Received: 12 October 2022 | Revised: 23 June 2023 | Accepted: 7 September 2023

DOI: 10.1002/ecy.4181

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Tropical forest mammal occupancy and functional diversity increase with microhabitat surface area

Daniel Gorczynski[1,2] | **Francesco Rovero**[3,4] | **Arafat Mtui**[4,5] | **Steven Shinyambala**[5] | **Joseph Martine**[5] | **Chia Hsieh**[1,2] | **Luke Frishkoff**[6] | **Lydia Beaudrot**[1,2]

[1]Department of Biosciences, Rice University, Houston, Texas, USA

[2]Program in Ecology and Evolutionary Biology, Rice University, Houston, Texas, USA

[3]Department of Biology, University of Florence, Florence, Italy

[4]MUSE—Museo delle Scienze, Trento, Italy

[5]Udzungwa Ecological Monitoring Centre, Mang'ula, Tanzania

[6]Department of Biology, University of Texas at Arlington, Arlington, Texas, USA

Correspondence
Daniel Gorczynski
Email: dg52@rice.edu

Funding information
Aage V. Jensen Foundation; American Philosophical Society; Conservation International; Diane McSherry and Patrick Poe; Fondazione Foresta Futura; MUSE- Museo delle Scienze; National Science Foundation, Grant/Award Number: NSF 2213568; Northrop Grumman; Sigma Xi

Handling Editor: F. Stephen Dobson

Abstract

Many animal–environment interactions are mediated by the physical forms of the environment, especially in tropical forests, where habitats are structurally complex and highly diverse. Higher structural complexity, measured as habitat surface area, may provide increased resource availability for animals, leading to higher animal diversity. Greater habitat surface area supports increased animal diversity in other systems, such as coral reefs and forest canopies, but it is uncertain how this relationship translates to communities of highly mobile, terrestrial mammal species inhabiting forest floors. We tested the relative importance of forest floor habitat structure, encompassing vegetation and topographic structure, in determining species occupancy and functional diversity of medium to large mammals using data from a tropical forest in the Udzungwa Mountains of Tanzania. We related species occupancies and diversity obtained from a multispecies occupancy model with ground-level habitat structure measurements obtained from a novel head-mounted active remote sensing device, the Microsoft HoloLens. We found that habitat surface area was a significant predictor of mean species occupancy and had a significant positive relationship with functional dispersion. The positive relationships indicate that surface area of tropical forest floors may play an important role in promoting mammal occupancy and functional diversity at the microhabitat scale. In particular, habitat surface area had higher mean effects on occupancy for carnivorous and social species. These results support a habitat surface area–diversity relationship on tropical forest floors for mammals.

KEYWORDS
camera traps, functional diversity, functional traits, Microsoft HoloLens, occupancy modeling, surface area

---

INTRODUCTION

Habitat is a critical concept in ecology, defined as the resources and conditions present in an area that produce occupancy by a species (Hall et al., 1997). Because of species-specific habitat requirements, the way that habitat structure (i.e., the physical organization of habitat, including vegetation and topography) relates to habitat availability may determine broader patterns of animal diversity within forests (Adila et al., 2017). That is, habitat structure may be associated with the diversity of resources (e.g., food, nesting) available to animals and may, thus, affect multiple aspects of animal diversity (MacArthur, 1964; Recher, 1969). For example, as the complexity of canopy, shrub, grass, and debris cover increases, the abundance of small ground-dwelling mammals also increases (Cork & Catling, 1996). Reduced standing tree density from tree thinning, greater fallen log density, and greater ground vegetation cover can also increase the abundance of animal species (Son et al., 2017).

In tropical forests, vegetation is highly productive, leading to complex habitat structure via increased growth form diversity and stratification (Spicer et al., 2020). Animals may choose to use different types of forest floor habitats based on their functional traits, such as body size, diet, and habitat use (Ikin et al., 2012). For example, browsing species occur in habitats with more woody and leafy material (Ehlers Smith et al., 2017). Thus, animal species occupancies vary with habitat type based on their ecological needs (Riordan et al., 2020). Some aspects of habitat structure, such as the abundance of vegetative structural attributes, are even associated with increased diversity of functional traits within mammal communities (Sukma et al., 2019).

The relationship between habitat structure and mammal functional trait diversity (i.e., the value, range, and relative abundance of traits in a given community; Díaz et al., 2007) is particularly important because of the ecosystem services that mammals provide, such as seed dispersal, maintenance of carbon stocks, nutrient cycling, and control of seedling recruitment (Lacher et al., 2019). Mammals encompass a broad range of body sizes, dietary niches, and home range sizes, allowing them to have significant and diverse roles in ecosystem dynamics. Mammals are particularly diverse in the tropics, further indicating their ecological importance. Finally, many mammals are endangered, putting the ecosystem services that they provide at risk as well (Flynn et al., 2009). Identifying the aspects of habitat structure relevant to mammal diversity is important given the ongoing biodiversity crisis, particularly for functional diversity as it relates to the quantity and quality of ecosystem services at local scales (Abelleira Martínez et al., 2016).

Despite the fundamental importance of habitat structure in determining animal diversity (MacArthur, 1964; Ralph, 1985; but see Recher, 1969) current assessment of forest floor structure is challenging, time consuming, and expensive (Buckley et al., 1999). Habitat surface area is a metric of structure that is associated with animal diversity in multiple systems, including coral reefs (Graham & Nash, 2013) and tropical forest canopies (Davies & Asner, 2014). On coral reefs, structural complexity generated by corals accommodates a wider variety of niches and facilitates heterogeneous microhabitat conditions for species (Graham & Nash, 2013). In tropical forest canopies, surface area and complexity measured from aerial LiDAR have been linked to greater species diversity due to increased microclimates and microhabitats (Schneider et al., 2020; Vogeler et al., 2014). In the present study, we measured forest floor habitat surface area using the active remote sensing capabilities of a mixed-reality device, the Microsoft HoloLens 2, which has been proposed as a new approach for measuring habitat structure (Gorczynski & Beaudrot, 2022). The remote sensing capabilities of the HoloLens 2 can effectively capture attributes of forest floor habitat structure and be used to quantify surface area.

We tested for associations between forest floor habitat surface area and mammal species occupancy (probability of site occupation by a species given the possibility of nondetection; MacKenzie et al., 2002), functional dispersion (mean distance in trait space of individual species to centroid all species; Laliberte & Legendre, 2010), and functional richness (volume of functional space occupied by a community; Villéger et al., 2008) at the microhabitat level while accounting for imperfect detection and elevation. We used camera trap data to estimate wildlife occupancy and functional diversity within the Udzungwa Mountains National Park, Tanzania, and measured habitat surface area using the Microsoft HoloLens 2. Previous work in the park demonstrated associations between mammal occupancy as detected by camera traps and habitat characteristics such as tree diversity and herbaceous cover (Bowkett et al., 2007; Martin et al., 2015), making this an excellent system in which to test for associations between mammals and habitat structure.

