Spatial Ecology of Reddish-Brown Cuxiú Monkeys (*Chiropotes sagulatus*, Pitheciidae) in an Isolated Forest Remnant: Movement Patterns and Edge Effects

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Abstract: Habitat loss, and subsequent fragmentation, can increase the amount of forest edge. Primate species vary in their responses to such changes in their habitat. We studied the movement ecology of a group of reddish-brown cuxiú monkeys (*Chiropotes sagulatus*, Pitheciidae) in a small (13 ha), isolated forest remnant that was <3% of the species' typical home range in the region. Every 5 min we recorded the group's latitude and longitude, and the behavior of all individuals in sight. We calculated distance, speed, and trajectory of travel routes, and distance from every location to the nearest forest edge. Using Lidar data, we calculated canopy height. Cuxiús traveled in all cardinal directions, but they turned left more often than right, and they traveled at a faster speed to locations where the monkeys fed than where they did not eat. Although cuxiús used forest from the edge to the interior, they concentrated their movements and activities >30 m from the forest edge. Furthermore, their food sites were located less often near the forest edge, and canopy height of food trees near the forest edge was lower than canopy height of food trees at a greater distance from the edge. Although edge effects impacted the monkeys' movement, trees >15 m at the forest edge can provide resources. Future research can examine ecological variables in more detail with the movement patterns.

Keywords: Amazon; bearded saki; conservation; forest fragmentation; patch; path trajectory; primate

1. Introduction

Globally, approximately 65% of nonhuman primate species (primates, hereafter) are listed by the IUCN as Vulnerable, Endangered, or Critically Endangered, and most of the threats to primate populations center on habitat loss, hunting, and disease [1–3]. In the tropical Americas, the last three decades have been marked by steady forest loss and increased agricultural expansion [2]. Often, but not always, such habitat loss is accompanied by habitat fragmentation, resulting in isolated habitat remnants in the landscape [4,5].

Forest remnants often differ from continuous forest in plant composition and structure [6,7]. These differences in forest composition and structure can impact primate presence and distribution [8,9], habitat quality [10], and food availability [11]. Primates living in habitat remnants can demonstrate changes in endocrinology, ranging patterns, diet, group size and density, genetics, functional diversity, and parasite prevalence [12–21]. Forest loss and fragmentation can also result in increased edge effects near the forest border [22,23], leading to a multitude of changes in the remaining forest's edge [24]. For example, near the edge there can be decreased canopy moisture that can extend 1–2.7 km towards the forest interior [25], more-frequent and more-intense forest fires [26], increased tree mortality [27], increased prevalence of successional trees [28], greater liana abundance [29], phenological

changes [30], and smaller trees [31,32]. Some of these forest structure changes can persist decades after initial isolation of the forest remnant [33].

The definition of forest edge can range from up to 20 m from the forest border to greater than 1 km [13,25,34,35]; such variation can impact the interpretation of the animals' responses to the edge [34,36]. To better understand the effects of habitat loss and fragmentation, it is important to know the distance or depth of edge influence [37] in context with how the animals use their remaining habitat. In addition, when the animals are living in a small forest remnant, much (or all) of the forest remnant may potentially be impacted by edge effects [38]. Therefore, context can be important.

There can be varied responses by mammals at these edges, which can be associated with the extent to which a species' resources are located and distributed across one or multiple habitat types [39]. For example, three primate species at the same study site in Costa Rica did not exhibit the same patterns in abundance and density along anthropogenic forest edges, riparian edges, and interior forest [40]. In Madagascar, four lemur species differed in their seasonal responses to forest edges [41]. In the Brazilian Amazon, four primate species had greater densities, one species had lower density, and one species did not exhibit any patterns when examining the edges between the primary forest and the secondary forest that was 19–30 years old [42].

Animal movements are directly linked to animal behavior, ecology, and evolution [43], as well as learning from past experiences [44–46]. Animal movement patterns can vary within and between individuals, groups, populations, and species, as well as temporally and spatially [47,48]. Spatial movements can be influenced by resource location and abundance, as well as predation risk [49,50]. Movement data can provide information about an animal's home range, habitat use, changes in movement speed or states, interactions with the landscape, and physiological state [51]. Such an understanding of animal movement can aid in species conservation [52]. A review of tracking data of 57 species (803 individuals) found that, overall, individuals in areas highly impacted by humans moved shorter distances than individuals in less-impacted areas [53].

Compared to other geographical regions, the Amazon still has large tracts of unfragmented forest [54,55]. However, deforestation of relatively intact areas can be associated with high conservation risk for the area's vertebrates [56]. Furthermore, when examining the region at a more refined scale, forest edges and their associated edge effects are widespread in the Amazon [57]. These edge effects and their demonstrated impacts on canopy structure [33] could greatly impact a range of species, including non-human primates.

There is overall agreement that habitat loss can be detrimental to many species, but there is ongoing debate about the extent to which habitat fragmentation per se impacts biodiversity and at which scale of effect [58–65]. Some primate species use human-modified landscapes, but some species are more likely to use such landscapes than others [66]. Furthermore, there can be behavioral and ecological differences in a species based on the extent to which habitat has been modified: the reddish-brown cuxiú monkey (*Chiropotes sagulatus*, Pitheciidae) differed in its behavior and ecology depending on whether it lived in small forest remnants, large forest remnants, or continuous forest: cuxiús in the small forest remnants had smaller group sizes but lived at greater population density, rested more and traveled less, traveled in more circular paths and revisited the same feeding sites more often during a single day, used fewer feeding sites per hour, had a uniform spatial use of the forest (versus a clumped distribution), used more trees within 50 m of the forest edge more often, and ate some plants that the cuxiús in the continuous forest primarily ignored [67–70]. However, the percentage of the cuxiús' diet consisting of lianas did not differ across forest size classes, nor did the diameter at breast height (DBH) of feeding trees [69].

These previous findings provided an understanding of how cuxiús in small forest remnants differed in behavior and ecology from cuxiús in larger forested areas [67–70]. Our primary objective in the current analysis was to examine detailed aspects of the spatial ecology of cuxiús living in a small forest remnant (less than 3% of the size of the species'

typical home range in continuous terra firme forest [67]) to address two questions: (1) What are main characteristics of cuxiú movement patterns in a small forest remnant? and (2) Do movement and behavioral profiles differ relative to the distance to the forest edge?

Question #1: What are main characteristics of cuxiú movement patterns in a small forest remnant? We knew a priori that cuxiús in small forest remnants used most of the available forest, traveled to the same locations within the forest remnant multiple times during a single day, and traveled more circular routes than cuxiús in larger areas of forest [67]. Furthermore, other monkey species have mental maps of resources and local landmarks [46,71,72]. Therefore, we predicted that the cuxiús would travel in all cardinal directions (north, south, east, and west), and would demonstrate a preference in turning patterns (preference for left or right turns) as they navigated the forest remnant in circular routes. Because other primate species have mental maps [46,71,72], we also predicted that as the cuxiús approached a food source, they would exhibit a preference in turning direction (left or right) and they would travel at a faster speed than when they were not approaching a food source.

