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RESEARCH ARTICLE

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High density of white-faced capuchins (*Cebus capucinus*) and habitat quality in the Taboga Forest of Costa Rica

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Abstract

Across the globe, primates are threatened by human activities. This is especially true for species found in tropical dry forests, which remain largely unprotected. Our ability to predict primate abundance in the face of human activity depends on different species' sensitivities as well as on the characteristics of the forest itself. We studied plant and primate distribution and abundance in the Taboga Forest, a 516-ha tropical dry forest surrounded by agricultural fields in northwestern Costa Rica. We found that the density of white-faced capuchins (*Cebus capucinus*) at Taboga is 2–6 times higher than reported for other long-term white-faced capuchin sites. Using plant transects, we also found relatively high species richness, diversity, and equitability compared with other tropical dry forests. Edge transects (i.e., within 100 m from the forest boundary) differed from interior transects in two ways: (a) tree species associated with dry forest succession were well-established in the edge and (b) canopy cover in the edge was maintained year-round, while the interior forest was deciduous. Sighting rates for capuchins were higher near water sources but did not vary between the edge and interior forest. For comparison, we also found the same to be true for the only other primate in the Taboga Forest, mantled howler monkeys (*Alouatta palliata*). Year-round access to water might explain why some primate species can flourish even alongside anthropogenic disturbance. Forest fragments like Taboga may support high densities of some species because they provide a mosaic of habitats and key resources that buffer adverse ecological conditions.

KEYWORDS
Cebus imitator, conservation, edge effect, fragmentation, tropical dry forest

1 | INTRODUCTION

The majority of non-human primates (hereafter, "primates") across the globe are either under threat of extinction or experiencing population declines (Estrada et al., 2018). Primate densities tend to decrease in unprotected areas, yet primates can nevertheless still flourish in areas of human activity, suggesting both a vulnerability and resilience to anthropogenic disturbance (Cavada, Barelli, Ciolli, & Rovero, 2016). Some species show remarkable behavioral flexibility and quickly adjust to new circumstances while others get pushed closer to extinction (Kulp & Heymann, 2015; Laurance et al., 2007; Ries, Fletcher, Battin, & Sisk, 2004). This variation is likely due to a number of factors, from species-specific characteristics (i.e., dietary breadth) to habitat characteristics (i.e., total fruit production vs. the timing of fruit availability: Stevenson, 2016). For example, across variously degraded Bornean forests, tree density predicts primate species richness much better than the degree of habitat disturbance (i.e., number of times logged) does (Bernard et al., 2016). Understanding how species and habitat characteristics together contribute to resilience is critical for effective conservation efforts.

One key habitat that remains relatively understudied is the tropical dry forest. Tropical dry forests are widely distributed, diverse habitats that simultaneously support a number of endemic species while also experiencing significant anthropogenic disturbance (Dryflor et al., 2016; Miles et al., 2006). Despite warnings about the vulnerability of these habitats (e.g., Janzen, 1988), tropical dry forests worldwide remain unprotected and understudied (Dexter et al., 2018). For example, over 90% of the tropical dry forests in North and Central America are vulnerable to anthropogenic disturbance (Miles et al., 2006), due in part to high fragmentation (e.g., in Costa Rica: Portillo-Quintero & Sánchez-Azofeifa, 2010). However, a variety of primate species are found in tropical dry forests, with some even continuing to flourish in fragments. For example, white-faced capuchins (*Cebus capucinus* or *C. capucinus imitator*: Lynch Alfaro, Izar, & Ferreira, 2014), mantled howler monkeys (*Alouatta palliata*), and black-handed spider monkeys (*Ateles geoffroyi*) are common sympatric species, yet they demonstrate markedly divergent responses to fragmentation and other forms of anthropogenic disturbance (e.g., Williams-Guillén, Hagell, Otterstrom, Spehar, & Gómez, 2013).

Understanding how primate species respond to anthropogenic disturbance has important implications for conservation and reforestation efforts. This is especially true when it comes to tropical dry forests, which were once the predominant forest type on the west coast of Central America (Gillespie, Grijalva, & Farris, 2000). Spider monkeys are not expected to thrive in highly fragmented landscapes due to their large home ranges (Spehar, Link, & Di Fiore, 2010), preference for taller trees (Chapman, 1990), and highly frugivorous diet (González-Zamora et al., 2009; though see Williams-Guillén et al., 2013). By contrast, capuchin and howler monkeys are often abundant in fragmented tropical dry forests. Capuchins, as behaviorally flexible omnivores, can opportunistically exploit a broad array of plants and animals (Ford & Davis, 1992; Panger et al., 2002; Perry, 2012; Rose, 1994) and can adapt to anthropogenic disturbances that threaten many other species (i.e., showing neutral or even positive edge effects: Bolt et al., 2018 (*C. capucinus*); surviving in fragmented habitats: Lins & Ferreira, 2019 (*Sapajus flavius*); and Cunha, Vieira, & Grelle, 2006 (*Cebus* sp.)). The factors that limit capuchin densities are mainly anthropogenic (e.g., human hunting, poaching, and the pet trade (Williams-Guillén et al., 2013)) or limited access to water. For example, in dry forests, where rainfall is scarce for months at a time, capuchins appear to be constrained by access to reliable above-ground water sources (Fedigan & Jack, 2001). Howler monkeys, in contrast, are perhaps less reliant on above-ground water sources (Glander, 1978) and more capable of tolerating fragmented habitats due to their leaf-based diet (Williams-Guillén et al., 2013; i.e., showing neutral or positive edge effects: Bolt et al., 2018 (*A. palliata*); Lenz, Jack, & Spironello, 2014 (*A. macconelli*); surviving in fragmented habitats: Asensio, Arroyo-Rodríguez, Dunn, & Cristóbal-Azkarate, 2009 (*A. palliata mexicana*); Boyle & Smith, 2010 (*A. macconelli*)). Nevertheless, when forest fragmentation is accompanied by other factors (e.g., fewer large trees, increased hunting pressure, etc.) even howler monkeys are negatively impacted (i.e., Arroyo-Rodríguez & Dias, 2010; Horwich, 1998). For example, a 1976 census of howler monkeys in forest fragments in Guanacaste, Costa Rica suggested that certain populations (including the one surveyed here) were in sharp decline, and perhaps even at their nadir (Heltne, Turner, & Scott, 1976).

