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Functional diversity and redundancy of tropical forest mammals over time

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Abstract

Globally, tropical rain forests comprise some of the most diverse and functionally rich ecosystems but are increasingly degraded by human impacts. Protected areas have been shown to conserve species diversity, but their effectiveness at maintaining functional diversity over time is less well known, despite the fact that functional diversity likely reveals more ecological information than taxonomic diversity. By extension, the degree to which species loss decreases functional diversity within protected areas is also unknown; functional redundancy may buffer communities from loss of functional diversity from some local extinctions. Using eight years of camera trap data, we quantified annual functional dispersion of the large mammal community in the Volcán Barva region of Costa Rica and tested for changes in functional dispersion over time in response to environmental and anthropogenic predictors. We quantified functional redundancy based on simulated declines in functional dispersion with species loss. Observed functional dispersion did not change significantly over time and was not associated with measured environmental or anthropogenic predictors. Quantitative modeling of observed functional traits over time did not identify significant changes. We did however find qualitative trends in relative trait proportions, which could be indicative of functional change in the future. We found high functional redundancy, with average simulated functional dispersion declining significantly only after 9 out of 21 large mammal species were lost from the community. We cautiously suggest that protected tropical rain forests can conserve functional diversity over the course of a decade even in heavily fragmented landscapes.

Abstract in Spanish is available with online material.

KEYWORDS

conservation, Costa Rica, ecology, extinction, fragmentation, protected area, rain forest

1 | INTRODUCTION

Mitigating human-induced loss of biodiversity is one of the most significant challenges of our time (Cardinale et al., 2012; Chapin et al., 2000). Globally, species extinction rates have risen to historically unprecedented levels (Barnosky et al., 2011). Global changes in land development and natural resource use are putting pressure on earth's natural systems and the species that utilize them (Foley et al., 2005; Houghton, 1994). Deforestation and fragmentation are often associated with defaunation—loss or decline of wildlife—and especially so in tropical ecosystems (Canale, Peres, Guidorizzi, Gatto, & Kierulff, 2012). Tropical rain forests are particularly vulnerable to detrimental effects because they contain greater species diversity than other regions (Rosenzweig, 1992) and extensive areas of tropical rain forest are converted for agricultural use every year (Achard et al., 2002; Etter, McAlpine, Wilson, Phinn, & Possingham, 2006). Protected areas have long been a cornerstone of biodiversity conservation (Bruner, Gullison, Rice, & da Fonesca, 2001; Kramer, van Schaik, & Johnson, 1997), but the extent to which they are able to maintain functional ecosystems in the face of increasing global change is a critical and urgent question (DeFries, Hansen, Newton, & Hansen, 2005; Guilhaumon et al., 2015; Laurance et al., 2012).

Evaluations of protected area effectiveness have largely focused on success in maintaining species (Coetzee, 2017; Gray et al., 2016; Reed & Merenlender, 2008; Rodrigues et al., 2004), but taxonomic diversity may not be representative of what is needed to maintain functional ecosystems. Indeed, loss or gain of species richness reveals very little about the loss or gain of functions within a community (Baiser, Olden, Record, Lockwood, & McKinney, 2012). Functional diversity, or the variety of functional traits in a community, provides a way to assess the breadth of ecosystem functions within a community through the richness, evenness and dissimilarity of its species' functional traits. Functional traits, such as organismal size or trophic level, act as mediators between environmental conditions and species, and offer a proxy for how organisms interact with the broader ecosystem (Flynn et al., 2009; Petchey & Gaston, 2006). A change in species abundance within a community that is associated with a specific functional trait implies a gain or loss of the ecosystem function provided by that functional trait (Díaz et al., 2013).

Varying environmental conditions accompanied by changes in functional trait abundances can alter the functional diversity of communities (Swenson et al., 2012). Changes in environmental conditions, such as precipitation (Dwyer & Laughlin, 2017), temperature (Zogg et al., 1997), and vegetation structure (Laurance, 1991), have been shown to affect community-wide functional trait compositions by altering selective pressures. In this way, ecological processes occurring within protected areas can alter functional trait abundances, and by extension, functional diversity. However, ecological processes and changes occurring outside of protected areas may also affect functional diversity within protected areas (DeFries, Rovero, et al., 2010). For example, the islandization of protected areas from deforestation and fragmentation can cause declines in species richness by decreasing species colonization rate relative to extinction (Newmark, 1987). Such declines not only reduce species abundances, but potentially also reduce functional diversity.