METHODS

Study site

The Udzungwa Mountains National Park is the southern-most and largest mountain block of the Eastern Arc Mountains, a chain of disjunct mountains extending from southern Kenya to southern Tanzania (Lovett et al., 2006).

This region holds outstanding levels of endemism and is part of the Eastern Afromontane biodiversity hotspot (Myers et al., 2000; Rovero, Menegon, et al., 2014). The study area, Mwanihana Forest, is located on the northeastern escarpment of the Udzungwa Mountains and is composed of tropical forest covering an elevation gradient from 290 to 2300 m above sea level (asl). Forest floors contain a variety of trees, saplings, seedlings, shrubs, lianas, and fallen vegetation including logs and leaf litter. The topography of the park is often very steep and complex. Outside of the park, lower elevations are dominated by agricultural and developed landscapes, with high human population densities (Defries et al., 2010).

Camera trapping

As part of an annual monitoring program in the Udzungwa Mountains National Park, a component of the Tropical Ecology Assessment and Monitoring (TEAM) initiative (Rovero & Ahumada, 2017), 31 Reconyx RM45 or Hyperfire camera traps were deployed in a grid with 1.4 km between cameras. All monitoring sites were within closed forested habitat within Mwanihana Forest, and camera trap surveys were conducted during the dry season from July to November 2021. Camera traps were affixed to trees at a height of ~1 m off the ground and directed toward game trails or clearings. Cameras were left active at each site for ~30 days, and each site was monitored during one of three separate deployment periods. Photographs from the camera traps were processed with ad hoc software Wild.ID (Fegraus & MacCarthy, 2016), and species were identified by Francesco Rovero, Arafat Mtui, and Steven Shinyambala. Detection ranges of camera traps can vary based on altitude, temperature, and humidity, which potentially introduces detection variability between cameras.

Habitat structure scanning

We used the VegSense application (Gorczynski & Beaudrot, 2022) on the HoloLens 2 to measure habitat structure at all 31 camera trap locations (Appendix S1: Figure S1) during November 2021. VegSense allows the user to control the HoloLens's built-in environmental scanners, which use reflected light rays to detect and digitally construct three-dimensional (3D) environments. As a result, environmental detection may be dependent on a variety of conditions, including incoming solar radiation, although we did not test for these effects. At each sampling site, we activated the scanners to map the area immediately surrounding the camera trap. The scanned area varied from site to site based on the topography but generally included the tree to which the camera was fixed and a 120° wedge in front of the camera roughly 5 m in radius. Although the area scanned at each site varied, the amount of area scanned was calculated and used to standardize measurements as a ratio (as described in the *Habitat structure processing* section). The scanning process involved walking the area and pivoting the head from the horizontal position downward to capture structures at all heights below eye level. This technique should control for height between plots, although further field testing is required. The application projects a holographic mesh on detected objects, allowing the extent of the scan to be monitored while it was occurring. Once the environment surrounding a camera trap was adequately mapped, the scanners were deactivated, and the mesh was saved as an .obj file to the HoloLens 2 for later spatial processing.

Habitat structure processing

Wavefront (.obj) files obtained from the HoloLens were imported and processed in Blender (Community, 2018; Appendix S1: Figure S2). To calculate habitat surface area, the scanned objects were oriented so that the ground was horizontal to the x–z plane. The surface area (i.e., the raw surface area of the scan) of the object was calculated using Blender's 3D print statistics. The object was then collapsed along the y-axis into only two dimensions. The surface area of the collapsed object (i.e., the scan footprint or floor space) was then calculated and served to control for area scanned in the habitat metric. The final measurement of surface area was calculated as the surface area of the scanned object divided by the two-dimensional area scanned (i.e., the surface area of the environment controlled by the amount of area scanned). We refer to this habitat surface area per unit area scanned as the habitat surface area ratio for the rest of the manuscript, and it is our main measurement of habitat structure. This process was repeated for each of the 31 sampling areas scanned. In addition, elevation values for each camera trap were obtained from previously published data (Jarvis et al., 2008). Because elevation is known to have effects on mammal occupancies (Cavada et al., 2019; O'Brien et al., 2020; Rovero, Martin, et al., 2014), we included this as a covariate in the occupancy model. In the study forest, elevation is correlated with other environmental variables including distance to park boundary and temperature (based on data from Beaudrot et al., 2016; Appendix S1: Figure S3) and corresponds to forest type (two broad types: montane and lowland deciduous). The habitat surface area ratio and elevation were not significantly correlated (Appendix S1: Figure S3).

Occupancy modeling

To test the effects of habitat structure on community-level occupancy and individual species occurrence, we ran a single-season multispecies occupancy model using data from the camera trap surveys (Kéry & Andrew Royle, 2020). Accounting for imperfect detection allowed us to calculate the probability of a species being present at a location even if it was not observed. Naïve occupancy values are available on figshare. Camera trap data were divided into 15 sampling periods, with each period lasting approximately 6 days. Species were either detected or not detected at each camera trap site for each of the sampling periods during which the camera was active. The occupancy model included species-level estimates for both detection and occupancy incorporated as random effects pulled from a common distribution describing all species. These random terms included both occupancy and detection intercepts, as well as two parameters describing the effects of occupancy covariates, including habitat surface area ratio and elevation (random slope terms). For each of these random slopes, the beta coefficient for species *i* was described by

$$\beta_i \sim \text{Normal}(\mu\beta, \text{sd}\beta),$$

where μβ and sdβ are the model estimated mean and standard deviation across all species. Vague priors were set for μβ and sdβ, specifically, $\mu\beta \sim \text{Normal}(0, 31.6)$ and $\text{sd}\beta \sim \text{Uniform}(0, 10)$. Because random intercept terms are bounded by 0 and 1 on the arithmetic scale, using a vague prior to draw these terms from a normal distribution on the logit scale results in high prior probability densities clumped around 0 and 1. To ensure a flat prior distribution for the intercept terms, we drew priors for the μβs associated with occupancy and detection intercepts from a Uniform(0,1) distribution and then transformed it to the logit scale prior to drawing species intercepts. That is:

$$\mu\beta 0 \sim \text{logit}(\text{Uniform}(0,1)).$$

Given that all camera traps had a clear view of game trails on which species were expected to occur, we did not include any covariates for the detection component of the model. Environmental covariates for the occupancy component of the model were standardized to compare effect sizes more easily, and none of the continuous variables showed directional skew in distribution as determined by visual inspection. To facilitate model convergence, we only included mammal species detected more than three times. The model was run using Bayesian formulation in R version 4.1.2 (R Core Team, 2021) using the R2Jags package (Su & Yajima, 2015). We ran four chains for 10,000 iterations of the model with a 1000-iteration burn-in and retained every 30th sample.

