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Down by the riverside: Riparian edge effects on three monkey species in a fragmented Costa Rican forest

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Abstract

Rivers represent natural edges in forests, serving as transition zones between landscapes. Natural edge effects are important to study to understand how intrinsic habitat variations affect wildlife as well as the impact of human-induced forest fragmentation. We examined the influence of riparian and anthropogenic edge on mantled howler, white-faced capuchin, Central American spider monkeys, and vegetation structure at La Suerte Biological Research Station (abbreviated as LSBRS), Costa Rica. We predicted lower monkey encounter rate, tree species richness, and median dbh at both edge types compared to interior and that monkeys would show species-specific responses to edge based on size and diet. We expected large, folivorous–frugivorous howler monkeys and small, generalist capuchins would be found at increased density in forest edge, while large, frugivorous spider monkeys would be found at decreased density in forest edge. We conducted population and vegetation surveys along interior, riparian, and anthropogenic edge transects at LSBRS and used GLMM to compare vegetation and monkey encounter rate. Tree species richness and median dbh were higher in forest interior than anthropogenic edge zones. Although spider monkey encounter rate did not vary between forest edges and interior, howler monkeys were encountered at highest density in riparian edge, while capuchins were encountered at highest density in anthropogenic edge. Our results indicate that diverse forest edges have varying effects on biota. Vegetation was negatively affected by forest edges, while monkey species showed species-specific edge preferences. Our findings suggest that riparian zones should be prioritized for conservation in Neotropical forests.

Abstract in Spanish is available with online material.

KEYWORDS

Alouatta, *Ateles*, *Cebus*, edge effects, forest fragmentation, natural forest edge, river edge, tropical rain forest

1 | INTRODUCTION

Forest edges are landscape boundaries where one type of habitat transitions to another with different biotic and abiotic qualities (Laurance, 1991; Schwitzer, Glatt, Nekaris, & Ganzhorn, 2011). Edges occur naturally and represent intrinsic transition zones between different regions of a landscape; for example, riparian (river) edge zones separate forests and rivers in undisturbed environments (Cadenasso, Pickett, Weathers, & Jones, 2003; Lovejoy et al., 1986; Swanson, Gregory, Sedell, & Campbell, 1982). In contrast to natural edges, anthropogenic edges are created by human-caused fragmentation of otherwise continuous landscapes. Sharp forest edges, such as borders between protected rain forest and developed land, are increasingly present worldwide, particularly in tropical environments (Lenz, Jack, & Spironello, 2014; Stevens & Husband, 1998). Both natural and anthropogenic forest edges are usually poor habitats for biota adapted to forest interior; tree mortality increases and there are greater canopy gaps (Laurance et al., 2002), and both plant and animal biomass typically decreases near edges or transition zones (Arroyo-Rodríguez & Mandujano, 2006; Estrada, Anzures, & Coates-Estrada, 1999; but see Laurance et al., 2002; Lopez de Casenave et al., 1998).

Few studies have compared the impact that both anthropogenic and natural edges have on plants and animals within the same forest landscape; doing so will lead to greater understanding of how diverse types of edge effects are manifested at the same site. In order to fully understand the impact of anthropogenic edge effects on biota, we need to quantify the effects of natural edges to establish a comparative baseline. As Murcia (1995) notes, the mechanics of edge effects must be better understood before conservation plans can effectively mitigate the damage caused by anthropogenic edges in fragmented forests.

This study focuses on how primate species and their habitat are affected by both natural and anthropogenic edge effects in a fragmented tropical rain forest at the La Suerte Biological Research Station (LSBRS), Costa Rica. As large-bodied mammals with specialized diets, primates are indicator species for the overall health of a forest (Mace & Balmford, 2000), making them important subjects for edge effects study. The present study focuses on three sympatric primates—mantled howler (*Alouatta palliata*), white-faced capuchin (*Cebus capucinus*), and Central American spider monkeys (*Ateles geoffroyi*)—and their response to both anthropogenic and natural riparian (river) edge at the same site. At LSBRS, the banks of the La Suerte River and surrounding forest comprise the riparian edge. Forest interior consists of a dense and continuous canopy of mature trees (Pruetz & Leasor, 2002) while anthropogenic edge sharply transitions from continuous forest to ranches and coconut and banana plantations (Molina, 2015), with little food available for monkeys outside the forest fragment. Previous work at LSBRS (Bolt et al., 2018) examined the impact of anthropogenic edges on primate populations and vegetation structure, while this study focuses on the role of riparian edge within the landscape and compares riparian edge to both forest interior and anthropogenic edge in order to more fully understand how biota respond to natural habitat boundaries.

Hypothesis 1 *Vegetation responds differently in Riparian versus Anthropogenic edges*

Based on previous findings from other sites suggesting lower plant biomass at natural forest edges compared to forest interior (Arroyo-Rodríguez & Mandujano, 2006; Estrada et al., 1999), but different and more hydrophilic vegetation present in riparian zones (Richardson & Danehy, 2007), we expected differences in tree characteristics when comparing riparian edge to forest interior and anthropogenic edge. Previous research on vegetation characteristics at LSBRS showed anthropogenic edge effects for vegetation (Bolt et al., 2019, 2018). Bolt et al. (2018, 2019) did not, however, consider riparian edges or compare how they differ from forest interior and anthropogenic edges in this environment. In the present study, we predicted there would be smaller median tree diameter at breast height (dbh), less canopy cover, and lower tree density in riparian edge compared to forest interior and in anthropogenic edge compared to riparian edge. We predicted that tree species richness would not vary across riparian and interior zones, while species richness would be greater in riparian edge than in anthropogenic edge. We made these predictions due to the lower species richness of trees (Skrinyer, 2016) and lower concentrations of flowers in the understory (Ramos & Santos, 2006) in anthropogenic edge compared to natural edge, coupled with the more gradual transition in abiotic characteristics expected of natural edges compared to anthropogenic edges (Cadenasso et al., 2003).

Hypothesis 2 *Monkey species respond differently to Riparian versus Anthropogenic edges, with less marked edge effects in riparian edges*

Given the vegetation differences across edge zones discussed above (e.g., Ramos & Santos, 2006), we expected monkeys to respond differently to riparian versus anthropogenic edges, with less marked edge effects in riparian edge zones. We predicted lower overall monkey encounter rates in riparian edge compared to forest interior and in anthropogenic edge compared to riparian edge, given that lower animal biomass is typical at forest boundaries (Arroyo-Rodríguez & Mandujano, 2006; Estrada et al., 1999) along with lower species richness in anthropogenic compared to natural edge (Magura, Lövei, & Tóthmérész, 2017). Previous research on mantled howler, white-faced capuchin, and Central American spider monkeys' responses to anthropogenic edges at LSBRS indicated that all primates responded to anthropogenic edges neutrally, with no significant differences in encounter rate at anthropogenic edge versus forest interior (Bolt et al., 2018); this research did not, however, compare monkey response to riparian edge. In the present study, we used the same monkey survey transects (Bolt et al., 2018) divided into four landscape zones rather than two and predicted there would be different encounter rates for sympatric monkeys in riparian edges compared to forest interior and anthropogenic edges based on species-level differences in body size, diet, and canopy height preferences (Lidicker, 1999).

