Forest cover and bird diversity: drivers of fruit consumption in forest interiors in the Atlantic forest of southern Bahia, Brazil

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Abstract

Forest loss and fragmentation change the dynamics and structure of remnant populations, ultimately affecting key processes with implications for ecosystem functioning. Fruit consumption has important consequences for seed dispersal, maintaining the plant demography, which is also critical to the populations of animals that utilize them for resources. Therefore, understanding how forest cover reduction affects fruit consumption and, consequently, seed dispersal is essential to informing conservation policy for the remaining forest patches. This study was conducted in 20 forest sites with varying amounts of forest cover (from 6% - 85%) located in the Atlantic forest of southern Bahia, Brazil. We investigated whether forest loss and local bird diversity affected fruit consumption rates in the forest edge and interior. We used artificial fruit to estimate fruit consumption by birds. At each site, we set up 14 experimental stations, one located on the forest edge (~ 3m) and the others in the forest interior (75 m), each one composed of 15 artificial fruits fixed to a plant. Our results showed that forest loss and the reduction of bird abundance led to a decrease in fruit consumption in the forest interiors, but not on the forest edges. This verifies that forest cover loss results in changes in fruit consumption, and has important consequences for seed dispersal by birds in forest remnants.

Keywords: Anthropogenic landscape, Atlantic forest, ecological function, frugivory, compensatory dynamics.

Resumo

Perda e fragmentação da floresta mudam a dinâmica e estrutura de populações remanescentes, afetando em última análise, processos-chave com implicações para o funcionamento do ecossistema. O consumo de frutos tem consequências importantes para a dispersão de sementes e manutenção da demografia de plantas, assim como das populações de animais que obtêm recursos dessas plantas. Portanto, compreender como a redução da cobertura florestal em escala de paisagem afeta o consumo de frutos, e consequentemente, a dispersão de sementes, é essencial para a conservação dos fragmentos florestais remanescentes. Este estudo foi conduzido em 20 áreas de floresta com diferentes quantidades de cobertura florestal em escala de paisagem (6-85%), localizadas na Mata Atlântica brasileira do sul da Bahia. Investigamos se a perda de floresta em escala de paisagem afeta as taxas de consumo de frutos em áreas de bordas e interior de floresta. Utilizamos frutos artificiais para estimar o consumo de frutos por aves. Em cada local, colocamos 14 estações experimentais, uma localizada na borda (~ 3 m) e outra no interior da floresta (75 m), cada uma composta por 15 frutos artificiais fixados em cada planta. Nossos resultados mostraram que a redução da cobertura florestal e a abundância de aves diminui o consumo de frutos no interior das florestas, mas não em bordas da floresta. Este resultado ilustra que a perda de cobertura florestal e diminuição da abundância local de aves levam a mudanças no consumo de frutos nos interiores da floresta, mas não nas bordas. Este resultado sugere consequências importantes para a dispersão de sementes mediada por aves no interior de remanescentes florestais.

Palavras-chave: Paisagens antrópicas, função ecológica, frugivoria, dinâmica compensatória.

Introduction

Currently, changes in land-use due to anthropogenic activities have transformed continuous forests into a myriad of small patches, often surrounded by an inhospitable matrix, such as pasture, sugar cane and palm oil plantations [1-3]. As a result of this massive habitat loss and fragmentation, there are striking changes in species composition in the ecological assemblages of small and isolated forest patches, with sensitive species being replaced by a proliferation of disturbance-adapted species, a process we call compensatory dynamics [4, 5]. These changes are in part a consequence of the increasing penetration of edge effects, which may change microclimate conditions (such as temperature and humidity) as well as the local vegetation structure [6, 7]. Although several studies have shown the negative effects of forest loss and fragmentation on biodiversity [8, 9], there is poor understanding of the effects of this biodiversity loss on species interactions and of the pervasive consequences to ecosystem functions [10-12].

Birds are among the most diverse group of vertebrates in tropical forests, and due to their high local diversity and abundance, they are involved in key ecological processes such as arthropod control, pollination, and seed dispersal [13]. However, because bird diversity often declines as a result of land-use changes [9, 10, 14], the ecological functions performed by them are also likely to be altered [13, 14]. Seed dispersal is one of the most important ecological processes carried out by birds in tropical forests that have been modified by land-use changes [15]. In some tropical forests up to 90% of the tree species are dispersed by animals, mainly mammals and birds [16, 17]. Therefore, loss of seed dispersers, such as frugivorous birds, can affect plant regeneration and impact heavily on forest structure and the phenotypic and genetic characteristics of plants species [13, 18].

