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Spatial variation in understory frugivorous birds in an Atlantic Forest fragment of southeastern Brazil

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RESUMO. **Variação espacial em aves frugívoras de sub-bosque em um fragmento de Mata Atlântica do sudeste do Brasil.** Entre abril de 1999 e março de 2000 estudamos as aves frugívoras de sub-bosque em um fragmento de Mata Atlântica em avançado estádio sucessional no Parque Estadual Intervales, SP, com a finalidade de verificar a existência de variação espacial no padrão de captura dessas aves, e se esta variação poderia ser explicada pelas características estruturais do sub-bosque, pela abundância de frutos e pela riqueza de espécies em frutificação. Foram estabelecidas cinco unidades amostrais na área de estudo, cada uma consistindo de uma trilha com uma linha de seis redes de neblina e duas parcelas de 250 m^2 adjacentes a esta trilha. A estrutura do sub-bosque foi caracterizada a partir de medições de altura total, altura do fuste, diâmetro à altura do peito e das freqüências das formas de vida em sub-amostras das parcelas. Mensalmente, as plantas no interior das parcelas foram vistoriadas quanto à presença de frutos ornitocóricos e as aves foram capturadas nas redes. O padrão de captura das aves frugívoras variou espacialmente na área de estudo, estando possivelmente relacionado à variação espacial da oferta de frutos e à baixa densidade do sub-bosque em pelo menos uma das unidades amostrais. O presente estudo mostra que frugívoros generalistas de sub-bosque podem ser influenciados por esses fatores, o que em última instância pode afetar a dispersão de sementes e o estabelecimento das plantas ornitocóricas desse ambiente em Mata Atlântica.

PALAVRAS-CHAVE: Aves frugívoras, sub-bosque, variação espacial, Floresta Atlântica.

ABSTRACT. Between April 1999 and March 2000 we studied the understory frugivorous birds in an late sucessional stage of an Atlantic Forest fragment at the Intervales State Park, SP. Our goal was to verify the existence of spatial variation in the capture pattern of these birds, and if this variation could be explained by structural characteristics of the understory, such as fruit abundance and species richness of fruiting plants. We set up five sample unities in the study area, each one consisting of a trail with a line of six mist nets along it and two 250 m^2 plots adjacent to this trail. The structure of the understory was characterized by the following descriptors: total height, bole height, circumference at breast height and frequencies of plant life forms, all of them taken inside sub-plots. Monthly, plants inside the plots were examined for the presence of ornithochorous fruits and birds were mist-netted. The capture pattern of frugivorous birds varied spatially in the study area, possibly following the spatial variation occurred in fruit production or due to the low vegetation density in the understory, at least in one of the sample unities. This study shows that understory generalist frugivorous birds can be influenced by these factors, what may ultimately affect seed dispersal and establishment of understory ornithochorous plants in the Atlantic Forest.

KEY WORDS: Frugivorous birds, understory, spatial variation, Atlantic Forest.

Habitat characteristics strongly affect the pattern of spatial distribution of birds in forest environments (Willson 1974, Pearson 1975, Cody 1981, Garcia *et al.* 1998). Birds may respond with variation in both species composition and abundance of individuals to different degrees of habitat modification, such as successional stage (Johns 1991), fragmentation (Willis 1979, Aleixo and Vielliard 1995) and vegetation structure (Karr and Roth 1971, Karr and Freemark 1983). However, studies in lower scales, within the same physiognomy (e.g., Schemske and Brokaw 1981, Blake and Hoppes 1986, comparing gap and interior forest), are less numerous.

Frugivorous birds comprise an important subset of bird communities in many neotropical forests (Lein 1972, Pearson 1977, Karr 1980: 25% of species in Panama and Costa Rica), being also affected by variation in habitat characteristics, such as structure (Willson *et al.* 1982), floristics, and distribution of food resources (Terborgh 1985, Loiselle and Blake 1993).

These frugivores play an important role as seed vectors (Howe and Smallwood 1982, Stiles 1985), and their preference on specific sites may influence seed dispersal patterns (Restrepo *et al*. 1999), ultimately contributing to germination, establishment, spatial distribution and genetic structure patterns for many plant species (Hamrick *et al.*1993, Horvitz and Le Corff 1993, Loiselle *et al.* 1995, Bleher and Böhning-Gaese 2001). On the other hand, their dependence on fruits year-round influences their pattern of distribution and movements inside the forest (Herrera 1985, Blake and Hoppes 1986, Loiselle and Blake 1993). However, few birds are exclusively frugivorous (Moermond and Denslow 1985, Izhaki and Safriel 1989), the same way that our study focuses many species that do not rely entirely on fruits. Therefore, one should expect to find understory frugivores being locally distributed according to the habitat features that better ensure the searching and foraging on fruits and insects.