The ability of a community to maintain ecosystem functions in the face of changing environmental conditions is dependent upon maintaining functional diversity within the community (Flynn et al., 2009). Organisms within a community can share functional traits for multiple reasons, such as similar resource use (Dwyer & Laughlin, 2017), and thereby impact the environment in a similar fashion (Walker, 1992). A community that has a high number of species with overlapping functional traits possesses high functional redundancy (Walker, 1992). We refer to functional redundancy as the degree to which a community can maintain functional diversity in the face of species loss. Theoretically, high functional redundancy can buffer communities from loss of functional diversity and the loss of ecosystem function associated with species extinctions. In this way, functional redundancy is a critical ecosystem feature, necessary to ensure the proper functioning of a community (Naeem, 1998) . Functional redundancy in animal communities is thought to be highest globally in tropical forests (Penone et al., 2016), potentially due to greater niche packing (Safi et al., 2011). Thus, tropical functional diversity may be less affected by species loss than functional diversity at higher latitudes. Functional diversity has been thoroughly studied in plants, but far less research has focused on animals (reviewed by Ahmed, van Bodegom, & Tukker, 2019) despite the fact that the functional roles of animals differ fundamentally from plants due to their lower taxonomic diversity, greater physical mobility, and higher trophic positioning. Moreover, the extent to which protected areas are able to maintain animal functional diversity has only been investigated in a limited number of systems and scales (Häkkilä et al., 2017; Laméris, Tagg, Kuenbou, Sterck, & Willie, 2019). Assessing functional diversity and functional redundancy within protected tropical forests over time can provide insight into the maintenance of ecosystem functions at the local scale at which they occur (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Petchey, Hector, & Gaston, 2004).

Here, using occupancy as a proxy for abundance (MacKenzie & Nichols, 2004), we examine temporal trends in functional diversity over an eight-year period in a tropical forest protected area. First, we test the *null hypothesis* and *trait abundance shift hypothesis* from Boersma et al. 2016 to evaluate if and how the large mammal community has responded to forest loss and fragmentation in the surrounding area. If the protected area is effective against anthropogenic disturbances, we do not expect consistent change in functional diversity over the course of the study period under the *null hypothesis*. Alternatively, under the *trait abundance shift hypothesis*, we expect the following (a) changes in mammal functional diversity that are significantly associated with ecological factors, such as precipitation or vegetation structure, or (b) a consistent change in functional diversity over time that is significantly associated with deforestation or fragmentation, indicating a deterministic change in

relative abundance of functional traits associated with human influences on the community.

In the second component of this study, we test for changes in the relative occupancies of individual functional traits over the eight-year study. Individual traits could change over time despite support for the *null hypothesis* described above if they do not significantly affect the diversity of traits in the community as a whole. Finally, in the third component of this study, we estimate functional redundancy by simulating how functional diversity declines with incremental species loss. Understanding the relationship between functional diversity and species loss will help us to predict how community functionality could change in the future as species are lost due to extinction.

Box 1: Definitions of terms as they are used throughout the manuscript

Term	Definition
Functional diversity	Broadly, the variety of functional traits in a community. It can encompass all functional diversity metrics (i.e., functional richness, and functional evenness).
Functional redundancy	Generally refers to the degree to which a community can maintain functional diversity in the face of species loss. Specifically refers to the degree to which a community can maintain functional dispersion in the face of species loss in this study.
Functional dispersion	A measure of functional diversity defined as the mean distance of individual species to the centroid of all species in a community along functional trait dimensions (Laliberté & Legendre, 2010).

2 | METHODS

2.1 | Study taxa

Large mammals have a disproportionate impact on their ecosystem because of their large body size, dietary requirements and home ranges (Bakker, Pagès, Arthur, & Alcoverro, 2016). For these reasons, large mammals also have the potential to respond strongly to environmental change based on their functional traits (Chiarello, 1999; Newbold et al., 2014). For millennia, large-bodied mammals have consistently exhibited the highest extinction rates (Dirzo et al., 2014), particularly within fragmented tropical landscapes (Crooks, 2002; Jorge, Galetti, Ribeiro, & Ferraz, 2013). Tropical mammal communities may therefore be particularly vulnerable to functional diversity loss in a changing environment.

We analyzed a terrestrial large mammal community, which had 21 species (Beaudrot, Ahumada, et al., 2016). We included all predominately ground-dwelling mammal species over 100 grams in average body mass. There were several additional co-occurring mammal species, but they either fell outside this definition or were excluded due to very low detection (Table S3). Functions performed by large mammal species were considered functionally distinct in this study, but may also be provided by other taxa (e.g., arboreal mammals, and birds).

2.2 | Study site

Volcán Barva in Costa Rica consists of tropical rain forest that encompasses La Selva Biological Research station and Braulio Carrillo National Park; La Selva has a long, rich history of ecological research (Pringle et al., 1984). With camera trap points ranging in elevation from 49 to 2,569 meters above sea level (Ahumada, Hurtado, & Lizcano, 2013), and an elevational coefficient of variation of 1.01, the survey area encompasses considerable habitat heterogeneity. The terrestrial mammal community at this site has been monitored annually with camera traps since 2007 as part of the Tropical Ecology Assessment and Monitoring (TEAM) Network. TEAM was established to monitor ground-dwelling mammal and bird communities in protected tropical forests worldwide using a standardized camera trapping protocol (Jansen, Ahumada, Fegraus, & O'Brien, 2014). We selected Volcán Barva because it is the longest running TEAM site. There is no evidence of large mammal species loss at Volcán Barva since 2007 (Beaudrot, Kroetz, et al., 2016), but populations of some mammal species have declined (Ahumada et al., 2013).