Mantled howler monkeys are large New World monkeys weighing 3.1–9.8 kg (Ford & Davis, 1992). They eat leaves as well as fruit when available (Arroyo-Rodríguez & Dias, 2010; di Fiore, Link, & Campbell, 2011; Glander, 1982). If only leaves are available, they prefer young leaves, which are higher in protein (di Fiore et al., 2011; Milton, 1979). Due to the greater amount of solar energy reaching trees in riparian edge compared to forest interior combined with the greater amount of moisture available (Swanson et al., 1982), riparian edge is likely to contain greater leaf production (van Schaik & Mirmanto, 1985) as well as a high concentration of mature trees and nutrient-rich young leaves (Matsuda et al., 2019) and therefore is expected to be preferred habitat for howler monkeys. We predicted that mantled howler monkeys, as large folivore–frugivores with preference for high canopy (Arroyo-Rodríguez & Dias, 2010; Fleagle & Mittermeier, 1980), would show positive riparian edge effects, with higher encounter rates at riparian forest edge compared to interior. Research on other howler species revealed positive edge effects (Lenz et al., 2014), suggesting mantled howlers may exhibit the same tendencies. As folivore–frugivores (di Fiore et al., 2011; Glander, 1982), their relatively flexible dietary strategy allows them to persist in relatively low-quality forest patches (Estrada, 2015). Howler monkeys' preference for young leaves compared to older leaves (di Fiore et al., 2011) and the "leaf flush" typical of edges (Murcia, 1995) would promote howler presence in all edge types compared to interior, but the potential lack of large trees in anthropogenic edge may mitigate this preference (Estrada, 1984; Munoz, Estrada, Naranjo, & Ochoa, 2006). We therefore predicted that mantled howler monkeys would be encountered at higher rates in riparian edge compared to anthropogenic edge.

White-faced capuchins are small-bodied monkeys weighing 2.6–3.9 kg (Ford & Davis, 1992). Capuchins are frugivorous, but have varied diets including insects, leaves, and flowers (Cunha, Vieira, & Grelle, 2006; Rose, 1994). We expected white-faced capuchins to exhibit positive edge effects with higher encounter rate in riparian edge compared to forest interior. Other capuchin species have shown positive edge effects (Lenz et al., 2014); as small frugivores with extreme dietary flexibility and preference for low-to-mid-forest canopy (Fleagle & Mittermeier, 1980; Ford & Davis, 1992), capuchins can thrive in small fragments (Cunha et al., 2006) and are predicted to flourish in riparian edge compared to forest interior. When comparing edge zone preferences, we predicted capuchins would prefer anthropogenic edge to riparian edge due to their preference for lower canopy (Fleagle & Mittermeier, 1980) and the smaller trees found at anthropogenic edge at LSBRS (Bolt et al., 2018).

Central American spider monkeys are large New World monkeys with adult weight ranging from 6 to 9.4 kg (Ford & Davis, 1992). They live in large fission–fusion social groups over wide home ranges (Klein & Klein, 1977; Shimooka, 2005) and as preferential frugivores, they rely mostly on fruit from mature trees (van Roosmalen, 1985). We predicted that Central American spider monkeys would show negative edge effects with lower encounter rate at riparian edge compared to forest interior, given that other spider monkey species exhibited negative edge effects (Lenz et al., 2014). We expected Central American spider monkeys to avoid riparian edge compared to forest interior due to their preference for high-canopy suspensory locomotion compared to sympatric primate species (Fleagle & Mittermeier, 1980) and the lack of continuous canopy across sections of the river, but to be encountered at a higher rate in riparian edge compared to anthropogenic edge given the larger number of mature trees available by the river.

2 | METHODS

2.1 | Study site and monkey population

We performed this investigation at the La Suerte Biological Research Station (LSBRS) in northern Costa Rica (10°26′ N, 83°46′ W). Our study site is composed of 3 km^2 of primary and secondary tropical lowland rain forest (Brandt & Singleton, 2018; Garber, Molina, & Molina, 2010; Pruetz & Leasor, 2002). We carried out our research in a smaller area at this site comprising two linked forest sections ("Small Forest" = 0.35-km^2 to the south and "Large Forest" = 0.94-km^2 to the north) with a clear-cut area for "camp" at the center (0.07-km^2)(Bolt et al., 2019, 2018; Molina, 2015; Figure 1). LSBRS is one of increasingly few substantive forest fragments in an area of Costa Rica that has been mostly deforested since the 1970s, mainly due to cattle ranching and corporate production of bananas and pineapples (Garber et al., 2010; Molina, 2015). The La Suerte River courses through the study site before meeting the Tortuguero River. Having natural riparian edges that span the length of the forest makes LSBRS a fitting site for investigation of riparian edge effects and a comparison with anthropogenic edges at the same site.

Previous population surveys at LSBRS suggest that the Large Forest contains six to eight groups of mantled howler monkeys, one to three groups of white-faced capuchin monkeys, and one community of approximately ten Central American spider monkeys, while the Small Forest contains two to three groups of mantled howlers and one group of white-faced capuchins (Garber et al., 2010; Huettman, 2015; Pruetz & Leasor, 2002).

2.2 | Vegetation survey

We collected data on monkey population and vegetation structure from May–August 2015 (population and vegetation surveys), May–July 2016 (population surveys), and May–June 2017 (vegetation surveys) (Bolt et al., 2019, 2018). All surveys were performed during the wet season, so all results are specific to this time of year. The