To test this assumption we investigated the spatial distribution of frugivorous birds as well as habitat characteristics of the understory of an old second-growth forest tract in southeastern Brazil. Ecological studies in this biome are highly recommended, especially those focusing fruit-eating vertebrates and plants with implications for forest conservation and management (Silva *et al.* 2002).

MATERIAL AND METHODS

The study was conducted in an Atlantic Forest area at 800 m inside Intervales State Park, southeastern Brazil (24°16'09"S, 48°24'56"W) (figure 1). The annual mean temperature in the study year was 16.7°C (max. 31°C and min. 1.6°C) and the annual rainfall was 1543 mm. The study site is a 4 ha tract of secondary forest bordered by dirty roads, a garden, and another forest tract smaller than this. Our tract is an abandoned plantation that has been regenerating into a secondary forest in the last 50 years. The upper canopy is about 22 m high and the understory is dense with many individuals of *Piper* spp. (Piperaceae), *Dichorisandra thyrsiflora* (Commelinaceae), *Heliconia velloziana* (Musaceae) and *Psychotria suterella* (Rubiaceae).

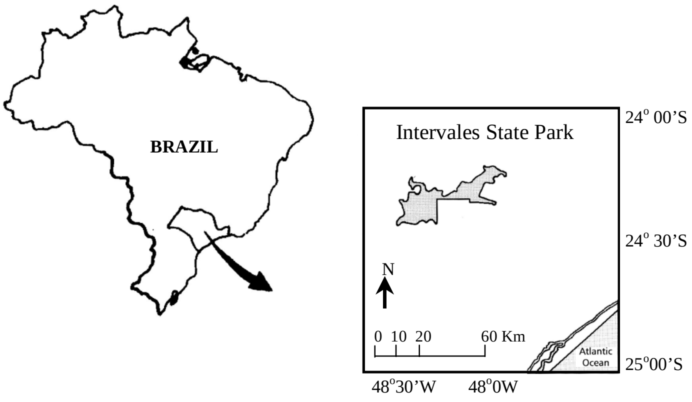

Figure 1. The location of Intervales State Park in southeast Brazil (adapted from Baider *et al.* 2001).

In an old trail that crosses the area we set up five sample unities (T1 to T5) consisting each of a transect 80 m long and two 250 m^2 plots along each transect (figure 2). Six mist nets (12 x 2.5 m long; 36 mm mesh) stayed opened for six hours in each transect in one morning per month, totaling 2160 net hours by the end of the study. We considered frugivorous birds those capable to evacuate seeds intact (Snow 1981, Sick 1997) and understory birds those that use this stratum regularly for foraging (Willis 1979, Allegrini 1997, Sick 1997). We used the number of bird captures as an estimation of habitat preference by the birds.

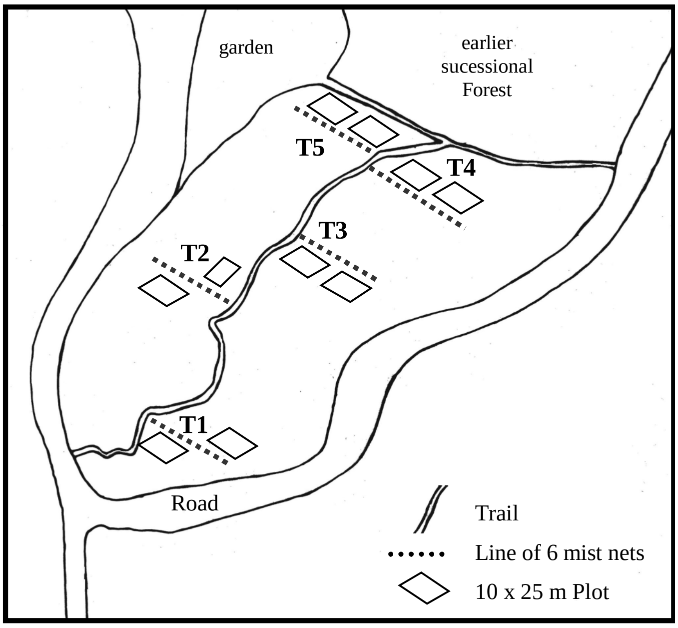

Figure 2. Distribution of the sample unities in the study site at Intervales State Park.