Human disturbance is also prevalent in and around Volcán Barva. Poachers are a threat to mammal species in the area, and deforestation occurs along the border of Braulio Carrillo National Park (Rovero & Zimmerman, 2016; Schelhas & Sánchez-Azofeifa, 2006). Over 50% of the park's border is classified as fragmented landscape (Ahumada et al., 2011). Nevertheless, little forest cover change has been observed within the protected area in recent years (Beaudrot et al., 2019), which suggests that human disturbance from illegal logging has been minimal.

2.3 | Data collection

2.3.1 | Camera trap data and occupancy estimates

We used camera trap data collected by TEAM between 2007 and 2014. TEAM surveys terrestrial (i.e., ground-dwelling) tropical mammal populations on an annual basis, using a standardized protocol with large-scale arrays of permanent camera trap points (Jansen et al., 2014). Sixty camera traps were deployed at a density of 1 camera per 1–2 km^2, encompassing a survey area of 21,049 hectares out of the 49,317 hectares within the boundaries of the protected area. Each camera trap was activated for 30 consecutive days annually at the same time every year during the dry season. This was done to account for seasonality across TEAM sites and across years. While mammal community compositions can shift in response to seasonal

differences such as plant productivity and fruit availability (Marshall, Beaudrot, & Wittmer, 2014; Ramírez-Bautista & Williams, 2019; Wen et al., 2014), the consistent temporal camera trap deployment each year likely reduced any potential bias. Camera trap images were identified by TEAM personnel following the standard IUCN Red List (IUCN, 2014).

Species-specific annual occupancy values for the Volcán Barva community were obtained from a previously published study (Beaudrot, Kroetz, et al., 2016), which used single species Bayesian dynamic occupancy modeling that provided a posterior distribution of 1,000 occupancy values for each species for each year based on the TEAM camera trap data. We selected the median species-specific posterior occupancy value for each species for use in this study.

2.3.2 | Functional trait data

We obtained mammal functional trait data through an extensive literature search in which all monitored terrestrial mammal species were assigned ranked values for six functional traits: average body mass, diet, average social group size, habitat type, activity period, and average litter size (Table 1; Tables S1 and S2). We selected these functional traits for their association with aspects of individual species ecology relevant to how species utilize their environment and impact their ecosystem (Weiss & Ray, 2019). For example, body mass affects the quality of resources needed for survival (Jarman 1974) and approximates the degree of impact that species will have on its ecosystem in terms of quantity of nutrients dispersed, quantity of food consumed and spatial range of impact (Wolf, Doughty,

TABLE 1 Functional trait rankings and descriptions used to classify species functional traits in the Volcán Barva large mammal community

Trait Value Rankings and Descriptions			
Trait	**Rank**	**Title**	**Value Description**
Diet	1	Grazer	>75% grasses
	2	Grazer-Browser	<75% grasses or browse, >75% grasses and browse
	3	Browser	>75% browse
	4	Browser-Frugivore	<75% browse or fruits, >75% browse and fruit
	5	Frugivore/Seed Predator	>75% fruits and seeds
	6	Omnivore	<75% plants or animals
	7	Insectivore	>75% Insects
	8	Zoophage	<75% insects or vertebrates, >75% animals
	9	Carnivore	>75% vertebrates
Average Social Group Size	1	Solitary/pairs	Groups of 1–2 when not raising young
	2	Coalitions	Occasional grouping between non-parent/progeny
	3	Family Groups	Groups includes mature offspring and some extended relatives
	4	Gregarious	Large groups, not all individuals necessarily related
Habitat	1	Terrestrial	Mostly restricted to terrestrial surfaces
	2	Scansorial	Able to move on land and climb trees
Activity Period	1	Diurnal	Active during daytime
	2	Non-restricted	Can be active at any time of day
	3	Crepuscular	Activity restricted to around dawn and dusk
	4	Nocturnal/Crepuscular	Activity generally occurs between dusk and dawn
	5	Nocturnal	Active during nighttime
Average Litter Size	Average number of offspring per litter		
Average Body Mass	Log Transformed Average Body Mass in Kilograms		

Note: Based on a literature search, each species was assigned a rank for each functional trait.

& Malhi, 2013). The selected traits are used extensively in studies of mammal functional traits (Flynn et al., 2009; Hempson, Archibald, & Bond, 2015; Jones et al., 2009). Nevertheless, functional traits studies are highly dependent on the selection of relevant functional traits (Petchey & Gaston, 2006), and although we cover a wide suite of ecological attributes, it is possible that important traits have been inadvertently omitted. In addition, although these ordered traits cover a breadth of functional aspects, their categorical nature may obfuscate patterns that would be revealed by continuous trait measurements (Kohli & Rowe, 2019).

