Distribution of birds in natural gaps of different sizes in a seasonal semideciduous forest in São Paulo state, Brazil

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Introduction

Habitat variation in a forest fragment is largely due to the falling of trees and their subsequent regeneration, forming a patchwork mosaic of gaps in different stages of succession, from recent tree falls, to regenerating and more mature stages (Brokaw 1985, Runkle 1981, Lima 2005).

The main differences between gap and understory environments are in the amount of radiation, or light intensity, temperature and humidity, as well as biotic factors and edaphic conditions, which also determine the floristic composition and the vegetation structure at these sites (Hartshorn 1980, Denslow 1987, Whitmore 1989, Jardim *et al*. 2007, Gandolfi *et al*. 2007, 2009).

The light intensity in gaps and on the soil surface increases with the canopy opening and may increase the temperature and reduce the air and the soil humidity (Denslow 1987; Champlin *et al*. 2009). The height and the direction of the shadow projected from the trees on the edge of the gap influence light intensity, and such incidence normally increases with the gap size (Denslow *et al*. 1998).

Thus, treefall gaps constantly provide habitats that contrast with the adjacent closed-canopy forest, and house a variety of organisms that inhabit these particular environments (Terborgh & Weske 1969, Schemske & Brokaw 1981, Hoppes 1988, Restrepo *et al*. 1999, Greenberg 2001, Guilherme & Cintra 2001, Moorman *et al*. 2007, Rosely *et al*. 2007, Banks-Leite & Cintra, 2008, Fuller 2000, Khamcha & Gale 2012, Forsman *et al*. 2013).

Studies have also shown that gap environments can be more attractive to birds due higher insect abundance (Richards & Coley 2007). Bird species select foraging substrates based on their feeding habits and on the availability of resources (Blake & Hoppes 1986, Cueto & Casenave 2002), sometimes showing preferences for certain types and sizes of prey found in gaps (Moorman *et al*. 2007, Manhães & Dias 2008).

Tree fall gaps, compared to the undisturbed understory environment, can also experience an increased density of insects due to changes in microclimate conditions and the density of regeneration growth (Richards & Coley 2007). It is possible that birds are attracted to the gaps by the high luminosity levels and foliage density (Champlin *et al*. 2009), expecting a greater abundance of insects.

However, most vegetation formations experience one or more periods of relative fruit scarcity throughout the year, obliging frugivorous animals to change their diet or disperse to new feeding environments (Galetti *et al*. 2003) or to increase the size of their territories to account for lower food abundance (Haché *et al*. 2013), thereby using the gaps.

About 20 to 50% of tropical bird species consume fruits at least during part of the year, acting as potential seed dispersers (Fleming *et al*. 1987, Jordano 2014) of 50 to 90% of the animal-dispersed trees on the tropics (Howe & Smallwood 1982).

The abundance of small frugivorous birds is higher at the edge of forest fragments, in part because of the presence of typical species of open areas frequenting this environment. As a result, plants at the edges have their fruit removed more often than plants within the fragments of tropical forest (Levey 1988a, 1990, Galetti *et al*. 2003, Saavedra et al. 2014). Often, the fruit-eating birds that frequent the edges of the fragments also attend to its surroundings. Thus, plants the edge can contribute greatly to the seed rain and possibly for the regeneration of the adjacent gaps. Consequently, birds frequently have been identified as a particularly important group of seed disperses in tropical forests (Stiles 1985, Levey 1988a, Medellin & Gaona 1999).

Understory fruits are dispersed by a diverse assemblage of birds, mostly generalist species, including manakins, tanagers and flycatchers (Loiselle & Blake 1999) which should not be affected by fragmentation (Willis 1979, Aleixo & Vielliard 1995, Galetti & Pizo 1996). On the other hand, canopy trees species with large seeds are dispersed by specialized large frugivores (such as toucans, guans and large cotingas) (Howe and Smallwood 1982) which are prone to become vulnerable due to dispersal failure in fragmented forests (Marsden *et al*. 2001).