Inside the plots we collected data on fruit abundance and vegetation structure. All ornithochorous (*sensu* van der Pijl 1982) or zoochorous plants potentially consumed by birds (Ladrum 1986 *apud* Pizo 2002, Levey 1988, V. S. M. G. pers. obs.) up to 10 m high had their fruits counted or estimated when counting was not precise. The Fruit Abundance Index proposed by Levey (1988) was calculated to minimize large crop effects and it was taken as a measure of fruit abundance.

Eight sub-plots of 10 m^2 were randomly chosen inside each plot to represent the local understory structure. Three vegetational descriptors were used, following Mueller-Dombois and Ellemberg (1974): number of individuals, frequency of life forms (tree, shrub, bamboo, fern, dead, liana, palm, herb), and circumference at breast height (used to calculate basal area), all of them taken from individuals with more than 1.3 m high. We assumed that these variables, plus bole height (height from the base till the beginning of the crown), could adequately describe the availability of microhabitats, which could be used by birds for foraging and nesting. Pluviosity, temperature and relative humidity were measured at a meteorological station less than 2km apart from the study area.

Chi-square pairwise comparisons were used with the Yates correction, as recommended by Zar (1996). Cluster analysis was used to classify the sample unities considering the occurrences of banded birds and structural variables. This analysis was run with the package PC-Ord (Mc Cune and Mefford 1999), using Sorensen qualitative and quantitative similarity indexes, respectively, and UPGMA

Table 1. Understory frugivorous birds captured between April 1999 and March 2000 (* sensu Stotz *et al.* 1996; ** habitat most frequently used, pers. obs.).

Family	Species	Habitat *	Micro-Habitat **	Diet	Number fecal samples	Number samples with fruits/ insects	Total captures
Emberizidae	*Habia rubica*	LF	Forest Interior	FI	6	3/6	21
	Saltator similis	LFe,GF,SF	Forest Edge	O	2	2/1	2
	Tachyphonus coronatus	LFe,MFe,SF	Forest Edge	O	18	18/3	21
	Trichothraupis melanops	LF,MF,SF	Forest Edge	O	20	16/13	37
Muscicapidae	*Turdus albicollis*	LF	Forest Interior	FI	16	14/2	28
	Turdus rufiventris	LFe,MFe,SF	Forest Edge	O	2	2/1	6
Pipridae	*Chiroxiphia caudata*	LF,MF,SF	Forest Interior	FI	23	23/4	35
	Schiffornis virescens	LF,MF,SF	Forest Interior	FI	14	11/9	19
Tyrannidae	*Attila rufus*	LF,MF	Forest Interior	FI	-		2
	Mionectes rufiventris	LF,MF	Forest Interior	FI	-		6
	Neopelma chrysolophum	LF,MF,SF	Forest Interior	FI	1	1/0	2
Vireonidae	*Vireo chivi*	LF,RF,DF,GF,SF	Forest Edge	O	-		1
	Hylophilus poicilotis	LF,MF,SF	Forest Interior	FI	3	2/1	4

Habitat: LF = Tropical Lowland Evergreen Forest; RF = River-edge Forest; MF = Montane Evergreen Forest; SF = Secondary Forest; DF = Tropical Deciduous Forest GF = Gallery Forest; e = Edge

Diet: FI = Frugivorous-Insectivorous; O = Omnivorous. OBS: The term "omnivorous" is used here to denote a generalist diet, which includes other items besides fruits and arthropods: leaves (*S. similis*), flowers (*T. coronatus*), other invertebrates (*T. rufiventris*). Sources: Sick (1997), Willis (1979), W. R. S. (pers. obs.).

as a grouping method in both cases (Ludwig and Reynolds 1988, Valentin 2000). Mantel's test was used to pairwise comparisons between Distance Matrices (as suggested by Rotenberry 1985) and carried out with PC-Ord (Monte Carlo test was performed in 1000 runs). Normality was verified with the Kolmogorov-Smirnov (KS) test (Sokal and Rohlf 1997), option Lilliefors (Systat 1990). Box plots, correlations and regressions, as well as KS, were run in the package Systat.