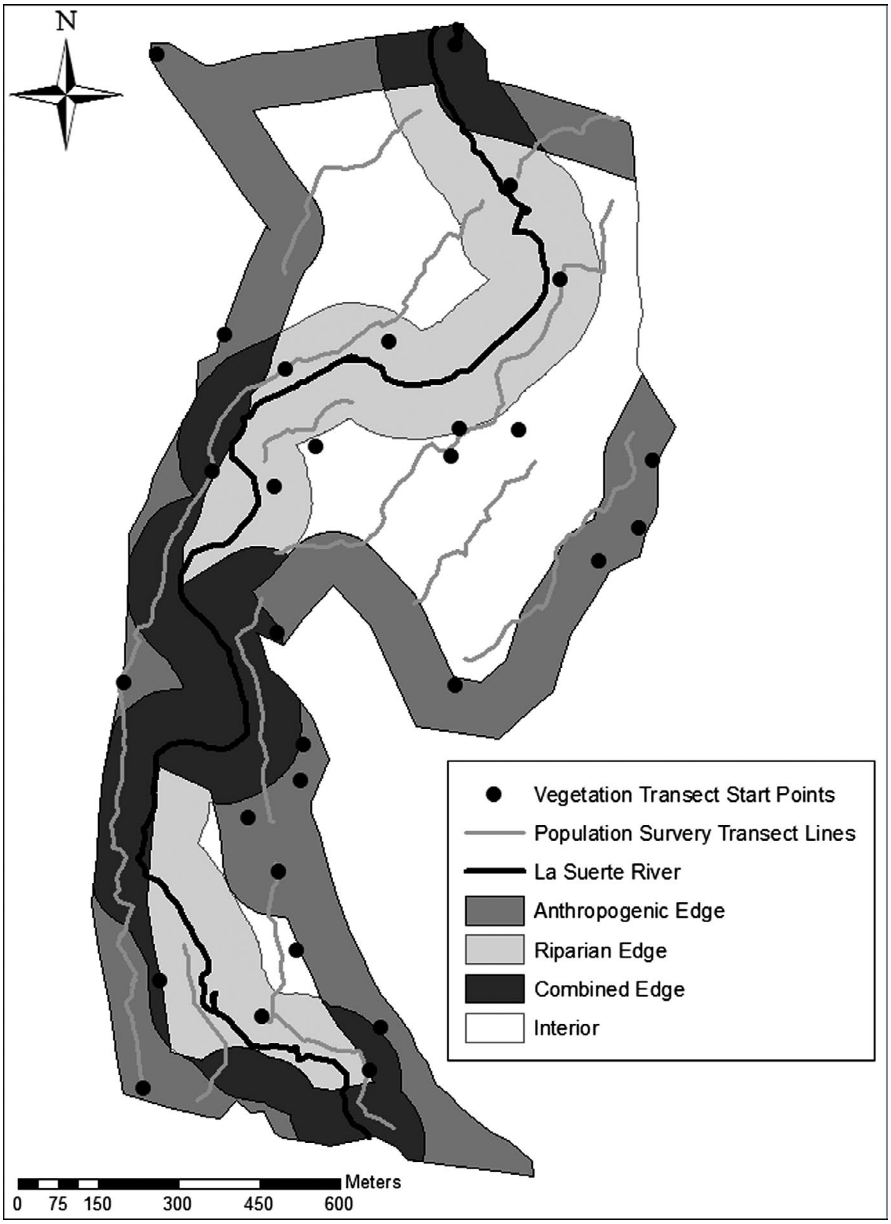

FIGURE 1 Map of the La Suerte Biological Research Station (LSBRS) displaying forest anthropogenic edge, riparian edge, combined anthropogenic and riparian edge, and interior zones, vegetation transects, and population survey transects. The Large Forest is to the north, the Small Forest is to the south, and camp is between them

vegetation data we recorded (i.e., tree species richness, dbh, tree density, canopy cover) were not expected to vary considerably between 2015 and 2017, thus allowing for comparison with monkey data from the same time of year in 2015 and 2016.

We surveyed vegetation along riparian edge (less than 100m from the La Suerte River), anthropogenic forest edge (within 100m of clear-cut area including cattle pasture, road, and camp), combined riparian and anthropogenic forest edge ("combined edge" – overlapping edge area within 100m of both anthropogenic and natural forest edge), and interior transects (more than 100m from any type of forest edge; Figure 1). We defined edge as 100m from any human-caused or natural forest border, following previous definitions (Bolt et al., 2019, 2018; Laurance, Goosem, & Laurance, 2009; Pohlman, Turton, & Goosem, 2009). Each vegetation transect was 50m × 5m. We conducted 29 randomly situated vegetation transects spanning riparian edge, anthropogenic edge, combined edge, and interior habitat zones (*n* = 7 riparian edge, *n* = 12 anthropogenic edge, *n* = 6 combined edge, and *n* = 4 interior transects). Vegetation was surveyed across the Large Forest (one transect/0.062 km^2), the Small Forest (one transect/0.044 km^2) and camp (one transect/0.035 km^2; Figure 1). Within each transect, we recorded tree species when possible along the entire transect line and within 2.5 m of either side of it, and measured circumference at breast height for trees with circumferences larger than 10 cm. Using these tree data, we calculated tree median dbh and density within each transect. For transects within the Large Forest, we calculated tree species richness through determining total number of tree species in each transect, but did not do so for Small Forest transects due to time constraints and limited personnel. To approximate level of canopy cover for every 1-m interval on each vegetation transect, we used a point sampling method by looking directly overhead and giving a canopy coverage score from 1–4 (1 = 0%–25% tree canopy coverage,

TABLE 1 Summary of generalized linear model comparisons for vegetation characteristics and monkey encounter rate at La Suerte Biological Research Station (LSBRS)

	Null model AICc	Forest zone model AICc	Forest zone ΔAICc	Null model weight	Forest zone model weight	Estimate from null model	95% CI from null model
Vegetation characteristics							
Richness (# species)	89.4	92.2	2.8	0.806	0.194	4.9	3.9–5.9
Density (trees/m^2)	79.6	86.8	7.2	0.974	0.026	0.064	0.045–0.090
dbh (cm)	61.2	64.3	3.1	0.821	0.179	22.1	17.2–28.3
Canopy cover (%)	80.6	87.6	7.0	0.971	0.029	71.7	63.6–78.6
Monkey encounter rate							
Capuchin (groups/km)	275.2	276.4	1.2	0.643	0.357	0.42	0.24–0.61
Howler (groups/km)	406.5	408.2	1.7	0.696	0.304	0.68	0.46–0.92
Spider (groups/km)	181.8	187.4	5.6	0.944	0.056	0.28	0.15–0.41
All Monkeys (groups/km)	643.7	645.4	1.7	0.700	0.300	1.15	0.81–1.53

Note: Although models including forest zone did not differ significantly from null models for vegetation characteristics or monkey encounter rates, models including forest zone did result in significant weights for certain responses. Estimates from null models represent the value across the entire study area irrespective of forest zone. These estimates were calculated from the null model's intercept and transformed to the scale of the original measurement.

2 = 26%–25% coverage, 3 = 51%–75% coverage, and 4 = 76%–100% coverage). The same data collectors estimated tree cover for all vegetation surveys, and inter-observer reliability was therefore not a confounding factor for analyses.

To assess similarities and differences in tree characteristics across riparian edge and other forest zones—anthropogenic edge, combined edge, and forest interior—we fit generalized linear models: one for each of the vegetation characteristics measured. We assumed that tree species richness followed a Poisson distribution whose log mean depended linearly on forest zone as a fixed effect. Similarly, we assumed that transformed vegetation responses (log(tree density), log(dbh), logit(canopy)) followed a normal distribution whose mean depended on the fixed effect of forest zone. For each vegetation response, we also fit a null (i.e., intercept-only) model for each appropriately transformed response, and subsequently calculated each model's AICc and corresponding AICc weights within each model pair (i.e., null and forest zone) (Burnham & Anderson, 2002). We then employed a multimodel inference approach to calculate and compare estimates for pairs of forest zones using generalized linear hypothesis tests. We fit models in R version 3.6.0 (R Core Team, 2019) with the glm function and calculated model-averaged estimates using the MuMIn package (Bartoń, 2019) and their corresponding confidence intervals using the glht function in the multcomp package (Hothorn, Bretz, & Westfall, 2008).