Here, we studied plant and primate abundance in the Taboga Forest (hereafter, "Taboga") of Costa Rica (Figure 1). Taboga presents an ideal opportunity to understand primate abundance in relation to habitat quality for a number of reasons. First, Taboga has an unusually high density of capuchins compared with other forests in the region (Table 1). Second, the 789-ha forest (of which 516 ha are protected and the focus of this study) is irregularly shaped, such that nearly 40% of the protected forest is within 100 m of an anthropogenic edge and therefore susceptible to the most significant effects of fragmentation (Laurance et al., 2002). Third, the forest is dissected by a series of canals used in irrigation and (according to aerial photos of the area: Google Earth Pro, Dec, 1984) has been completely surrounded by sugar cane and rice farmland for at least three decades, when a portion of the fragment became protected as the Taboga Forest Reserve. Therefore, we are able to look at the long-term impacts of two types of human disturbance that may have opposing effects: habitat fragmentation caused by agriculture and year-round, artificial water sources. These water sources may be particularly important because Taboga is a tropical dry forest, where the dry season would normally limit the viability of many animals that depend on above-ground water (e.g., capuchins: Fedigan & Jack, 2001).

We address three questions related to capuchin density, forest composition, and the location of capuchin group sightings: (1) What is the density of white-faced capuchins in Taboga, and how does this compare to densities at nearby sites with long-term capuchin studies?

(2) Does the composition of forest near (i.e., ≤100 m) an anthropogenic edge (e.g., roads, farmland, pasture, etc.; hereafter, "edge forest") differ from the composition of interior forest (i.e., >100 m from an anthropogenic edge) at the Taboga site? Specifically, we test three sets of predictions: (2a) We predict higher species richness, higher mean diameter at breast height (DBH), and higher canopy coverage (across seasons) in interior compared with edge forest (Bolt et al., 2018). However, because capuchins have been shown to have neutral or even positive edge effects (e.g., Bolt et al., 2018), (2b) we expect to find no significant differences in species richness and mean DBH for tree species associated with capuchins (i.e., that capuchins use for food or fur-rubbing; Table S1). Finally, because of the long-term anthropogenic activity around Taboga, (2c) we expect to find higher species richness and larger DBH for indicator tree species (i.e., those associated with the first stage of forest succession in tropical dry forests: Kalacska et al., 2004; Table S1) in edge compared with interior forest.

Finally, we ask: (3) Do the rates of capuchin sightings differ by location? Specifically, we compare rates of capuchin sightings between the edge and interior forest and between forest ≤100 m of reliable water sources (e.g., rivers and large canals; i.e., "near water sources") and forest >100 m from these water sources (i.e., "far from water sources"). As the

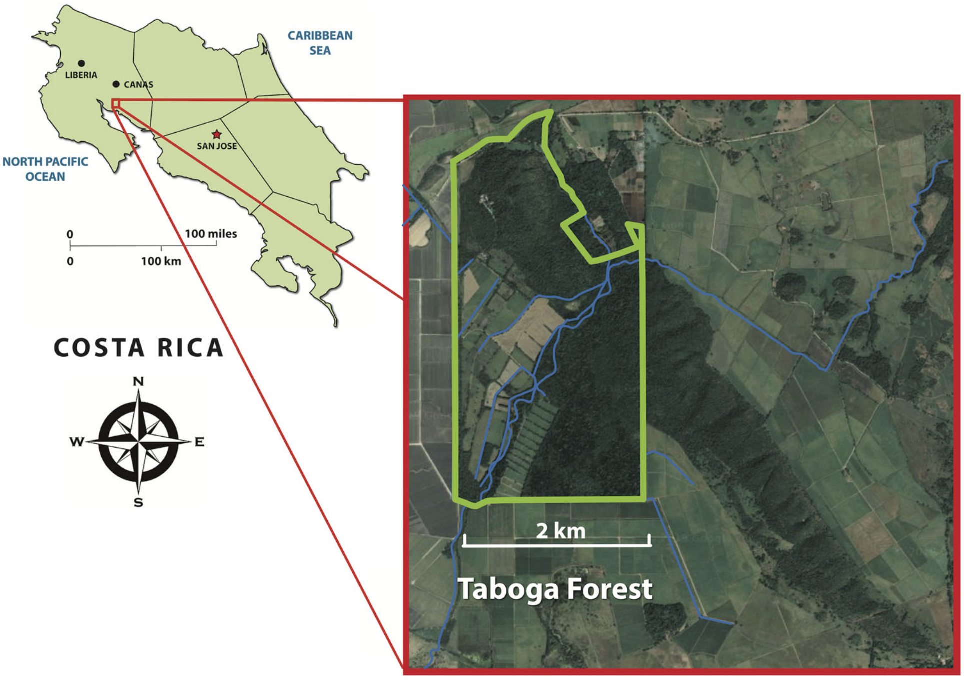

FIGURE 1 Location of the Taboga Forest in Costa Rica. The official Taboga Forest Reserve boundary (established in 1978) is within this larger reserve held by the Universidad Técnica Nacional (see Figure 2a). However, for simplicity, we refer to this entire area as the Taboga Forest or "Taboga"