In this study we investigated how forest cover reduction can affect the fruit consumption of birds in the fragmented Brazilian Atlantic forest, testing whether fruit consumption varies between the forest edge and the interior. A previous study in the same region reported that deforestation affected frugivorous birds [9]. Therefore, we also investigated the influence of the abundance of frugivorous birds on fruit consumption, among both forest interior specialist species and forest edge species. We expected that the amount of fruit consumed would decrease in more deforested landscapes, but that the pattern would be different between the forest edge and the interior and would vary according to bird abundance [19-22]. As forest patches embedded in more deforested landscapes often lose disturbance-sensitive species such as forest interior specialist birds, while favoring the proliferation of generalist birds [5, 23], we also predicted that fruit consumption would only be affected in plants located in forest interiors and that fruit consumption would increase at the edges

of forests. We also predicted that the abundance of frugivorous birds would be a key factor explaining local variations in fruit consumption, and that the decreasing diversity of frugivorous species due to forest loss would negatively influence fruit consumption rates. In this paper we discuss the potential implication of our results for seed dispersal and, ultimately, for the maintenance of forests within anthropogenic landscapes.

Methods

Study forest sites

This study was conducted in the Atlantic forest of southern Bahia, Brazil (Fig. 1), a tropical wet forest region [24]. Unlike other areas of the Brazilian Atlantic forest, southern Bahia is still densely forested [25], albeit in different successional stages ranging from secondary to old-growth forest. The region has a mosaic of land-use that is mainly composed of shade cacao plantations, cattle pasture and rubber tree and *Eucalyptus* sp. plantations [26]. The average annual temperature is 24 °C, and the mean annual rainfall is 2000 mm. There is no defined seasonality, although a dry period may occur from December to March [27].
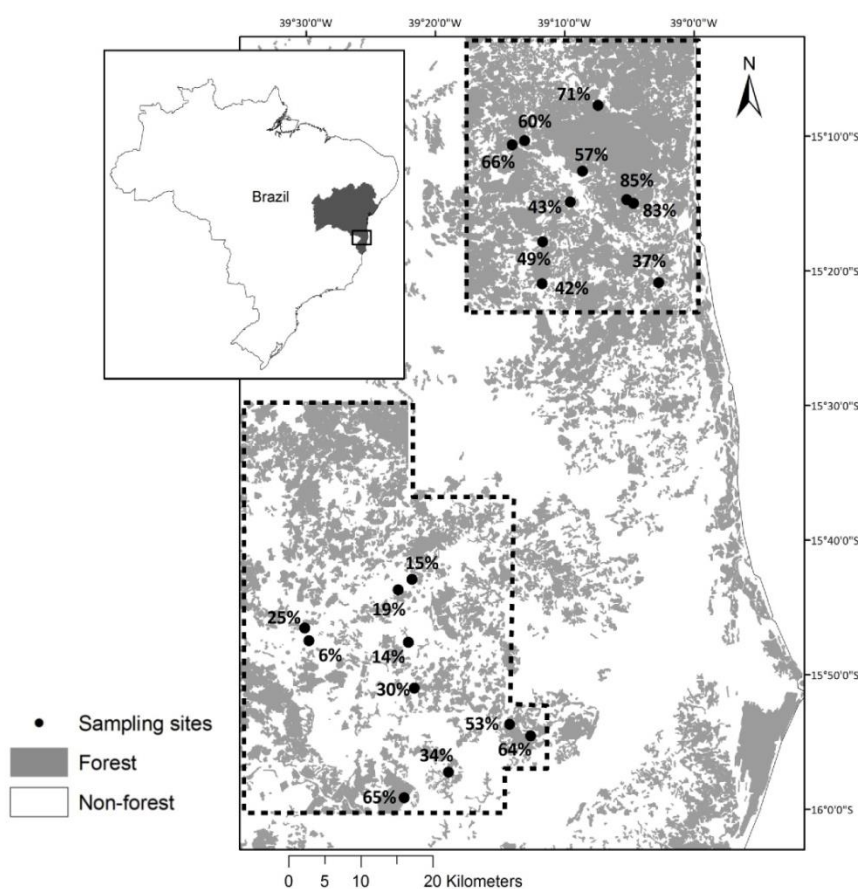
Fig.1. Study area located in northeastern Brazil highlighting the forest cover (gray areas) and the distribution of 20 sampling sites (black dots), each depicting the amount of forest (%) remaining within a 2 km radius. Dashed lines show the areas that were specifically mapped for this study while the remaining map of forest cover was obtained from the SOS Mata Atlântica, Instituto Nacional de Pesquisas Espaciais (2012).

