and *Vachellia gerrardii* made up 90% of the total stems

(with N = 243 and 555 stems per site). Although slope habitat sites tended to contain, on average, greater phylogenetic diversity per site than did either of the other habitats, it did not contain significantly greater phylogenetic diversity than random expectations based on our null models. Habitat type also had an effect on woody plant community *ses*MNTD (ANOVA, $F_{2,30} = 9.58$, $P < 0.001$). Plateau sites had lower nearest-taxon distances in the phylogeny than did low plain or slope habitats (mean *ses*MNTD plateau = -1.1; low plain = 0.2, slope = 1.6). Thus, across all metrics, the high plateau had the lowest woody plant abundance and diversity whereas slope and low plain habitats had woody plant communities that were both more abundant and diverse.

Whereas the plant community results were broadly consistent with our first hypothesis in that the ecosystems that harbored greater plant abundance also harbored greater plant diversity, this was not the case for large herbivores. Herbivore abundance differed significantly between habitats (ANOVA, $F_{2,30} = 8.42$, $P = 0.001$; Fig. 2e). Cumulative herbivore RAI at low plain sites was over 250% times greater than that in slope sites (means = 127 vs. 49 detections/100 working days) and also significantly greater than plateau sites (mean = 60), but plateau and slope sites did not differ in their mean site-level abundance (Fig. 2e). Mean herbivore richness also differed significantly between habitat types (ANOVA, $F_{2,30} = 12.70$, $P < 0.001$; Fig. 2f). Surprisingly, plateau sites, on average, supported the most species rich herbivore assemblages (11.4 species/site) compared to the low plain (9.8 species/site) and slope sites (6.3 species/site). Differences in mean species richness were statistically significant when comparing camera trap sites in the plateau slope habitats to the low plain sites (Tukey $HSD_{\text{plateau-low plain}}$ $P = 0.004$; Tukey $HSD_{\text{slope-low plain}}$ $P = 0.013$) but were not significantly different when comparing the plateau to the slope habitat (Tukey $HSD_{\text{plateau-slope}}$ $P = 0.594$), potentially reflective of the unequal sampling across habitat types. Species accumulation curves (Fig. S2) indicated that slope sites had

consistently fewer herbivore species per site than either major habitat unit when considering just our sampling grid, but that extrapolating past our current sample may be difficult due to undersampling this region of the landscape. Expanding species diversity measures through the use of Hill numbers (Chao, Chiu, & Jost, 2014; Colwell et al., 2012) that are able to incorporate information on the relative abundance of species within assemblages provided additional insights into how diversity differs across habitat types. For example, when considering the diversity of "typical" species (q=1), the slope habitats were consistently less diverse than either major habitat unit, indicated by the complete lack of overlap in the 95% confidence intervals of interpolated and extrapolated species diversity curves (Fig. S2). Investigating species-specific abundance measurements suggests that this may be attributable to the disproportionate abundance of dik-dik (*Madoqua guentheri*), a locally abundant small antelope, that made up a vast majority of herbivore detections in slope habitat sites relative to more rarely detected species such as elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*) and kudu (*Tragelaphus strepsiceros*, Fig. S5). The phylogenetic diversity and structure of camera trap site-level herbivore assemblages differed in subtle ways between habitat types. Mean values of herbivore community *ses*MPD differed significantly across habitat types (one-way ANOVA, $F_{2,30} = 33.88$, $P = 2.01 \times 10^{-8}$). Herbivore communities at camera trap sites in the plateau tended to include more phylogenetically diverse lineages (mean *ses*MPD = 1.1) compared to those sampled in slope (mean = 0.2, Tukey HSD $P = 0.003$) and low plain (mean = -0.1, Tukey HSD $P < 0.001$) habitats. However, herbivore community *ses*MPD was not significantly different between slope and low plain habitats (Tukey HSD $P = 0.551$). Herbivore mean nearest-taxon distance (*ses*MNTD) did not differ significantly across habitats ($F_{2,30} = 2.82$, $P = 0.076$; Fig. 2h). Within habitats, mammalian herbivore phylogenetic diversity did not differ significantly from zero

within any sampling site for either metric based on null model randomizations (Fig. 2f, h, Table 1).

In contrast with hypothesis *ii*, the diversity of woody plants and large herbivores did not exhibit a monotonic positive correlation within or across habitats based on any metric that we evaluated (Fig. 3). To the contrary, both abundance and species richness exhibited a significant negative correlation between local plant and herbivore communities (Fig. 3a, b), and these correlations did not differ significantly between habitats in their slope (P-values > 0.05). In the case of abundance, intercepts differed significantly between habitats (P-value < 0.001), reflective of the greater baseline abundance of herbivores in the lowlands. Intercepts did not differ significantly in the case of relationships between plant and herbivore species richness (P-value = 0.98; Fig. 3a, b). Herbivore *ses*MPD was not related to woody plant *ses*MPD in either habitat type ($F_{1,29} = 0.03$, $P = 0.860$) but, as demonstrated in Fig. 2, significantly higher in the plateau than in the low plain ($F_{1,29} = 44.30$, $P < 0.001$, Fig. 3c). There were no significant relationships between herbivore *ses*MNTD and woody plant *ses*MNTD (P-value > 0.05, Fig. 3d). We also examined relationships between woody plant and herbivore abundance and diversity and site-level measures of continuous abiotic covariates. These relationships further illuminate the opposing abundance and diversity gradients (Figs. S3 and S4). Slope and convexity were negatively correlated with herbivore abundance species richness while positively correlated with corresponding measures for woody plant communities, highlighting their potential role in mediating plant-herbivore spatial relationships. Surprisingly, herbivore abundance and species richness were relatively invariant with regard to site-level TWI at least at the spatial scale of our measurements, in contrast to previous findings that highlight its positive effects on herbivore spatial aggregation (Hopcraft et al., 2012).

Although the abundance and diversities of plant communities were not locally correlated as we had predicted, both communities exhibited significant differences in composition with respect to a shared set of habitat characteristics underlying the ForestGEO plot. Consistent with hypothesis *iii*, we found that PCD differed significantly for woody plants (perMANOVA, pseudo-$F_{1,32} = 11.9$, $R^2 = 0.28$, $P \leq 0.001$) and large herbivores (pseudo-$F_{1,32} = 25.8$, $R^2 = 0.45$, $P \leq 0.001$) across major habitat classes. Differentiation between communities was stronger when considering just the taxonomic component of PCD (PCDc) for both plants (pseudo-$F_{1,32} = 21.6$, $R^2 = 0.41$, $P \leq 0.001$) and herbivores (pseudo-$F_{1,32} = 46.8$, $R^2 = 0.60$, $P \leq 0.001$). Both plant and herbivore communities showed stronger taxonomic dissimilarity than phylogenetic dissimilarity between habitat types (Fig. 4b, d): between the high plateau and slope/low plain habitats, turnover in the local composition of plant communities corresponded with turnover in large herbivore communities. Plant and herbivore community dissimilarity values based on both PCD and PCDc metrics were positively correlated (PCD: Mantel $r = 0.36$, $P \leq 0.001$; PCDc: Mantel $r = 0.64$, $P \leq 0.001$; Fig. 4e, f). After accounting for the effect of spatial proximity between sampling sites using partial Mantel tests, these positive correlations remained statistically significant but were reduced in magnitude, suggesting that at least a portion of the spatial correspondence between plant and herbivore communities reflects the short distances between sampling sites (minimum distance between adjacent sample sites = 100m; PCD: partial Mantel $r = 0.26$, $P \leq 0.001$; PCDc: partial Mantel $r = 0.50$, $P \leq 0.001$, Fig. 4e, f).