The plant species established in gap areas produce fruits with the same levels of attractants as those produced in the understory (Levey 1988a), generally showing high fruit production during long fruiting periods (Levey 1988a, 1990) and increased density according to the gap size. Some studies have also revealed that the fruits in these areas receive greater luminosity and thus may be more easily noted by birds and consequently more readily attractive to them (Willson *et al*. 1982).

Differences in the regeneration composition between gaps of different sizes (Denslow 1980) and higher fruit abundance in some gaps (Levey 1988b, 1990) may also be responsible for the preference by many birds for gap habitats.

Regeneration in these environments, i.e., increased coverage in levels close to the soil, provides shelter to animals that look for protection against predators (Blake & Hoppes 1986, Guenette & Villard 2005), acting even as a resource center for species of insectivorous nesting birds in the proximate understory (Fuller 2000, Greenberg & Lanham 2001).

Forest birds also may be affected by cle-arcut edges in boreal mixed-wood forest of Alberta, Canada, perhaps responding to edge-to-interior gradients in vegetation, ranging both with landscape context and with time since edge creation (Villard *et al.* 2007).

Smith & Dallman (1996) also observed a greater ease in establishing territories by reproductive males in these environments due to high visibility and more projection of sound, setting clearer territory boundaries. Forest-breeding birds may be more abundant in early-successional than mature forest habitat, especially during the post-breeding period (Marshall *et al.* 2003).

Others forest bird species use the gaps only seasonally, with an increased risk of predation in newly formed gaps, tending to take care of their young in older gaps that have greater vegetation cover (Khamcha & Gale 2012).

In others studies, the birds are attracted to the gaps primarily by the abundance of food resources (fruits or insects), material for nesting (Rosely *et al.* 2007), a greater visibility of the fruit because of more light in the gaps compared to the understory (Schemske & Brokaw 1981), a greater availability of places to nest, or by vegetation structure for protection (Moorman *et al.* 2007, Greenberg & Lanham 2001, Forsman *et al.* 2013).

However, Haché *et al.* (2013, 2014) observed negative effects for the closed canopy birds and understory birds which were more sensitive to the environment changes of reduced vegetation cover and associated food (Depreau *et al.* 2016, Villard & Taylor 1994).

These factors associated with treefall gaps, have resulted in greater richness and abundance of tropical forest birds (Terborgh & Weske 1969, Hoppes 1988, Wunderle *et al.* 2005, Banks-Leite & Cintra 2008); thus many bird species seem to have a marked preference for gap environments (Schemske & Brokaw 1981, Banks-Leite & Cintra 2008; Gharehaghaji *et al.* 2012).

In addition, gaps play an essential role in the dynamics of tropical forests (Runkle 1981, 1992, Hartshorn 1980, Denslow 1987), representing the basis for the forest renovation through the natural regeneration cycle and providing habitats upon which many tree species depend to reach maturity (Murray 1988, Lima 2005).

Given the reported significance of treefall gaps to birds in temperate forest (Thompson & Willson 1978), tropical montane forest (Restrepo *et al.* 1999), evergreen tropical forest (Khamcha & Gale 2012), lowland tropical forest (Rosely *et al.* 2007), boreal forests (Forsman *et al.* 2013), Amazonian forests (Banks-Leite & Cintra 2008) and tropical wet forest of Costa Rica (Levey 1988a), we investigated whether environments formed by treefalls and the creation of natural gaps of different sizes within a seasonal semideciduous forest fragment result in variation in use by birds or become barriers to the movement of understory birds (Gobeil & Villard 2002, Robichaud *et al.* 2002, Villard & Haché 2012). Species more sensitive to changes in habitat are less efficient in detecting and colonizing new habitats and hence
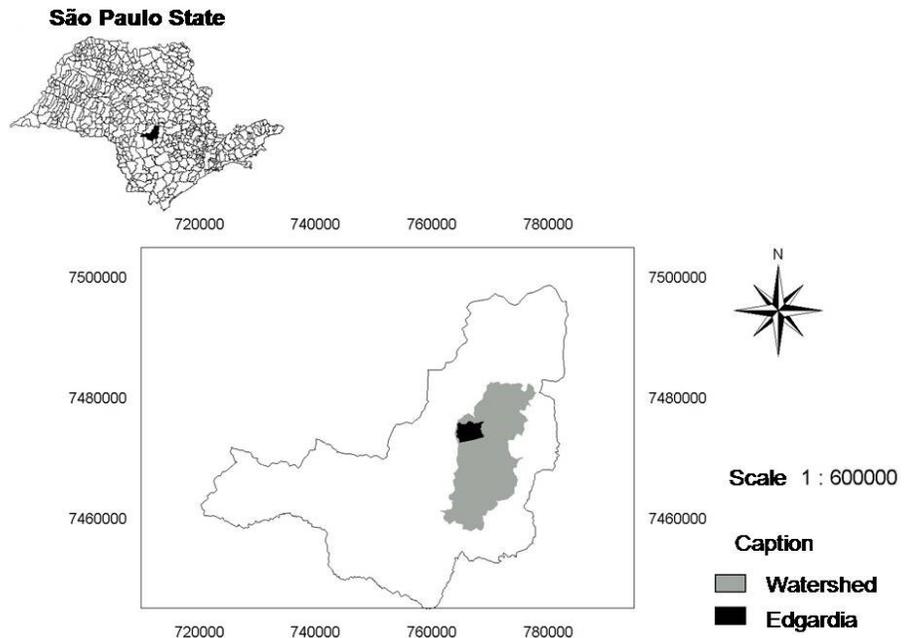