We analyzed satellite images (RapidEye, from 2009-2010, QuickBird and WorldView, from 2011) and added the data to a map of 3,500 km^2 of the study region (Fig. 1). The scale of the map is 1:10,000, which is suitable for identifying forest patches based on visual observation. The forest patches were classified according to different forest types following the typologies provided by IBGE [28]. Using this map, we selected 48 potential sample sites located within forest patches. We used a sample site-landscape approach, in which the landscape attributes surrounding sites (such as the amount of forest cover) were measured within a specific radius from the center of each focal site [29]. In particular, we estimated the amount of forest remaining in a 2000 m radius (1256 ha) to each forest site. A prior study at this scale in our region showed that there was a strong relationship between

forest cover and the abundance and richness of frugivorous birds [9]. We considered the percentage of both old-growth and secondary forest in our estimations of native forest cover. This classification may be a simplification of the ecological requirements of bird species, but we believe that this broad definition is appropriate because many recommendations for landscape conservation and management are based on fragmentation or habitat loss in general [30]. Furthermore, it is unlikely that empirical analyses can quantify the conditions that limit the occurrence of every species [31]. This is particularly true in Neotropical regions because of their high species diversity and because of a lack of scientific knowledge regarding the ecological requirements of the birds. Finally, we randomly selected 20 sites that had 6% to 85% of forest cover within the 2000 m radius.

Artificial fruit Consumption
We used artificial fruit made of non-toxic modeling clay (ACRILEX®) to estimate fruit consumption by birds [20, 32]. This technique has been applied successfully in a variety of ecological studies to estimate fruit consumption [32, 33]. We used red fruit because red is common in ornithochoric fruits and, because of its contrast, is one of the colors most clearly visible to visually oriented frugivores such as birds [34]. Each fruit measured approximately 14 mm in diameter [32]. We set up two parallel 420 m x 2 m plots at each site, one located on the forest edge (~ 3m) and other in the forest interior. In the interior, the plot was randomly located 75 m from the edge because previous studies in the region have found significant changes in forest structure [35] and in the composition of ecological groups occurring at this distance [26]. In each plot, we established 14 experimental stations at 30 m intervals. Each station was composed of 15 artificial pieces of fruit distributed in a plant (without flowers or fruit) ranging from 100 cm to 200 cm in height (Fig.2 A, B). After 96 hours we removed the artificial fruit and examined them for signs of consumption, indicated by beak marks [36, 37]. The analysis did not include 89 pieces of fruit that had either disappeared or showed signs of consumption by other groups such as mammals.

Fig. 2. Example of an experimental station used in this study (a), with an artificial fruit pecked by bird (b).

Bird survey

We sampled the bird community using the point-count method [38, 39]. The sampling took place during three periods from January 2013 to April 2014, May to September 2013 and October 2013 to April 2014. During each period we monitored all the sites. Sampling at each point was performed for 15 minutes twice a day: between 06:00 and 09:00 and between 15:00 and 17:00, totaling six hours of sampling per site. We avoided sampling on rainy days, as rain interferes with bird data collection [39]. At each sampling site, we established four point-counts with a fixed radius of 50 m, each separated by a minimum distance of 150 m. The point-counts were distributed 100 meters from any forest edge to minimize contamination from adjacent habitats and to ensure the bird communities at each sample site were representative [9].

Although we recorded bird species with different diets (insectivorous, frugivorous, nectarivorous, omnivorous, and granivorous), for the purposes of the present study we only considered frugivorous species, as they represent potential dispersers of fruits in the forest. Because all our sampling took place within forest interiors, the study did not generate data on local species abundance along forest edges. However, we classified each species according to a preferred habitat type, whether it was forest edge or interior and, for each species subset, we used their summed abundance as a proxy for their local diversity in each habitat type. When a given species occurred in both areas (edge and interior), it was considered in both categories. For this classification, we relied on literature available information regarding dependence on forest habitats, the occurrence of habitat type (forest edge or interior), the foraging layer, and sensitivity to anthropogenic disturbance [40].