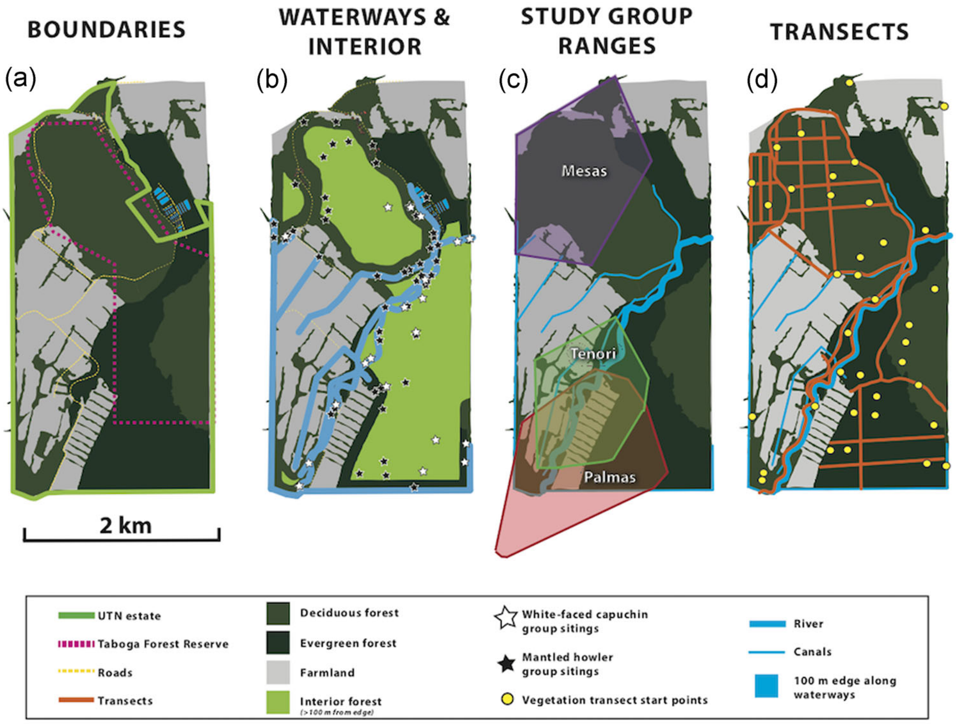

FIGURE 2 (a–d) Maps of (a) the Universidad Técnica Nacional (UTN) Estate and the Taboga Forest Reserve (together, the "Taboga Forest"), with overlays displaying: (b) 0.1 km buffer zones for forest edges and year-round water sources, (c) home ranges as convex polygons for three groups of wild white-faced capuchins (note that farmland area within the convex polygons for each capuchin group was estimated and subtracted from home ranges for density analyses), and (d) both primate and vegetation transect locations

TABLE 1 Group size and density comparison for this ("Taboga") and other white-faced capuchin sites

Sites	Description	Individuals	km^2	Individuals/km^2	Source
Lomas	Mean (3 groups)	29.00	3.64	7.97	Vogel (2004)
Lomas	Total population	216.00	36.99	5.84	Perry (personal communication)
Palo Verde	Total population	–	–	9.40	Panger et al. (2002)
Santa Rosa	Mean (7 groups)	20.10	1.98	10.15	Campos et al. (2014), Fedigan and Jack (2012)
Santa Rosa	Total population	673.00	57.70	11.66	Campos (personal communication)
BCI	Mean (4 groups)	15.00	1.16	12.93	Crofoot (2007)
BCI	Total population	300.00	15.00	20.00	Crofoot (2007)
BCI (after 2010 crash)	Total population	84.00	15.00	5.60	Milton and Giacalone (2014)
Taboga	Mean (3 groups)	21.00	0.97	21.65	Tinsley Johnson et al. (this publication)
Taboga	Total population	187.00	5.16 (7.89)	36.24 (23.70)	Tinsley Johnson et al. (this publication)

Note: The total population density estimate of Taboga includes two calculations, one based on the area of the forest surveyed and another (in parentheses) based on the total area of the contiguous forest.
Abbreviation: BCI, Barro Colorado Island.

only other primate in the Taboga Forest, we also compare how mantled howler monkey distribution maps onto these variables. As two species that typically do well in fragmented habitats, we expect that (3a) both species will show neutral edge effects (Bolt et al., 2018). However, because howler monkeys are less dependent on water sources and because our primate sighting survey took place during the dry season (when arboreal primates are easier to spot), we also expect that (3b) capuchin sighting rates will be higher near water sources while howler sighting rates will be unrelated to distance from water sources.

2 | METHODS

2.1 | Study site and subjects

We conducted this study at the Capuchins at Taboga research site, established in June 2017 in the Guanacaste province of Costa Rica. The Capuchins at Taboga research project (directed by Thore Bergman, Jacinta Beehner, Marcela Benítez, and Elizabeth Tinsley Johnson) focuses on the behavioral biology, endocrinology, and cognition of wild white-faced capuchins (*C. capucinus*; note that the taxonomy of Central American capuchins is in flux and some authors refer to Costa Rican capuchins as *C. capucinus imitator*: e.g., Hogan, Fedigan, Hiramatsu, Kawamura, & Melin, 2018; Lynch Alfaro et al., 2014; Melin et al., 2017; Ruiz-Garcia et al., 2012). The project is based in the Taboga Forest Reserve (created in 1978), which contains 296 ha of forest and represents an important piece of the fragmented biological corridor connecting the Guanacaste Mountains to the Tempisque River Basin (Figure 1). The Universidad Técnica Nacional (UTN) of Costa Rica operates an experimental farm of 702 ha that encompasses the reserve along with agricultural land and additional forest (hereafter, we use Taboga to refer to the contiguous forest in the Reserve and the UTN estate, 516 ha total: Figure 2a; however, the forest also extends beyond these boundaries, bringing the total forested area to 789 ha: Figure 1). The UTN farm consists of irrigated land dedicated to the cultivation of sugarcane (100 ha), rice (30 ha), and grass for cattle (4.5 ha). There is also a tilapia fish farm and research center as well as a water research laboratory. Taboga is almost exclusively bordered by sugarcane and rice fields, aside from a 2 km perimeter that borders private forested land and 1 km bordering public forested land. As such, the forest is characterized by distinct forest edges (i.e., farm land and roads) as well as more transitional or "natural" forest edges (i.e., canals and rivers: Figure 2b). Aerial photos of this forest from the 1940s indicate that many of these edges are at least 70 years old (Sistema Nacional de Información Territorial, Costa Rica, 1940), while aerial photos from the 1980s indicate that all of the edges used in our analyses were already in place by this time, making even the newest edges at least 35 years old (Google Earth Pro, Dec, 1984).