Model results provided estimates of individual species occupancies, as well as the effect size for both environmental variables on mean species occupancy and individual species occupancies. We visually assessed trace plots and Brooks-Gelman-Rubin (Rhat) convergence diagnostic (<1.05) to ensure model convergence. We then derived distributions of camera-trap level functional dispersion and functional richness from the occupancy model to get the mean and SD of these metric estimates. Distributions of estimated functional dispersion and functional richness values were derived from binomial species-specific occupancy values from the posterior distribution of each of the 1200 retained model iterations for each camera trap location. We calculated the mean and SD of functional dispersion and functional richness estimates for each camera trap location from the distribution of derived values. Functional dispersion and functional richness were calculated with the FD package in R (Laliberté et al., 2015) using six relevant functional traits (body mass; diet composition—five categories: graze, browse, fruits/seeds, vertebrates, invertebrates; sociality—form groups with more than two mature individuals; substrate use—terrestrial or scansorial; activity period—three categories: diurnal, crepuscular, nocturnal; and average litter size; Gorczynski et al., 2021; Gorczynski & Beaudrot, 2021, Appendix S1: Table S1). Generally, these traits capture quantitative and qualitative environmental requirements of species. For example, body mass, sociality, and average litter size can indicate the amount of resource use by a species on a small scale, while diet, substrate use, and activity period can indicate the type of resources used.

To assess the effects of the environmental covariates on the functional diversity metrics, we modeled the derived mean values of functional dispersion and functional richness weighted by the variance (inverse of the standard deviation squared) of the respective diversity metric for each camera trap as the response variable using the "lm" function from the stats package in R (R Core Team, 2021). We used Gaussian distributions to model functional dispersion and functional richness, visually inspected for normal distribution of residuals of the resulting models, and checked for outliers with high leverage using Cook's distance (cutoff >1). For each functional diversity metric, we ran two separate regression models, each of which contained either habitat surface area ratio or elevation as a predictor. We also ran unweighted versions of these models for comparison (Appendix S1: Figure S5). We visually examined model fit and residuals to ensure model assumptions were met.

Finally, we ran backward linear model selection to assess the relationship between mean environmental effects on individual species occupancy and species functional traits to determine whether species with particular traits had higher average estimated effect sizes for environmental conditions. All traits that were not strongly correlated with one another ($r < 0.6$) were included as potential predictor variables (diurnal and nocturnal activity periods were negatively correlated, so the nocturnal trait was removed) and mean species environmental effects were the response variable (weighted by the inverse of the SD squared). We ran backward model selection using the MASS package (Ripley et al., 2022) in R for all environmental variables that had a significant effect on mean community occupancy.

RESULTS

Nineteen species were detected more than three times and were included in this analysis. Species ranged in average body mass from 0.453 kg (*Rhynchocyon cirnei*—checkered sengi or checkered elephant shrew) to 76.6 kg (*Potamochoerus larvatus*—bushpig). At camera trap sites, the habitat surface area ratio ranged from 1.12 to 1.46. Elevation ranged from 408 to 1710 masl. Mean functional dispersion ranged from 0.259 to 0.309, and functional richness ranged from 0.133 to 0.306.

The results of the multispecies occupancy model revealed a significant positive association (95% credible interval did not include 0) between habitat surface area ratio and occupancy at the community level (Figure 1). Elevation showed a weak nonsignificant positive association with occupancy.

Generalized linear regression revealed a significant positive relationship between habitat surface area ratio and functional dispersion (Figure 2a). We found that no data point in the model had substantial leverage (Cook's distance <1 for all points). Functional richness showed a positive relationship with habitat surface area ratio that approached significance (Figure 2c). Both diversity metrics showed nonsignificant relationships with elevation (Figure 2b,d). Unweighted regression outputs were qualitatively the same as reported results, except that the positive relationship between habitat surface area ratio and functional richness was significant (Appendix S1: Figure S5).

Occupancy for all individual species had a positive relationship with habitat surface area ratio (Figure 3), although the mean effect size varied among species. *Genetta servalina* (servaline genet; mean = 0.78,

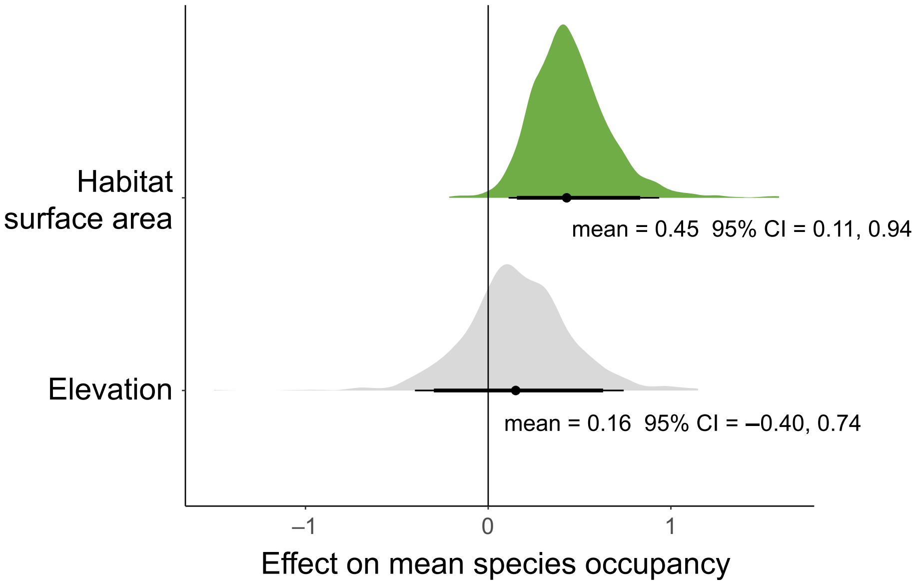

FIGURE 1 Coefficient plot showing relative effect sizes of standardized environmental covariates on mean species occupancy from multispecies occupancy model used. Points represent mean effect size, thin bars represent 95% credible intervals, and thick bars represent 90% credible intervals. Distribution colors indicate credible interval inclusion of zero (green 95% CI does not include zero; gray 90% CI includes zero). Surface area shows a significant positive relationship (as defined by a nonzero 95% credible interval) with mean species occupancy.