2.3 | Population survey

We conducted a systematic primate population survey using 11 line transects (T1-T11) which were spaced approximately 150m apart throughout the Large and Small Forests and camp (Figure 1), following methods by Pruetz and Leasor (2002). The total length of transects in each habitat were 1.59 km in anthropogenic edge, 1.76 km in forest interior, 1.64 km in combined edge, and 1.69 km in riparian edge. Transects were walked 10–34 times each throughout the study (n = 253 times in total; T1 = 13 times in 2015 and 10 times in 2016, T2 = 10 times in 2015 and discontinued in 2016 due to safety concerns, T3 = 16 times in 2015 and 10 times in 2016, T4 = 21 times in 2015 and 13 times in 2016, T5 = 14 times in 2015 and 11 times in 2016, T6 = 12 times in 2015 and 9 times in 2016, T7 = 13 times in 2015 and 9 times in 2016, T8 = 15 times in 2015 and 11 times in 2016, T9 = 10 times in 2015 and 9 times in 2016, T10 = 10 times in 2015 and 9 times in 2016, T11 = 16 times in 2015 and 12 times in 2016), with differences in number of times walked caused by variation in transect accessibility with changing weather conditions. In order to minimize habitat disturbance at LSBRS, we relied primarily on established trails but included some off-trail area for most transects. We independently walked each transect at a speed of ~ 1.5 km/hour (Peres, 1999) during daylight hours, pausing every 100m for 2 minutes to thoroughly search the area for primates (Pruetz & Leasor, 2002). Although transects were sampled between 0530–1730, most sampling took place between 0730–1145 and 1230–1600, meaning that groups were no longer in their sleeping trees yet any change in monkey detectability based on time of day would be accounted for given the broad spectrum of sampling times (Matsuda, Otani, Bernard, Wong, & Tuuga, 2016). To avoid the likelihood of repeated sampling of the same primate individuals and groups on the same day, adjacent transects were not sampled on the same day (i.e., only odd or even-numbered transects were sampled on a given day to ensure that all transects sampled during a single day were separated by at least 300m) and individual transects were sampled a maximum of once daily, with one to three transects sampled concurrently in randomized order at any given time. Individual monkey and group identity were unknown in this population; throughout the course of the study, individuals and groups were likely sampled multiple times, although not on the same day. During sampling, upon encountering at least two howler and capuchin individuals or at least one spider monkey, we recorded the time and location (GPS point taken with a Garmin GPSMAP 62s Handheld GPS Navigator). Every GPS point recorded was considered a single sighting of a monkey group (Pruetz & Leasor, 2002), whether the sighting consisted of single spider monkeys, two individuals of howler and capuchins, or a large group. Sightings of single howler and capuchin monkeys were excluded from data collection to ensure we were not including lone males or other outliers in our group measure, while sightings of single spider monkeys were included because individuals can range alone within their fission–fusion social system (di Fiore et al., 2011).

To compare group encounter rates between riparian edge and other forest zones—anthropogenic edge, combined edge, and interior—we fit four generalized linear mixed models (GLMM): one representing each primate species and one grouping all primate encounters together. Within every model, we presumed that the number of group sightings for every transect survey followed a Poisson distribution whose log mean depended linearly on forest zone as a fixed effect with transect as a random effect. Additionally, every model employed a constant offset term to control for differing effort on transects of different length. We statistically assessed differences in encounter rates by forest zone using the same protocol that we used for vegetation responses. We fit models with the glmer function in the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) using R version 3.6.0 (R Core Team, 2019) and calculated model-averaged estimates using the MuMIn package and their corresponding confidence intervals with the glht function in the multcomp package (Hothorn et al., 2008).

3 | RESULTS

For vegetation characteristics, null models were favored over forest zone models according to AICc (Table 1). However, model-averaged estimates of tree species richness and dbh differed by forest zone. As predicted, tree species richness was similar in the forest interior (5.61, 95% CI: 3.60–7.40) and the riparian edge (4.51; 95% CI: 3.63–5.61), while tree species richness was higher in riparian edge than in anthropogenic edge (2.91; 95% CI: 2.25–3.74). Tree dbh in the forest interior (24.4 cm; 95% CI: 14.2–41.8 cm) was greater than dbh in anthropogenic edge (11.2 cm; 95% CI: 9.6–13.0 cm), but only marginally higher than dbh in riparian edge (14.3 cm; 95% CI: 10.5–19.6 cm; Figure 2). Null models were strongly favored over forest zone models for canopy cover and tree density, resulting in similar model-averages across forest zone (Figure 2).

For monkey encounter rates, null models were favored over forest zone models according to AICc (Table 1). However, the model-averaged estimate of mantled howler monkey encounter rate in riparian edge (1.23 groups/km; 95% CI: 0.89–1.72 groups/km) was roughly twice (2.1 times, 95% CI: 1.0–4.3 times) that in forest interior (0.60 groups/km; 95% CI: 0.33–1.05 groups/km; Figures 3 and 4), but only marginally higher than in anthropogenic edge (0.88 groups/km; 95% CI: 0.54–1.43 groups/km). On the other hand, the model-averaged estimate for capuchin monkey encounter rate in riparian edge (0.29 groups/km; 95% CI: 0.15–0.56) was less than half (0.4 times, 95% CI: 0.2–1.0) that in anthropogenic edge (0.70 groups/km; 95% CI: 0.50–0.99 groups/km), but only marginally lower than in the interior (0.41 groups/km; 0.24–0.72 groups/km; Figures 3 and 4). Because the null model was strongly favored for spider monkeys, model-averaged estimates were quite similar across forest zones (Figures 3 and 4). Combined monkey sightings in the riparian edge (1.41 groups/km; 95% CI: 1.02–1.94 groups/km) overlap with both anthropogenic edge (1.67 groups/km; 95% CI: 1.22–2.29 groups/km) and forest interior (1.08 groups/km; 95% CI: 0.73–1.61 groups/km; Figures 3 and 4).

4 | DISCUSSION

We found limited support for our hypothesis (H1) that vegetation would differ in how it responded to riparian versus anthropogenic edges. Tree species richness was higher in riparian edge than anthropogenic edge, but other vegetation characteristics were similar between riparian and anthropogenic edge zones. Consistent with previous work (Bolt et al., 2019, 2018), tree species richness and median tree dbh were higher in forest interior than anthropogenic edge, even with the additional forest edge zones now incorporated. However, our vegetation results should be interpreted with a degree of caution, in that the number of transects surveyed for each vegetation type was relatively small (range of n = 4–12 transects per habitat zone). A larger-scale survey consisting of a greater number of vegetation transects in each forest zone may yield different results.