Taboga is largely characterized by seasonally dry tropical forest, featuring a closed canopy and seasonal deciduousness (Janzen, 1988; Miles et al., 2006). In addition to the dry forest, there are also riparian, semideciduous forests along the river and a palm forest dominated by the native species *Attalea rostrata*, part of which becomes inundated during the wet season. The area experiences two distinct seasons (Figure 3): a hot, dry season from late November to April (mean daily maximum temperature = 35.38 ± 0.20°C (*SE*); mean daily rainfall = 0.66 ± 0.27 mm (*SE*)) and a cooler wet season from May to early November (mean daily maximum temperature = 32.57 ± 0.21°C (*SE*); mean daily rainfall = 8.93 ± 1.09 mm (*SE*)). Mean daily minimum temperatures remain consistent throughout the year (dry season: 26.25 ± 0.10°C (*SE*); wet season: 25.46 ± 0.11°C (*SE*)). Importantly, the river provides fresh water year-round and many of the canals used by the farm for irrigation are consistently full throughout the dry season.

2.2 | Capuchin density

We calculated capuchin density in two ways. First, we used demographic and ranging data collected from our three habituated groups ("Tenori," "Mesas," and "Palmas"). These three groups range in size from 16 (Mesas) to 17 (Tenori) to 29 individuals (Palmas). The breakdown of age/sex categories can be found in Table 2. We

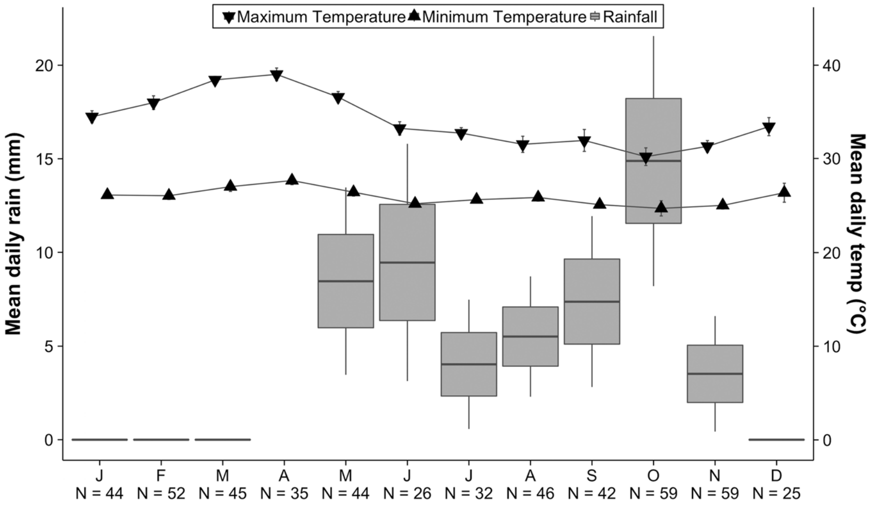

FIGURE 3 Temperature (black triangles) and rainfall (gray boxes) data from the Taboga Forest from July, 2017 to May, 2019. Numbers along the *x* axis indicate the number of days of weather data measured per month. Vegetation surveys occurred between July–early November, 2018 (late wet season) and March–April, 2019 (late dry season). Primate sighting surveys occurred between February and April, 2019 (late dry season)

collected ranging data between January, 2018 and April, 2019, spending a total of 1,471 hr (131 dry season and 88 wet season observation days) with Tenori, 481 hr (41 dry season and 31 wet season observation days) with Mesas, and 512 hr (56 dry season and 28 wet season observation days) with Palmas. Whenever possible, groups were followed from their morning sleeping site to their evening sleeping site. Observers recorded group locations on handheld global positioning system (GPS) units (Garmin eTrex 10 and 20) using the "track" function, which marks a point every 10 m or 10 s, whichever comes first. When observers lost sight of their group they turned the track function off.

Location data were uploaded to Google Earth Pro version 7.3.2.5776 (Google LLC 2019) and used to create convex polygons encompassing each group's home range (Figure 2c). All three home range polygons contained areas not traversed by the monkeys (agricultural fields, buildings, and cattle pasture) that were excluded from the polygon area measures (Di Bitetti, 2001). The river area was conserved in ranging area, as canopy cover is generally continuous over the river and the capuchins cross it freely. For each group, we calculated the number of individuals per home range area (km^2), and our first capuchin density estimate is the average of the three values.

For our second approach to calculating capuchin density, we estimated the total number of capuchins in the Taboga forest based on counts of all individuals encountered on an *ad libitum* basis (including both habituated and nonhabituated groups, i.e., total estimated population). We recorded the following data when we found unhabituated groups (which occurred during intergroup encounters, searches for habituated groups, primate sighting surveys, vegetation surveys, and trail maintenance): date, time, location, number of individuals observed across different age/sex classes, and notes on any distinguishing features of specific individuals (e.g., scars, missing appendages, etc.). We compiled 49 of these *ad libitum* observations from January, 2018 to May, 2019 to estimate the minimum possible number of groups (e.g., during one primate sighting survey we sighted four different unhabituated groups along the same line transect) and their minimum possible sizes (e.g., from multiple sightings of the same group with a distinct alpha male we were able to calculate the minimum number of individuals). To calculate capuchin density, we divided the estimated total number of individuals by the area of the Taboga forest (5.16 km^2). We believe this is a conservative estimate because we suspect that several capuchin groups were not censused during our primate surveys (a portion of the forest continues into private land that we are not allowed to survey; note that the area of this part of the forest is not included in the 5.16 km^2 area of Taboga used here, which only represents the parts of the forest we were allowed to survey). In addition, the size estimates of unhabituated groups are likely underestimated. However, we also calculated this density estimate using the area of the total contiguous forest (i.e., including the area we were unable to survey, 7.89 km^2 total), and present both estimates here.