Question #2: Do movement and behavioral profiles differ relative to the distance to the forest edge? Because tree canopy height is often lower near forest edges than non-edge locations [32], and cuxiús rarely use low canopy and terrestrial substrates compared to other pitheciid monkeys [73], we predicted that cuxiús would use edge forest to a lesser extent than non-edge forest and that the forest used as a travel path would have higher forest canopy than the areas that were not part of the travel paths. Furthermore, we predicted that cuxiús would engage in feeding behavior and travel behavior at all distances from the forest edge to maximize resource availability in the small forest remnant. However, we predicted that cuxiús would engage in resting behavior more often near the interior of the forest remnant because monkeys often use larger trees as resting sites, as such site selection is often associated with reducing predation risk [74,75]. Cuxiús and similar-bodied primates are prey for large raptors [76,77]. Lastly, because trees near the forest edge tend to be smaller, we predicted that the cuxiús' food trees near the forest edge would have smaller diameter at breast height (DBH) and lower canopy height than food trees located further from the forest edge.

A detailed picture of how cuxiús navigate their surroundings in a small forest remnant can provide more context to understanding to what extent primate species have similar movement patterns and to what extent there are differences between species; there remains a gap in our knowledge on this topic for many primate species [46]. Furthermore, a better understanding of animal movement patterns could be helpful in assessing current and future conservation concerns [52], such as primate species in fragmented landscapes.

2. Materials and Methods

2.1. Study Subjects and Study Sites

We collected data on a cuxiú group living in an isolated, 13 ha forest remnant (2°24′15″ N, 59°52′18″ W) at the Biological Dynamics of Forest Fragments Project (BDFFP) study area, located approximately 80 km north of Manaus, Brazil (Figure 1). There have been four decades of research at the BDFFP study area, which consists of tropical terra firme forest that does not vary greatly in elevation (50–100 m above sea level) [6,78].

The BDFFP's forest remnants' structural diversity has been negatively impacted by edge effects [32]. Canopy height is decreased at the forest edge, and this decrease continues for up to 20 m from the edge [32,79,80]; however, other edge effects (e.g., plant species composition, soil moisture) have been noted up to 100 m from the edge [81,82]. Liana abundance has also been greater at the edges [29], as has tree density [33]. Since the isolation of the forest remnants in the 1980s, the presence of six primate species in the region has varied greatly, with howler monkeys being most consistently present in the forest remnants and black spider monkeys being least present [83].
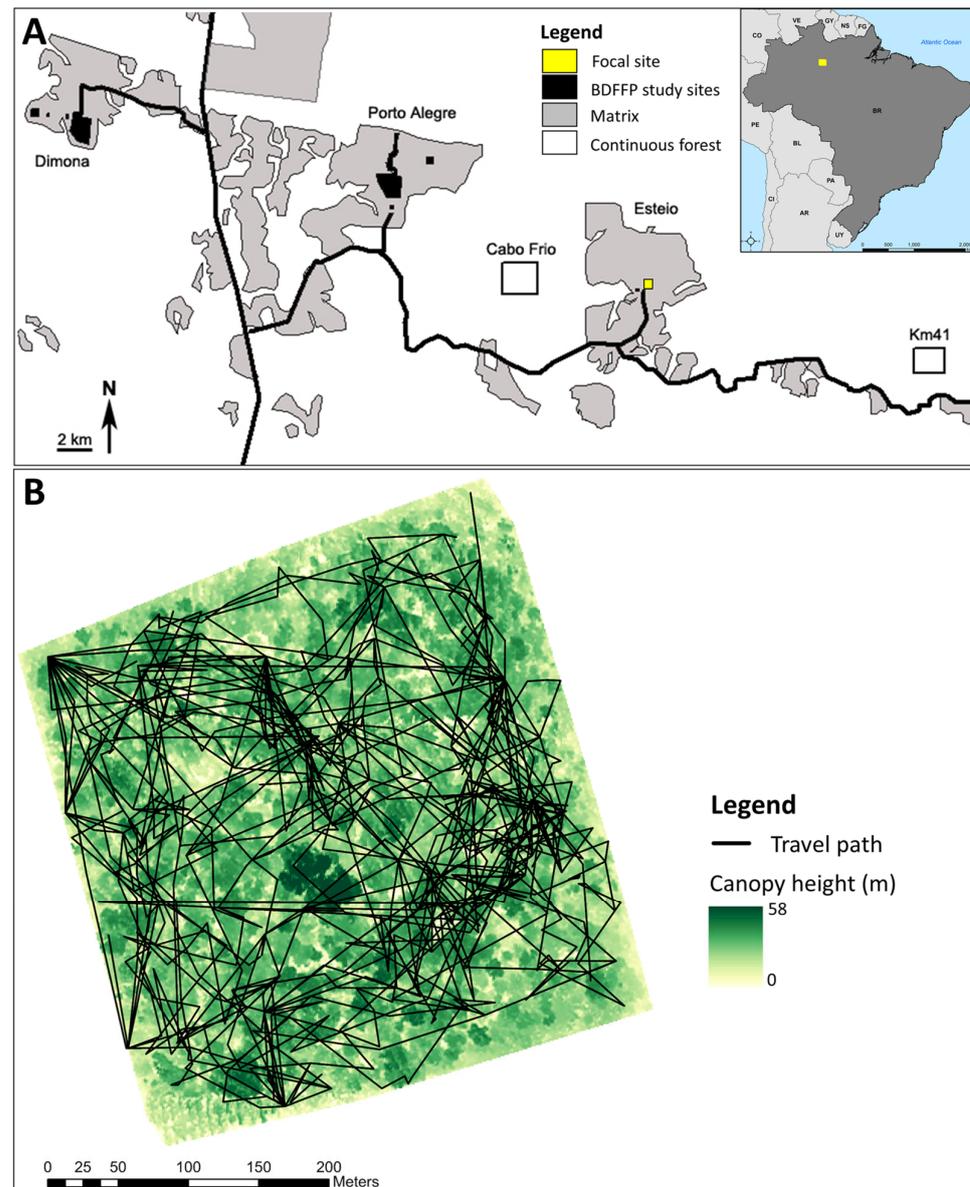
Figure 1. The study site was (**A**) located at the Biological Dynamics of Forest Fragments Project, in central Brazilian Amazonia, and (**B**) consisted of an isolated, 13 ha forest remnant that contained one group of cuxiú monkeys that moved throughout the forest remnant (black lines). Canopy height (m) was derived from Lidar [79,80].