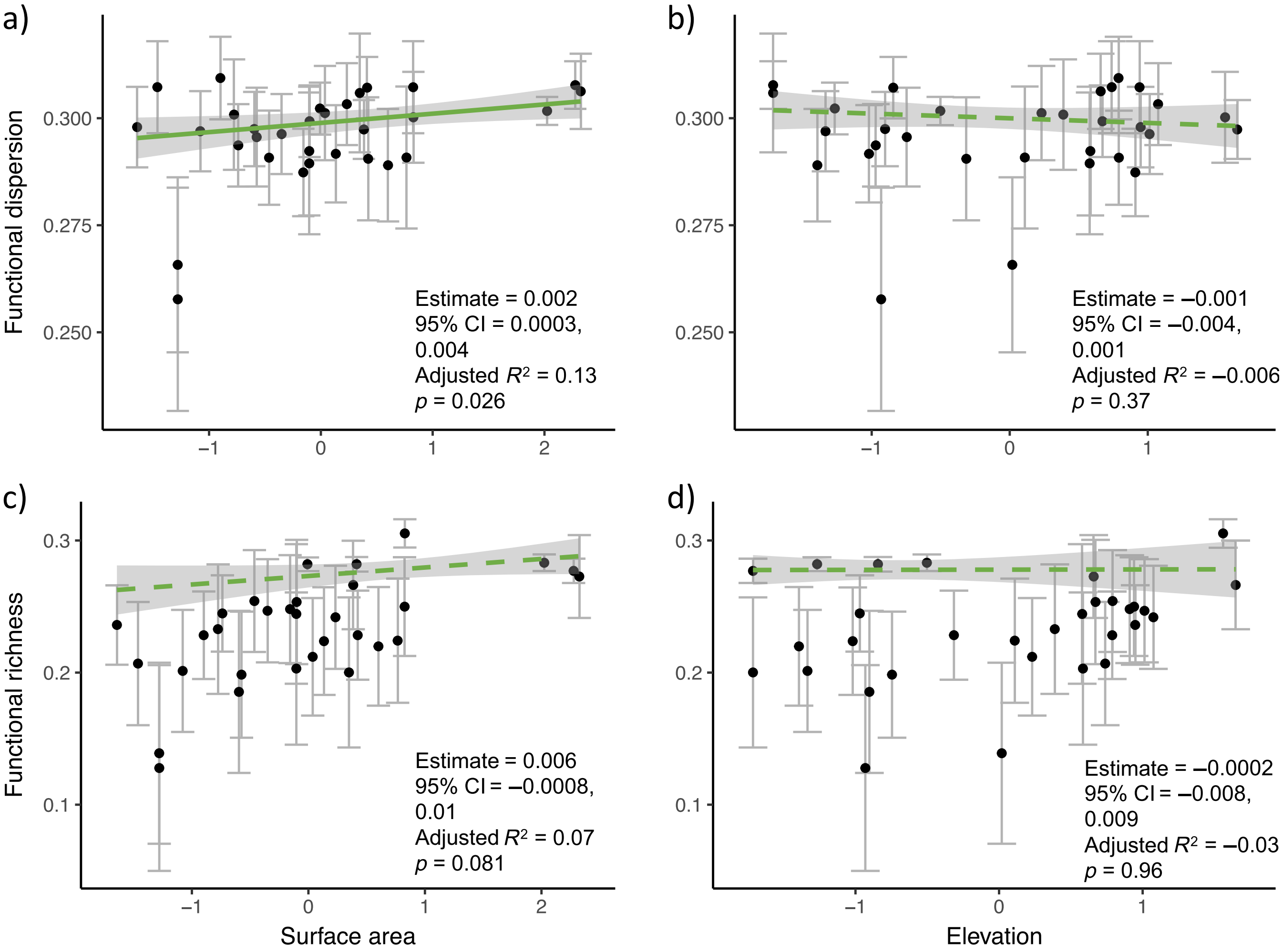

FIGURE 2 Linear relationships between standardized environmental metrics (habitat surface area and elevation) and functional diversity metrics (functional dispersion and functional richness). Green lines indicate weighted regressions, while gray shaded areas indicate 95% CIs of the regressions. Values reported for each regression include the parameter estimate and the 95% CI. Fitted regressions were weighted by the inverse SD squared of the diversity estimates, and the point error bars represent one SD. Habitat surface area (solid line) showed a significant positive relationship with functional dispersion. Dashed lines indicate nonsignificant relationships.

95% CI = 0.11, 1.84) showed the most positive mean association with habitat surface area ratio and a 95% credible interval that did not include zero.

Because habitat surface area ratio was the only variable to have a significant association with mean community occupancy, we ran a backward model selection to test the relationship between species functional traits and individual species surface area associations (Appendix S1: Table S2). The output model from the selection process included significant positive effects of vertebrate diet and sociality on species response to surface area ratio (Figure 4). This means that species that consumed vertebrates and species that were social responded more strongly to habitat surface area than species that did not have these traits. This model also had a positive association with scansoriality that approached significance.

DISCUSSION

We tested the extent to which tropical forest floor habitat surface area predicted the occupancy and functional diversity of ground-dwelling mammals. Mean species occupancy and functional dispersion increased significantly with surface area. This result supports the habitat surface area–diversity hypothesis in tropical forest floors, even for large, highly mobile species in localized microhabitats.

Habitat surface area is an important correlate of animal diversity in many systems due to its provision of increased microhabitat, microclimate, and resource diversity (Davies & Asner, 2014; Johnson et al., 2003; MacArthur, 1964; Ralph, 1985; Recher, 1969; Torres-Pulliza et al., 2020). Our results suggest that greater forest floor habitat surface area may also provide