TABLE 2 Group size and composition for three habituated white-faced capuchin groups at Taboga

Groups	Adult males	Adult females	Subadults and juveniles	Infants	Total
Mesas	2	4	6	4	16
Tenori	3	4	7	3	17
Palmas	5	8	12	4	29

2.3 | Forest composition

From July to early November, 2018 (late wet season) and March to April, 2019 (late dry season), we conducted a vegetation survey of the reserve to examine potential impacts of anthropogenic activity on forest composition. The most significant effects of fragmentation are known to penetrate up to 100 m from the forest boundary (Laurance et al., 2002). Even the fragmentation that created the edges of the Taboga Forest, which occurred over 35 years ago (Google Earth Pro, Dec, 1984; and some over 70 years ago: Sistema Nacional de Información Territorial, Costa Rica, 1940) can have a lasting impact on forest composition within these edges (e.g., influencing species prevalence, wind speeds, and tree mortality rates: Kalacska et al., 2004). Moreover, sustained anthropogenic activity along forest boundaries can continue to alter the adjoining forest composition even after it has recovered from the initial clearing (Gascon, Williamson, & Fonseca, 2000). For this analysis, we were primarily interested in whether we could detect any anthropogenic effects (past or present) on forest composition at Taboga; therefore, we defined edge forest as forest within 100 m of a forest boundary. Forest boundaries were created by agricultural and cattle pasture fields, land cleared for buildings, and various roads that traverse the reserve. We used a Google Earth image of Taboga to calculate the 100 m edge and then randomly dispersed vegetation transect start points within edge ($n = 20$) and interior ($n = 20$) forest using a random number generator selecting numbers associated with points on a grid overlaid on a map of Taboga (Figure 2d). Once at the start point, observers randomly selected the transect direction by a spin of a compass bezel. If the direction selected did not allow for a full 50 m transect, then the opposite direction was chosen.

Along each vegetation transect and within 2.5 m of either side of the transect, we recorded the species (identified by one of the authors, J. C. O.) and DBH (using a diameter or girthing tape) of every tree with a circumference at breast height ≥10 cm (FAO, 2004). We recorded canopy coverage on a scale from one to four (reflecting the percentage of the sky blocked by canopy when the observer looked directly up: 1 = 1–25% coverage; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%) every meter along the transect line, first during the late wet season (July to early November, 2018) and again during the late dry season (March to April, 2019).

For each vegetation transect, we calculated the following: mean DBH, mean canopy cover (wet and dry season), density (trees/m^2), species richness (S; i.e., the number of tree species), and Shannon's Diversity Index (H; which accounts for both species richness and the distribution of individuals across the species represented in the sample: Shannon & Weaver, 1949; Spellerberg, 2005). To determine whether forest edges contained more resources for capuchins and to quantify the degree of anthropogenic disturbance seen along the edges, we also categorized tree species into two nonmutually exclusive groups (Table S1): (a) species used by capuchins for foraging or fur rubbing (determined by cross-referencing with Vogel, 2005 and with a list of species our study groups have been observed to use at least once at Taboga), and (b) species characteristic of the early stage of successional dry forests (i.e., forest with a history of intense anthropogenic disturbance, such as fire and clearing for pasture: Kalacska et al., 2004). The early stage describes patchy, young forest, but because the three stages of forest succession represent more of a continuum than discrete phases of regrowth (i.e., species present in the early stage remain through the intermediate and even late stages of regrowth, resulting in forest that is distinct from untouched forest), here we focus on early-stage species as indicators of past anthropogenic disturbance (hereafter, "indicator species"). For each category, we calculated mean DBH, density, species richness, and Shannon's Diversity Index along each transect.

Finally, for ease of comparison across sites, we calculated the overall mean Shannon's Diversity Index and Shannon's Equitability (J', i.e., the distribution of individuals across the species in a sample: DeJong, 1975; Pielou, 1969). Shannon's Equitability ranges from 0 to 1, with 0 indicating an uneven distribution and 1 indicating an equitable distribution of species (DeJong, 1975; Pielou, 1969; Table S2).

2.4 | Forest composition analyses

First, we examined whether there were vegetation differences between the edge and interior forest types. Because our data were not normally distributed, we used Mann–Whitney *U* tests to compare edge and interior transects with respect to mean DBH, density (trees/m^2), species richness (S), and Shannon's Diversity Index (H). Identical comparisons were then conducted: (a) after restricting species to those used by capuchins for foraging and fur-rubbing, and (b) after restricting to indicator species. Second, to test whether canopy cover varied between edge and interior forest and/or if canopy cover changed seasonally, we fit a linear mixed model with transect location (edge or interior), season (wet or dry) and the interaction between the two as fixed effects. We controlled for transect number as a random effect and log transformed canopy cover as the dependent variable.

2.5 | Primate sighting rates

Between February and April, 2019 (late dry season), we conducted a primate sighting survey using 32 line transects comprising pre-existing roads and paths (i.e., along canals or firebreaks) and a network of trails created by the project (19 cut trails total, each at least 0.2 km apart: Figure 2d). Transect lengths ranged from 0.2 to 2.2 km, and we walked most transects twice (once in the morning between 6:00 and 10:00 and once in the afternoon between 14:00 and 16:00), each time in an alternate cardinal direction, for a total of 55 km walked. Three transects were only walked once due to lack of trail maintenance. Transects were not surveyed when it was raining.

Transects were walked by teams of observers (typically two and no more than five), traveling at a speed of 1.5 km/hr and stopping every 100 m for 2 min of detailed observation (Bolt et al., 2018; Pruetz & Leasor, 2002). When more than one team searched on the same day, teams walked transects that were more than 0.2 km apart to avoid double-counting primate groups. Upon sighting a primate group (defined here as seeing one or more individuals), observers recorded the time of day, primate species, and location (using a Garmin eTrex 10 or 20 handheld GPS unit). Observers paused for 10 min to count individuals of each age/sex class, when possible, and then returned to the transect.

2.6 | Primate sighting rates analyses

We then determined whether primate group sightings were more likely in different forest types (i.e., edge vs. interior: Figure 2b) or in proximity to a permanent water source (i.e., ≤100 vs. >100 m or "near water sources" vs. "far from water sources": Figure 2b). For each species of monkey (i.e., capuchins, howlers), we fit a generalized linear mixed model where the dependent variable was the number of primate group sightings for each species (left-skewed count data). We assumed the number of sightings on each transect followed a Poisson distribution whose log mean depended on forest type and proximity to water as fixed effects and transect number as a random effect allowing for random intercepts (but not slope) by transect. We also added a constant offset term to each model to account for different research effort on transects of different lengths.