The history of re-isolation of the forest remnants has varied across the study site, but the forest remnant for the current study has remained isolated [33]. At the time of the study, the forest remnant was isolated from other forest by low vegetation (e.g., pasture). While some arboreal primates will descend to the ground and travel across open spaces [73], we never observed any of the cuxiús in the isolated forest remnants traveling terrestrially. Therefore, we did not study the animals' movements outside of the context of the forest remnant because we never saw the animals leave or re-enter the forest remnant.

2.2. Field Data Collection

We collected data from January 2005 to April 2006 as part of a larger study that examined primate species richness [84] and the behavioral differences in cuxiús across different habitat sizes [67–69,85]. We collected data on the animals in this forest remnant for six cycles across 16 months, with each cycle typically consisting of 4 consecutive days of

spatial and behavioral data; two cycles consisted of 3 consecutive days due to bad weather that reduced visibility. We followed the cuxiús from the time they became active in the morning until they reached their evening sleeping site (approximately 0600 h to 1700 h). Every 5 min we recorded the location of the group via a handheld GPS, noted the behavior of all individuals in sight, and flagged all feeding locations so we could return later to measure DBH and identify the plant species [68,69]. We noted the latitude and longitude of all feeding sites, measured at the trunk of the tree or at the base of the liana at the ground. In January 2005, there were four individuals (two males and two females), but by October 2005 there were three individuals (an adult female disappeared and was never seen again during the study) [68]. Prior to the current study, only presence–absence data were recorded for cuxiús in this forest remnant [83]. This noninvasive research project followed the guidelines of the American Society of Mammalogists [86], and it was approved by the Conselho Nacional de Desenvolvimento Científico e Tecnológico in Brazil.

2.3. Forest Canopy Analysis

Previous studies found that forest canopy diminished near the forest edge at the BDFFP study area [33,79], but our goal was to examine in detail the variations in forest canopy height and its use by the monkeys. We used Lidar data from Mokross et al. [80] to create a forest profile of the forest remnant. We calculated the distance from the centroid of each 1 m × 1 m pixel to the forest-matrix boundary, and then quantified canopy height for each pixel based on its distance to the edge. We quantified canopy height across the entire forest remnant, including areas of canopy gaps, because such information is important when analyzing the forest remnant from the perspective of the cuxiús, which are arboreal animals. We used the forest canopy profile to confirm that the forest remnant had lower canopy height within 20 m of the forest edge. We conducted all spatial analyses using ArcGIS Pro 2.5, ESRI, Redlands, CA, USA [87] and we conducted all statistical analyses in R, R Foundation for Statistical Computing, Vienna, Austria [88].

2.4. Movement Analysis

For each of the behavior and location scans taken every 5 min, we associated the location (latitude and longitude) of the monkeys with the behaviors they exhibited, the distance (m) to the closest forest edge, and the height (m) of the canopy at that location. Because the monkeys moved together, these paths represent the movement of the group, not of individuals. We created paths, connecting consecutive points, for each of the daily travel periods. Using the latitude and longitude of the cuxiús' locations at each behavioral and location scan, we calculated the distance (m) between consecutive points and the speed (km/h) traveled. We also calculated the bearing of the movement trajectory (direction of travel; degrees) for each instance where the cuxiús moved to another location. Lastly, we examined all movements and calculated if the cuxiús moved in a relatively consistent direction (angle made by three travel points <15°), or if they turned right or left (angle ≥15° in either direction). We quantified the angles of movement because this variable provides information on whether the monkeys have directional biases in their movement patterns in particular habitats [47,89].

We tested if there was a difference in the bearing of the movement using a chi-square test, with bearings ($n = 730$) grouped by 22.5°. We then used a Mann–Whitney U to test if the travel behavior differed based on whether the cuxiús were moving to a food site (and eating during the behavioral scan) or moving to a location where they did not eat. Because travel distances varied daily, we also paired travel to a food site versus travel to a non-food site by day and used a Wilcoxon Signed Ranks test to determine if speed differed. We then tested if there were differences in the turning behavior of the cuxiús by comparing the total number of turns (left versus right) using a chi-square goodness of fit test. Lastly, we tested if turning behavior (left versus right) differed when the cuxiús were traveling to a food site or not traveling to a food site using a chi-square test.

We had previously calculated home range using both minimum convex polygon and kernel density estimators and had found that the cuxiús had a home range that was equivalent to the area of the forest remnant [67]. However, such information did not necessarily identify specific details about smaller areas that the monkeys may avoid within their home range. With typical GPS accuracy error up to 5 m, we created a 5 m buffer around the travel path. For each travel path (and its buffer), we calculated mean forest canopy height and mean distance to forest edge. We then took all combined travel paths (and their 5 m buffers), and we tested if there was a difference in (1) distance to edge and (2) canopy height between the areas of the forest remnant that the monkeys used and the areas that were not used by the monkeys during the study using Mann–Whitney U tests. We then examined the data based on distance from edge in 10 m increments to determine if the percent of space used by the cuxiús matched the predicted percent, indicated by the percent of pixels located within each 10 m band. We used these predicted values because 10.1% of the pixels (therefore, area of the forest remnant) were <10 m from the edge, while only 1.0% were 170 m or greater from the edge; therefore, our predicted values were based on the likelihood of being within a particular distance from the edge. The greatest distance from the edge from anywhere in the forest remnant was 184.0 m (mean $\pm$ SE distance from edge: 63.54 m $\pm$ 0.12 m). Our distance groupings increased by increments of 10 m from the edge, but we grouped all values 170 m and greater together due to the limited area (1.0%) within the forest remnant that was at that distance from the remnant's edge.

2.5. Behavioral Location Analysis

For each of the behavioral scans, we calculated the distance to forest edge based on three common behaviors (rest, eat, travel, which comprised >90% of the behavioral scans). We tested if there was a difference in distance to edge in the three behaviors using a Kruskal–Wallis test. Then, we examined all behavioral scans, and then each of the three behaviors individually, to compare the percent of these behaviors that occurred within each distance category (e.g., <10 m, 10–19.9 m,) from the edge. We did not want to arbitrarily define a distance for determining forest edge vs. not forest edge, so we compiled the data for all behavioral observations and the three individual behaviors to see at which distance the actual percent of behaviors differed from the expected. We noted where there was 30% or more deviation (positive or negative) from the expected value.