Indicator species analyses revealed highly heterogeneous patterns in habitat associations across woody plants and herbivores. All plant taxa exhibited a significant association with at least one habitat type, and 57% of the significant associations involved the slope habitat (Fig. 5a).The majority of plant taxa were significantly negatively associated with the high plateau

habitat (N=17 species) and only three were significantly associated with it (*Balanites aegyptica*, *Cadaba farinosa*, *V. drepanolobium*). A total of six plant taxa were significantly associated with the low plain habitat (*Euclea divinorum*, *Vachellia gerrardii*, *Vachellia etbaica*, *Senegalia brevispica*, S*enegalia mellifera*, and *Grewia kakothamnos*), and two of these species also exhibited significant associations with both the slope and low plain habitats (*E. divinorum* and *S. brevispica*), contributing strongly to the similarity between these two topographically distinct parts of the habitat gradient. In contrast, 59% (N=10) of large herbivore species exhibited significant avoidance of the slope habitat (Fig. 5b), and no species exhibited significant positive association with the slope.

Discussion

We used fine-scale data on savanna woody plant and large-herbivore communities to determine the levels and extent of local correspondence in abundance and diversity across trophic levels. Results were partially consistent with our first hypothesis in that habitat patches with the most abundant woody plant communities also supported the greatest taxonomic richness and phylogenetic diversity of woody plants. However, this increase in plant abundance and diversity did not translate into a greater abundance and diversity of large herbivores either between (hypothesis *i*; Fig. 2) or within (hypothesis *ii*; Fig. 3) habitats. Surprisingly, correlations between the local abundance and diversity of plants and herbivores were either non-significant or significantly negative (Fig. 3), potentially reflecting the opposing responses of woody plants and herbivores to underlying topographic and/or edaphic conditions (Figs. S3 and S4). Despite this negative correlation between the abundance and taxonomic diversity of plants and large herbivores, both communities exhibited significant and spatially concordant differences in

459 composition across edaphically and topographically distinct habitats. Thus, the abundance,
460 diversity, and composition of plant and animal communities were all strongly associated with a
461 gradient in soil composition underlying the habitats at this plot. However, these differences did
462 not correspond in ways that were consistent with either the resource-specialization hypothesis or
463 the more-individuals hypothesis.

464 The resource-specialization and more-individuals hypotheses provide two possible
465 mechanisms that give rise to spatial correspondence in the abundance and diversity of plants and
466 herbivores. Niche-based theories of limiting similarity underpin the resource specialization
467 hypothesis such that as the total number of potential plant resources increase, available niche
468 space also increases, magnifying the opportunity for partitioning among more species of
469 herbivores that may specialize on sub-sets of plant taxa (R. H. MacArthur & MacArthur, 1961;
470 R. MacArthur & Levins, 1967). This hypothesis is suited for plant-herbivore systems that are
471 composed of relatively highly specialized feeders—such as phytophagous insects or insect
472 pollinators with close host-plant eco-evolutionary histories—that differ substantially in both
473 foraging modes and nutritional requirements from ungulate herbivores that are capable of
474 consuming a wide range of plant species (Kartzinel & Pringle, 2020). The more-individuals
475 hypothesis is based on the premise that overall increases in resource availability enables more
476 species to establish (Srivastava & Lawton, 1998; Storch, Bohdalková, & Okie, 2018), perhaps
477 through the alleviation of competitive exclusion (Hutchinson, 1959; Wright, 1983). However,
478 our results reveal inverse relationships between the abundance and diversity of local plant and
479 that of herbivore communities (Fig. 3), in stark contrast to several studies reporting positive
480 correlations between the abundance and diversity of plants and herbivores at local to global

scales (Dinnage, Cadotte, Haddad, Crutsinger, & Tilman, 2012; Haddad et al., 2009; Jetz et al., 2009; Schuldt et al., 2019; Wang et al., 2019).

Several non-mutually exclusive mechanisms could underpin the opposing gradients in herbivore and woody plant abundance and diversity plant and large herbivore communities that we observed in the ForestGEO plot. The local habitats with the greatest abundance and diversity of plant species could be (*i*) topographically complex and difficult to access refuges that enable plants to escape suppression by herbivores, (*ii*) risky environments in which herbivores are suppressed through behaviorally mediated fear responses to predators, and/or (*iii*) less productive than the other habitats despite a greater standing crop of woody plants. Although we cannot yet fully distinguish between *i* and *ii*, our data are inconsistent with *iii*. Specifically, the slope and low plain habitats are most similar in soil composition and woody plant community composition, and yet they differ starkly in their local abundance of large herbivores (Fig. 2). Further, although the highly productive black-cotton soils underlying the high plateau habitat could support a relatively high-quality/low-biomass plant community—and hence similar large-herbivore diversity to the low plain despite significantly lower woody plant abundance (Fig. 2)—these differences in productivity cannot fully explain the inverse correlations that we observed and we must consider alternate explanations.

Topographic complexity, such as variation in slope, aspect, and surface roughness are thought to be associated with increases in plant community diversity. Similar to the niche-based resource specialization hypothesis that has been used to link herbivore community diversity to the diversity of their food resources, increases in abiotic habitat conditions can expand the niche space available for partitioning among co-occurring plant species, facilitating the accumulation of plant taxa. Evidence of the positive effects of habitat heterogeneity on plant species richness

has been borne out in a range of ecosystems (Hortal, Triantis, Meiri, Thébault, & Sfenthourakis, 2009; Irl et al., 2015; Thuiller, Midgley, Rougeti, & Cowling, 2006). The same factors that generate these highly variable growing conditions that may facilitate the spatial accumulation of plant diversity may also simultaneously negatively influence the ability of herbivores to access those plants, effectively creating topographic refugia. Rapid changes in topography can impose both mechanical and energetic constraints on the large-bodied herbivores that may lead them to avoid these topographically challenging areas. Megaherbivores such as giraffe and elephants in our study tended to avoid the steep escarpment sites of the slope habitat (Fig. 4), as they do across East African savannas (Wall, Douglas-Hamilton, & Vollrath, 2006). Beyond just these megabrowsers, community-wide herbivore abundance and diversity tended to decrease with increases in topographic complexity (Fig. S4). This hypothesis provides a potential explanation for the overall greater abundance of plant stems (Fig. 2) in the slope habitat (particularly along the steepest regions of the topographic escarpment) and the prevalence of rare plant species with strong associations to the slope habitat (Fig. 4). Large-scale experimental exclusions of megaherbivores highlight the ability of herbivores in savanna systems to exert strong top-down effects on the abundance and diversity of vegetation in this (Goheen et al., 2018) and other savanna ecosystems across Africa (Guyton et al., 2020; Owen-Smith, Page, Teren, & Druce, 2019; Staver, Bond, Stock, Rensburg, & Waldram, 2009). Findings derived from the Kenya Long-term Exclosure Experiment (KLEE; T. P. Young et al., 1997), which is situated in the plateau habitats dominated by the clay-rich 'black cotton' soils, indicate that reductions in large herbivore browsing pressure by both small- and large-bodied herbivore species leads to increases in the recruitment of some shrub taxa (e.g. *Cadaba farinosa*) as well as accelerated growth and reproduction in the locally dominant *V. drepanolobium* (Riginos & Young, 2007). Further

527 experimental investigation is needed to determine the degree to which herbivore browsing affects
528 the local abundance and distribution of species beyond the locally dominant acacia species under
529 natural topographic and edaphic variation. The methodologically similar UHURU experiment
530 conducted at Mpala Research Centre (Goheen et al., 2013), which systematically excludes
531 ungulate herbivores of different size classes and spans the same edaphic conditions as our low
532 plain sites (volcanic red sands), also provides preliminary evidence supporting this hypothesis.
533 At least a subset of the relatively rare taxa that we observed had significant positive associations
534 with the slope sites (e.g. both species in the genera *Maerua*, *Boscia angustifolia*) also tended to
535 increase in their abundance in the five years following exclusion of large herbivores (Kartzinel et
536 al., 2014). The defensive strategies employed by other abundant and positively associated slope
537 species also provide clues as to the potential plant-herbivore trophic interactions that contribute
538 to their differential abundance across habitat types. For example, two woody plant species that
539 were strongly associated with steepest escarpment habitats invest heavily in anti-herbivore
540 defenses that are probably effective against smaller-bodied ruminants that require high quality
541 plant resources but less effective against very large hind-gut fermenting species like elephants:
542 *C. dichogamus* produces a noxious latex and *E. divinorum* is an evergreen shrub that possesses
543 tough, fibrous, and tannin-rich leaves (Hattas, Hjältén, Julkunen-Tiitto, Scogings, & Rooke,
544 2011). Although these plant species are consumed occasionally by many large herbivore species
545 in this ecosystem, consumption tends to occur under very dry conditions when more palatable
546 resources are depleted and competition among herbivores is greatest (Kartzinel, Hsing, Musili,
547 Brown, & Pringle, 2019; Kartzinel & Pringle, 2020). The inverse spatial relationships between
548 plant and animal diversity and abundance that we observed provide insight into how trophic