Our hypothesis (H2) that monkeys would vary in how they responded to riparian edge was partially supported. Our predictions about monkey response to riparian zone were met for the mantled howler monkey, were partially supported for the capuchin monkey, and were not supported for the spider monkey. Consistent with predictions, howler monkey encounter rate was highest in riparian edge, lower in anthropogenic edge, and lowest in forest interior, while capuchin monkey encounter rate was highest in anthropogenic edge, but contrary to predictions, capuchins were encountered at lower rates in riparian edge than in forest interior. In contrast, spider monkeys were encountered at similar rates throughout the forest. While

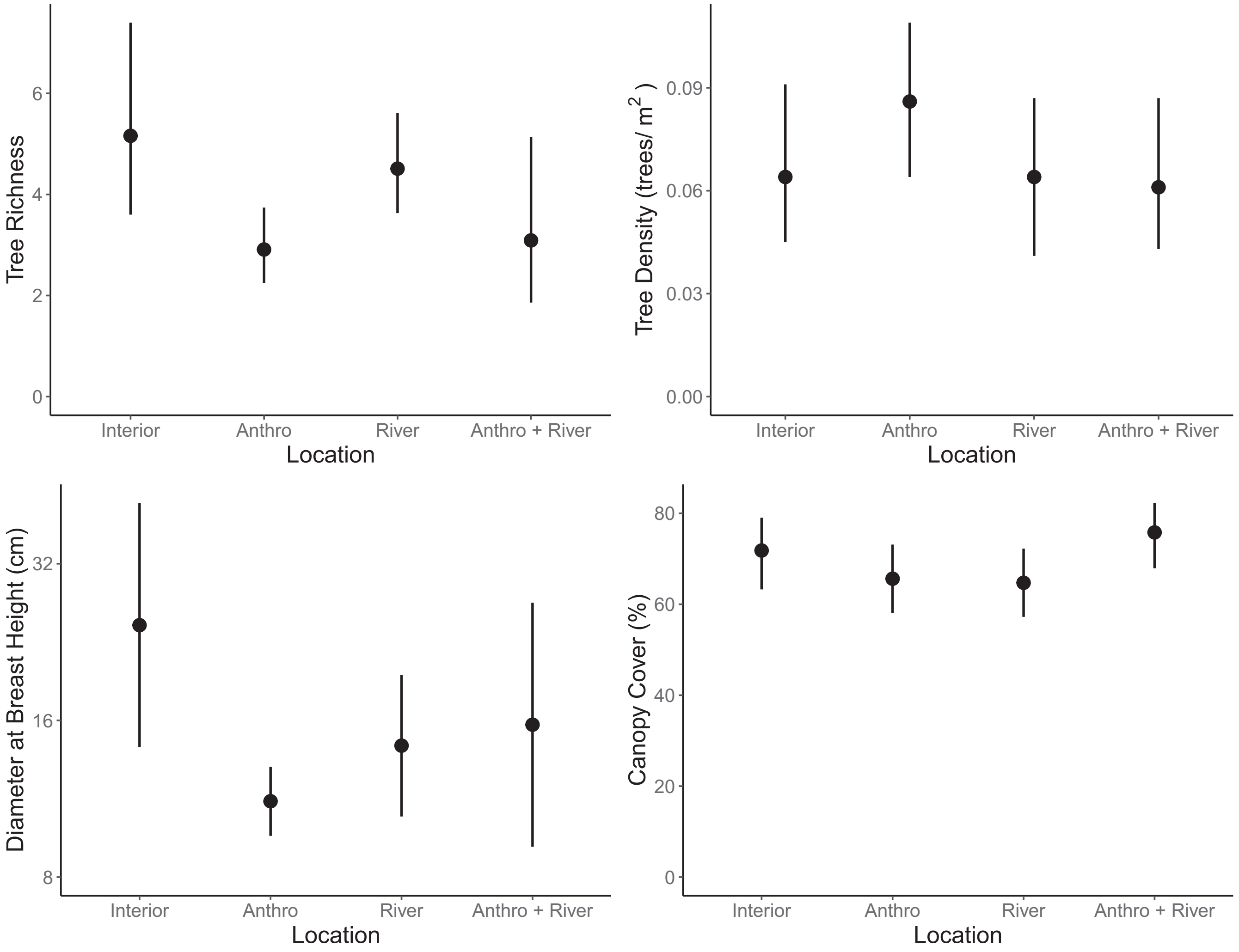

FIGURE 2 Vegetation characteristics (tree species richness, tree density, median tree dbh and mean percent canopy cover, all with 95% confidence intervals) across edge zones and interior of LSBRS forest

our spider monkey results are consistent with previous work at LSBRS showing equal encounter rates for all three monkey species across forest interior and anthropogenic edge (Bolt et al., 2018), with the inclusion of additional edge zones (i.e., riparian and combined edge), both howler and capuchin monkeys tended to prefer forest edges.

Howler monkeys were encountered at a higher rate at riparian edge compared to forest interior, indicating a positive edge response. Our findings are in line with edge-positive results from Guianan howler monkeys (Lenz et al., 2014) and mantled howler monkeys (Skrinyer, 2016) from the Osa Peninsula in Costa Rica. However, our study shows that mantled howlers are selective about the type of edge environment they favor; they are found at higher density in riparian edge compared to anthropogenic edge. Lenz and associates (2014) surveyed edge transects at the boundary of lightly logged primary forest, which given the proximity to undisturbed forest may have contained a variety of howler monkey food sources. Similarly, Skrinyer (2016) did not differentiate between natural and anthropogenic edge when investigating howler monkey preferences in his study. The natural edges likely had more food sources available for howler monkeys than anthropogenic edges; riparian edge in particular had a larger number of tree species compared to anthropogenic edge (Skrinyer, 2016). The difference in tree species richness between riparian and anthropogenic edge at LSBRS in our study suggests that howler monkey preference for riparian area could be influenced by the presence of more and/or larger preferred howler monkey feeding trees at the river's edge compared to other forest zones.