2.6. Food Site Analysis

We mapped all feeding sites (trees and lianas), noted the distance to the closest forest edge, and calculated mean canopy height within a 5 m buffer of the GPS point taken. We compared the percent of food sites within each distance-to-edge category to the predicted distribution based on the amount of area present in the forest remnant that distance from the forest edge. These distance groupings were in increments of 10 m, as noted earlier. We then compared DBH of food trees and canopy height of all food sites based on their distance to edge categories, noting where there was a deviation by 30% or more. These distance groupings for comparison were also in increments of 10 m until 70 m from the edge, at which time we combined groupings. We combined groupings once a distance category had <5% of all food sites represented; doing so allowed for several categories, for example, with only three food sites to not be influenced strongly by a handful of samples. We tested if DBH of food trees differed between food sites close to the edge versus further from the edge using the Mann–Whitney U test; we defined close to the edge as <10 m, <20 m, and <30 m to not arbitrarily define the edge distance before placing the data in context to the cuxiús' feeding behaviors. We repeated the same analysis with the canopy height (5 m buffer around the base of the feeding site) at distances <10 m, <20 m, and <30 m from the forest edge versus the other feeding sites.

3. Results

3.1. Movement Trajectories and Speed

When cuxiús moved from one location to another, the bearings included all cardinal directions and there was no difference in direction traveled (X^2 = 7.05, df = 15, p = 0.96; Figure 2A). When they traveled, more than 50% of the movements (three consecutive points) were at an angle of <15°; however, left turns (59.6% of turns) were more common than right turns (40.4% of turns; X^2 = 11.74, df = 1, p < 0.001; Figure 2B).
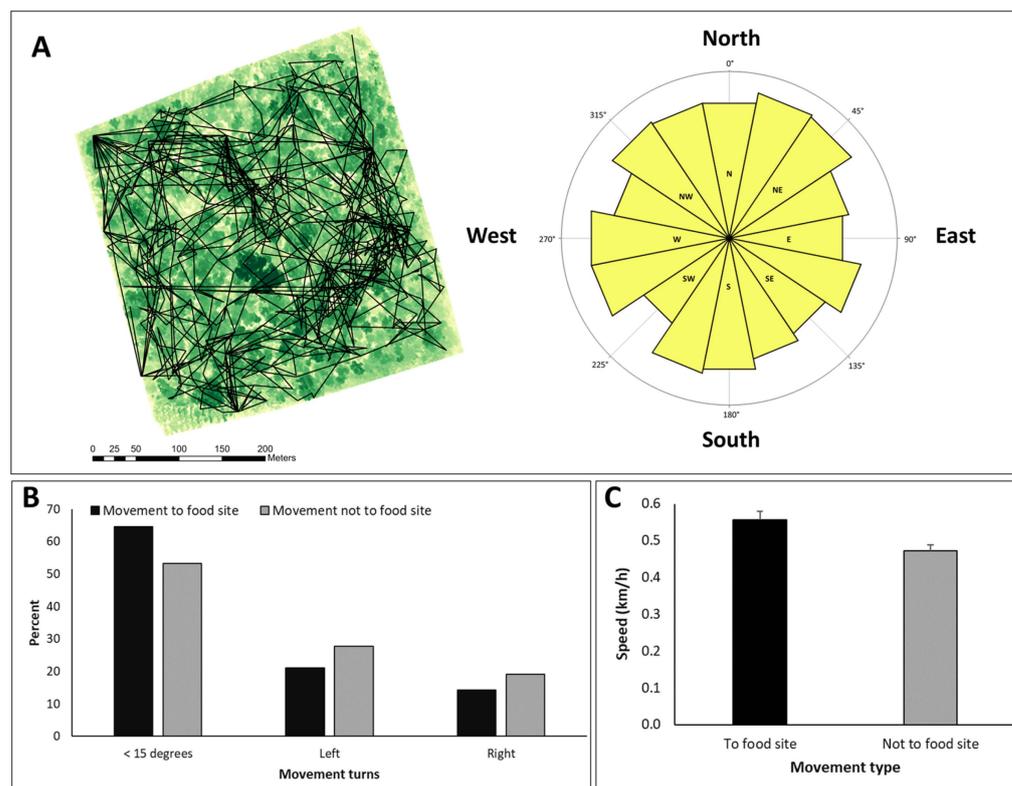

Figure 2. Cuxiú movement patterns. (**A**) When cuxiús moved to a new location, the bearings of such movement represented all cardinal directions, which was not surprising given the circular movements of the monkeys. (**B**) When traveling, most movements (three consecutive points) were at an angle of <15°, and left turns were more common than right turns, but there was no difference in turn direction when moving to a site where they ate than where they did not eat. (**C**) When moving from one location to another, they traveled at a faster speed (mean ± SE) when moving to a site where they ate than where they did not eat.

When cuxiús moved from one location to another during the 5 m interval, mean distance (±SE) was 41.79 m (±2.09), which was a mean speed of 0.49 km/h (±0.023). Mean maximum speed was 1.41 km/h (±0.12). Cuxiús traveled at a faster speed (mean ± SE) when moving to a food site than when they moved to a location where they did not eat (all data together: U = 50,654, N_1 = 268, N_2 = 460, p < 0.0001; paired averages/day: W = 53, n = 21, p = 0.031; Figure 2C). There was no difference in these patterns when the monkeys were moving to a food site versus when they were not moving to a food site (X^2 = 2.66, df = 2, p = 0.26; Figure 2B).

3.2. Forest Canopy and Cuxiú Use of the Canopy

Based on the pixels generated from the Lidar data, 28.9% of the forest remnant was <30 m from the forest edge and 22.6% was ≥100 m from the edge. Forest canopy height ranged from no canopy to 57.9 m (mean: 24.7 m). Within the forest remnant, 50.7% of the area consisted of forest canopy of 25 m or greater, 25.67% was 30 m or greater, and