Statistical analysis

We adjusted linear models to assess how the abundance of frugivorous birds related to forest cover. The total frugivorous bird abundance at each site was considered as the sum of the number of individuals, recorded during the three field study periods at the four counting points. To assess whether variation in fruit consumption could be explained by changes in forest cover, we adjusted the generalized linear mixed model (GLMM) to include habitat type (forest edge or interior) as categorical variables as well as the local abundance of frugivorous birds at forest edges and in the interior. We considered the abundance of frugivorous birds, and not species richness, because fruit consumption may depend more strongly on the number of individuals rather than the number of species present in each forest patch. We assumed a Poisson error distribution for all variables and considered habitat type as a categorical factor (forest edge or interior) and forest site as a random factor in the models. Because of the limitations of our sampling we created non-interactive models composed of combinations of the aforementioned variables. We also calculated Akaike information criterion corrected for small samples (AICc) for all models and selected the model with the lowest AICc. We considered both models as equally plausible when the difference in the AICc (ΔAICc) between the lowest two models was smaller than 2. We also used the Akaike weighting (wAICc) that ranges from 0 to 1, and thus enables the ranking of models, showing the probability of which one is most parsimonious [41]. The statistical analysis was performed in R software [42], using lme4 [43], bbmle [44] and nlme [45] packages. An adopted alpha of ≤ 0.05 was considered significant.

Results

Of the total amount of fruit used during our experiment (n = 8400), only 697 pieces (8.3%) were consumed and 89 removed from plants. We identified 49 frugivorous bird species, of which 37 species (914 individuals) were considered potential consumers of fruits in the understory of the forest. The most abundant species were *Tangara palmarum* (n = 143 individuals), *Manacus manacus* (n = 83), *Machaeropterus regulus* (n = 74) and *Pipra rubrocapilla* (n = 70). The latter is classified as a species of the forest interior. We found that forest reduction did not impact on the abundance (R^2 = 0.003, p = 0.31, Fig.3) of frugivorous birds associated with edge habitats (n = 31). However, the decrease in forest cover triggered a decline in the abundance patterns (R^2 = 0.40, p 0.001, Fig.3) of bird species associated with the forest interior (n = 17). Our results showed that two models were

equally plausible to explain fruit consumption by birds (Table 1). Reduction of both landscape-scale forest cover and local bird abundance negatively affected fruit consumption and were the main variables shown in the two models selected (Table 1 and 2). Habitat type also explained fruit consumption, in this case with significantly higher consumption in the forest interior (Table 1 and 2, Fig. 4).
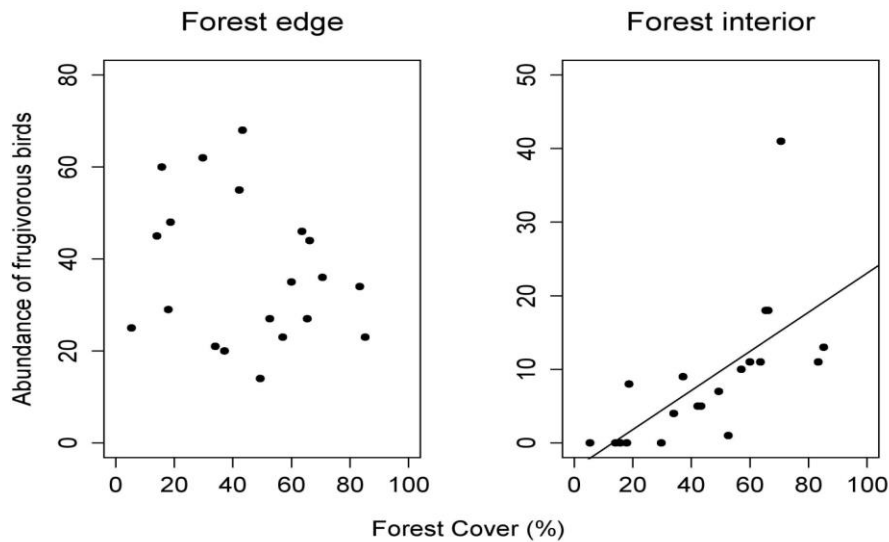