Mantled howler monkeys are known to be species-selective feeders that mostly eat from trees (Estrada, 1984). At LSBRS, preliminary investigation shows that howlers spend more time in larger trees, and feed from trees that are taller and have wider trunks than the average tree size across forest zones (Russell, 2018; A.L. Schreier & L.M. Bolt, unpublished data). Further, mantled howler monkeys consumed leaves from a total of six tree species while within 50m of the river's edge, while eating leaves, fruit, and flowers from at least ten tree species in forest interior (Russell, 2018). These results suggest that when forest zones are

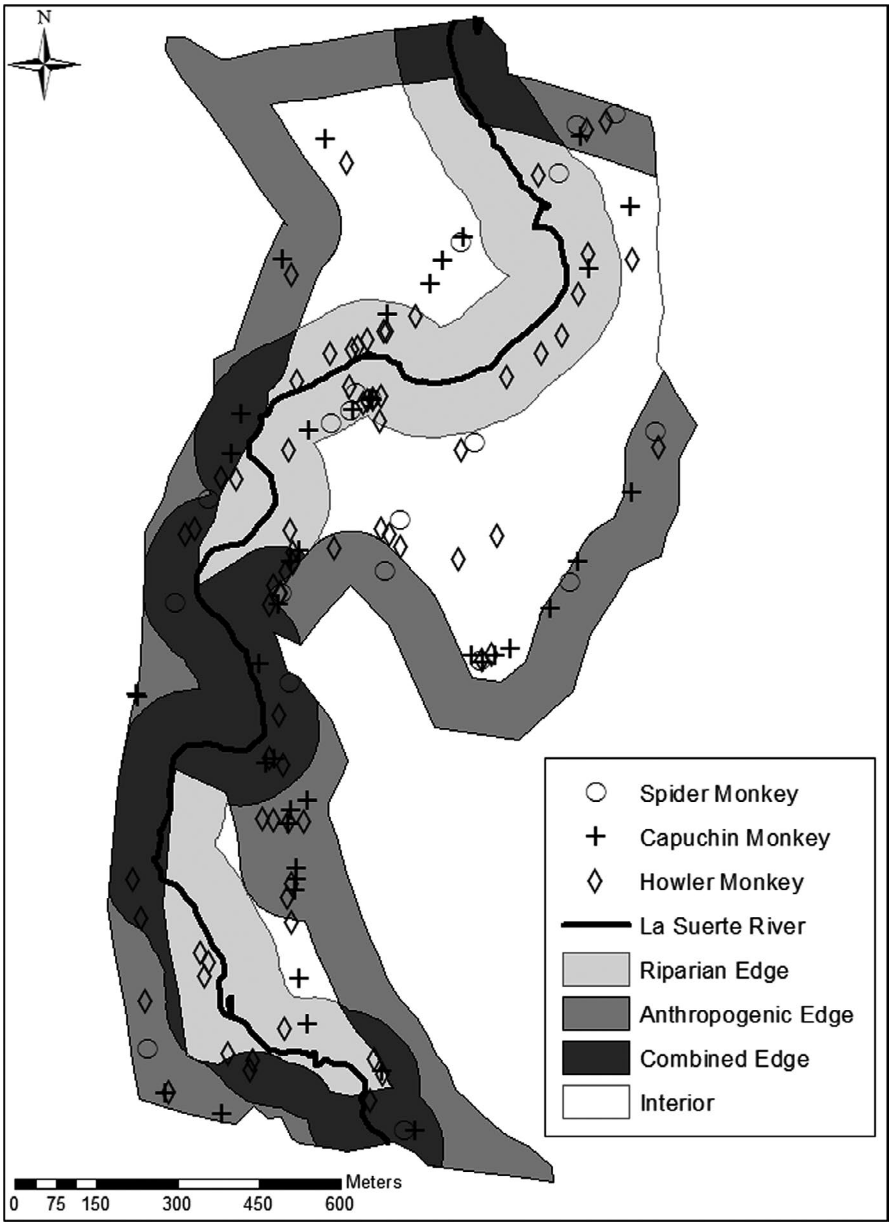

FIGURE 3 Map showing monkey sightings by species in edge zones and interior of LSBRS forest

compared, differences in species richness for howler monkey feeding trees may not ultimately be driving the results in our present study. Russell (2018) found that howler monkeys primarily fed from *Ficus insipida* and *Cecropia insignis* trees at LSBRS, which are both light-demanding pioneer species that can survive in forest edges. With both tree species found across habitat zones at LSBRS (Russell, 2018), factors other than preferred feeding tree species availability are likely influencing riparian edge preferences. Feeding tree size should be investigated across habitat zones as a possible driver for riparian edge preference. Howler monkeys prefer larger trees within forest fragments (Munoz et al., 2006), and given the high light levels and availability of water near the river, these preferred large trees may be more common at riparian edge than within forest interior.

In accordance with predictions, we found that white-faced capuchin monkeys were encountered at the highest rates in anthropogenic edge, but contrary to predictions, were encountered at the lowest rates in riparian edge, not forest interior. Our results are consistent with edge-positive findings for the brown capuchin monkey (Lenz et al., 2014), but contradict results for the white-faced capuchin at another tropical wet forest site in Costa Rica (Skrinyer, 2016). Skrinyer (2016) found that capuchin monkeys used both edge and interior zones for feeding and resting, suggesting that sufficient food resources were distributed throughout forest zones. In contrast, at LSBRS, preliminary data showed capuchins using trees from all forest zones for resting (R. Schlaht, unpublished data) but mostly anthropogenic edge trees for feeding (A.L. Schreier & L.M. Bolt, unpublished data). In addition to consuming native plant species such as *Ficus* throughout habitat zones, capuchins consistently fed from photophilic, invasive fruit trees such as *Nephilium lappaceum* and *Garcinia mangostana*, which are primarily found in anthropogenic edge at LSBRS (A.L. Schreier