549 interactions between plants and large herbivores could be mediated by shared abiotic habitat
550 characteristics.
551 Perceived threats of predation can also decrease herbivore activity in certain
552 environments with implications for the physical structure and composition of local plant
553 communities. Wild large herbivores perceive risk cues associated with the presence of predators
554 and—generally but not universally—prefer habitats with low tree density and good sight lines
555 (Riginos & Grace, 2008). Steep habitats with high predator density, high tree density, and a
556 challenging terrain to flee from threats should thus be avoided by most large herbivore species
557 compared to more flat and open habitats. Thus, habitat distributions driven by predator
558 avoidance behaviors could also alleviate herbivore pressure on plant communities through non-
559 consumptive predator-prey interactions (Beschta & Ripple, 2009; Carpenter, Kitcheil, &
560 Hodgon, 1987; Schmitz, 2006). Whereas we had originally conceptualized stem abundance as a
561 measure of resource abundance and had hypothesized that it would be positively related to that
562 of herbivores, this measure of vegetation structure could also conceptualized as a measure of
563 viewshed obstruction, an important contributor to predation risk for many small and medium-
564 sized ungulate herbivores in savanna ecosystems (Ford et al., 2014; Hopcraft et al., 2012;
565 Hopcraft, Olff, & Sinclair, 2010; Riginos & Grace, 2008). Topographic features, particularly
566 indices of landscape curvature that further interrupt long sight lines such as slope and convexity,
567 may also exert species-specific influences on herbivore habitat use (Ford et al., 2014; Hopcraft et
568 al., 2012). In our study, the most abundant medium-sized herbivore is impala, which exerts
569 significant browsing pressure on woody species (Goheen et al., 2013; Kartzinel et al., 2014; H.
570 S. Young et al., 2013). Impala had a strong negative association with the steep escarpment
571 habitats, lending provisional support to this hypothesis. Analyses of camera trap data to quantify

site-specific predator abundance across our study site is ongoing and can improve our ability to ascertain the non-consumptive effects of large carnivores on plant community structure and diversity.

The same physical habitat features that obstruct herbivore sightlines and potentially increase predation risk may also have methodological implications for our ability to detect animals. In our sampling approach, we standardized vegetation sampling by centering circular polygons with 25m radii over an exhaustively mapped spatial grid of individual plant stems, effectively reducing the potential probability of missing existing individual plants. However, this approach also makes the implicit assumption that herbivore detection probabilities were also uniform both within the area of the sampling polygons and between camera trap sites across habitat types. If this is, in fact, not the case, then this methodological approach could lead to abundance and diversity estimates that are biased low in densely vegetated or steeply sloping sites compared to sites that are less obstructed. This potential drawback in our analytical approach could be addressed through more sophisticated statistical treatment of the factors affecting both herbivore habitat use and the probability that we detect them given they actually occur – e.g. through the application of hierarchical occupancy modeling procedures that can simultaneously quantify detection and occupancy probabilities (Dorazio, Royle, Söderström, & Glimskär, 2006; MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003; MacKenzie et al., 2017). As such, the results of our analyses as presented should be interpreted conservatively. The future application of multi-species occupancy modeling approaches for estimating community-level herbivore richness and diversity may provide additional avenues for parsing the local- and landscape-scale relationships between woody plants and their consumers in this particular environment.

595 Our analysis incorporated both taxonomic and phylogenetic data into our understanding
596 of plant-herbivore diversity relationships and their spatial manifestations. Prior studies found
597 positive correlations between plant species turnover and that of herbivorous consumers at both
598 large and small spatial scales, including lepidopterans in the Swiss Alps (Pellissier et al., 2013)
599 and general arthropods in the Cape Floristic Region of South Africa. (Kemp, Linder, & Ellis,
600 2017). Thus, one of the unexpected results from our study was the lack of correlation between
601 the phylogenetic diversity of plants and animals as we had predicted in our second hypothesis.
602 One relevant difference between our study and prior work is that prior studies tended to focus on
603 plant-arthropod associations whereas we focused on plant-ungulate associations. Large, wide-
604 ranging, generalist ungulates evolved to specialize on major clades of plants (e.g., grasses vs.
605 non-grasses (Codron, Codron, et al., 2007; Codron, Lee-Thorp, et al., 2007) and exhibit
606 phylogenetic structure in diet composition (Kartzinel et al., 2019). Whereas our current analysis
607 took a broad community approach to quantifying herbivore diversity that did not distinguish
608 between major feeding guilds (e.g. grass-eating grazers vs. non-grass-eating browsers), the
609 herbivores that forage most intensively on trees might exhibit differential sensitivity to the local
610 woody plant community. Analyses based on subsets of local herbivores that are locally known to
611 include substantial amounts of woody plants in their diets are ongoing.
612 Another surprising insight from the integration of taxonomic and phylogenetic
613 information into our analysis of community composition was the extent to which plant and
614 herbivore *species* exhibited strong habitat associations whereas plant and animal lineages were
615 widely dispersed throughout the 1.2-km^2 plot. Some species-specific associations within species-
616 rich lineages of plants have been the focus of prior studies locally. For example, ant-acacia plant
617 *V. drepanolobium* is competitively dominant in the physiologically stressful plateau habitats, but

618 it is unable to withstand browser pressure in the less fertile sandy loams of the lowlands given
619 the high energetic cost of supporting its ant mutualists—and thus other acacias such as *Senegalia*
620 *brevispica* and *Vachellia etbiaca* predominate in these low plain habitats (Mutuku & Kenfack,
621 2019; Pringle et al., 2016). In contrast, other acacia species are less abundant and less strongly
622 associated with any habitat and are relatively abundant across the gradient (e.g., *S. mellifera*).
623 Because acacia species from the genera *Senegalia* and *Vachellia* (Kyalangalilwa, Boatwright,
624 Daru, Maurin, & van der Bank, 2013) are both cumulatively dominant (52% of all main stems in
625 the plot) and widespread, community differentiation between habitat types is driven strongly by
626 species-specific habitat associations. Species-specific habitat associations are stronger for
627 herbivores than plants in this community. As with the plants, however, some closely related
628 herbivore species exhibited very strongly divergent habitat associations. For example, congeneric
629 plains zebra (*Equus burchellii*) were strongly associated with the high plateau whereas Grevy's
630 zebra (*Equus grevyi*) were strongly associated with the low plains; closely related Grant's gazelle
631 (*Nanger grantii*) was strongly associated with plateau whereas impala (*Aepyceros melampus*)
632 was strongly associated with low plains (Fig. 4). Taxonomic differentiation despite phylogenetic
633 similarity in both plants and animals across habitats is consistent with expected patterns resulting
634 from competitive exclusion under the principle of limiting similarity, since closely related
635 species should not be able to stably coexist on the same limiting resources (R. MacArthur &
636 Levins, 1967). Such spatial niche partitioning is a common among large herbivore communities
637 in savanna ecosystems (J. P. G. M. Cromsigt & Olff, 2006; J. P. G. M. Cromsigt et al., 2009;
638 Hopcraft et al., 2012; Kleynhans, Jolles, Bos, & Olff, 2011).
639 As our study highlights, the negative correlations in the abundance and diversity of plants
640 and herbivores can develop against the backdrop of a shared local environment. Inverse

relationships in consumer-resource abundance or diversity are understudied and more research is needed to establish their prevalence within and across food webs. Yet several lines of evidence suggest they may be more common than currently appreciated, including the growing recognition that physically and behaviorally mediated refuges can have strong effects on ecological communities and interactions. There are thus timely opportunities to disentangle where, when, and why we observe spatial covariation in ecological communities.