0.76% was 45 m or greater. Canopy height was lowest <20 m from the forest-matrix border (mean height was 17.0 m and 22.6 m <10 m from the edge and 10–19.19.9 m from the edge, respectively; Figure 3A). Canopy height continued to increase until 40 m from the edge, at which time the variation decreased (mean canopy height ≥20 m from the edge was 26.0 m).
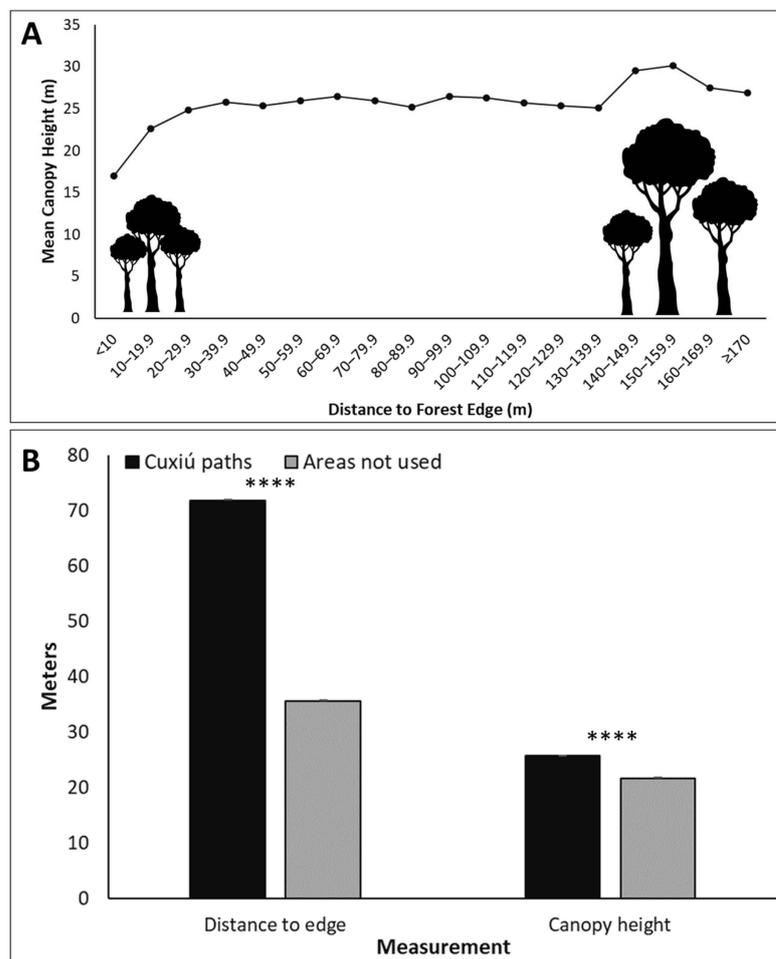

Figure 3. Canopy height and cuxiú travel paths. (**A**) Canopy profile of the isolated forest remnant, based on pixel values (1 m pixel resolution) from Lidar imagery [80]. Values represent canopy profile for the entire forest remnant, including areas of canopy gaps, because this information is an important component of examining the use of the forest by the arboreal cuxiús. Mean canopy height was lowest at the forest edge, but >30 m from the edge the mean canopy height did not vary much until the interior of the forest remnant, where mean canopy height was higher than in areas <130 m from the forest edge. (**B**) Cuxiú movement paths (5 m buffer), indicating forest used by the monkeys, were at a further distance from the edge (mean + SE) and had a higher canopy height (mean + SE) than areas that were not used by the cuxiús (**** $p < 0.0001$).

The paths traversed by the cuxiús (represented as the connection between GPS points with a 5 m buffer along the line), intersected 77.2% of the pixels represented by the area of the forest remnant. Although the use of the forest ranged from the forest edge (0.0 m from the edge) to the forest remnant's interior (max: 184.0 m from the edge), the areas of use were a greater distance from the edge than areas that the monkeys did not use ($U = 832,314,201$, $N_1 = 143,055$, $N_2 = 32,603$, $p < 0.0001$; Figure 3B). Moreover, forest used by the cuxiús had higher canopy height than areas the monkeys did not use ($U = 1,257,158,450$, $N_1 = 143,055$, $N_2 = 32,603$, $p < 0.0001$). For example, vegetation height in the southwestern corner of the forest remnant was very low, and they did not travel into that area; Figure 1B).

Although cuxiús used the forest edge to the interior of the forest remnant (Figure 4A), the greatest discrepancies between the area used versus the expected area used was in distances <20 m from the forest remnant's edge (Figure 4B). Examining the data by distance grouping, they used >80% of the pixels within each distance grouping (range: 84.3–97.1%) ≥30 m from the edge; however, within 30 m of the edge, these percentages were much lower (Figure 4C). These paths indicate areas that the cuxiús traversed but they do not indicate the frequency that these monkeys traveled through particular areas of the forest. In fact, when we considered such frequency data, the percentage of time that they traveled near the forest edge was even lower, due to more frequent movements closer to the interior of the forest remnant. For example, the percent of time (daily mean ± SE) <10 m from the edge was 1.69% (±0.53) and for <20 m from the edge it was 5.07% (±1.26).
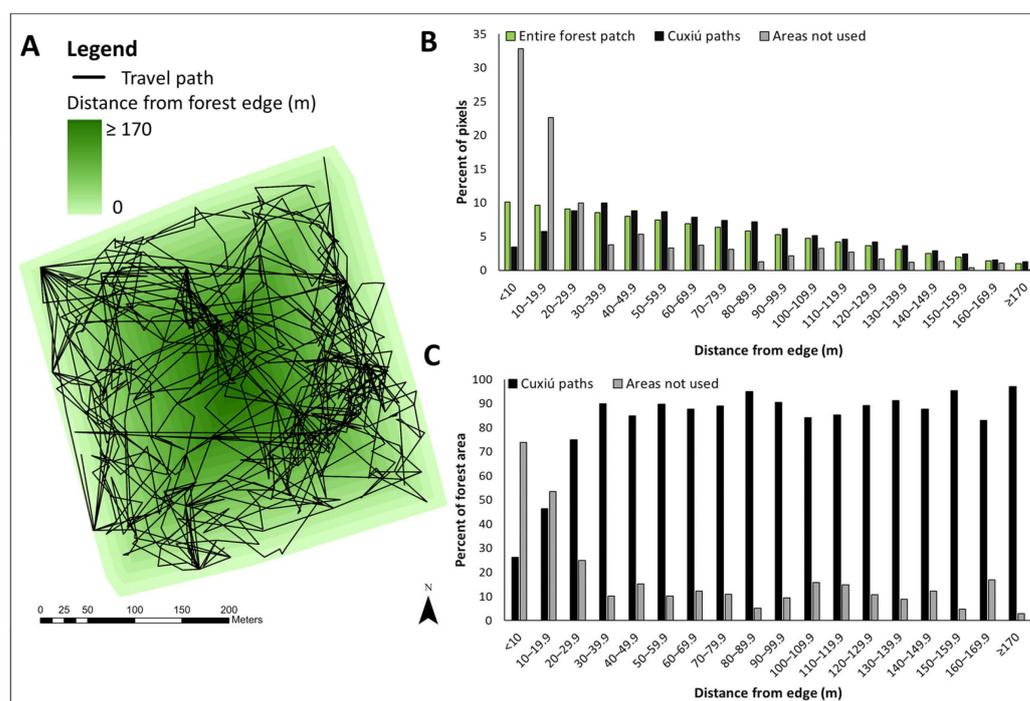

Figure 4. Forest use. (**A**) Cuxiús used most of the forest remnant, but they typically traveled interior to the forest edge. (**B**) The entire area used by the cuxiús (path with 5 m buffer) ranged from forest edge to interior, but the greatest discrepancies between the percent of area available within a given distance from the edge (green: entire forest remnant) and the percent used by the cuxiús (black: cuxiús paths) were <10 m and 10–19.9 m from the edge (−denotes ≤30% of the expected value; +denotes ≥30% of the expected value). (**C**) Within each distance category (at 10 m increments), cuxiús did not use >50% of the area <20 m from the edge; however, at distances ≥20 m from the edge, cuxiús used >70% of the area within each category.