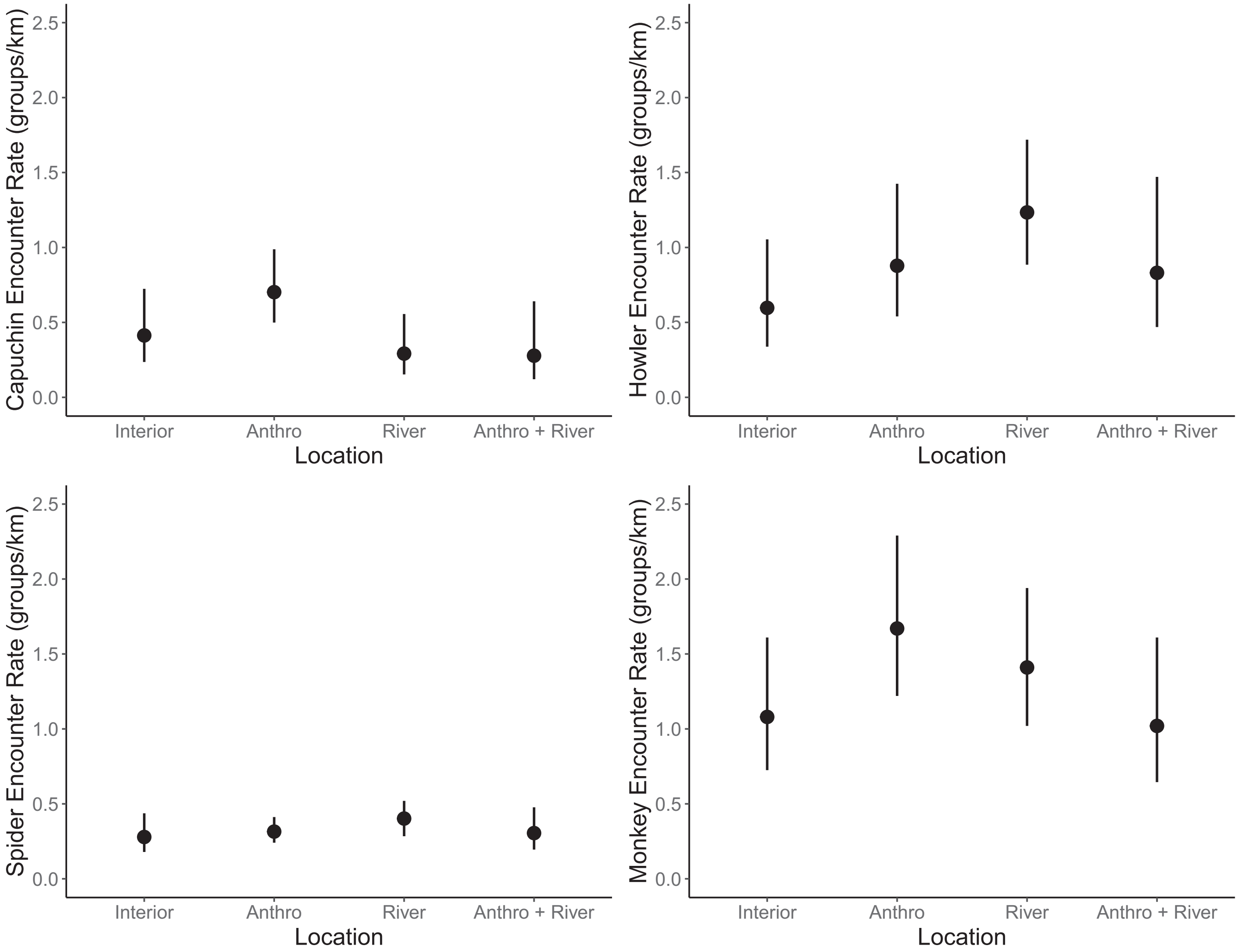

FIGURE 4 Monkey encounter rate (groups/km with 95% confidence intervals) overall and by species in edge zones and interior of LSBRS forest

& L.M. Bolt, unpublished data). Capuchin preference for these food sources may be driving their higher encounter rate in anthropogenic edge zones, with these preferred foods being much more prevalent near human-modified habitat (A.L. Schreier & L.M. Bolt, unpublished data). In contrast, the absence of preferred *N. lappaceum* and *G. mangostana* trees in riparian edge may explain the lower capuchin encounter rate by the river (A.L. Schreier & L.M. Bolt, unpublished data). With small body size and lower canopy preference (Fleagle & Mittermeier, 1980; Ford & Davis, 1992), capuchins can easily move through the smaller trees in anthropogenic edge and also may encounter less feeding competition from sympatric primate species in this habitat zone, thus likely further driving their preferences. Further study of white-faced capuchin feeding ecology and tree use is needed at LSBRS to better understand the factors driving their habitat zone preferences.

Contrary to predictions, Central American spider monkeys were found equally across forest zones, exhibiting neutral edge effects. These results contradict edge-negative findings for the Guianan spider monkey (Lenz et al., 2014), but are similar to findings for Central American spider monkeys at another Costa Rican site (Skrinyer, 2016). Skrinyer (2016) found that spider monkeys used edge and interior zones equally and suggested this was due to spider monkey food tree species including *Ficus insipida* being abundant in edge habitat. *Ficus insipida* and other spider monkey food species are found throughout LSBRS, spanning forest interior and edge zones including riparian edge (Russell, 2018). Although spider monkey feeding behavior has not been studied in detail at LSBRS, they have been observed feeding throughout diverse edge and interior forest zones and using some of the same feeding trees as howler and capuchin monkeys (A.L. Schreier & L.M. Bolt, unpublished data), suggesting feeding tree species are sufficiently abundant throughout the site to allow some feeding in each zone. They have also been consistently observed feeding on invasive species such as *N. lappaceum* in anthropogenic edges, which means that although their overall edge response is neutral, they may be feeding from different tree species while in different forest zones. Further research is necessary to explore the range of factors contributing to the neutral edge response of Central

American spider monkeys at LSBRS, including closer examination of their feeding behavior and feeding tree distribution.

In addition to feeding ecology, predation pressure may also be driving species-specific edge responses at LSBRS. While Central American spider monkeys and white-faced capuchins may be adapted to range across forest zones to fulfill their energetic requirements, and have evolved fast locomotory behavior (Fleagle & Mittermeier, 1980) that enables them to effectively flee from predators, mantled howlers may be encountered more frequently near riparian forest edge due to higher predation pressure in forest interior combined with their energy-minimizing activity budget and slow-moving locomotory behavior (Milton, 1980). Howler monkeys may engage in riverine refuging behavior in order to have the ability to detect potential predators from greater distances than in other forest zones (Matsuda, Tuuga, & Bernard, 2011) and therefore may have spent more time near the river in order to more effectively avoid predators. Although smaller sympatric monkey species such as the capuchin may be at higher overall predation risk than larger howler monkeys (Cheney & Wrangham, 1987; di Fiore, 2002), and sympatric spider monkeys are also at risk of predation (Cristóbal-Azkarate, Urbani, & Asensio, 2015), the howler monkeys at LSBRS may be especially likely to engage in riverine refuging behavior due to their energy-minimization dietary strategy and comparative inability to quickly flee from threats (Milton, 1980). At LSBRS, known monkey predators including the ocelot (*Leopardus pardalis*), harpy eagle (*Harpia harpyja*), tayra (*Eira barbara*), and dog (*Canis familiaris*) (reviewed in Miller & Treves, 2007; Raguet-Schofield, 2008; reviewed in Cristóbal-Azkarate et al., 2015; Molina, 2015) are found across forest zones, and the howler monkeys howl more frequently in response to potentially threatening species in forest interior compared to anthropogenic forest edge (Bolt et al., 2019) but did not howl more than expected by chance in riparian zones (Bolt, Russell, et al., 2020), suggesting that a higher level of vigilance may be necessary when in forest interior at LSBRS.