Data availability: Camera trap records and all code used for filtering datasets will be posted to Data Dryad upon submission for publication. Tree data can be requested from plot Principle Investigators using the Smithsonian Institution's ForestGEO data portal. DNA barcode data generated for this project will be posted to boldsystems.org.

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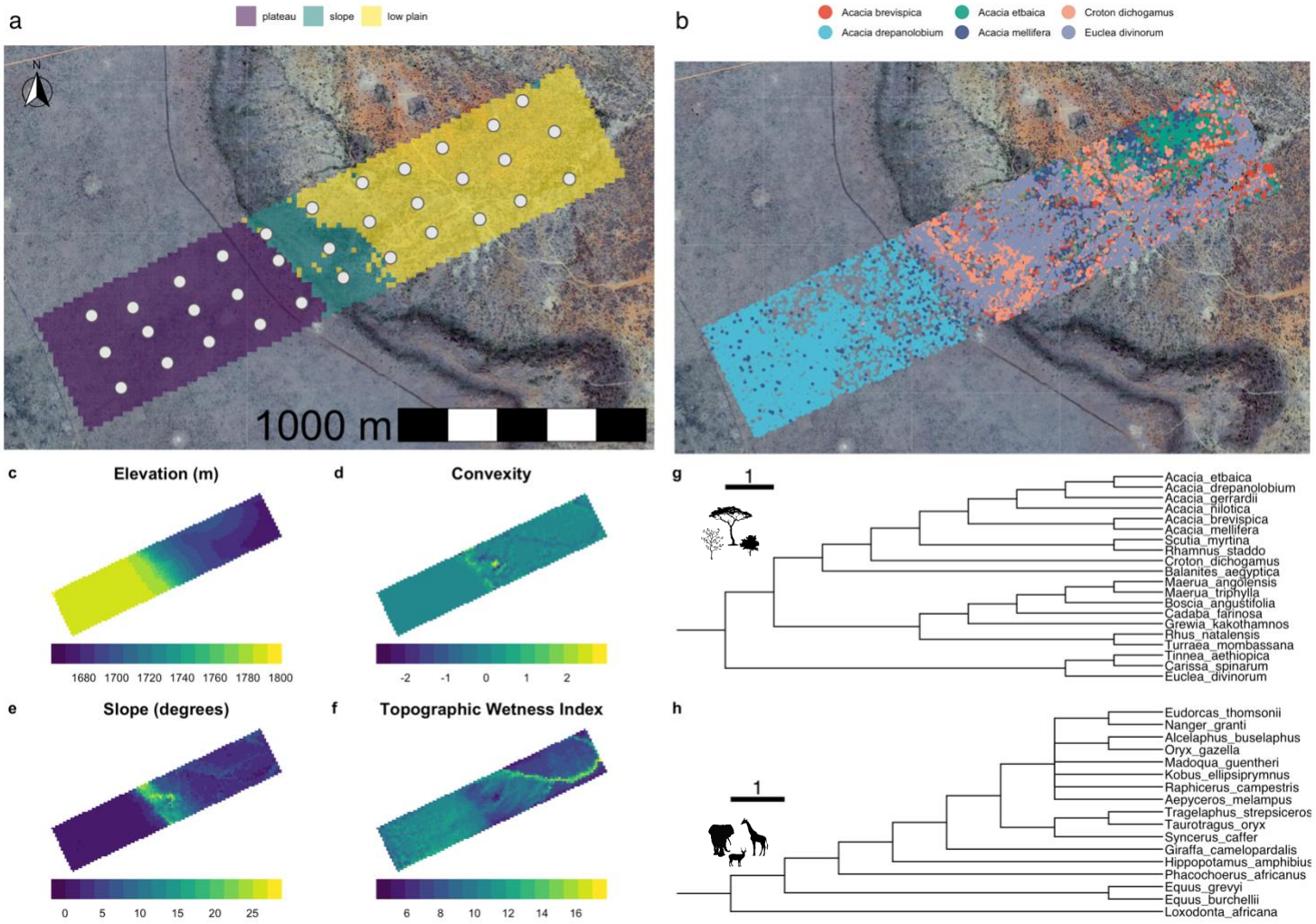
937

Tables

Table 1. Mean values for site-level measures of abiotic variables, and woody vegetation and large herbivores abundance, taxonomic richness, and phylogenetic diversity. Standard deviations of all values are in parentheses.

		Abiotic variables				***Woody Vegetation***				***Large Herbivores***			
Habitat	N	*Elevation(m)*	*Convexity*	*Slope (rad)*	*TWI*	*Total Stems*	*Richness*	*sesMPD*	*sesMNTD*	*Cum. Herbivore RAI*	*Richness*	*sesMPD*	*sesMNTD*
Plateau	14	1787 (3.73)	0.0190 (0.049)	1.04 (1.03)	10.6 (0.42)	238 (247)	4.43 (3.20)	-1.45 (1.17)	-1.08 (1.24)	60.40 (15.2)	11.40 (1.40)	1.12 (0.29)	-0.60 (0.98)
Slope	3	1754 (17.7)	0.556 (0.59)	12.3 (1.51)	7.86 (0.35)	1604 (1714)	14.3 (2.08)	0.85 (0.28)	1.56 (0.99)	49.0 (4.00)	6.30 (0.60)	0.20 (0.15)	-0.29 (0.08)
Low plain	16	1692 (11.4)	-0.0219 (0.10)	4.10 (1.59)	8.99 (1.69)	855 (659)	9.45 (2.56)	-0.15 (1.48)	0.174 (0.99)	127.0 (68.6)	9.81 (2.00)	-0.05 (0.48)	0 (0.36)

947 **Figures**



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949

950 *Figure 1*. Mpala Research Centre ForestGEO plot, Laikipia, Kenya. **(a)** The N=33 camera traps plots are represented as white points
951 centered on the location of plots, with circles of 25-m radii representing the range of remotely triggered photographic imagery and of
952 vegetation survey data used for analysis. The three primary habitats are distinguished by color (purple = "high plateau", teal = "slope",
953 yellow = "low plain"). **(b)** The distribution of six woody plant taxa comprising >70% of woody plant biomass in the plot are
954 represented with different color points. Major topographic layers used in our analysis include **(c)** elevation, **(d)** convexity, **(e)** slope,
955 and **(f)** Topographic Wetness Index (TWI). Cladogram representations of DNA barcode-inferred woody plant barcode phylogeny (g,
956 Gill et al., 2019) and a published mammalian megaphylogeny (h, Fritz et al., 2009) used for all phylogenetic analyses. Vector art used
957 in this and subsequent figures attributable to vecteezy.com.