Fig. 3. The abundance of frugivorous birds in 20 sampling sites located in landscapes with different amounts of surrounding forest cover (%), along the Atlantic rainforest of southern Bahia, Brazil. Results are shown separately for edge and forest interior habitats. Significant relationship (*P< 0.05*) is indicated by the solid line.
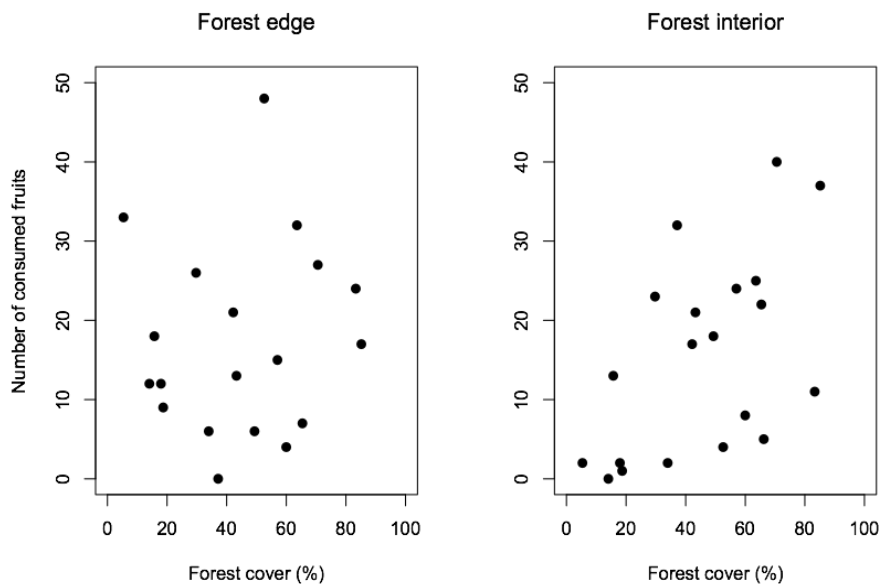

Fig. 4. Number of consumed fruits in 20 sampling sites with different amounts of surrounding forest cover. We show the results separately for edge and forest interior.

Table 1. Model selection parameters, based on Akaike's Information Criterion (AIC), relating fruit consumption to forest cover, habitat type (edge or forest interior), abundance of frugivorous birds classified as edge or forests interiors, showing the best models in bold. AICc: Akaike information criterion corrected; Δi: difference in AICc between the best model and the ith model; k: parameter number of the model; wi: AICc weight. Models are ranked by AICc values.

Models	Δi	K	wi
1. **forest cover and local abundance**	**0**	**4**	**0.48**
2. **forest cover, habitat type and local abundance**	**0.3**	**5**	**0.4**
3. local abundance	4	3	0.06
4. habitat type and local abundance	4.2	4	0.06
5. forest cover and habitat type	16.2	4	<0.001
6. habitat type	19.8	3	<0.001
7. forest cover	22.0	3	<0.001
8. (Null)	26.7	2	<0.001

Table 2. Parameters estimated by the best fit generalized linear mixed model (GLMM).

Fixed effect	Parameter estimate	Standard error	z value	P
1. intercept	1.85	0.25	7.34	<0.001
forest cover	0.01	0.004	2.77	0.01
local abundance	0.01	0.002	5	<0.001
2. intercept	1.66	0.27	5.97	<0.001
forest cover	0.01	0.004	2.75	0.01
habitat type	0.18	0.12	1.52	0.23
local abundance	0.01	0.003	4.29	<0.001

Discussion

Our study showed that fruit consumption decreased following the reduction of forest cover in anthropogenically modified landscapes. This is a consequence of the demise or decrease in abundance of many disturbance-sensitive frugivorous birds commonly recorded in forest interiors, particularly in landscapes with intermediate to high levels of forest cover [9, 20]. Forest specialist birds are likely to depend on a large amount of forest to maintain viable populations [9, 46], especially frugivorous species. As fruit is a seasonal resource, frugivorous birds must move among different habitats daily to obtain food [47, 48], and the loss of landscape connectivity triggered by the reduction of forest cover impairs such movement [49]. In addition, increasing deforestation and anthropogenic land use intensity often results in a simplification of the surrounding matrix, further lessening the permeability of the landscape to species movement [50-52]. The combined effect of an inhospitable matrix and increased distance between forest patches can further hamper species dispersal due to an increasing demand on energy and a greater risk of predation [48]. This results in a reduction of the diversity of frugivorous birds in more deforested landscapes.