We fit all the models with the lme4 package (Bates et al., 2015) in R version 3.3.2 (R Core Team, 2016; RStudio Team, 2016). Figures were created using the ggplot2 package (Wickham, 2016). This study was approved by the Institutional Animal Care and Use Committee (Protocol ID: PR00007911) and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

3 | RESULTS

3.1 | Capuchin density

Our first capuchin density estimate using the mean group and home range size from our three habituated groups (Tenori, Mesas, and Palmas) was 21.65 individuals/km^2 (Table 1). Tenori (16 individuals) had the smallest range size (60.5 ha) in comparison with Mesas (17 individuals, 129.4 ha), and Palmas (29 individuals, 102.1 ha; Figure 2c). Our second density estimate using the total population and forest size was 36.24 individuals/km^2 (using the area of the forest surveyed) or 23.70 individuals/km^2 (using the area of the total contiguous forest). Using primate surveys, we have identified at least 12 distinct capuchin groups in Taboga since June 2017, ranging in size from 15 to 40 individuals.

3.2 | Forest composition

We did not find significant differences between the interior (*N* = 20 transects) and the edge (*N* = 20 transects) forest for mean tree DBH (edge mean ± standard error: 12.53 ± 1.31 cm; interior: 14.30 ± 1.72 cm; Mann–Whitney *U*, *U* = 185.5, *p* = .70), mean tree density (edge mean ± standard error: 0.13 ± 0.01 trees/m^2; interior: 0.15 ± 0.03 trees/m^2; *U* = 203.5, *p* = .94), mean tree species richness (edge mean ± standard error: 12.30 ± 1.01; interior: 11.15 ± 1.23; *U* = 234.5, *p* = .37), or Shannon's Diversity Index (edge mean ± standard error: 2.10 ± 0.11; interior: 1.89 ± 0.14; *U* = 244, *p* = .24; Table 3). We identified 1,367 individual trees representing 110 species, six of which are not native to the area (Table S1); 28 of these species were only found on edge transects, 22 species were only found on interior transects, and the remaining 60 species were found on both edge and interior transects.

In comparing trees species used by capuchins (49 species; 15 of which were also identified as indicator species; Table S1), we again found no significant differences between edge and interior for mean tree DBH (edge mean ± standard error: 12.85 ± 1.31 cm; interior: 15.23 ± 1.96 cm; Mann–Whitney *U*, *U* = 185, *p* = .70), mean tree density (edge mean ± standard error: 0.08 ± 0.01 trees/m^2; interior: 0.07 ± 0.04 trees/m^2; *U* = 241, *p* = .27), mean tree species richness (edge mean ± standard error: 7.40 ± 0.61; interior: 6.90 ± 1.50; *U* = 264.5, *p* = .08), or Shannon's Diversity Index (edge mean ± standard error: 1.65 ± 0.12; interior: 1.34 ± 0.13; *U* = 264, *p* = .09; Table 3). The majority of tree species used by capuchins were found on both edge and interior transects (*n* = 34 species), while eight species were only found on edge transects and seven were only found on interior transects (Table S1).

For indicator species (i.e., those associated with the first stage of forest succession in tropical dry forests and thus reflective of past anthropogenic disturbance: 28 species), we found that trees on the edge had a significantly greater DBH than indicator trees in the interior (edge mean ± standard error: 16.21 ± 1.55 cm; interior: 11.30 ± 1.72 cm; Mann–Whitney *U*, *U* = 274, *p* = .046; Table 3). We found no difference between edge and interior forest for mean tree density (edge mean ± standard error: 0.03 ± 0.01 trees/m^2; interior: 0.08 ± 0.03 trees/m^2; *U* = 234.5, *p* = .36), mean indicator species richness (edge mean ± standard error: 3.00 ± 0.61; interior: 4.45 ± 0.72; *U* = 144.5, *p* = .132), or Shannon's Diversity Index (edge mean ± standard error: 0.67 ± 0.15; interior: 0.99 ± 0.17; *U* = 153, *p* = .20; Table 3). The majority of indicator species were found on both edge and interior transects (*n* = 19), while three were only found on edge transects and six were only found on interior transects (Table S1).

We found that there was more canopy coverage in the wet season months than in the dry season (Figure 4: wet season mean ± standard error: 3.78 ± 0.04; dry season: 2.60 ± 0.20;

TABLE 3 Mean ± standard error of vegetation measures in the edge and interior of all trees ("Overall"), capuchin-associated trees (i.e., those capuchins use for food or fur-rubbing), and indicator tree species (i.e., those associated with the first stage of forest succession in tropical dry forests, Kalacska et al., 2004)

	Overall		Capuchin-associated trees		Indicator trees	
	Edge	Interior	Edge	Interior	Edge	Interior
DBH (cm)	12.53 ± 1.31	14.30 ± 1.72	12.85 ± 1.31	15.23 ± 1.96	**16.21 ± 1.55**	**11.30 ± 1.72***
Density (trees/m^2)	0.13 ± 0.01	0.15 ± 0.03	0.08 ± 0.01	0.07 ± 0.04	0.03 ± 0.01	0.08 ± 0.03
Richness	12.30 ± 1.01	11.15 ± 1.23	7.40 ± 0.61	6.90 ± 1.50	3.00 ± 0.61	4.45 ± 0.72
Diversity index (*H*)	2.10 ± 0.11	1.89 ± 0.14	1.65 ± 0.12	1.34 ± 0.13	0.67 ± 0.15	0.99 ± 0.17

Note: Bold indicates significant differences between edge and interior.
*Denotes *p* < .05

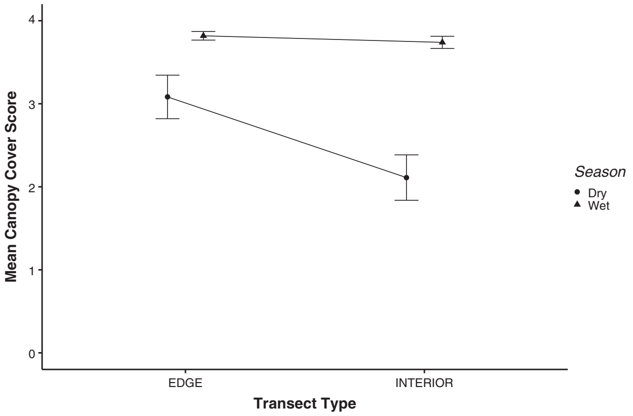

FIGURE 4 Mean canopy cover score (±standard error) across season and transect type. Canopy coverage was recorded on a scale from one to four (reflecting the percentage of the sky blocked by canopy when the observer looked directly up: 1 = 1–25% coverage; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%) every meter along the transect line, first during the wet season (July to November, 2018) and again during the dry season (March to April, 2019)

generalized linear model [GLM]: Wet Season $\beta = 0.31$, $SE = 0.12$, $p = .014$). We also found that in the dry season, interior transects had significantly less canopy cover than edge transects (mean ± standard error: dry season interior: 2.11 ± 0.27; dry season edge: 3.08 ± 0.26; GLM: Interior × Wet Season $\beta = 0.42$, $SE = 0.17$, $p = .020$).