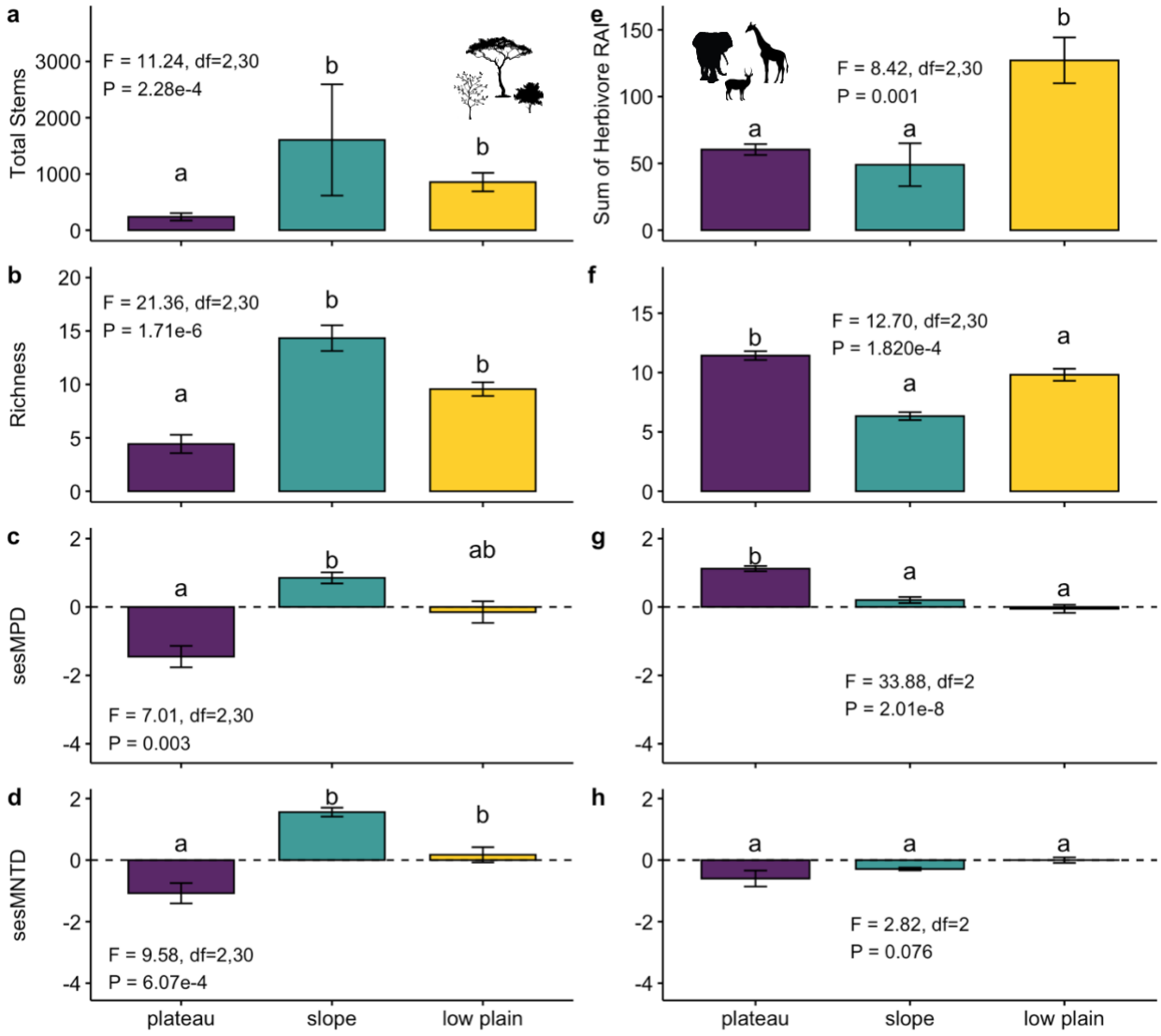

Figure 2. Abundance, taxonomic, and phylogenetic diversity of woody plant **(a-d)** and large mammalian herbivore **(e-h)** communities across habitat types. Bars indicate mean values and error bars are ± SEM. Results of one-way ANOVA tests are indicated in panels. Bars that do not share the same letter are statistically significantly different based on Tukey's HSD tests. The dashed zero-line for phylogenetic diversity metrics represents sites with community compositions that are indistinguishable from random draws from the phylogeny while

968 controlling for site-level richness, with positive values indicating phylogenetic overdispersion
969 and negative values indicating phylogenetic clustering.
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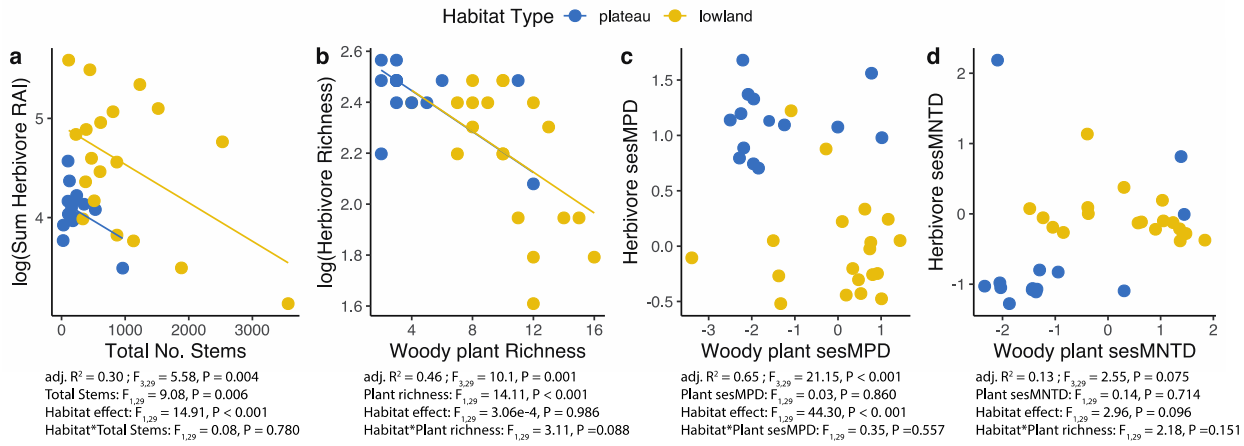

973 *Figure 3.* Relationships between **(a)** herbivore abundance, **(b)** taxonomic richness, **(c)** sesMPD
974 and **(d)** sesMNTD with corresponding measures for woody plant communities at N=33 camera
975 trap sites across two major habitat types. For each pair of metrics, we show relationships based
976 on linear models including the woody plant variable, habitat type, and the abundance/diversity
977 measure × habitat interaction. Line and point colors indicate habitat type (low plain/slope sites v.
978 plateau sites). Summary statistics from ANCOVA analyses are reproduced below each panel.
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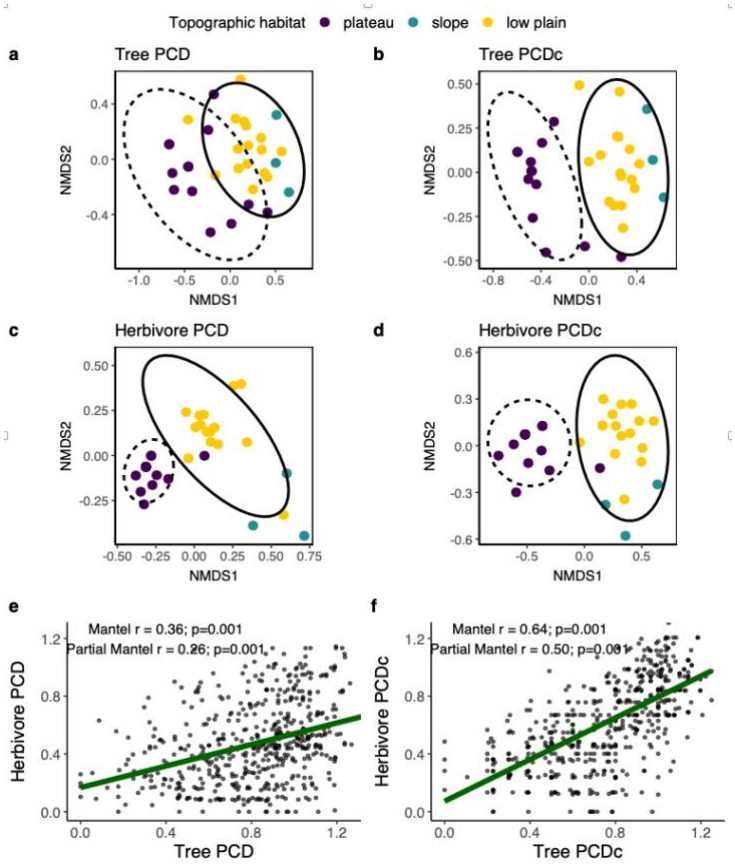

Figure 4. Woody plant and herbivore communities diverge in their taxonomic but not phylogenetic composition across habitat types. **(a-f)** Non-metric multidimensional scaling (NMDS) ordinations reveal compositional dissimilarity in both plant and herbivore communities between habitat types. Point colors describe the topographic microhabitat (plateau, slope, low plain) at each camera trap site. Ellipses indicate 95% confidence intervals for the two major habitat classes (plateau v. lowland). **(e)** Woody plant and large herbivore phylogenetic community dissimilarity were positively correlated even when accounting for spatial proximity of camera trap sites using partial Mantel tests. **(f)** Correlations in community turnover were stronger when considering only the taxonomic component of the PCD metric.