São Paulo State

Figure 1. Location of Edgárdia Experimental Farm, at the watershed of Capivara River, Botucatu-SP, Brazil (Fonseca 2005).

may have a lower dispersal ability (Villard & Taylor 1994), consequently influencing the arrival of birds that disperse seeds in these gap environments (Carlo *et al.* 2013).

Methods
Study area
This study was conducted at the 1,150 ha Edgárdia Experimental Farm, which belongs to the School of Agronomical Sciences of UNESP-Univ Estadual Paulista, Botucatu (22°47'30''S, 48°26'15''W). The gaps were located within a forest fragment named "Mata da Bica", which is represented by approximately 60 ha of seasonal semideciduous forest (Figure 1).
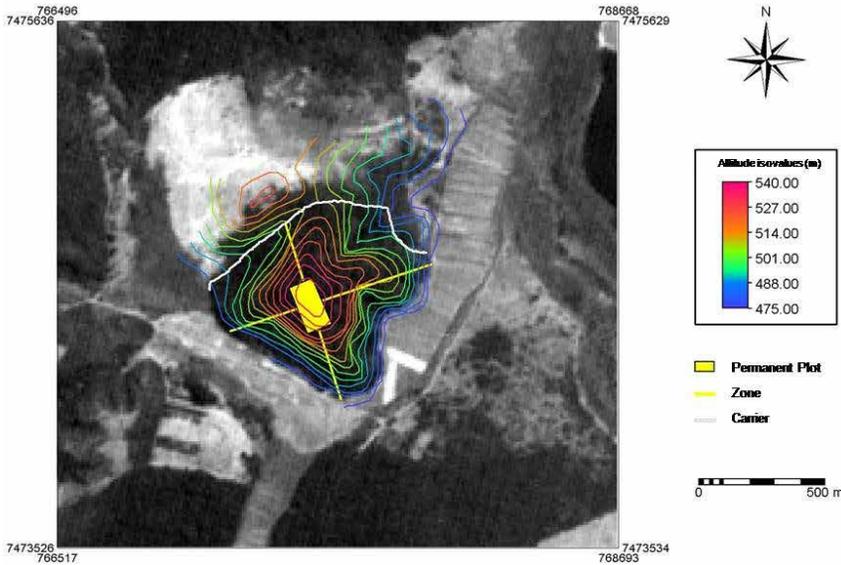
Despite the existence of proposed standardized methods and choices of variables for research on gaps, these methods and variables have yet to be adopted by the scientific community. The most variable and arbitrary part of gap definitions is distinguishing when a gap merged with the background vegetation. Clearly, many gaps fill from below; that is, saplings within gaps grow steadily upward, obscuring the distinctiveness of the gap (Kunkle 1992).In this study, the gaps were considered areas without canopy formed by death of at least half a tree and measured on the forest ground, under a canopy opening extending to the bases of the surrounding trees. The distinction between the gaps and background vegetation is clear enough that criteria based on sapling height are not needed. A more detailed description of the gap delimitation method can be found in Runkle (1981, 1992), Lima (2005), Santos (2007), Pardi (2007) and Hunter (2015).