RESULTS

From a total of 184 captures encompassing 13 species of understory frugivorous birds, 73% of the individuals and 85% of the species were food and habitat generalists (table 1). Bird species richness was not spatially correlated to fruiting plant species richness (Spearman Rank Correlation, $0.25 > p > 0.10$, N = 5 sample unities) nor total bird capture was related to total abundance of fruiting plants (Linear Regression, $p = 0.97$, N = 5 sample unities). Relationships among sample unities represented in the bird capture similarity matrix was not correlated to the fruiting plants abundance matrix (Mantel's test: $r = 0.182$, $p = 0.28$), as well as bird occurrence matrix was not correlated to plants occurrence matrix (Mantel's test: $r = 0.151$, $p = 0.35$). Thus, spatial variation in bird capturing was not related to the spatial abundance of fruiting plant species nor was spatial variation in the occurrence of bird species related to the spatial variation in the occurrence of fruiting plant species.

The monthly variation in the number of captures of frugivores presented a significant difference only between T2 and T4 (figure 3). There was also no recapture in T2, although the percentages of individuals recaptured in T1, T3, T4 and T5 were 26, 9, 23 and 15 respectively. There were marked differences in plant life form frequencies between T1 and T2 and the rest, as T1 presented more ferns and T2 more bamboos and less shrubs (figure 4). The distribution of basal area or bole heights values among the sample unities presented no significant differences. Although T5 had the greatest total basal area (table 2), this sample unity presented few plants with high basal area values, which affected the total value. Fruit abundance was significantly greater in T4 than in the other sample unities, which did not differ from each other (figure 5). T4 was also the only sample unity with a significant difference between the occurrence of edge and interior banded birds ($X^2 = 4.83$; $p = 0.05$; 1 d.f).

The greatest monthly variation of captures at T1 may have been caused by many factors. However, whichever

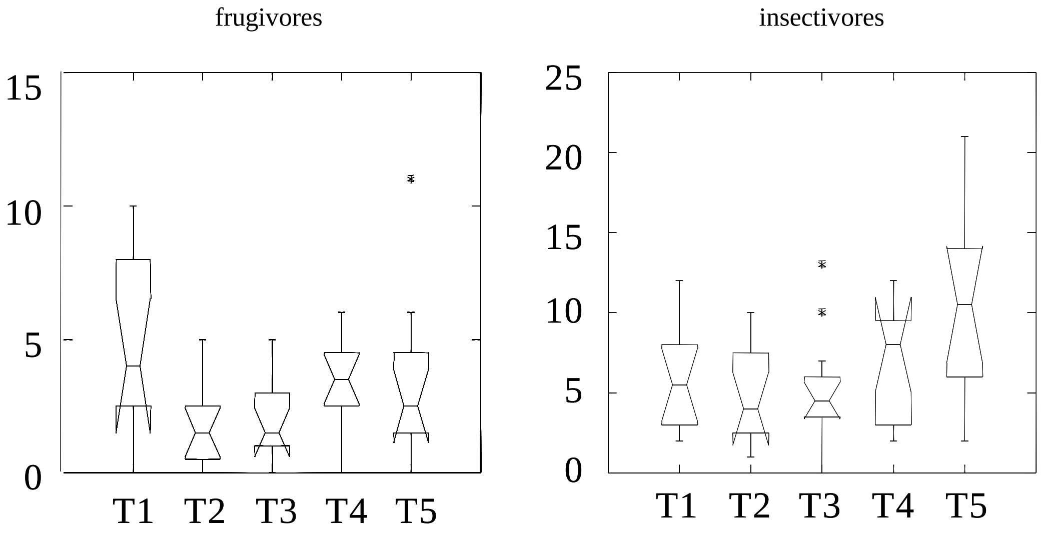

Figure 3. Variation of year-round bird capture in the five sample unities for frugivores and insectivores (internal horizontal line = median; whiskers = minimum and maximum values; box horizontal limits: inferior = 25 % quartile, superior = 75 % quartile; asterisks and circles = two levels of outliers. Boxes are notched at the median and return to full width at the lower and upper 95 % confidence limits of the median).

Table 2. Total number of plants and total basal area for 160 m^2 sampled in each sample unity.