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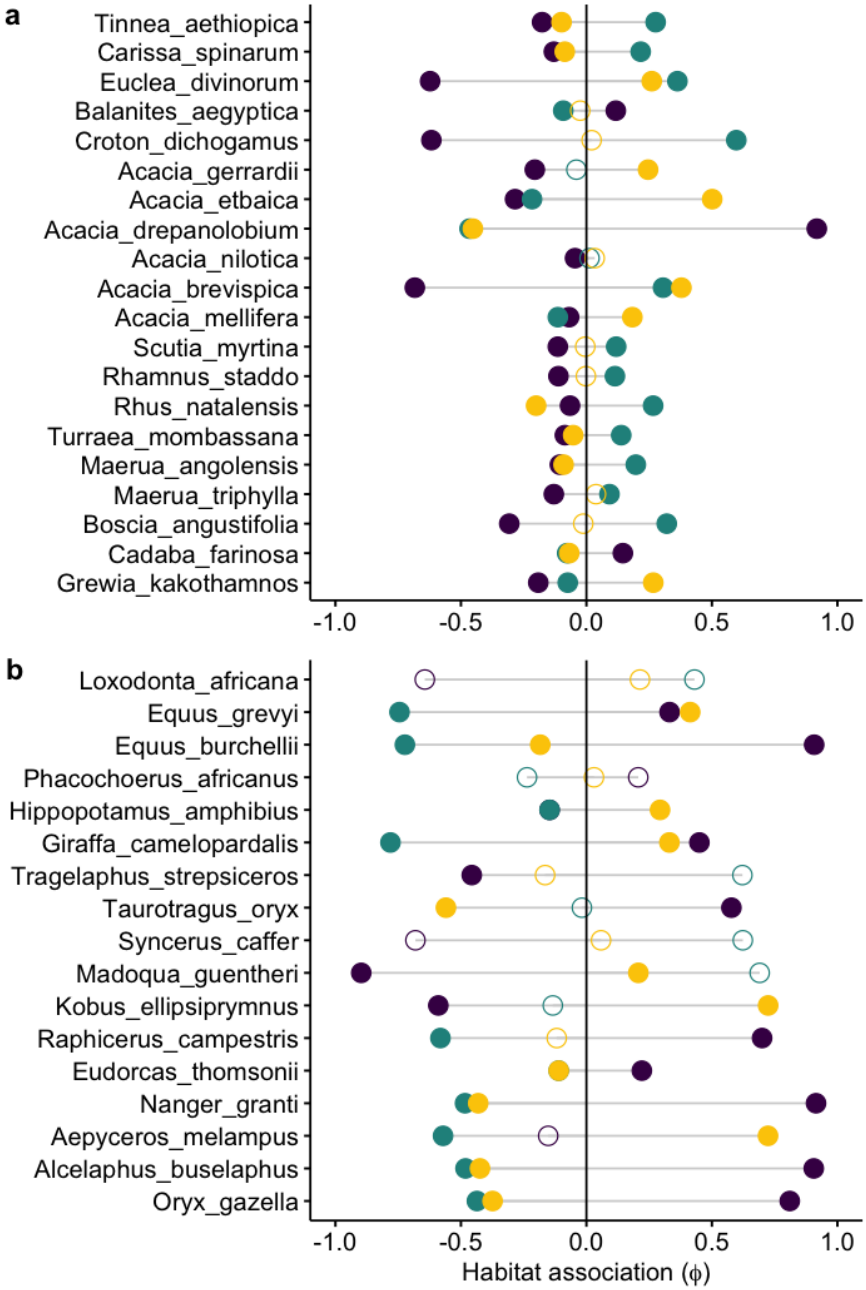

994 Figure 5. Most woody plant and herbivore taxa exhibit significant association with at least one of
995 three microhabitats. Woody plant associations are calculated based on plot-wide survey data
996 across 3,000 400-m2 quadrats. Herbivore data are derived from the 33 camera trap sites. The
997 strength of habitat preferences is represented by the abundance-weighted counterpart to
998 Pearson's phi coefficient of association (Chytrý et al., 2002), with positive values indicating a

habitat preference and negative values indicate avoidance. Statistically significant associations or avoidances (bootstrapped 95% confidence intervals do not include 0) are indicated by filled circles while insignificant relationships are indicated with open circles.

Supplementary figures:

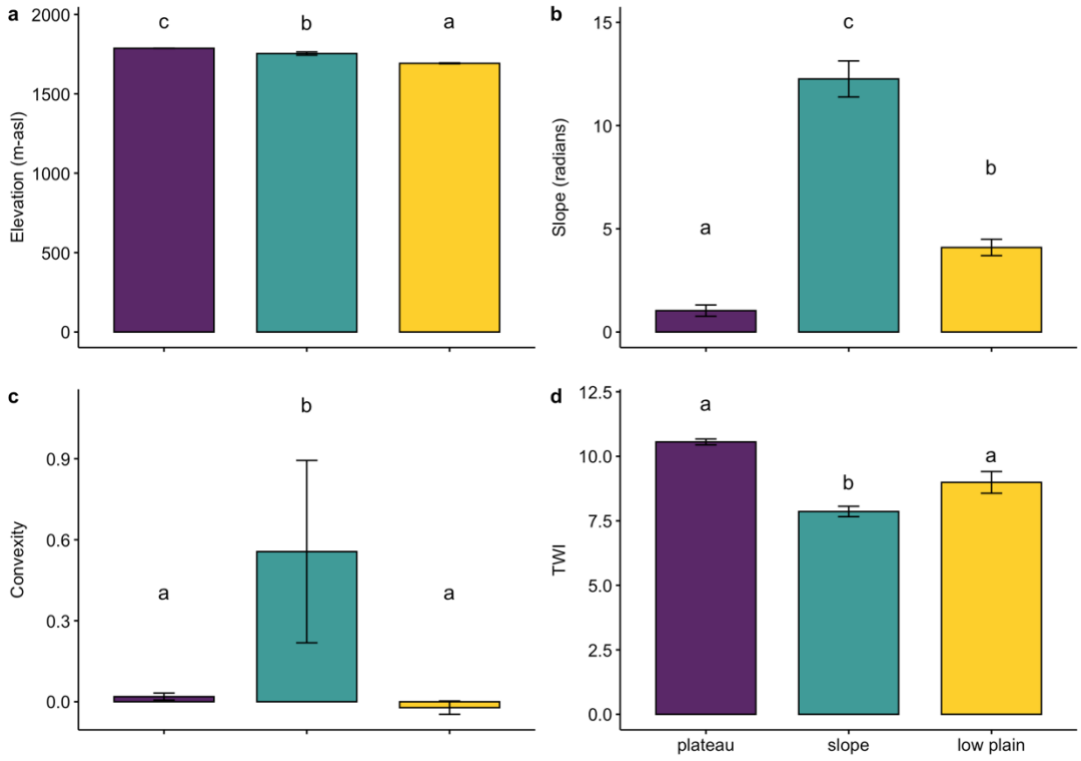

Figure S1. Mean ± SEM of site-level measurements of continuous topographic variables at N=33 camera trap sites in the three microhabitats. Pairwise differences between habitat types were assessed using Tukey HSD tests with statistical significance indicated by bars that do not share the same compact letter.