A previous study in the same region showed that as landscape-scale forest cover decreases and the more sensitive species are lost, there is a concomitant proliferation of disturbance-adapted birds in forest interiors [5], a pattern also reported elsewhere [14, 23]. Yet, despite numerical compensation for the local richness and abundance patterns of frugivorous assemblages, fruit consumption was still negatively affected by landscape-scale forest loss. Such shifts in species composition are likely to be an important driver changing patterns of fruit removal with consequences on seed dispersal, and may well reveal the low functional redundancy among species. Recent evidence has shown that rather than reducing the overall number of ecological functions, communities in more deforested and disturbed landscapes play different roles, indicating that changes in species traits following the dramatic species turnover after deforestation are likely to result in a concomitant change in the repertoire of ecological functions they provide [23].

Contrary to earlier studies using artificial fruit [20], we found no evidence of a higher probability of artificial fruit consumption on forest edges to forest interiors. Deforestation increases the proportion of edges in a given fragment [2, 53], and it is likely to favor the presence of more generalist birds [14, 26]. In addition, the increase of edge effects following deforestation is known to alter the availability of resources within forest remnants in fragmented landscapes [54], increasing or decreasing the availability of fruits, seeds and nectar resources, for instance, compared to within the forest interior [55, 56]. However, in most studies, edge effects negatively influence fruit production and the visitation rates of birds [57], although species with diets composed of different classes of food, such as omnivores, and those that occur in disturbed areas, such as generalist birds, may benefit by landscape scale forest loss [9, 58].

Our results showed that local bird abundance on forest edges was not affected by large-scale deforestation and, consequently, that fruit removal rates on forest edges were constant regardless of deforestation. In particular, we observed a high variability of fruit removal rates at forest edges located within similar ranges of landscape forest cover. Such high spatial variability on forest edges may be related, for instance, to differences in the surrounding matrix composition. Although our edge transects comprised the boundary between forests and open areas such as pasture or annual crops, we did not control for differences in other aspects of the landscape structure that may directly affect species composition on the edges, such as the nature and the amount of different habitats in the surrounding matrices [5]. Such features may contribute to variations in local assemblages of generalist frugivorous birds [59].

Implications for conservation

It is important that more conservation-oriented studies evaluate not only the local patterns of species diversity in anthropogenic landscapes but also the possible changes in functional processes, such as seed dispersal, that different species perform [12]. Most species of birds occurring in the Brazilian Atlantic forest require a high amount of forest cover (≥ 50%) [9, 60] due to their high habitat specificity and, thus, sensitivity to environmental disturbances. If the continued functionality of tropical forests is to be maintained it is essential to determine the ecological functions of bird species most vulnerable to environmental changes [61].

The replacement of ecological groups of frugivorous birds triggered by deforestation in our study region indeed influenced local patterns of fruit consumption [5]. Forest specialists are likely to perform more specialized functions, consuming and dispersing a specific array of fruit, with only a few overlapping between species, while generalist species may be more ecologically redundant [62, 63]. This means that even if there is a proliferation of generalist species following the reduction of forest cover, these species cannot maintain the range of fruit consumption within and on the edges of forests. It is still unclear how changes in species diversity and ecological functions can interfere with the future trajectory of forest patches in human-modified landscapes [64, 65]. However, the disappearance of more specialized frugivorous birds can alter seed dispersal patterns [66, 67], ultimately changing key aspects of forest composition and dynamics [68]. If our results serve as a proxy for actual fruit removal rates, such a decrease indicates less efficiency in seed dispersal, both in numbers of seeds dispersed and in the likelihood of seeds being moved long distances [69-71]. Thus, the seeds produced by a parent plant may end up falling only in their vicinity, where they are subject to predation and greater competition for the establishment and growth of seedlings [72, 73]. The effect of a lower fruit removal rate in forest interiors can ultimately change the trajectory and dynamics of forest regeneration [74, 75]. It is essential for the maintenance and functionality of tropical forests that the functional characteristics of the species most vulnerable to environmental changes are determined [61]. For the long-term persistence of frugivorous birds, and probably for the maintenance of the key ecological functions that they play, the amount of forest cover at the greater landscape scale is an important factor to take into account [76, 77].

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