2.3.3 | Environmental data

We collected data on climatic, biological, and anthropogenic factors that could impact mammal functional diversity (Table S4). We selected four variables that were not strongly correlated with other considered variables ($r < 0.6$) as potential predictors of mammal functional diversity. The four predictors were as follows: (a) annual precipitation, (b) area of new canopy gaps within Volcán Barva each year, (c) mean area of forest fragments within the Zone of Interaction (Defries, Karanth, & Pareeth, 2010) each year, and (d) area of forest loss within the Zone of Interaction each year. The Zone of Interaction is the spatial extent believed to most likely affect biodiversity within the sampling area and is systematically quantified based on human settlements, watersheds, and migration corridors (Beaudrot, Kroetz, et al., 2016; DeFries, Karanth, et al., 2010).

We selected the above variables for the following reasons. Annual precipitation can affect plant and animal functional traits because water is required by all organisms for metabolism and is a limiting resource for many (Dwyer & Laughlin, 2017; Wright, Carrasco, Calderón, & Paton, 1999). Canopy gaps are critical components of vegetation dynamics and represent important aspects of plant community diversity (Denslow, 1987). For example, approximately 75% of the tree species in La Selva are dependent on canopy gaps for seed germination and growth (Hartshorn, 1978). Vegetation dynamics, in turn, have the potential to strongly affect mammal community functional traits by altering resource availability and habitat structure (Laurance, 1991; Laurance et al., 2008). Edge effects and isolation from fragmentation have been shown to affect community composition in other systems (Krishnadas, Bagchi, Sridhara, & Comita, 2018; Malcolm, 1994; Newmark, 1987). Deforestation has also been shown to be one of the primary drivers of defaunation in the tropics (Canale et al., 2012) and has the potential to disturb community structure.

Mean annual precipitation data were collected from the NASA POWER project at a 0.5°×0.5° resolution (POWER data access viewer). We used remotely sensed vegetation classification data (Hansen et al., 2013) to calculate canopy gaps, mean fragment size, and forest loss over the study period (package "SDMTools" in R; VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014).

2.4 | Analysis

2.4.1 | Overview

First, we calculated annual functional diversity for the mammal community in the Volcán Barva region of Costa Rica for an eight-year period and assessed these values for linear trends over time. We then used linear regression to examine the relationship between temporal change in functional diversity and our four environmental predictor variables. We tested for temporal trends in occupancy-weighted trait values to examine quantitatively how individual functional traits changed over time within the Volcán Barva large mammal community. Lastly, we used bootstrapping to quantify functional redundancy and segmented linear regression to analyze how functional diversity changed with simulated removal of species from the community.

2.4.2 | Functional traits

We selected functional traits for assessment and ranking based on established methods for examining effects of anthropogenic change on mammalian functional traits that reflect species responses to environmental conditions (response traits) (Díaz et al., 2013; Flynn et al., 2009). The selected traits were also doubly valuable as they are associated with functional impacts of mammals (effect traits) on the environment (Hempson et al., 2015). Two of the trait variables were continuous (i.e., average body mass, litter size), and one was an ordered category (i.e., average social group size). For the remaining three traits, we imposed ordered categories following previous work on mammal functional traits (Flynn et al., 2009; Hempson et al., 2015; Jones et al., 2009). Specifically, we ordered diet from the lowest quality food (grass - grazers) to the highest quality food (vertebrate meat - carnivore), habitat from the most horizontally oriented (terrestrial) to the most vertically oriented (scansorial), and activity period from highest light (diurnal) to lowest light (nocturnal). The traits with natural or imposed ordered categories (diet, social group size, habitat, activity period) were analyzed as ordinal variables in the functional diversity calculations and in our assessment for temporal trends. No traits were strongly correlated with each other ($r < 0.6$).

2.4.3 | Functional diversity

We used the abundance-weighted functional dispersion metric (package "FD" in R; Laliberté & Legendre, 2010) to calculate annual functional diversity in Volcán Barva over the eight-year study, using occupancy values as a proxy for abundance weights. We determined that a functional diversity metric based on functional dispersion would be the most effective for understanding the functional effects of this community on its ecosystem based on extensive work showing the link between community functional dispersion and ecosystem

functioning (Cadotte, 2017; Frainer, McKie, & Malmqvist, 2014). Functional dispersion is the mean distance of individual species to the centroid of all species in a community along functional trait dimensions (Laliberté & Legendre, 2010). Because species occupancy changed and species richness remained constant over the eight-year study period (Beaudrot, Kroetz, et al., 2016), we determined that an investigation into a potential trait abundance shift measured with an occupancy-weighted functional dispersion metric would give the most meaningful results for assessing functional diversity within a single site (Boersma et al. 2016). Laméris and colleagues (2019) found differences in functional dispersion in large mammal communities in Cameroon based on conservation efforts, further justifying our selection of this metric.

2.4.4 | Linear modeling

To test for change in functional dispersion over time, we ran a simple linear regression model with year as the predictor. We evaluated the estimate, standard error and p-value of the year coefficient from this model. We also constructed linear models using Gaussian distributions and performed model selection (package "MuMIn" in R; Barton, 2019) to evaluate the predictive power of environmental and anthropogenic variables for functional dispersion. The environmental variables were annual precipitation, new canopy gap area within Volcán Barva, mean fragment size within the Zone of Interaction of the protected area, and annual rate of deforestation in the Zone of Interaction. We used AICc model selection to compare models and defined the best model as the model that had the lowest AICc value by a margin of 2 or more (Anderson & Burnham, 2004).