Sample Unity	Total number of plants	Total basal area (m2)
T1	171	0.56
T2	196	1.00
T3	182	0.38
T4	208	0.90
T5	186	1.97
Total	943	4.80

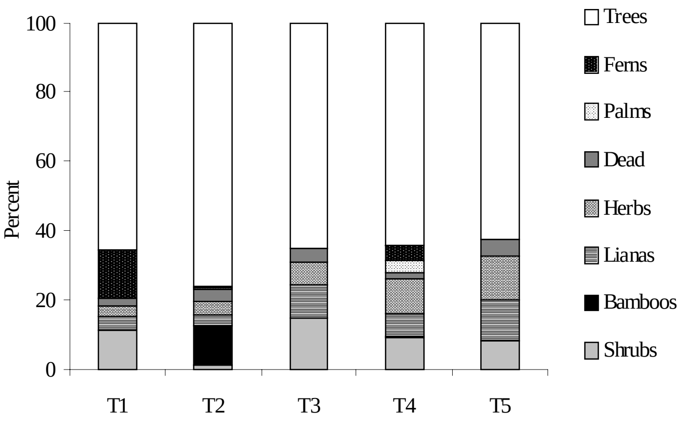

Figure 4. Proportional distribution of plant life forms within each sample unity.

factor affecting bird capture in this trail, only frugivorous birds were considerably affected (figure 3). Regarding fruit resources, T1 was not the most variable sample unity in terms of monthly fruit abundance (figure 5). Also, both captures of total frugivores and individual species were not correlated with monthly number of plant species or individuals fruiting at T1 (Spearman Rank Correlations: $r_s < 0.30$, $p > 0.10$ for all comparisons). The fact that birds were mist netted in each sample unity in different days of each month does not seem to have influenced the pattern obtained, because bird capture was not related to climatic variables ($r^2 < 0.06$; $p > 0.07$).

To assess bird movements in the study site we clustered sample unities considering the occurrence of banded birds, thus eliminating the individual preference for a site. T3 and T4 were the sample unities that shared more individuals with each other and T2 was the most isolated one (figure 6). The clustering pattern could not be explained by the distances among the sample unities, as shown by the correlation between the matrices of banded birds distances and geographical distances (Mantel's test: r = 0.44, p =

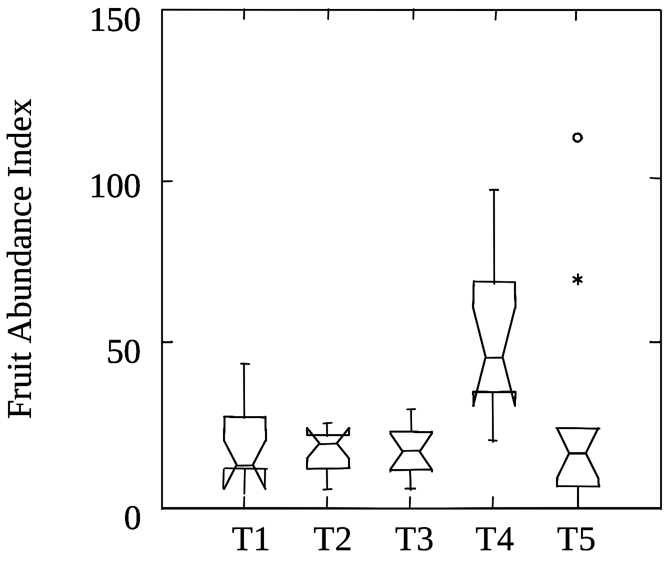

Figure 5. Year-round variation in the Fruit Abundance Index for each sample unity (box plots described as in figure 3).