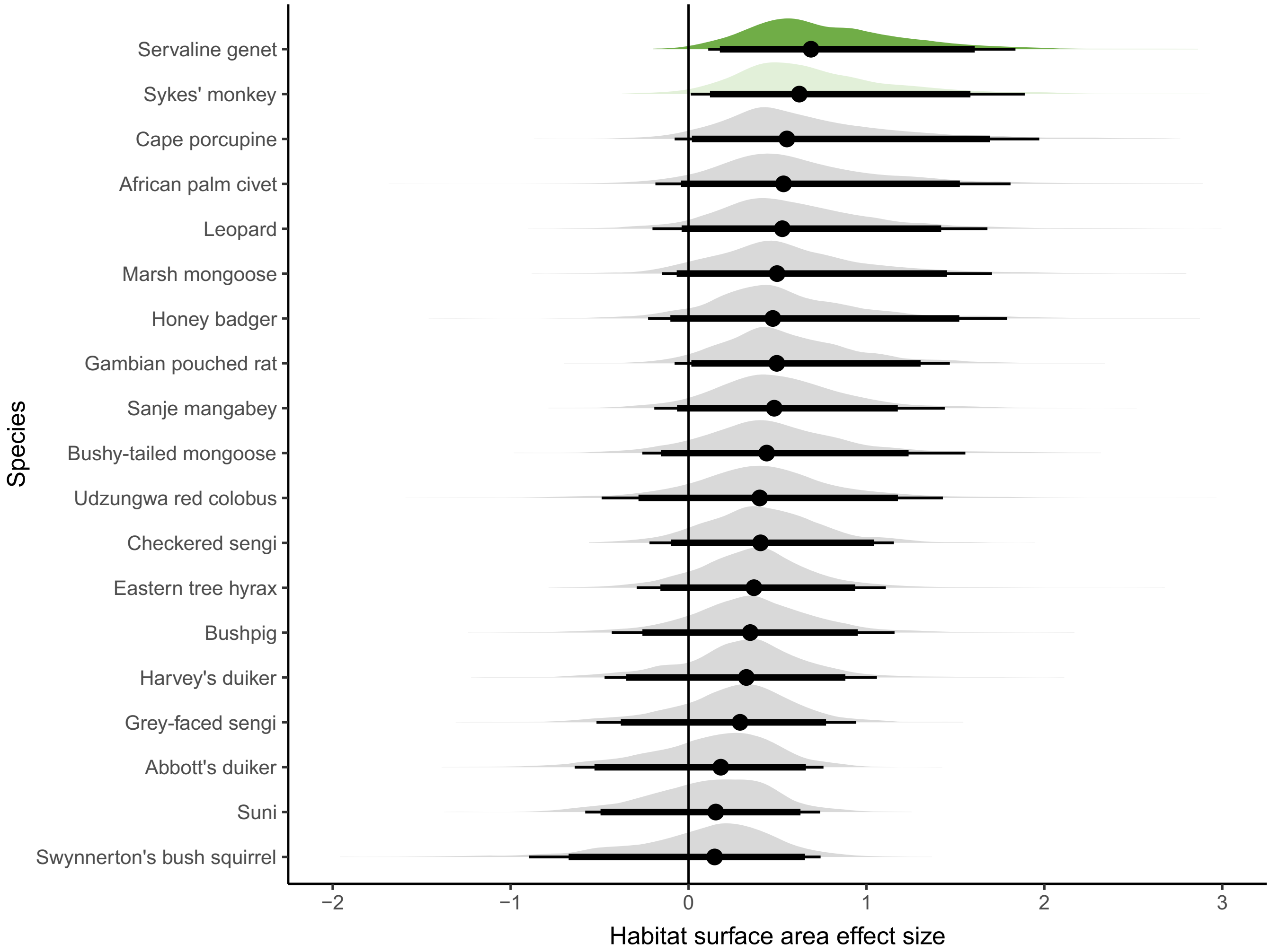

FIGURE 3 Individual species occupancy associations with habitat surface area. Points represent mean effect size, thin bars represent 95% credible intervals, and thick bars represent 90% credible intervals. Distribution colors indicate credible interval inclusion of zero (dark green—95% CI does not include zero; light green—90% CI does not include zero; gray—90% CI includes zero). Species occupancies showed positive mean relationships with habitat surface area, but to varying degrees. In particular, the 95% credible interval of this effect for *Genetta servalina* does not include zero, indicating that this species had the most positive association with microhabitats with more surface area. See supporting data on figshare for species scientific names.

higher resource or microhabitat diversity for a greater variety of mammal species. On coral reefs, greater surface area leads to greater niche and microhabitat diversity that supports a greater variety of species at higher abundances. For large ground-dwelling mammals, species ranges are larger than camera trap sampling locations, and so the mechanism for this relationship may differ. Nevertheless, habitat surface area is associated with biological diversity in multiple layers of forest structure, from the forest floor to the canopy (Davies & Asner, 2014).

The positive relationship between habitat surface area and mammal diversity was significant for mean species occupancy and functional dispersion. This indicates that greater habitat surface area was related to higher species occupancy overall and a greater proportion of functionally unique species, as indicated by the increased functional dispersion. Low habitat surface area may be suitable to a limited number of species with similar functional traits, for example, those that forage in open forest floors (Son et al., 2017), leading to lower functional dispersion. In forest floors with higher habitat surface area, functionally unique species may be more likely to find necessary resources or microhabitats for feeding, movement, and nesting, leading to higher functional dispersion.

The positive relationship between mammal functional dispersion and habitat surface area on the forest floor at a small scale is in accord with previous results identifying a relationship between protected area-level mammal functional dispersion and Normalized Difference Vegetation Index (NDVI) using satellite-based

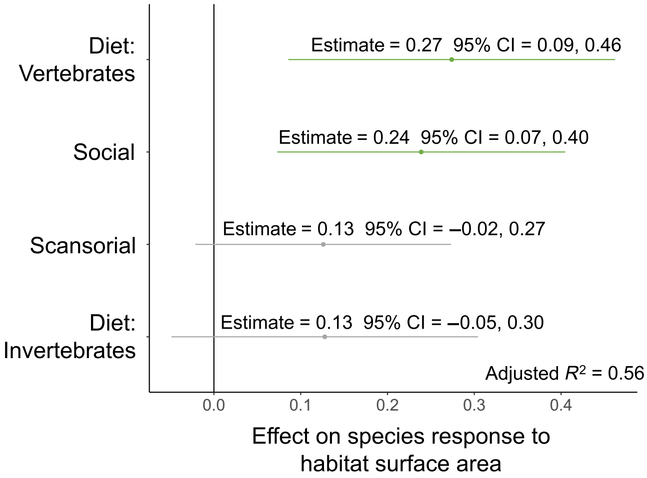

FIGURE 4 Associations between functional traits and species response to habitat surface area. Points represent mean effect size, and lines represent 95% CIs, with both values specified to the right of the plot. Line and point color represent significance based on a 95% CI (green—significant, gray—nonsignificant). This model is the output of backwards stepwise model selection to identify the most relevant traits. Diets incorporating vertebrates and some degree of social behavior both had a significant positive relationship with species association to surface area, indicating that species with these traits were significantly more likely to occupy habitats with high surface area.

remote sensing (Gorczynski et al., 2021). Habitat area indices and NDVI can provide important estimates of ecosystem productivity, but on very different scales (Asner et al., 2003) and in different parts of the forest (forest floor vs. canopy, respectively). This might indicate that relationships between productivity-associated resource availability and dispersion of mammal functional traits in tropical forests (Evans et al., 2005) exist across scales and within different aspects of forest vegetation. In measuring fine-scale species occurrence at individual camera traps, the relevant metrics for habitat quality may thus also be fine-scale and localized in the relevant habitat (in this case the forest floor). In addition, tropical forest mammal communities have high functional redundancy (Gorczynski & Beaudrot, 2021; Safi et al., 2011), a pattern that is reflected in this study through the asymptotic relationship between mean species occupancy and functional dispersion (Appendix S1: Figure S4).