2.4.5 | Functional trait distributions over time

To test for changes in individual functional traits over time, we ran linear regression models for quantitative traits (i.e., body mass, litter size) and ordinal regression models for ordered traits (i.e., diet, group size, habitat, activity period) with year as a predictor. We weighted the response variable for each trait based on the occupancies of the species with the given trait. We used the estimates, standard deviations and p-values to assess the statistical significance of temporal trends.

2.4.6 | Functional redundancy

To estimate functional redundancy, we used occupancy and functional data to simulate how community functional dispersion changed as species were removed from the community. We calculated this change with bootstrapping, randomly drawing subsets of species from the community and calculating their functional dispersion (see above). Species richness values ranged from 3 to N-1, where N was the number of species in the full community ($N = 21$). We randomly selected 1,000 species combinations without replacement of each species richness value to generate a distribution of functional dispersion values and used the mean functional dispersion value in our calculations. For higher species richness, repetition of species combinations was necessary in the analysis to generate 1,000 functional dispersion values, but the combinations were still selected randomly without replacement. We performed this analysis for each year using occupancy values from the respective year of the eight-year study period.

We fit a segmented linear regression model (package "strucchange" in R; Zeilies et al., 2002) to the bootstrapped functional dispersion models from all eight years and performed model selection to determine the number of break points (0–4) in the most robust regression. The best-fit model was determined by the lowest AIC value. We used break points to identify functional redundancy, or the number of species lost from the community before rate of functional dispersion loss increased, if ever.

3 | RESULTS

3.1 | Mammal community

The large mammal community monitored by TEAM camera traps in Volcán Barva during the study period consisted of 21 species ranging in size from 0.25 kg (red-tailed squirrel, *Sciurus granatensis*) to 240 kg (Baird's tapir, *Tapirus bairdii*). Diet ranged from browser to carnivore. Social grouping ranged from solitary to gregarious. Habitat varied between terrestrial and scansorial. Activity period varied from fully diurnal to fully nocturnal. Average litter size ranged from 1 (Baird's tapir, *Tapirus bairdii*) to 5.1 (Virginia opossum, *Didelphis marsupialis*). Species richness and composition did not change over the course of the study period. Annual species occupancy probabilities within Volcán Barva ranged from 0.006 to 0.767 with a median of 0.100. Change in species occupancy ranged from a decrease of 0.433 to an increase of 0.333 with a median change of 0. Capture events on camera traps and minimum and maximum occupancy values for each species over the study period are given in Table S3.

3.2 | Environmental change over time

During the eight-year study, annual precipitation ranged from 1,277 mm to 2,090 mm, the area of new canopy gaps ranged from 0.53 hectares to 3.78 hectares per year, mean fragment size within the Zone of Interaction varied between 99.52 hectares and 105.94 hectares, and deforestation in the Zone of Interaction varied between 637 hectares and 2,764 hectares per year (Figure 1).

3.3 | Functional dispersion and linear modeling

We did not detect significant change in functional dispersion over time (Est. = −0.002, $SE = 0.001$, $p = .254$). We performed model