While predator species' habitat zone preferences at LSBRS have not been studied, in other forest fragments, predation risk can be very high in specific forest areas and is generally higher in a fragment than in a larger continuous forest (Irwin, Raharison, & Wright, 2009). Primates are known to vary habitat use based on predator distribution within an environment (Willems & Hill, 2009) and to modify ranging and foraging patterns to avoid predators (Miller & Treves, 2007). Some Old World monkey species prefer exposed riparian areas as sleeping sites in order to better detect approaching predators (e.g., Proboscis monkey [*Nasalis larvatus*], long-tailed macaque [*Macaca fascicularis*]; Matsuda et al., 2011; Salter, Mackenzie, Nightingale, Aken, & Chai, 1985; van Schaik, van Amerongen, & van Noordwijk, 1996) and use these riparian areas at higher rates in order to avoid predators (Matsuda et al., 2011), suggesting that howler monkeys may be doing this at LSBRS. While it is currently unknown whether monkey predators may prefer edge or interior zones at LSBRS, at other sites, predators are encountered at equal rates in both edge and interior (e.g., snakes and owls) or situate themselves around available resources (e.g., mammalian predators) (Larivière, 2003; Michel, Jiménez-Franco, Naef-Daenzer, & Grüebler, 2016). With predators potentially situating themselves around interior prey resources and/or across habitat zones at LSBRS, slow-moving howler monkeys may be able to engage in more efficient vigilance at riparian edge through riverine refuging (Matsuda et al., 2011), thus driving their preferences for this habitat zone rather than forest interior. Further research on predator abundance and habitat use at LSBRS is necessary to explore these alternatives.

Inter-species interactions among sympatric primates may have additionally affected monkey ranging patterns in this study. Although all three sympatric species found at LSBRS are able to neutrally co-exist in large fruiting trees such as *Ficus* species (Cristóbal-Azkarate et al., 2015; Haugaasen & Peres, 2009; A.L. Schreier & L.M. Bolt, unpublished data), mantled howler monkeys are also impacted by the approach or close proximity of white-faced capuchin and Central American spider monkeys when they are feeding, with howlers typically losing in inter-species agonistic interactions and being displaced from fruiting trees (Cristóbal-Azkarate et al., 2015; Rose et al., 2003). This negatively impacts howler monkey access to fruit, with howler monkeys likely losing in competitions with other primate species due to their energy-minimization strategy (Cristóbal-Azkarate et al., 2015; Milton, 1980). In fragmented habitats, competition between howler monkeys and sympatric species is thought be greater than in undisturbed landscapes (Cristóbal-Azkarate et al., 2015) due to the smaller size of trees and smaller amount of fruit available in fragments (Arroyo-Rodriguez & Mandujano, 2006). In these lower-quality habitats, howler monkeys have been observed eating fallback foods such as eggs (Bicca-Marques, Muhle, Prates, Oliveira, & Calegaro-Marques, 2009) and performing species-atypical behaviors such as traveling on the ground (Pozo-Montuy & Serio-Silva, 2007). In the fragmented forest at LSBRS, while howlers have not been observed eating eggs and have only rarely been observed traveling on the ground (A.L. Schreier & L.M. Bolt, unpublished data), howlers may be found at greater frequency in riparian zone trees due to being displaced from other forest areas by sympatric species rather than due to any preference for the riparian zone. With LSBRS vegetation results showing that the forest interior has the largest trees and higher-quality vegetation than anthropogenic edge (Bolt et al., 2019, 2018), howler monkeys may have concentrated themselves in the riparian zone not because they prefer it, but because they have been driven from forest interior by both sympatric species and from the anthropogenic edge zone by capuchin monkeys, leaving the riparian zone available to occupy. Alternately, if there are more large preferred feeding trees, which all three species favor (e.g., *Ficus* trees, Haugaasen & Peres, 2009), in riparian edge than in other forest zones, capuchin and spider monkeys may tolerate howler monkeys more than in other zones, accounting for howlers' tendency to be found at higher frequency in riparian edge. Further study of primate interspecific relationships at LSBRS is needed to test this range of possibilities.

Overall, our results show some support for Lidicker's (1999) prediction that the body size and general dietary adaptations of animals will condition species-level response to habitat fragmentation. We conducted primate population surveys from May–August, during the wet season in northeastern Costa Rica. This restricted surveying time is a study limitation, as some studies (e.g., Chapman, 1987) have shown seasonal and monthly variation in food availability for these species, which would influence their ranging patterns. If we had conducted monkey population surveys during other months of the year, such as the dry season, we may have found different ranging patterns for each species. Chapman (1988) studied foraging and ranging in the same three monkey species across seasons at another site in Costa Rica, but did not find any association between feeding behavior or range use and seasonality. Given these results (Chapman, 1988), seasonal differences may have some effect, but are not necessarily expected to strongly impact species-level preferences for edge or interior zones in our study. Our population survey results may also have been influenced by our methods, with 11 short transects sampled repeatedly to calculate encounter rates rather than longer transects surveyed less frequently. Given the relatively small size of the forest fragment at LSBRS, however, longer transects were not feasible. Additionally, forest zone sizes differed at La Suerte, with riparian (0.62 km^2) and anthropogenic edge (0.58 km^2) zones covering more than twice the area of interior (0.252 km^2) and combined (0.22 km^2) zones, but population survey transect lengths were comparable across forest zone (ranging from 1.59 to 1.76 km). These differences in forest zone size coupled with similarities in surveying effort were not ideal, but any potential oversampling of interior and combined zones were controlled for by the statistical tests we employed. Finally, Small and Large Forests at LSBRS were different sizes (Bolt et al., 2018); thus, edges may show differing effects between fragments. Although this study did not differentiate between fragments, future study will investigate these potential differences.

Previous work at LSBRS indicated that the three monkey species did not prefer interior forest zones to anthropogenic edge, suggesting the resilience of these primates at withstanding some degree of habitat fragmentation (Bolt et al., 2018). Our results from the present study show that although all three sympatric species are found across edge and interior forest zones at LSBRS, mantled howler monkeys are found at higher density in riparian forest edge compared to forest interior, while white-faced capuchin monkeys are found at higher density in anthropogenic forest edge compared to interior. Although our results suggest that capuchin monkeys may be able to flourish in forest adjacent to human-modified landscapes, they also demonstrate that howler monkeys prefer natural rather than anthropogenic edges; their preference for riparian forest edge should be accounted for in long-term Neotropical conservation planning. For example, during deforestation or selective logging, destruction of riparian zone vegetation should be minimized in order to preserve a greater amount of preferred howler monkey habitat. This could help mitigate the decline of howler monkey populations. As rampant deforestation continues in northeastern Costa Rica, it is vitally important to further study how monkeys use their remaining areas of habitat while some large fragments still exist. Within forest fragments, better understanding how monkeys and vegetation are faring within different edge and interior forest zones will allow conservationists to more effectively plan long-term initiatives; while capuchins thrive in modified forest edges, it is critical to ensure that mantled howler monkeys remain “down by the riverside” for years to come.

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AUTHOR CONTRIBUTIONS

LMB designed the study, performed research, and wrote the paper. ALS designed the study, acquired funding, performed research, performed data curation and analysis, contributed to writing the paper, and contributed critically to drafts. KAV performed data curation and analysis, produced figures and tables, contributed to writing the paper, and contributed critically to drafts. ELS performed data curation and analysis, produced figures, and reviewed final drafts of the paper. NLB designed the study, performed research, and reviewed final drafts of the paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.qz612jm9t (Bolt, Schreier, Voss, Sheehan, & Barrickman, 2020).

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