Sampling
Six gaps were mapped in November 2008 using a 200x100m grid with 200 plots of 10x10m, established within the fragment (Figure 2).

The area of each gap was calculated by using the ellipse area formula: A = p x B x C; where: A = ellipse area, p = 3.1416; B = larger radius/2 and C = smaller radius/2 (Caldato *et al.*1996).

Considering Spiegel (1979), the minimal number of size clas-

Figure 2. Location of the permanent plot where the gaps were delimited at "Mata da Bica", Botucatu-SP, Brazil on a SPOT satellite image, with elevation iso-values. These gaps were characterized based on their area, floristic composition of their perimeter and light intensity.

Data analysis

The frequency of occurrence (FO) of each bird species captured in the mist nets was determined (D'Angelo Neto *et al*. 1998). Bird distribution among gaps of different sizes (small, medium and large) was compared based on their abundance and richness, and the results were statistically analyzed according to the non-parametric Kruskal-Wallis method (Zar 1999).

To verify possible relationships between the different gap sizes and the light intensity found in each gap, Spearman's correlation was used with the aid of the statistical software SIGMAPLOT 11.0.

The similarity in the bird composition between gaps was verified through the Jaccard similarity index, represented in a cluster analysis diagram, using the PAST software.

The captured birds were categorized as to their diet according to Willis (1979).

Results
Characterization of Gaps
Light intensity:

Despite the light intensity is higher at the gaps than in the understory, Spearman correlation coefficient ($r_s = 0.429$; $p = 0.419$) indicated that there was no significant correlation between gap area and light intensity in the studied gaps (Table 1).

For large gaps (LG1 and LG2), light intensity decreased due to the higher density of species under regeneration and due to bamboos of the genus *Chusquea* sp. taller than 1m, i.e., the height of radiation measurement.

In the large gap (LG2) the canopy was more open. This, in addition to the absence of *Chusquea* sp. (Bamboos) in areas adjacent to large gap (LG2) provided a greater amount of sunlight

ses and their amplitude were determined, and gaps were subsequently grouped into three classes: Small (from 0 to 230m²), Medium (from 231 to 460m²) and Large (from 461 to 690m²).

A light meter (ROTH, Roline RO-1332) was used to measure the light intensity at bird capturing sites, and differences between sun radiation on the sampled gaps and on the understory environments were verified (Saganuma 2008). Sun radiation intensities were recorded at six sites along the mist nests, at the height of 1m above the soil, and the mean luminosity for each site was subsequently calculated.

To capture the birds, mist nets of 12x2 m and 36 mm mesh were established both in the center of each one of the six studied gaps and, in the respective understories at 20m distance, for a total of 12 mist nets. The nets were opened for two days every month during a 12 month period, from soon after sunrise until 11 a.m. and from 3 p.m. until the beginning of the evening. The captured birds were identified as per the Brazilian Committee

Table 1: Solar radiation intensity (Lux) recorded at six sites of each mist net and their mean. Caption: SG = mist net located in the small gap (0 to 230m2); SU = mist net located in the understory at 20m from the net located in the small gap; MG = mist net located in the medium gap (231 to 460m2); MU = mist net located in the understory at 20m from the net located in the medium gap; LG = mist net located in the large gap (461 to 690m2) and LU = mist net located in the understory at 20m from the net located in the large gap.

Location of Mist nets	1	2	3	4	5	6	Average
SG1	622	1184	1446	1014	813	321	**900**
SU1	313	422	262	208	327	330	**310**
SG2	1480	1335	1323	769	290	261	**910**
SU2	246	259	232	393	348	356	**306**
MG1	1078	1253	1999	1940	1950	1999	**1703**
MU1	538	613	549	484	411	419	**502**
MG2	1010	1092	1150	1807	2320	1628	**1501**
MU2	730	564	540	432	570	545	**563.5**
LG1	1801	1560	1273	661	1051	1979	**1387.5**
LU1	606	503	707	598	689	1032	**689**
LG2	1030	1068	1038	1404	1202	1328	**1178**
LU2	1032	611	781	932	844	599	**800**

in the relevant understory (LU2) and consequently less difference between these two environments.