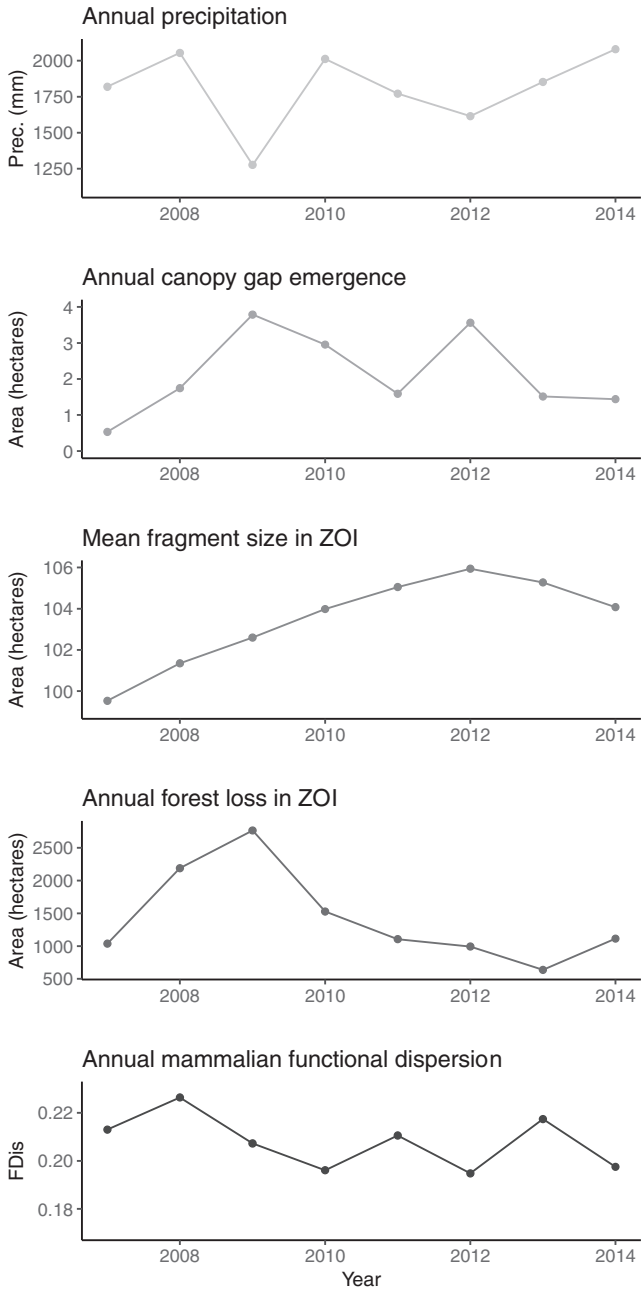

FIGURE 1 Measured values of environmental variables and functional dispersion over the eight-year study period

selection to identify the model that best predicted functional dispersion during the study period. Neither annual precipitation, the area of new canopy gaps, the mean area of forest fragments, nor the area of forest loss performed better than the model without covariates based on AICc model comparison (Table S5).

3.4 | Functional trait distributions over time

Linear and ordinal regression models revealed that none of the functional traits shifted significantly in relative occupancy over time (Table S6). However, a qualitative assessment of proportional occupancy of trait values showed directional trends over time for some traits (Figure 2). Specifically, species with larger body mass, browser/frugivore intermediate diets, and non-restricted activity periods showed non-significant increases in relative occupancy during the study period.

3.5 | Functional redundancy

AICc model selection for the segmented linear regressions identified four breakpoints in the best-fit model of the relationship between species richness and functional dispersion (Figure 3, Table S7). Each breakpoint marks a change in the slope for this relationship. Functional dispersion only began declining after the second break, which occurred when nine species had been removed from the community (Figure 3. dashed line). There was little loss of functional dispersion with species loss prior to the second break point, with the communities remaining well within the range of measured annual functional dispersion fluctuations. In fact, after the first breakpoint, functional dispersion actually increases with species loss. Beyond nine species, functional dispersion begins declining with species loss and each species extinction led to a steep decline in functional dispersion. This rate of loss increases after the third breakpoint and then again after the fourth breakpoint.

4 | DISCUSSION

We examined change in functional dispersion, functional traits, and functional redundancy over time in the large mammal community of a tropical forest protected area. Our results suggest that the protected area maintained functional dispersion over an eight-year period, without significant declines or increases in functional dispersion over time. We therefore reject the *trait abundance shift hypothesis* and retain the *null hypothesis* (Boersma et al. 2016). Furthermore, we did not detect significant change over time in any individual functional traits. We did, however, identify qualitative trends in some functional traits, which may signal the possibility of future change. We cautiously suggest that Volcán Barva supports a mammal community with high functional redundancy that has the potential to buffer declines in functional dispersion following the loss of some species, but emphasize the importance of continued monitoring for assessment of long-term trends, as some processes that affect functional dispersion and functional redundancy operate on time scales longer than eight years.

4.1 | Functional diversity

Despite previously identified declines in occupancy for some individual species at Volcán Barva (Ahumada et al., 2013; Beaudrot, Kroetz, et al., 2016), our results suggest that functional dispersion did not change significantly at this site over the course of the eight-year study. Furthermore, functional dispersion was not predicted