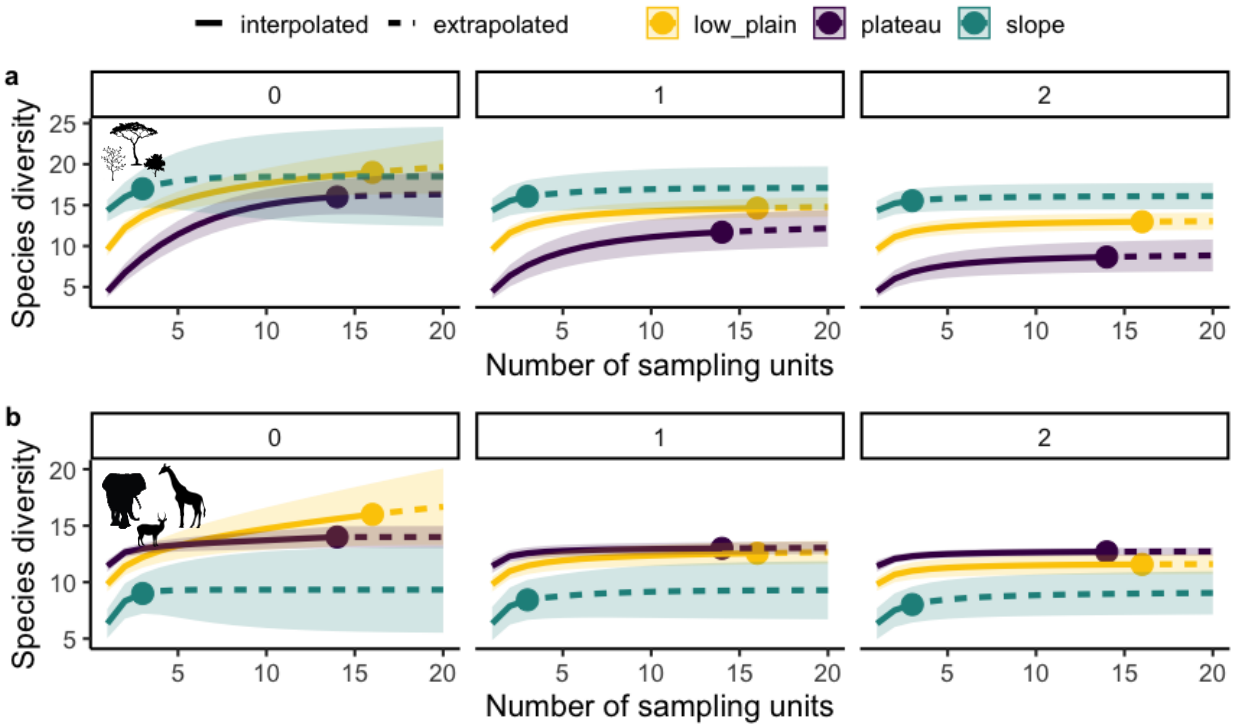

Figure S2. Sample-based interpolation (solid) and extrapolation (dashed) curves for three orders of species diversity based on Hill numbers (q=0, 1, 2) for **(a)** woody plant and **(b)** large herbivore community reference samples (filled circles) at camera trap sites located in the three topographic microhabitats under the Bernoulli product model with 95% unconditional confidence intervals. Species diversity differences across habitat types can be conservatively assessed as statistically significant when 95% confidence intervals do not overlap, but caution should be applied when extrapolating beyond three times the size of reference samples as variance estimates may be inflated (Colwell et al., 2012). Expanded sampling in comparatively undersampled habitats (e.g. the steep slope) may provide more accurate estimation of unconditional confidence intervals. Curves derived from our sampling largely recapitulate the inverse gradients in species diversity for woody plants and large herbivores, with the highest

plant and lowest herbivore diversity occurring in the steep slope habitats. When q=0, only species presences are counted when considering species diversity, yielding the equivalent of species richness. Significant cross-habitat differences in woody plant and herbivore diversity are most apparent when considering orders of diversity that incorporate incidence frequency. For q=1 (middle panels), species are weighted in proportion to their frequency, yielding an exponential of the Shannon diversity index which, in essence, represents the diversity of "typical" species. When q=2, the frequencies of abundant species are weighted more heavily and rare species are discounted, yielding a measure of Simpson diversity, which can be considered a measure of the diversity of "dominant" species (Chao, Chiu, et al., 2014; Chao, Gotelli, et al., 2014).

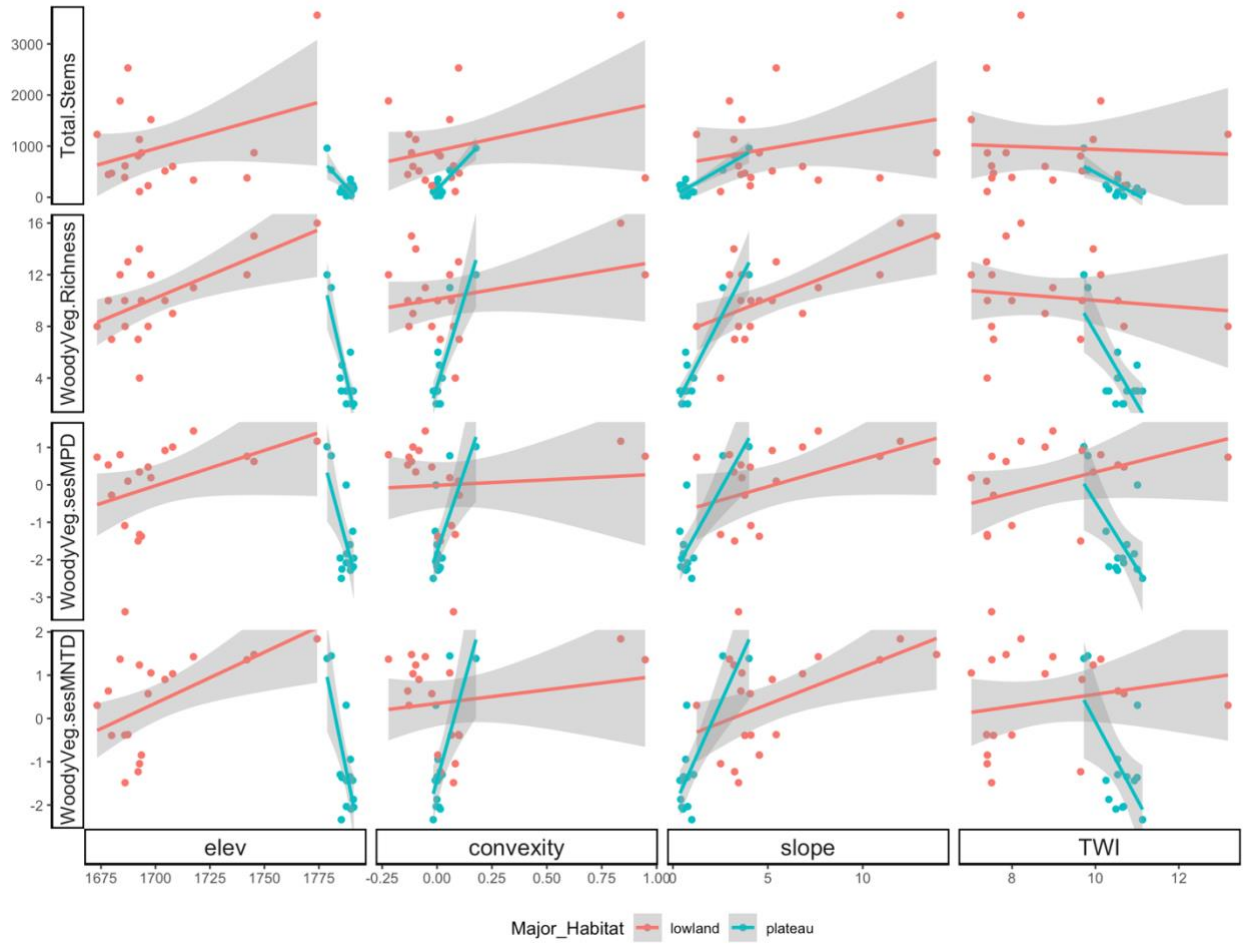

Figure S3. Bivariate relationships between site-level woody plant community characteristics and continuous abiotic variables for 33 camera trap sites. Linear trendlines (± 95% confidence intervals) are shown for both major habitat classes—the plateau (blue) and the lowlands (red) comprised of sites in both low plain and steep slope habitat types.