Overall, we found a high tree species richness ($S = 111$), diversity ($H = 3.84$), and equitability ($J' = 0.82$) in Taboga, indicating a large number of species and relatively equal representation of individuals from different species (Table S2).

3.3 | Primate sighting rates

As predicted, both capuchin and howler monkeys showed neutral edge effects (i.e., no significant difference between group sighting rates along transects in edge vs. interior forest). Observers walked a total of 54.98 km of transects, with 26.80 km in edge forest and 28.18 km in interior forest. Capuchin sighting rates were lower overall compared with howler sighting rates and did not differ between edge (0.34 groups/km; confidence interval [CI]: −2.10, 0.48) and interior forest (0.46 groups/km; CI: −0.48, 2.10; $p = .25$; Figure 5a). Although there was a higher sighting rate for howlers in edge (1.31 groups/km; CI: −0.38, 0.85) compared with interior forest (0.75 groups/km; CI: −0.85, 0.38; Figure 5b), this difference was not significant ($p = .43$).

Of the total 54.98 km of transects walked, 33.08 km was far from permanent water sources and 21.91 km was near permanent water sources. As predicted, capuchin group sightings were higher near permanent water sources (i.e., the river or large canals: 0.78 groups/km; CI: 1.42, 4.41) compared with farther from water (0.15 groups/km; CI: −4.41, −1.42; $p = 1.73 \times 10^{-4}$; Figure 5c). However, contrary to our predictions, howler group sighting rates were also significantly higher near water sources (1.69 groups/km; CI: 0.42, 1.72) compared with farther from water (0.57 groups/km; CI: −1.72, −0.42; $p = 1.24 \times 10^{-3}$; Figure 5d).

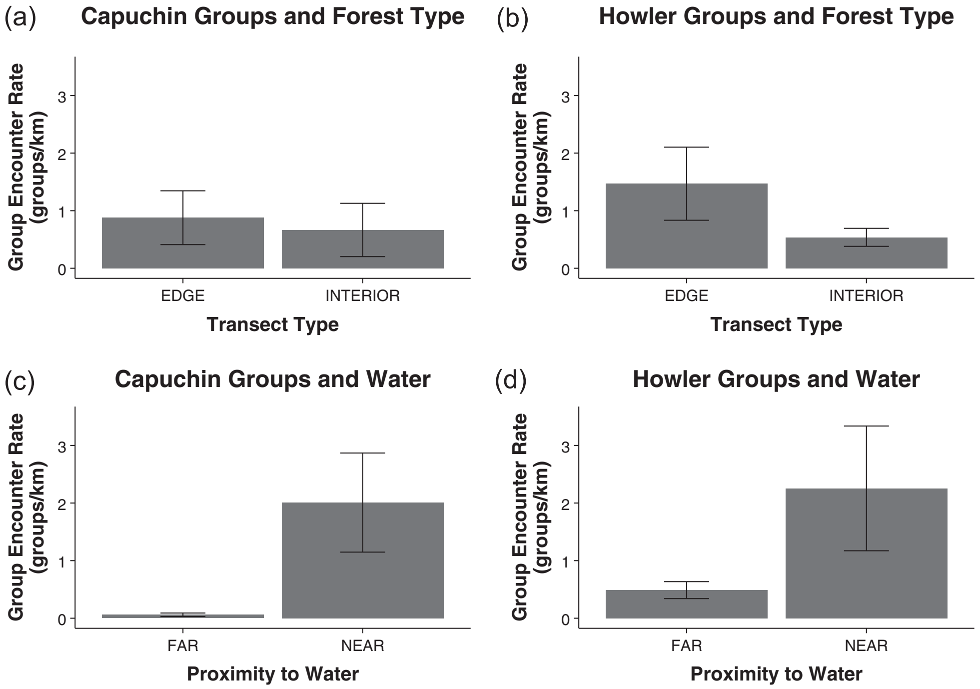

FIGURE 5 (a–d) Mean group encounter rate (groups/km walked ± standard error) by forest type in Taboga. (a) capuchin groups in edge and interior forest; (b) howler groups in edge and interior forest; (c) capuchin groups far from (>0.01 km) or near (<0.01 km) a permanent water source; (d) howler groups far from or near a permanent water source

4 | DISCUSSION

The density of capuchins in Taboga is higher than that reported from all other long-term white-faced capuchin sites (Table 1). This high density emerges whether we use the mean group and home range size from individual groups (21.65 individuals/km^2) or the total population and total forest area (36.24 individuals/km^2 using the area of the forest surveyed; 23.70 individuals/km^2 using the area of the total contiguous forest). For other sites, the group-based estimates range from 7.97 to 12.93 individuals/km^2; and the total population-based estimates range from 5.60 to 20.00 individuals/km^2. Therefore, with the exception of Barro Colorado Island, the Taboga population is 2–6 times denser than other white-faced capuchin sites.

The floral composition of the Taboga Forest itself differs from other sites in two ways. First, we report a relatively high species richness, diversity, and equitability compared with other tropical dry forests (Table S2). Second, in contrast to other sites (e.g., Arroyo-Rodríguez & Mandujano, 2009; Bolt et al., 2018; Harris, 1988; Lehman, Rajaonson, & Day, 2006; Saunders, Hobbs, & Margules, 1991), in Taboga the edge forest did not significantly differ from the interior forest along a number of measures (mean DBH, density, species richness, or diversity). We recognize that this difference could be due to our definition of edge (compared with interior) forest. Here, we defined the edge as any forest within 100 m from an anthropogenic edge, which represents the maximum penetration of the most significant effects of fragmentation (Laurance et al., 2002) and characterizes nearly 20% of the world's forests (Haddad et al., 2015). As we collect more data on the ecology of Taboga, we will modify and refine this definition to examine the impact of historical anthropogenic disturbance and fragmentation on the forest (i.e., Didham et al., 2015; Harper et al., 2005). One possibility is that the different forest types represented within the forest (tropical dry forest, riparian forest, alluvial palm forest) contribute to the high species richness, diversity, and equitability reported here. However, we also suspect that a more fine-grained analysis of edge effects that accounts for the type and age of anthropogenic disturbance may reveal more significant edge effects than what we are able to report here.