Our results demonstrated that mammal species with certain traits responded more positively to habitat surface area. Species that consumed vertebrates or exhibited social behavior had a higher mean effect of surface area on occupancy than other species. Some examples of species with high mean effects of habitat surface area on occupancy that consumed vertebrates included the servaline genet (*Genetta servalina*), African palm civet (*Nandinia binotata*), and leopard (*Panthera pardus*), while social species, defined as those forming groups of more than two mature individuals, included Sykes' monkey (*Cercopithecus mitis*) and Sanje mangabey (*Cercocebus sanjei*). Species associated with high habitat surface area may favor complex habitats when hunting prey or may require large amounts of localized resources to feed groups. High-surface-area habitats may contain more cover for predators while hunting and provide more food for foraging groups of social species. Increased occupancy of these species in high surface area microhabitats may also increase functional dispersion.

The Udzungwa Mountains National Park is a biologically unique region encompassing a variety of habitat types, including deciduous tropical forest in the lower elevation parts of the park. The fact that this study was conducted in the dry season, when some vegetation was dry and falling on the ground, may have affected the habitat structure of the forest floor in some locations, with larger amounts of leaf litter and lower quantities of green vegetation. In addition, it is possible that mammals alter their behavioral patterns based on the season, although previous work in this area showed minimal effects of seasonality on mammal occupancy (Martin et al., 2017). The interaction between forest floor habitat structure and mammal diversity may be dynamic, and this study is only the first step in teasing apart this relationship. Conservationists should be sure to consider forest floor and understory habitat integrity when planning management, as these aspects of the environment may be relevant to the biodiversity of animal taxa in a system. Ensuring that forest floor habitat complexity is not lost due to disturbances, such as those found at forest edges, may be critical.

AUTHOR CONTRIBUTIONS

Daniel Gorczynski conceived the idea for the manuscript. Daniel Gorczynski, Arafat Mtui, Steven Shinyambala, Joseph Martine, Chia Hsieh, and Luke Frishkoff collected and analyzed the data. Francesco Rovero coordinated the camera trapping data collection, annotation, and screening. Lydia Beaudrot, Francesco Rovero, and Luke Frishkoff advised data collection and analysis. Daniel Gorczynski wrote the manuscript with feedback and editing from Lydia Beaudrot and others. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

This work was supported financially by Northrop Grumman, Conservation International, the American Philosophical Society, Sigma Xi, Diane McSherry, Patrick Poe, and others. Field data collection was approved and permitted by the Tanzania Commission for Science and Technology (COSTECH- Permit No. 2021-576-NA-2021-098), the Tanzania Wildlife Research Institute (TAWIRI- Ref. No. TWRI/RS/22″ E″/52), and the Tanzania National Park Authority (TANAPA- Ref. No. BE.161/376/01). Camera trapping was funded through a grant from the Aage V. Jensen Foundations, Fondazione Foresta Futura, MUSE—Museo delle Scienze and other donors. Ruben Mwakisoma and Emilian Omari provided invaluable help during data collection and annotation. We thank Dr. Emanual Martin, the leadership and staff of Udzungwa Mountains National Park, the Udzungwa Ecological Monitoring Centre, and the Tanzania Conservation Resource Center (TZCRC) for providing extensive logistical support for this project. We also give special thanks to Dr. Amy Dunham, Dr. Volker Rudolf, Dr. Daniel Kowal, Dr. Tom E. X. Miller, Dr. Carsten Grupstra, and Dr. Joshua Fowler for feedback and support on the project. Finally, we thank editors Dr. Kathryn Cottingham and Dr. Stephen Dobson, as well as Dr. Christian John and an anonymous reviewer for their peer review of the manuscript. This work was supported by NSF 2213568 to Lydia Beaudrot.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All code and data (Gorczynski, 2023) are available from figshare at https://doi.org/10.6084/m9.figshare.21136258.v2.

ORCID

Daniel Gorczynski https://orcid.org/0000-0003-0395-0434
Francesco Rovero https://orcid.org/0000-0001-6688-1494
Chia Hsieh https://orcid.org/0000-0002-3715-4113
Luke Frishkoff https://orcid.org/0000-0001-5738-2140
Lydia Beaudrot https://orcid.org/0000-0001-8135-7519

REFERENCES

Abelleira Martínez, O. J., A. K. Fremier, S. Günter, Z. R. Bendaña, L. Vierling, S. M. Galbraith, N. A. Bosque-Pérez, and J. C. Ordoñez. 2016. "Scaling up Functional Traits for Ecosystem Services with Remote Sensing: Concepts and Methods." *Ecology and Evolution* 6(13): 4359–71. https://doi.org/10.1002/ECE3.2201.

Adila, N., S. Sasidhran, N. Kamarudin, C. L. Puan, B. Azhar, and D. B. Lindenmayer. 2017. "Effects of Peat Swamp Logging and Agricultural Expansion on Species Richness of Native Mammals in Peninsular Malaysia." *Basic and Applied Ecology* 22(August): 1–10. https://doi.org/10.1016/J.BAAE.2017.04.002.

Asner, G. P., J. M. O. Scurlock, and J. A. Hicke. 2003. "Global Synthesis of Leaf Area Index Observations: Implications for Ecological and Remote Sensing Studies." *Global Ecology and Biogeography* 12(3): 191–205. https://doi.org/10.1046/j.1466-822X.2003.00026.x.

Beaudrot, L., J. A. Ahumada, T. O'Brien, P. Alvarez-Loayza, K. Boekee, A. Campos-Arceiz, D. Eichberg, et al. 2016. "Standardized Assessment of Biodiversity Trends in Tropical Forest Protected Areas: The End Is Not in Sight." *PLoS Biology* 14(1): 1002357. https://doi.org/10.1371/journal.pbio.1002357.

Bowkett, A., F. Rovero, and A. R. Marshall. 2007. "Understanding Forest Landscape Restoration: Reinforcing Scientific Foundations for the UN Decade on Ecosystem Restoration View Project Tropical Ecology Assessment and Monitoring (TEAM) Program View Project." https://doi.org/10.1111/j.1365-2028.2007.00881.x.

Buckley, D. S., J. G. Isebrands, and T. L. Sharik. 1999. "Practical Field Methods of Estimating Canopy Cover, PAR, and LAI in Michigan Oak and Pine Stands." *Northern Journal of Applied Forestry* 16(1): 25–32. https://doi.org/10.1093/njaf/16.1.25.