Floristic composition surrounding the gaps:

The plant species in the perimeter (surrounding) of each gap were sampled and identified:

Small Gap 1: *Aspidosperma polyneuron* Mill. Arg.; *Campomanesia guaviroba* (DC.) Kiaersk.; *Celtis* aff *iguaneae* (Jacq.) Sargent.; *Chrysophillum gonocarpum* Mart. & Eichl; *Diatenopterix sorbifolia* Radlk.; *Holocalyx balansae* Mich.; *Metrodorea nigra* St. Hil.; *Parapiptadenia rigida* (Benth.) Brenan and *Trichilia catigua* A. Juss.

Small Gap 2: *Aspidosperma polyneuron* Mill.Arg.; *Chrysophillum gonocarpum* Mart. & Eichl.; *Piper* aff. *amalago* L.; *Trichilha catigua* A. Juss.; *Trichilia clausseni* C. DC. and *Urera baccifera* (L.) Gaud.

Medium Gap 1: *Aspidosperma polyneuron* Mill. Arg.; *Machaerium stipitatum* (D.C.) Vog.; *Parapiptadenia rigida* (Benth.) Brenan; *Patagonula americana* L.; *Trichilha catigua* A.Juss.; *Trichilha clausseni* C.DC.; *Trichilia elegans* A. Juss. and *Trichilha casarettii* C. DC.

Medium Gap 2: *Aspidosperma polyneuron* Mill. Arg.; *Centrolobium tomentosum* Guill. Ex Benth; *Chrysophillum gonocarpum* Mart. & Eichl.; *Jaracatia spinosa* (Aubl.) DC.; *Parapiptadenia rigida* (Benth.) Brenan; *Patagonula americana* L. and *Trichilia clausseni* C. DC.

Large Gap 1: *Acacia polyphilla* DC.; *Aloysia virgata* (Ruiz & Pav) A. Juss.; *Aspidosperma polyneuron* Mill. Arg.; *Astronium graveolens* Jacq.; *Casearia gossypiosperma* Briquet.; *Chusquea* sp., *Gallesia integrifolia* (Spr.) Harms.; *Holocalyx balansae* Mich.; *Jaracatia spinosa* (Aubl.) DC.;*Paullinia* sp.; *Piper* aff. *amalago*; *Trichilia catigua* A. Juss.; *Trichilha clausseni* C. DC. and *Trichilha elegans* A. Juss.

Large Gap 2: *Aspidosperma polyneuron* Mill. Arg.; *Bauhinia* sp.; *Campomanesia guazumifolia* (Camb.) Berg; *Chorisia speciosa* St. Hil.; *Dicella holosericea* (Juss.) Griseb.; *Gallesia integrifolia* (Spr.) Harms.; *Machaerium stipitatum* (DC.) Vog.; *Metrodorea nigra* St. Hil.; *Myrcianthes pungens* (Berg.) Legr.; *Patagonula americana* L.; *Piper* aff. *amalago*; *Trichilha catigua* A. Juss.; *Trichilia clausseni* C. DC. and *Trichilia casarettii* C. DC.
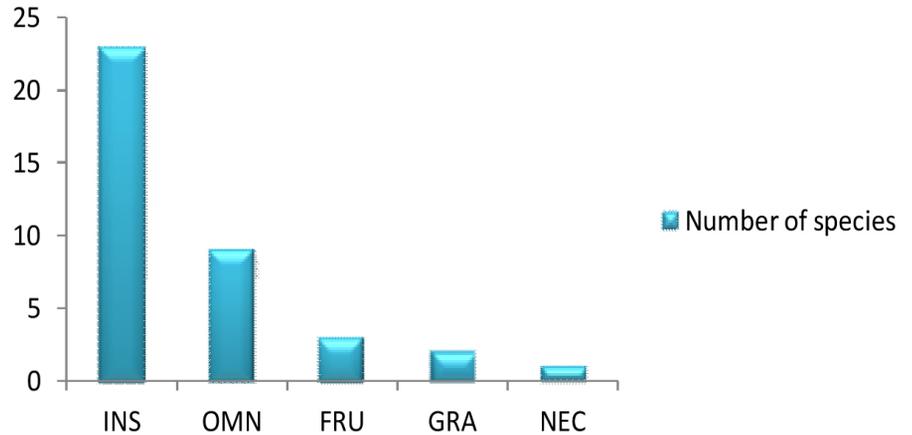
DIET