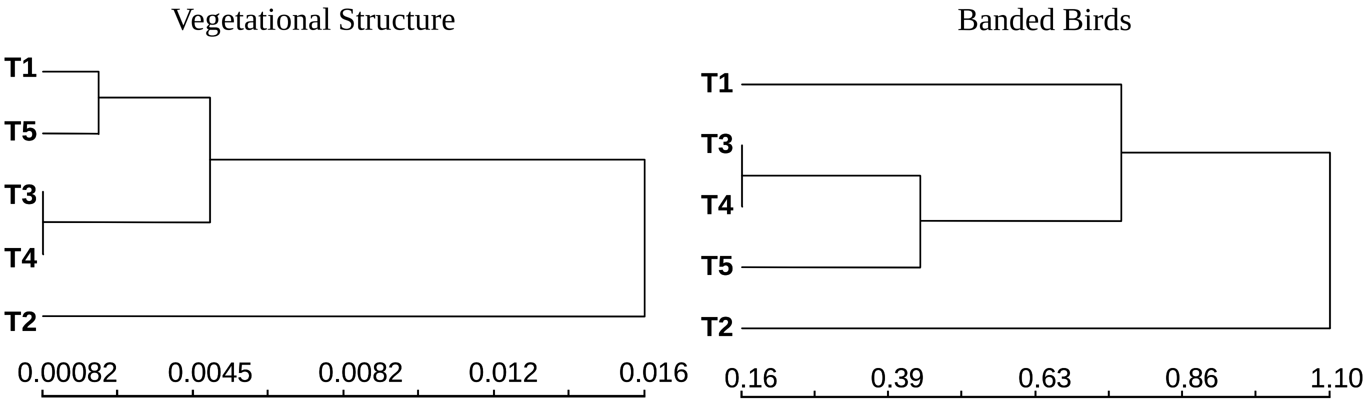

Figure 6. UPGMA distances between sample unities considering the occurrence of 99 individual banded birds (right) and 14 structural variables (left). Structural variables: density of plants (no. plants/ m^2), bole height (median), total height (med), total basal area (m^2/m^2), crown depth (med), basal area of individual plants (median), number of trees/ m^2, number of shrubs/ m^2, number of lianas/ m^2, number of herbs/ m^2, number of dead plants/ m^2, number of ferns/ m^2, number of palms/ m^2 and number of bamboos/ m^2.

0.08). However, it could be in part explained by structural similarities among the sites, what was revealed by the correlation between the matrices of banded birds and vegetation structure (Mantel's test: $r = 0.53$, $p = 0.04$).

DISCUSSION

Fruiting plant species composition did not seem to influence the spatial patterns of bird capture in our area. Apparently, there was no species specific or group specific association between frugivores and plants, like that verified for Melastomataceae and Rubiaceae fruits and frugivores in Panama (Loiselle and Blake 1993). Although our study site is an old sucessional stage forest, Melastomataceae are scarcely represented in the understory and the Rubiaceae present did not prove to be largely consumed by these birds. In addition, many seed species from the forest edge were present in fecal samples, revealing that the frugivorous birds in the study site do not rely entirely upon the fruit supply from the forest interior.

The low number of captures and recaptures at T2 may be the only evidence that the structure of the understory may influence site occupancy by birds. The life form spectrum was the only structural variable that could explain any clear difference between sites. The low availability of microhabitats in the understory, reflected by the low occurrence of shrubs, might be related to the high abundance of the bamboo *Merostachis* sp., which could inhibit the development of such plants (Oliveira-Filho *et al*. 1994, Tabarelli and Mantovani 2000). The high availability of fruits in T4 may have increased the differences in the captures between this and the other sample unities, although a significant difference was obtained only between T4 and T2. Other studies have shown the relationship between local availability of fruits/ insects and the abundance of frugivores (Blake and Hoppes 1986; Levey 1988). Furthermore, the captures of banded birds in our area indicate that species from the forest interior are more prone to take advantage of locally abundant fruit supplies than birds from the forest edge, what could make generalist frugivores less influenced by the local resource variation inside the forest tract.

Neither variation in climatic conditions nor in the spatial and temporal distribution of fruit abundance inside the forest seems to be determining the greatest monthly variation in captures observed at T1. Some other undetermined factor, like the fruit production of edge plant species, could be accounted for this pattern. In fact, most of the frugivores recorded in this study use to forage on fruit in the edge or secondary habitats very frequently (Stotz *et al.* 1996). We suggest that there might be a habitat-dependent fruiting pattern determining the spatial distribution of frugivores, as shown by Levey (1988, 1990) in Costa Rica.

Movement of individual birds between trails may be related to similarities in vegetation structure, which suggests that individual birds may prefer similar habitats for foraging. This movement pattern of frugivores may influence seed rain and ultimately the spatial patterns of plant regeneration. Our results show that habitat preference by individual birds may develop, inside the same physiognomy, through a fine-tuned spatial scale, while the overall preference for a particular species may occur in a broader scale, between physiognomies or well-established microhabitats, such as gaps and forest interiors.

In general, the capture of frugivores was low and recapture was null where the understory was less dense. On the other hand, capture was high where fruits were locally abundant, a pattern that possibly influenced most of the captures in the forest interior. However, the great monthly variation of captures in a single sample unit can not be explained by the variables tested, probably because most of the understory frugivores found in the area are habitat and food generalists.

Unlike other regions in the neotropics (*e. g*. Central America), where information on fruit-frugivore relationships are the result of long-term and broad-focused studies, the Atlantic Forest biome represents a new and complex scenario for the study of the interactions between birds and their food plants. Our data suggest that generalist frugivores in the Atlantic Forest, a large group of birds rarely under threat, can be also affected by fine-tuned variations in the fruit availability and the vegetational structure of the understory.

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