Cavada, N., R. W. Havmøller, N. Scharff, and F. Rovero. 2019. "A Landscape-Scale Assessment of Tropical Mammals Reveals the Effects of Habitat and Anthropogenic Disturbance on Community Occupancy." *PLoS One* 14(4): e0215682. https://doi.org/10.1371/JOURNAL.PONE.0215682.

Community, B. O. 2018. *Blender—a 3D Modelling and Rendering Package*. Amsterdam: Stichting Blender Foundation.

Cork, S. J., and P. C. Catling. 1996. "Modelling Distributions of Arboreal and Ground-Dwelling Mammals in Relation to Climate, Nutrients, Plant Chemical Defences and Vegetation Structure in the Eucalypt Forests of Southeastern Australia." *Forest Ecology and Management* 85(1–3): 163–175. https://doi.org/10.1016/S0378-1127(96)03757-7.

Davies, A. B., and G. P. Asner. 2014. "Advances in Animal Ecology from 3D-LiDAR Ecosystem Mapping." *Trends in Ecology & Evolution* 29(12): 681–691. https://doi.org/10.1016/J.TREE.2014.10.005.

Defries, R., F. Rovero, P. Wright, J. Ahumada, S. Andelman, K. Brandon, J. Dempewolf, A. Hansen, J. Hewson, and J. Liu. 2010. "From Plot to Landscape Scale: Linking Tropical Biodiversity Measurements across Spatial Scales." *Frontiers in Ecology and the Environment* 8(3): 153–160. https://doi.org/10.1890/080104.

Díaz, S., S. Lavorel, F. De Bello, F. Quétier, K. Grigulis, and T. Matthew Robson. 2007. "Incorporating Plant Functional Diversity Effects in Ecosystem Service Assessments." *Proceedings of the National Academy of Sciences of the United States of America* 104(52): 20684–89. https://doi.org/10.1073/pnas.0704716104.

Ehlers Smith, Y. C., D. A. Ehlers Smith, T. Ramesh, and C. T. Downs. 2017. "The Importance of Microhabitat Structure in Maintaining Forest Mammal Diversity in a Mixed Land-Use Mosaic." *Biodiversity and Conservation* 26(10): 2361–82. https://doi.org/10.1007/s10531-017-1360-6.

Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. "Species-Energy Relationships at the Macroecological Scale: A Review of the Mechanisms." *Biological Reviews of the Cambridge Philosophical Society* 80: 1–25.

Fegraus, E., and J. MacCarthy. 2016. "Camera Trap Data Management and Interoperability." In *Camera Trapping for Wildlife Research*, edited by F. Rovero and F. Zimmermann. Exeter: Pelagic Publishing.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield, and F. DeClerck. 2009. "Loss of Functional Diversity under Land

Use Intensification across Multiple Taxa." *Ecology Letters* 12(1): 22–33. https://doi.org/10.1111/j.1461-0248.2008.01255.x.

Gorczynski, D. 2023. "Supporting Data and Code for Tropical Forest Mammal Occupancy and Functional Diversity Increase with Microhabitat Surface Area." Figshare. https://doi.org/10.6084/m9.figshare.21136258.v2.

Gorczynski, D., and L. Beaudrot. 2021. "Functional Diversity and Redundancy of Tropical Forest Mammals over Time." *Biotropica* 53(1): 51–62. https://doi.org/10.1111/btp.12844.

Gorczynski, D., and L. Beaudrot. 2022. "Measuring Understorey Vegetation Structure Using a Novel Mixed-Reality Device." *Methods in Ecology and Evolution* 13(9): 1949–54. https://doi.org/10.1111/2041-210X.13927.

Gorczynski, D., C. Hsieh, J. T. Luciano, J. Ahumada, S. Espinosa, S. Johnson, F. Rovero, et al. 2021. "Tropical Mammal Functional Diversity Increases with Productivity but Decreases with Anthropogenic Disturbance." *Proceedings of the Royal Society B: Biological Sciences* 288(1945): 20202098. https://doi.org/10.1098/rspb.2020.2098.

Graham, N. A. J., and K. L. Nash. 2013. "The Importance of Structural Complexity in Coral Reef Ecosystems." *Coral Reefs* 32(2): 315–326. https://doi.org/10.1007/S00338-012-0984-Y/METRICS.

Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. "The Habitat Concept and a Plea for Standard Terminology." *Wildlife Society Bulletin* 25(1): 173–182.

Ikin, K., E. Knight, D. B. Lindenmayer, J. Fischer, and A. D. Manning. 2012. "Linking Bird Species Traits to Vegetation Characteristics in a Future Urban Development Zone: Implications for Urban Planning." *Urban Ecosystems* 15(4): 961–977. https://doi.org/10.1007/S11252-012-0247-2.

Jarvis, A., H. I. Reuter, A. Nelson, and E. Guevara. 2008. "Hole-Filled SRTM for the Globe: Version 4: Data Grid." Web Publication/Site, CGIAR Consortium for Spatial Information. http://srtm.csi.cgiar.org/.

Johnson, M. P., N. J. Frost, M. W. J. Mosley, M. F. Roberts, and S. J. Hawkins. 2003. "The Area-Independent Effects of Habitat Complexity on Biodiversity Vary between Regions." *Ecology Letters* 6(2): 126–132. https://doi.org/10.1046/J.1461-0248.2003.00404.X.

Kéry, M., and J. Andrew Royle. 2020. *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS: Dynamic and Advanced Models*, Vol. 2. London, UK: Academic Press.

Lacher, T. E., A. D. Davidson, T. H. Fleming, E. P. Gómez-Ruiz, G. F. McCracken, N. Owen-Smith, C. A. Peres, and S. B. Vander Wall. 2019. "The Functional Roles of Mammals in Ecosystems." *Journal of Mammalogy* 100(3): 942–964. https://doi.org/10.1093/JMAMMAL/GYY183.

Laliberte, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91(1): 299–305. https://doi.org/10.1890/08-2244.1.

Laliberté, E., P. Legendre, and B. Shipley. 2015. "FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology." R Package. http://www.elaliberte.info.

Lovett, J. C., A. R. Marshall, and J. Carr. 2006. "Changes in Tropical Forest Vegetation along an Altitudinal Gradient in the Udzungwa Mountains National Park, Tanzania." *African Journal of Ecology* 44(4): 478–490. https://doi.org/10.1111/J.1365-2028.2006.00660.X.

MacArthur, R. H. 1964. "Environmental Factors Affecting Bird Species Diversity." *The American Naturalist* 98(903): 387–397. https://doi.org/10.1086/282334.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, A. A. Royle, and C. A. Langtimm. 2002. "Estimating Site Occupancy Rates when Detection Probabilities Are Less than One." *Ecology* 83(8): 2248–55. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.