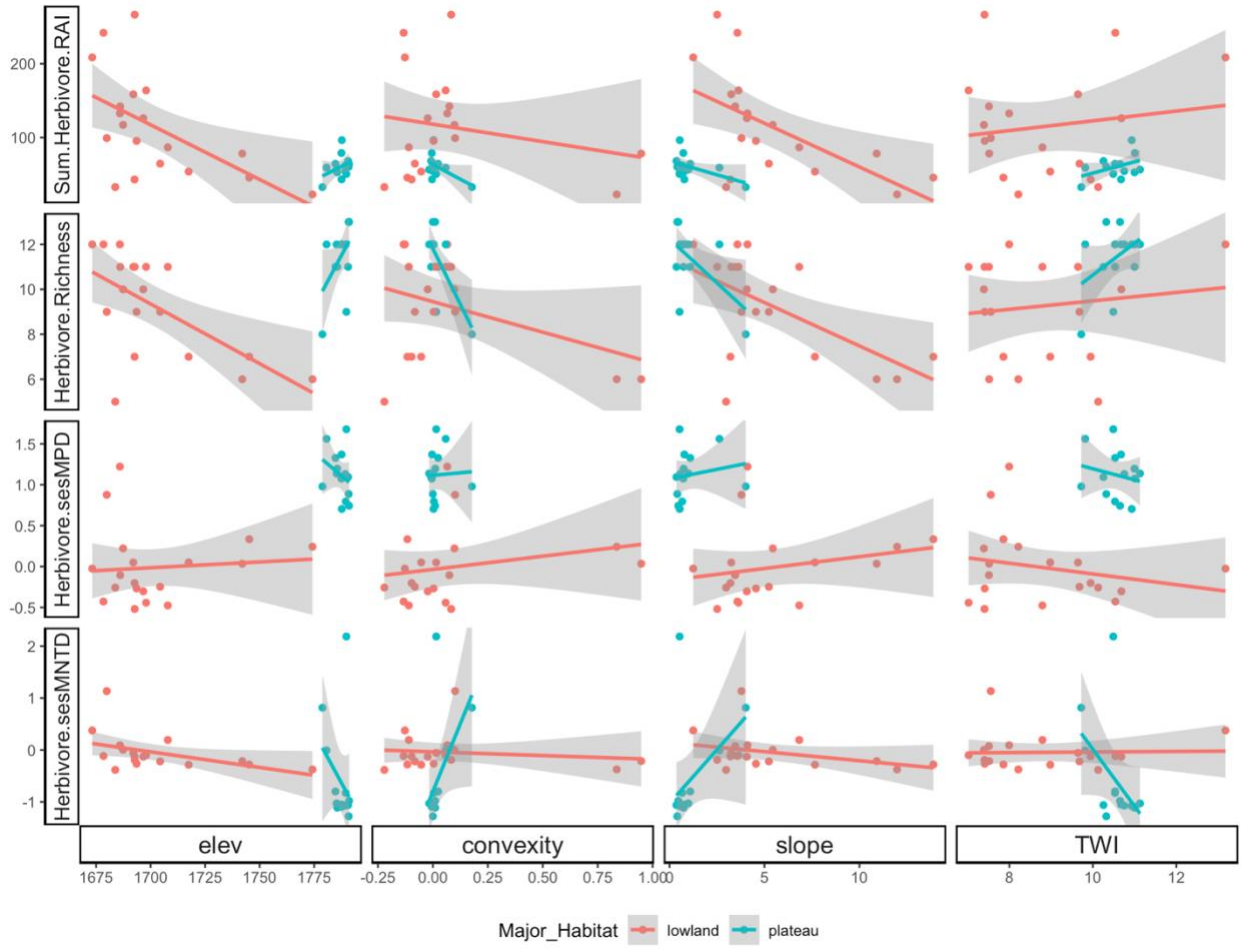

Figure S4. Bivariate relationships between site-level large herbivore community characteristics and continuous abiotic variables for 33 camera trap sites. Linear trendlines (± 95% confidence intervals) are shown for both major habitat classes—the plateau (blue) and the lowlands (red) comprised of sites in both low plain and steep slope habitat types. Herbivore abundance and species richness tended to decline in with increases in elevation, convexity, and slope in both major habitats.

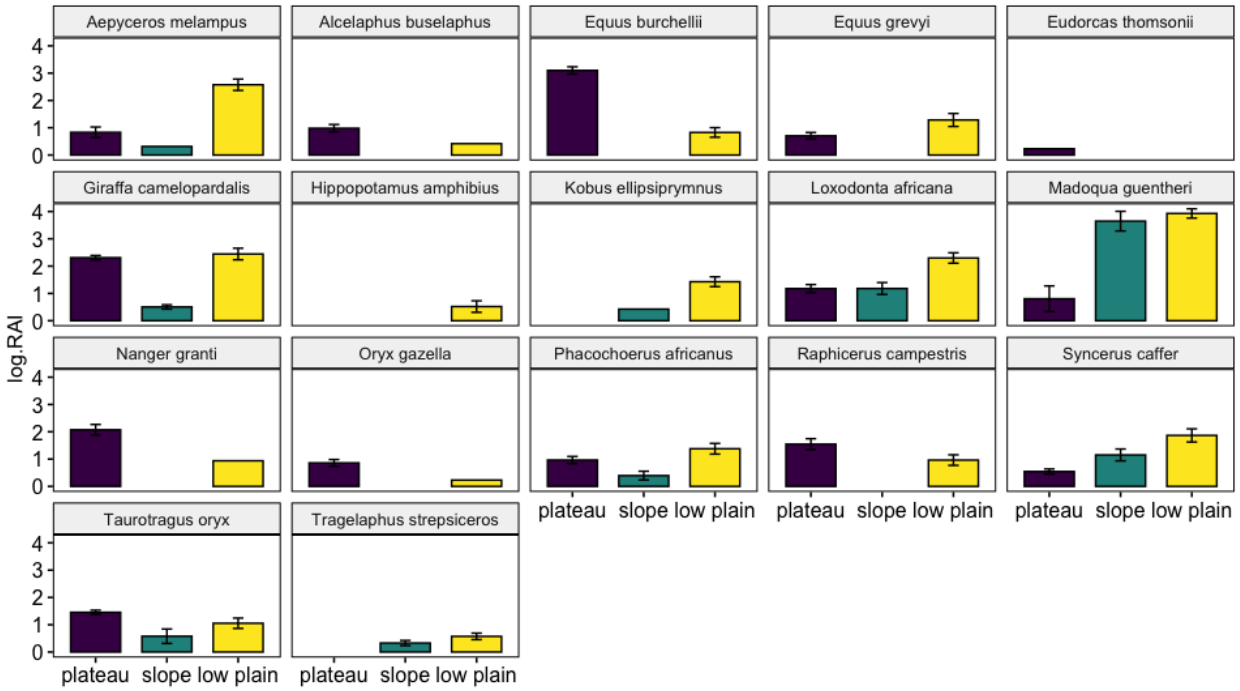

Figure S5. Herbivore species-specific relative abundance indices (detections/100 camera days) ± SEM for each microhabitat (represented on a log scale for cross-taxa comparison). Camera trap were largely dominated in the plateau habitats by plains zebra (*Equus burchelli*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Nanger granti*) and steenbok (*Raphicerus campestris*). Low plain sites were comparatively dominated by dik-dik (*Madoqua guentheri*), impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*), and elephant (*Loxodonta africana*). Camera traps in the slope sites were almost exclusively dominated by dik-dik, with RAI values several orders of magnitude greater than other co-occurring species in this habitat type (e.g. elephant and buffalo—*Syncerus caffer*).