The edge forest did differ from the interior forest in two important ways. First, tree species that characterize the first stage of tropical dry forest succession (i.e., indicator species) were well-established in the forest edge. Specifically, these trees had a significantly higher mean DBH in edge forest compared with interior forest. The stages of forest succession represent a continuum rather than a set of discrete characteristics; accordingly, the majority of the indicator species identified at Taboga are also characteristic of the intermediate (25 out of the 28 indicator species) and late (19 out of the 28 indicator species) stages of dry forest regeneration (Kalacska et al., 2004). The presence and maturity of these species in the forest edge may reflect the age of the Taboga Forest's anthropogenic disturbance (35–70 years). Past land-use patterns (i.e., anthropogenic fire, clearing for pastures, etc.) can have a long-term impact on forest composition up to 100 m from the boundary itself (Laurance et al., 2002) by contributing to tree death and influencing recolonization rates of specific species (Kalacska et al., 2004). However, in this study, we also cannot rule out the potential effect of continuing disturbance (i.e., selective logging) in some areas.

Second, we found that the edge forest in Taboga was semi-evergreen and maintained canopy cover throughout the year. We present three nonmutually exclusive possible explanations for this finding: (a) Floral composition: of the 29 tree species only observed on edge transects, two are evergreen (*Cecropia peltata* and *Pisonia aculeata*: Frankie, Baker, & Opler, 1974) and seven additional species maintain their leaves year-round at Taboga (unpublished data; Table S1); (b) Elevation: much of the interior forest is more elevated and may be drier than the edge forest; (c) Anthropogenic water sources: flood-irrigation of agricultural land during the dry season might spillover into edge forests, thus allowing for year-round soil moisture. Future studies will test these hypotheses and also account for how the different forest types present at Taboga (tropical dry forest, riparian forest, and alluvial palm forest) contribute to canopy cover.

In line with previous research that found neutral edge effects for both primate species (e.g., Bolt et al., 2018), we found no difference between capuchin or howler group sighting rates in edge or interior forest. Combined with the overall high capuchin population density, this suggests that despite a large percentage of edge forest (nearly 40% of the protected 516 ha), capuchins appear to thrive in forest fragments (Cunha et al., 2006). Indeed, we found that capuchins were equally likely to find staple food and fur-rubbing species in the edge compared with the interior forest and that the DBH of these staple species did not vary significantly between edge and interior. In addition, year-round canopy cover in the forest edge may provide shade through the hottest months and/or the hottest hours of the day (Fedigan & Jack, 2001; Fedigan, Rose, & Avila, 1996), and therefore both capuchins and howlers might spend more time in edge forest during the dry season (when our primate survey took place) than they do during the wet season. Longitudinal data will determine whether ranging patterns vary seasonally.

We found significant differences between capuchin and howler group sighting rates when we compared forest near versus far from the river or canals. Both species were more likely to be found near water sources. The presence of reliable year-round water sources (which may also impact fruit productivity, tree size, and canopy cover) is critical for many primates living in seasonally dry habitats. For example, capuchins in Santa Rosa National Park (another tropical dry forest in Costa Rica) rely on a limited number of water holes during the dry season, and access to these water holes is thought to be the primary constraint on the capuchin population (Fedigan & Jack, 2001; Fedigan et al., 1996; Fedigan, Rose, & Avila, 1998). In contrast, Taboga has two types of year-round water supply: the river and a system of canals. *Ad libitum* observations indicate that capuchins drink from both water sources and play in the canals. For howlers, proximity to water sources is thought to have more to do with the forest subtype (i.e., evergreen and riparian) or tree height than the need to drink water daily (Fedigan & Jack, 2001). However, we have observed a howler drinking from a canal, suggesting the water itself might be an important resource for both howlers and capuchins. While we could not compare plant transects according to distance from water sources due to sample size, future studies will assess how forest characteristics vary with proximity to the river and canals (and the associated riparian/semideciduous forest type). We are also collecting sighting data across seasons to see if there are seasonal differences in primate sightings. Another question that remains is why Taboga has a much higher density of capuchins compared with the nearby Lomas Barbudal site, which also contains year-round water sources. The capuchins in Taboga spend a significant amount of time in the alluvial palm forest, a forest type not present at Lomas. Primate habitats that feature a mosaic of different forest types may provide a buffer from the effects of temporal variation in fruit productivity (Stevenson, 2016) and we suspect the palm fruits may represent an important dietary staple for the Taboga population. Indeed, the largest of our habituated groups (Palmas, 29 individuals) primarily ranges in the palm forest. This is certainly a hypothesis we plan to test in the future.

The abundance of the capuchins in Taboga has important implications for conservation efforts (Chazdon et al., 2009). For certain species, the size and disturbance of a forest fragment may matter less than the forest composition and the availability of key resources, like year-round water access. Our analysis here adds to our understanding of factors that influence primate abundance and also establishes Taboga as a critical case study in tropical dry forest dynamics. Future studies will provide a more fine-grained analysis of the possible interaction between edge effects, habitat type, and season, and how these factors predict primate sightings (Gogarten et al., 2012). For example, we were not able to test here whether primate sighting rates are higher along the river or along anthropogenic canals (or vice-versa). We are also working on a complete howler census to compare with an earlier study suggesting that the howler population in Taboga was on the verge of collapse (Heltne et al., 1976). For capuchins, the next question is how the high density in Taboga influences ranging patterns, home range overlap, and the frequency and intensity of intergroup encounters (Perry, 1996, 2012). Preliminary data suggest that intergroup encounters are higher at Taboga than at other sites, but that the intensity of such encounters is lower, which may represent a behavioral adaptation to frequent encounters due to high population density.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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SUPPORTING INFORMATION

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

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