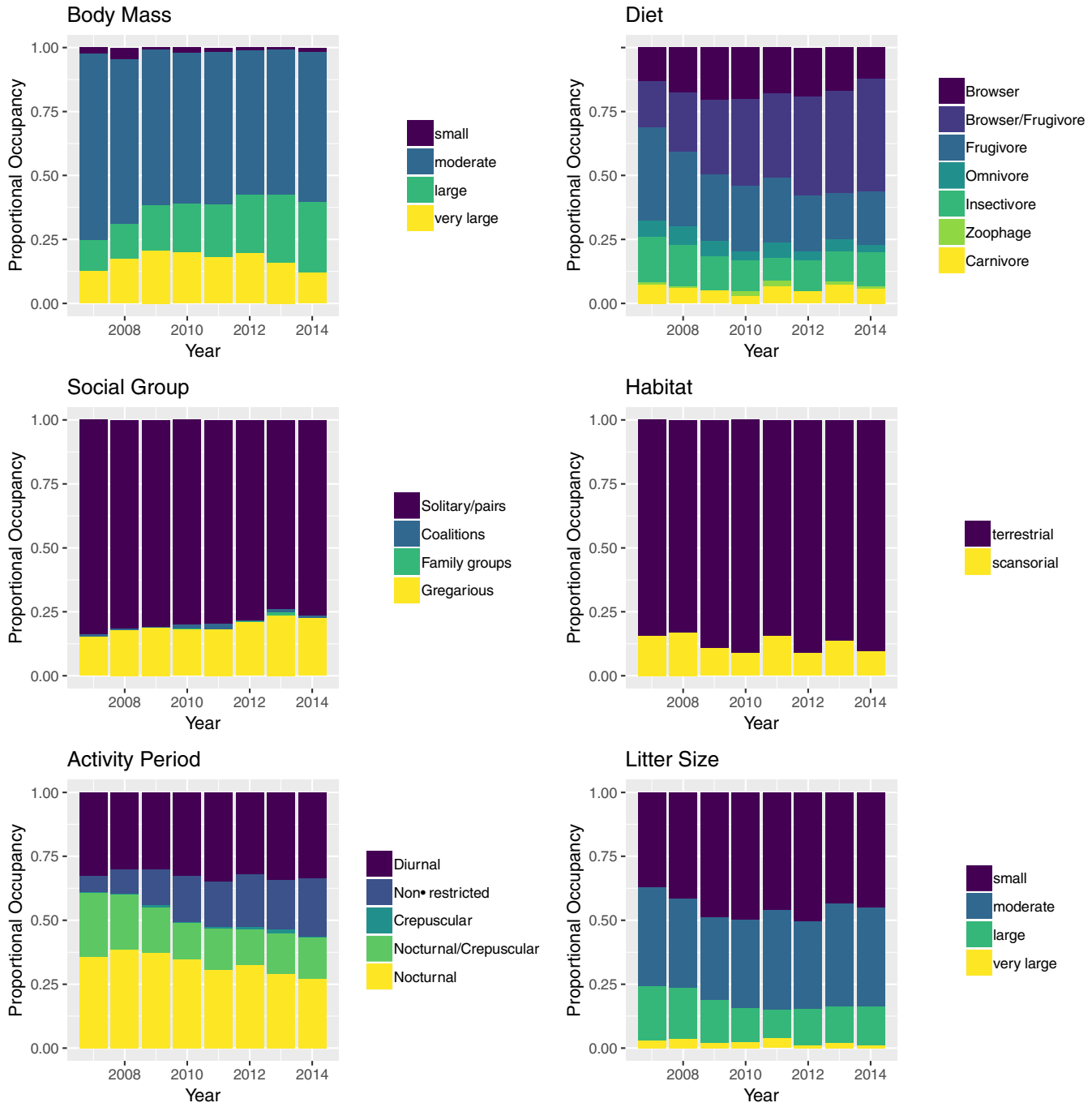

FIGURE 2 Plots showing change in distribution of trait values in the mammal community of Volcán Barva over the study period. Numeric traits were grouped into ordered categories to be represented with the categorical traits as stacked bar graphs showing the proportional occupancy of each trait value in the community. For body mass, the categories are small (<1 kg), moderate (1–9.9 kg), large (10–99.9 kg), and very large (100 + kg). For litter size, the categories are small (0–1.5 offspring), moderate (1.5–3 offspring), large (3–5 offspring), and very large (5 offspring)

by fragmentation or deforestation in the protected area's Zone of Interaction. We therefore reject the trait abundance shift hypothesis and suggest that these anthropogenic disturbances did not significantly affect functional dispersion within Volcán Barva during the study period.

Empirical data have demonstrated that community functional diversity is deterministically altered by disturbance level in riparian plant communities (Biswas & Mallik, 2010) and that edge effects reduce biotic interactions and taxonomic diversity in forest plant communities (Krishnadas et al., 2018). Although empirical data addressing the direct relationship between forest fragmentation and animal functional diversity are limited, observational data have shown that ecological communities surrounded by degraded matrices demonstrate altered functional diversity in correlation with landscape-level disturbances (Häkkilä et al., 2017). In addition, work by Laméris and colleagues (2019) has shown that mammal functional

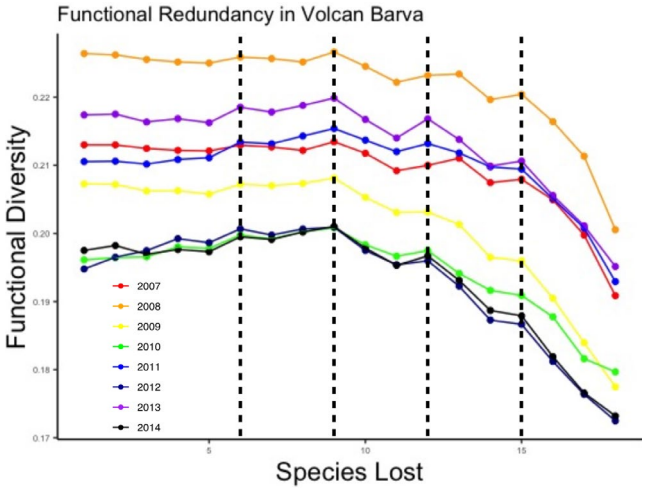

FIGURE 3 Functional redundancy quantified from bootstrapped estimates of functional dispersion and segmented linear modeling. Functional dispersion was calculated 1,000 times for each year with species loss ranging from 1 to 18 species. Break points from the best-fit segmented linear model indicate values at which the slope of the relationship between species loss and functional dispersion changes substantially and were used to determine functional redundancy (indicated by the dashed lines occurring at 6, 9, 12, and 15 species lost). We assessed functional redundancy by the number of species lost before functional dispersion declined, indicated by the dotted line at 9 species lost

dispersion was lower in communities with less protection and in areas with historically high logging. With these studies in mind, we might expect lower functional dispersion with greater degradation of the matrix, yet we do not see this in the results. Degradation of the matrix around Volcán Barva may not have been substantial enough to have affected the functional dispersion of the mammal community within the protected area if the mechanisms that filter functional traits in disturbed protected areas (e.g., edge effects, dispersal limitation) were not strong enough to influence the mammal community. Alternatively, the protected area is large and management may have mitigated consequences. Continued monitoring of the protected area community is necessary to evaluate these alternatives.