Cuxiú movement paths included canopy heights that were less than 1% higher or lower than the mean canopy height of the entire forest remnant at a particular distance, with the exception of <10 m from the edge, which differed from the forest remnant average by being 11.0% more, and 160–169.9 m from the edge, where the cuxiú paths had mean canopy height that was 7.9% smaller than the mean canopy size for all areas of the forest remnant at that distance (Figure 5). Within the interior of the forest remnant, mean canopy height was greater in areas not used as a path. These areas contained some emergent trees that were not used by the monkeys.
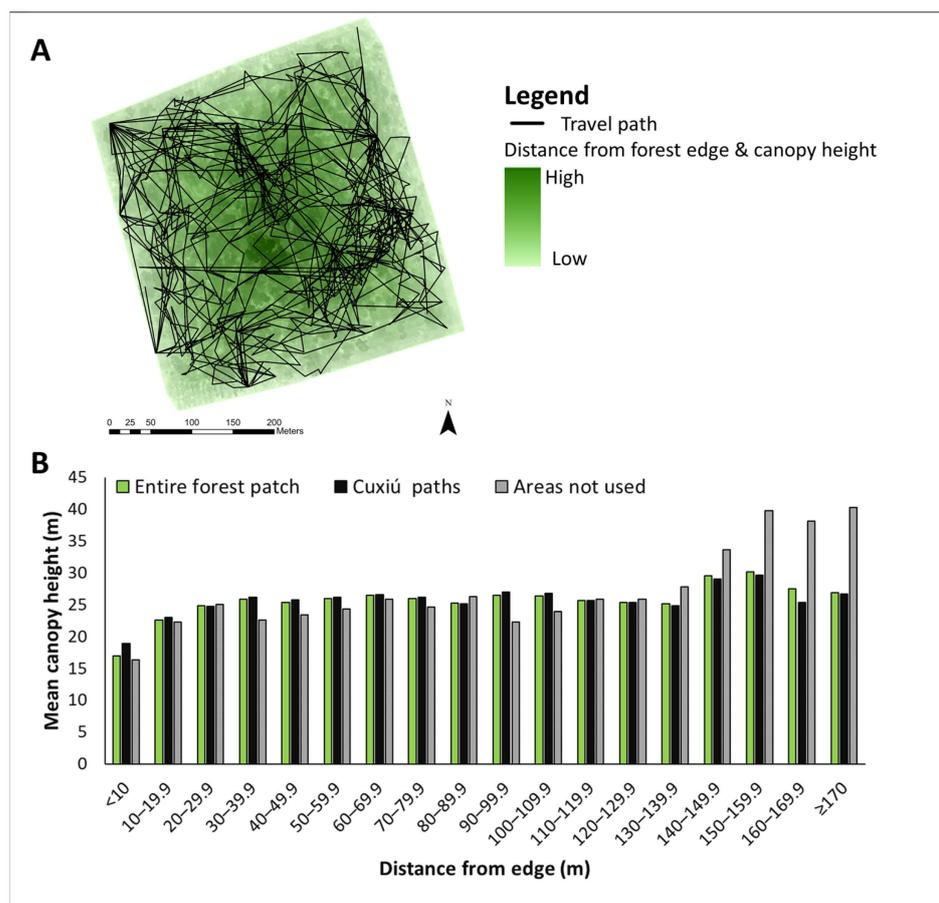
Figure 5. Cuxiú travel paths: forest edge and mean canopy height. (**A**) Cuxiús traveled throughout the forest remnant, with most paths not along the edge or in very low or very high canopy. (**B**) There were no large differences in mean canopy height within each distance-from-edge category, except for distances ≥150 m from the edge, where there were emergent trees not used by the monkeys.

3.3. Cuxiú Behavioral Locations

For all behavioral scans, mean daily distance from the edge (±SE) was 66.8 m (±4.82); for context, mean distance to the edge from any location within the forest remnant was 63.54 m (±0.12). Although mean distance to the edge (±SE) was ≥24% for traveling (83.5 ± 18.02) than resting (67.9 ± 6.17) or eating (64.7 ± 3.85), there was no statistical difference in distance to the edge among all three behaviors (X^2= 0.39, df = 2, *p* = 0.82).

Examining the location of the behaviors in greater detail, there consistently were patterns of a lower percentage of behaviors occurring <30 m from the edge compared to what was expected based on the amount of the forest remnant located <30 m from the edge (Figure 6). Almost 30% of the forest remnant was less than 30 m from the forest edge (green bar), but <20% of all behavioral scans combined, resting, and traveling were less than 30 m from the edge (Figure 6A): for all behaviors combined, as well as resting and traveling, cuxiús differed by 30% or more from the expected values. When we examined the edge distances at a finer scale, none of the behaviors were exhibited 30% or more from the expected values when distance to the edge was <30 m (Figure 6A–E).
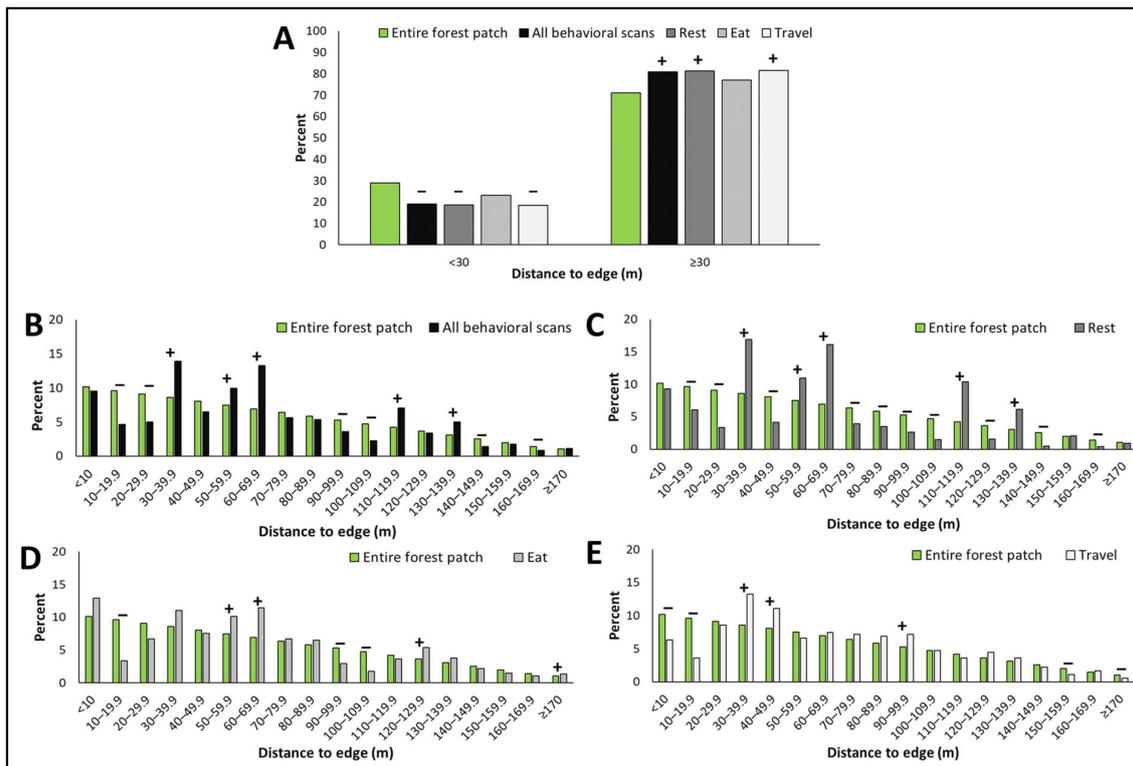
Figure 6. Cuxiús used forest edge to the interior of the isolated forest remnant, but not in an equal proportion to the amount of forest available at a given distance from the forest edge. (**A**) Almost 30% of the forest remnant was less than 30 m from the forest edge (green bar), but <20% of all behavioral scans combined, resting, and traveling were less than 30 m from the edge. For all behaviors combined, as well as resting and traveling, cuxiús differed by 30% or more from the expected values ($-$ = 30% or smaller of the expected value; + = 30% or larger of the expected value). The behavioral profiles, as a percent of behavioral scans exhibited based on distance to the forest edge, indicated variability in (**B**) all behavioral scans, (**C**) resting, (**D**) eating, and (**E**) traveling.