Martin, E. H., N. Cavada, V. G. Ndibalema, and F. Rovero. 2015. "Modelling Fine-Scale Habitat Associations of Medium-to-Large Forest Mammals in the Udzungwa Mountains of Tanzania Using Camera Trapping." *Tropical Zoology* 28(4): 137–151. https://doi.org/10.1080/03946975.2015.1078568.

Martin, E. H., V. G. Ndibalema, and F. Rovero. 2017. "Does Variation between Dry and Wet Seasons Affect Tropical Forest Mammals' Occupancy and Detectability by Camera Traps? Case Study from the Udzungwa Mountains, Tanzania." *African Journal of Ecology* 55(1): 37–46. https://doi.org/10.1111/AJE.12312.

Myers, N., R. A. Mittermeler, C. G. Mittermeler, G. A. B. Da Fonseca, and J. Kent. 2000. "Biodiversity Hotspots for Conservation Priorities." *Nature* 403(6772): 853–58. https://doi.org/10.1038/35002501.

O'Brien, T. G., J. Ahumada, E. Akampurila, L. Beaudrot, K. Boekee, T. Brncic, J. Hickey, et al. 2020. "Camera Trapping Reveals Trends in Forest Duiker Populations in African National Parks." *Remote Sensing in Ecology and Conservation* 6(2): 168–180. https://doi.org/10.1002/rse2.132.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ralph, C. J. 1985. "Habitat Association Patterns of Forest and Steppe Birds of Northern Patagonia, Argentina." *The Condor* 87(4): 471–483. https://doi.org/10.2307/1367943.

Recher, H. F. 1969. "Bird Species Diversity and Habitat Diversity in Australia and North America." *The American Naturalist* 103(929): 75–80. https://doi.org/10.1086/282583.

Riordan, C. E., C. Pearce, B. J. F. McDonald, I. Gynther, and A. M. Baker. 2020. "Vegetation Structure and Ground Cover Attributes Describe the Occurrence of a Newly Discovered Carnivorous Marsupial on the Tweed Shield Volcano Caldera, the Endangered Black-Tailed Dusky Antechinus (*Antechinus arktos*)." *Ecology and Evolution* 10(4): 2104–21. https://doi.org/10.1002/ECE3.6045.

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, and D. Firth. 2022. "Package 'MASS'." http://www.stats.ox.ac.uk/pub/MASS4/.

Rovero, F., and J. Ahumada. 2017. "The Tropical Ecology, Assessment and Monitoring (TEAM) Network: An Early Warning System for Tropical Rain Forests." *Science of the Total Environment* 574(1): 914–923. https://doi.org/10.1016/J.SCITOTENV.2016.09.146.

Rovero, F., E. Martin, M. Rosa, J. A. Ahumada, and D. Spitale. 2014. "Estimating Species Richness and Modelling Habitat Preferences of Tropical Forest Mammals from Camera Trap Data." *PLoS One* 9(7): e103300. https://doi.org/10.1371/JOURNAL.PONE.0103300.

Rovero, F., M. Menegon, J. Fjeldså, L. Collett, N. Doggart, C. Leonard, G. Norton, et al. 2014. "Targeted Vertebrate

Surveys Enhance the Faunal Importance and Improve Explanatory Models within the Eastern Arc Mountains of Kenya and Tanzania." *Diversity and Distributions* 20(12): 1438–49. https://doi.org/10.1111/DDI.12246.

Safi, K., M. V. Cianciaruso, R. D. Loyola, D. Brito, K. Armour-Marshall, and J. A. F. Diniz-Filho. 2011. "Understanding Global Patterns of Mammalian Functional and Phylogenetic Diversity." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366(1577): 2536–44. https://doi.org/10.1098/RSTB.2011.0024.

Schneider, F. D., A. Ferraz, S. Hancock, L. I. Duncanson, R. O. Dubayah, R. P. Pavlick, and D. S. Schimel. 2020. "Towards Mapping the Diversity of Canopy Structure from Space with GEDI." *Environmental Research Letters* 15(11): 115006. https://doi.org/10.1088/1748-9326/ab9e99.

Son, S. H., H. S. Hwang, J. K. Lee, T. K. Eom, C. R. Park, E. J. Lee, J. H. Kang, and S. J. Rhim. 2017. "Influence of Tree Thinning on the Abundance of Mammals in a Japanese Larch *Larix kaempferi* Plantation." *Animal Cells and Systems (Seoul)* 21(1): 70–75. https://doi.org/10.1080/19768354.2016.1276961.

Spicer, M. E., H. Mellor, and W. P. Carson. 2020. "Seeing beyond the Trees: A Comparison of Tropical and Temperate Plant Growth Forms and their Vertical Distribution." *Ecology* 101(4): e02974. https://doi.org/10.1002/ECY.2974.

Su, U.-S, and M. Yajima. 2015. "R2jags: Using R to Run 'JAGS'." R Packages, 12 https://cran.r-project.org/web/packages/R2jags/R2jags.pdf.

Sukma, H. T., J. Di Stefano, M. Swan, and H. Sitters. 2019. "Mammal Functional Diversity Increases with Vegetation Structural Complexity in Two Forest Types." *Forest Ecology and Management* 433(2): 85–92. https://doi.org/10.1016/J.FORECO.2018.10.035.

Torres-Pulliza, D., M. A. Dornelas, O. Pizarro, M. Bewley, S. A. Blowes, N. Boutros, V. Brambilla, et al. 2020. "A Geometric Basis for Surface Habitat Complexity and Biodiversity." *Nature Ecology & Evolution* 4(11): 1495–1501. https://doi.org/10.1038/s41559-020-1281-8.

Villéger, S., N. W. Mason, and D. Mouillot. 2008. "New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology." *Ecology* 89(8): 2290–2301.

Vogeler, J. C., A. T. Hudak, L. A. Vierling, J. Evans, P. Green, and K. T. Vierling. 2014. "Terrain and Vegetation Structural Influences on Local Avian Species Richness in Two Mixed-Conifer Forests." *Remote Sensing of Environment* 147(May): 13–22. https://doi.org/10.1016/j.rse.2014.02.006.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gorczynski, Daniel, Francesco Rovero, Arafat Mtui, Steven Shinyambala, Joseph Martine, Chia Hsieh, Luke Frishkoff, and Lydia Beaudrot. 2023. "Tropical Forest Mammal Occupancy and Functional Diversity Increase with Microhabitat Surface Area." *Ecology* 104(12): e4181. https://doi.org/10.1002/ecy.4181