4.2 | Functional trait distributions over time

The relative trait composition of the Volcán Barva large mammal community did not shift significantly for any of the individual functional traits. This suggests that any trait filters affecting the large mammal community of Volcán Barva, either ecological or anthropogenic, did not act strongly or consistently enough to alter individual functional trait occupancies during the eight-year study and further indicates that functional traits in the mammal community are relatively stable.

We note, however, that qualitative assessments of trait proportions suggest directional trends over time for some individual functional traits. Notably, we observed a qualitative increase in the relative occupancy of mammals with large body size, browser/frugivore intermediate diets, and non-restricted activity periods. These patterns correspond with the increase in occupancy of the red brocket (*Mazama temama*), a species which possesses all of these traits and showed the largest increase in occupancy over the study period. An increase in larger-bodied species seems to reinforce that this protected area is not experiencing selective pressures typical of anthropogenically disturbed mammal communities, which usually show declines in larger-bodied mammals (Dirzo et al., 2014). But the decline in relative occupancy of frugivores and insectivores coupled with the rise of frugivore/browser intermediates does reflect other studies that show a decline in dietary specialist vertebrates (i.e., insectivores) in anthropogenically disturbed landscapes (Flynn et al., 2009).

This pattern suggests that underlying ecological or anthropogenic processes could have selectively affected the large mammal community functional structure without causing statistical changes in trait composition or overall declines in functional diversity. Shifts in functional traits as a result of environmental change have been demonstrated to precede population decline both mathematically and experimentally (Baruah, Clements, Guillaume, & Ozgul, 2019). Qualitative trait shifts over the course of the study suggest that some species in the community may be vulnerable to population declines in the near future and that continued monitoring is critical.

4.3 | Functional redundancy

Functional redundancy is a critical component of community structure and strongly impacts a community's ability to fulfill its ecosystem functions (Naeem, 1998). Our functional redundancy results suggest the large mammal community may be able to maintain ecosystem functions associated with the measured functional traits in the face of the loss of multiple species from the community. This finding is consistent with broader understanding of tropical communities and supports the claim that tropical mammal communities exhibit high functional redundancy (Safi et al., 2011). Importantly, our simulation analysis identifies the extent of functional redundancy, which only extends to a certain point (nine large mammal species lost). After this point, functional dispersion declines in the community, and accelerates its decline thereafter, indicated by the third and fourth breakpoint. This can be interpreted as a type of tipping point, after which the functional consequences of further extinction increase dramatically as more species are lost. Many studies have found tipping points in many ecological systems after which the negative consequences of disturbance rapidly increase (for review, see Reyer et al., 2015). For example, reduction in functional herbivory in coral reef fishes due to overfishing causes macroalgae to escape top-down control after a certain level (Holbrook, Schmitt, Adam, & Brooks, 2016). We could expect similar ecological consequences (e.g., loss of top-down control on prey species) if species loss were to reach a tipping point in Volcán Barva.

We note that the loss or decline of functionally dissimilar species could disproportionately affect declines in functional dispersion. Our analysis assumes random loss of species, yet species extinctions are generally non-random (Dirzo et al., 2014). If more functionally distinct species were to go extinct first, the consequences of species loss on functional dispersion could occur following the loss of fewer

species. For example, Flynn and colleagues (2009) found that functional diversity declined more significantly than predicted by loss of species richness alone in agricultural landscapes, meaning that functionally dissimilar species were more likely to be lost from the community. Therefore, our simulations must be taken with caution, as non-random extinction events could alter their trajectory.

5 | CONCLUSIONS

We found consistent functional dispersion, consistent functional trait occupancies, and high functional redundancy of tropical forest mammals during an eight-year period. These results suggest that the protected area likely maintained the ecosystem functions performed by large mammals over the better part of a decade and that anthropogenic factors did not predictably alter or degrade functional structure within this large mammal community during that time. Our results support the utility of protected areas for conservation. Further investigation is required over longer time periods and in other systems including comparisons between protected and non-protected areas to understand the extent to which protected areas themselves conserve functional diversity and ecosystem multifunctionality.

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AUTHOR CONTRIBUTION

DG provided conceptualization, data curation, formal analysis, investigation, methodology, resources, software, validation, visualization, and writing—original draft and review and editing. LB provided conceptualization, data curation, formal analysis, funding acquisition, project administration, resources, software, supervision, validation, and writing—review and editing.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cvdncjt23 (Gorczynski & Beaudrot, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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