3.4. Food Sites

Of the 169 food sites (individual trees and lianas) used by the cuxiús, the distribution of the food sites ranged from the forest edge to the interior, but food sites typically were located further from the forest edge than expected based solely on amount of the forest remnant available (Figure 7A). However, these patterns did not hold when examining the food trees' DBH and the canopy height of the food sites. There was no difference in DBH between food trees <10 m from the edge and the rest of the food trees (U = 465.5, N_1 = 10, N_2 = 105, p = 0.56; Figure 7B). This pattern remained with trees <20 m (U = 906.5, N_1 = 18, N_2 = 97, p = 0.80), and <30 m (U = 1238, N_1 = 29, N_2 = 86, p = 0.96) from the forest edge. Yet, the canopy height was lower for food sites (trees and lianas) close to the edge compared to food sites elsewhere in the forest remnant (<10 m from the edge: U = 1764, N_1 = 15, N_2 = 154, p <0.001); <20 m from the edge: U = 2611, N_1 = 26, N_2 = 143, p = 0.0011; <30 m from the edge: U = 3207, N_1 = 39, N_2 = 130, p = 0.012). Canopy height of food sites had the lowest values closest to the edge, but none of the groupings by distance to the edge had an average canopy height of food sites that differed from the mean canopy of the entire forest remnant at that particular distance 30% or more (<10%: food sites were 16.8% larger; 130–159.9 m: food sites were 23.0% smaller (Figure 7C).
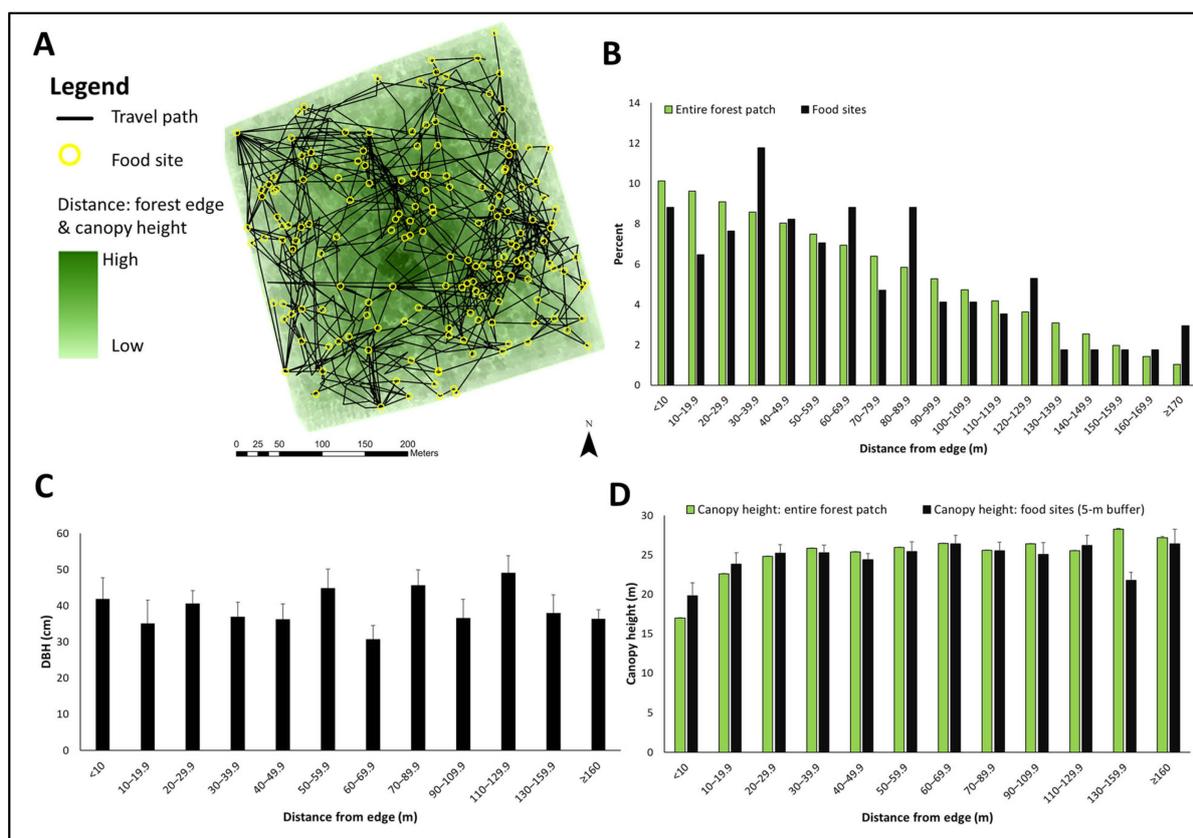
Figure 7. Of the 169 food sites (individual trees and lianas) used by the cuxiús, (**A**) the distribution of the food sites ranged from the forest edge to the interior. (**B**) Comparing the percent of the forest remnant located at varying distances from the forest edge, food sites typically were less often found than expected at distances close (<20 m) to the forest edge (− = 30% or smaller of the expected value; + = 30% or larger of the expected value). However, (**C**) the diameter at breast height (DBH) of feeding trees was relatively consistent across the forest remnant. The number of groups for distance from edge is smaller than in other figures because some of the distances did not have many food sites, and we did not want three trees, for example, to represent the entire group. There were no differences in DBH of feeding trees located <10 m from the edge, compared to the remaining feeding trees in the forest remnant. The same pattern held (no difference in DBH) when comparing the food trees <20 m from the edge, and then when comparing the food trees <30 m from the edge. (**D**) Canopy height of food sites was lowest closest to the edge, but none of the distances from edge had a difference of 30% or more between the overall canopy height and the canopy height of the food sites.

4. Discussion

Much of the previous research focusing on primates and forest edges have focused on the extent to which primate density changes from the edge to the forest interior [40,42,90], but understanding how animals behave in modified habitats is very important for understanding the edge effect on primates [36]. In our study, the cuxiús lived in a small, isolated forest remnant that was <3% of the size of their home range in continuous forest; 28.9% of the forest remnant was <30 m from the forest edge and 22.6% was ≥100 m from the edge. Therefore, these cuxiús had greater exposure to the forest edge than monkeys that lived in nearby continuous forest [67]. The remnant in this study had a minimum of three cuxiús; however, group size can get to be as large as 65 individuals [91], and in a nearby continuous forest the typical group size was >20 individuals [68]. The density of cuxiús in this small remnant was larger than that in larger remnants (100 ha) and continuous forest [68], and the cuxiús in this small forest remnant had a less diverse diet than those monkeys in larger forested areas [69]. Our findings on cuxiú movement patterns are in this context of monkeys living in a small forest remnant that is not typical for this species.

Our first objective was to determine the main characteristics of cuxiú movement patterns in a small remnant. Primates can use mental maps and remember the location of and path to resources [46]. We found that movement bearings were consistent in all cardinal directions; such findings make sense given that the cuxiús at BDFFP in the smaller forest remnants traveled in circular (vs. straight) patterns during a given day [67]. We found, however, that when the cuxiús made a turn during their travels (defined as an angle $\geq 15°$), the monkeys turned left more than right. While we had predicted that there would be a preference in turning, given that we knew the monkeys traveled circular routes, we did not have a prediction regarding which direction they would turn. In our examination of the literature, turning behavior in monkeys is a topic that has not been widely studied.

Consistent with our predictions, cuxiús traveled more quickly to areas that were food sources than to areas that did not provide food at a given time. While more research is needed to fully understand their traveling patterns, these findings for one group of cuxiús suggest that the animals tracked their resources, similar to findings for other primate species [46,71,72]. We think additional focus on these factors is a future direction of our research, given that animal movement angles can be used in combination with habitat assessments to better understand movement patterns [47,89].

Our second objective was to determine if cuxiú movement and behavioral profiles differed relative to the distance to the forest edge. We found that the monkeys used forest from the edge to the interior of the forest remnant. However, overall, the monkeys used forest <30 m from the edge less often than predicted. This finding was not surprising, given that some sections of the forest's edge were void of trees >15 m in height; however, cuxiús used areas of the edge where there was higher forest canopy. This forest canopy that the monkeys used was shorter near the edge, but it was several meters taller than the average canopy height along the edge. These findings highlight that even with heavy forest loss and fragmentation, and the resulting edge effects on the forest, mid-size trees (20–30 m) can be resources for the monkeys. Within the interior of the forest remnant, mean canopy height was greater in areas not used as a path. These areas contained some taller, emergent trees which were not used by the monkeys. While we do not know why the monkeys did not use the canopy of the emergent trees, we hypothesize that the canopy was at such a higher level than the main tree canopy (maximum canopy height was 57.9 m; only 2.1% of the forest remnant had a canopy height ≥ 40 m) that getting in and out of the emergent canopy may be energetically costly; the emergent canopy may also not have allowed for as much protection from predation given that the emergent trees were relatively isolated and predation of monkeys in the study area has been primarily by raptors [76,77].

Examining behaviors and their locations, we found that cuxiús used most of the forest that was available to them but concentrated their time in areas >30 m from the edge. Traveling and resting behaviors both were less frequent near the forest edge than expected, while eating behavior did not differ more than 30% than what was expected based on forest area. These findings could be related to predator avoidance: in the study area primates have been predated upon in the forest remnants, but also in continuous forest [76,77].

The cuxiús used food resources from the forest edge to the interior, but, overall, the food trees were located further from the forest edge than what was expected based on the relative area of forest in the remnant. The food trees that were near the forest edge were shorter than food trees closer to the interior of the forest remnant, but DBH did not differ based on distance from forest edge. These findings indicate that the monkeys used food resources throughout the forest remnant, but they concentrated their efforts on trees located further from the edge. While predation avoidance could potentially be a reason for this pattern, it may also be that food resources were less abundant near the forest edge, given that forest edges often differ from interior forest in the tree composition [6,7].

Globally, it is likely that forest remnants will increase in abundance and decrease in size [92]. Therefore, more populations, including primate populations, will likely encounter such habitat remnants. Edge effects and their demonstrated impacts on canopy structure [33] could further exacerbate the forest loss and fragmentation. For example,

cuxiús used the relatively larger trees that remained near the forest remnant's edge. If edge effects (e.g., increase in tree mortality, decrease in canopy height, plant species that are not used as food by the monkeys) were to increase, even without increased forest loss, there could be an increased impact on these monkeys. Such changes could further reduce how much of the forest remnant is available to the monkeys.

Small habitat remnants can be important for conservation [4]. This small habitat area could be important in a larger landscape for the long-term success of cuxiús in the region. At BDFFP, Lenz et al. [42] documented cuxiús in the secondary forest of 19–30 years of regrowth, and we found the monkeys used tall secondary-growth forest near previously isolated forest remnants [67]. These findings suggest that older secondary growth could be important in maintaining habitat connectivity for the monkeys. Although cuxiús used areas <20 m in height near the forest edge, most of the canopy used was 20–30 m in height.

The current study focused specifically on primate movements where the animals remained in an isolated forest remnant that was substantially smaller than the area used by individuals in nearby continuous forest. Moving forward, it will also be important to have a landscape perspective [93] to understand population dynamics, movement, and conservation. Understanding the extent to which the animals remain in isolated forest remnants, versus traveling in and out of forest remnants, is important for understanding how a species will use (or not use) a particular landscape. Such information could be an important consideration as people determine the best way to design landscapes for conservation [94–96].

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