Figure 3. Diet of birds captured at the gaps and undestory of "Mata da Bica", located in Botucatu-SP. Legend: INS = Insetivorous birds, OMN = Omnivorous birds, FRU = Frugivorous birds, GRA = Granivorous birds and NEC= Nectarivorous birds.

The large gaps showed a higher plant species richness (n = 22), followed by small gaps (n = 12) and medium gaps (n = 11); the longer perimeter of the large gaps provides a larger area for the establishment of plant species that may be dispersed to these environments. We can also observe a high similarity in species composition between the gaps of different sizes, also probably due to the similarity of gaps and understory as found by Santos (2007).

Most seedlings were recorded as having dispersed from individuals fruiting within short distances, as found in Murray (1988) and Penhalber & Mantovani (1997). Therefore, the composition of seed dispersal is closely related to its surroundings, that is, to the immediate vicinity (Wiswanathan *et al.* 2015) and the landscape in which located.

The large abundance of the genus *Trichilia* and others representatives of the families Meliaceae and Myrtaceae in the gaps may be attractive for seed-dispersers, and the genus *Piper* may be attractive for mammals seed-dispersers, such the bats. Fonseca (2005) registered 45 species of trees dispersed by animals on the "Mata da Bica".

Avian Sampling

During 2,304 hours/net, or 69,120 hours.m^2, 253 birds were captured; they were represented by 38 species belonging to 27 families (Appendix 1). The species captured in larger numbers were *Basileuterus culicivorus* (37), *Sittasomus griseicapillus*

Table 2. Species captured at "Mata da Bica" and number of captures per gap. Where: SG= small gap; SU= understory adjacent to the small gap; MG= medium gap; MU= understory adjacent to the medium gap; LG= large gap; LU= understory adjacent to the large gap.

Species	SG	SU	MG	MU	LG	LU	Total
Basileuterus culicivorus	12	10	3	8	2	2	37
Sittasomus griseicapillus	2	3	6	4	4	3	22
Conopophaga lineata	4	0	2	8	2	3	19
Tiaris fuliginosus	2	0	6	1	4	3	16
Myiothlypis flaveola	3	3	2	1	3	2	14
Habia rubica	2	0	1	2	5	4	14
Platyrinchus mystaceus	4	2	1	2	3	2	14
Lathrotriccus euleri	0	6	3	2	2	0	13

Species	SG	SU	MG	MU	LG	LU	Total
Synallaxis ruficapilla	2	0	2	2	3	1	10
Thamnophilus caerulescens	2	0	3	2	1	2	10
Trichothraupis melanops	1	2	1	0	6	0	10
Tachyphonus coronatus	1	1	1	2	3	1	9
Chiroxiphia caudata	0	0	2	2	2	2	8
Tolmomyias sulphurescens	0	3	0	1	1	2	7
Hemitriccus orbitatus	1	1	0	0	4	0	6
Corythopis delalandi	1	1	0	1	0	2	5
Malacoptila striata	0	0	2	2	0	1	5
Turdus albicollis	0	0	0	0	2	2	4
Automolus leucophthalmus	0	0	0	1	0	2	3
Myiarchus swainsoni	0	0	0	3	0	0	3
Turdus rufiventris	0	0	0	1	1	1	3
Campylorhamphus falcularius	0	0	1	1	0	0	2
Cyanocorax chrysops	0	0	2	0	0	0	2
Leptopogon amaurocephalus	0	1	0	0	1	0	2
Saltator similis	0	0	0	0	0	2	2
Thlypopsis sordida	0	0	0	0	0	2	2
Dysithamnus mentalis	1	0	0	0	0	0	1
Lepdocolaptes angustirostris	0	0	0	0	0	1	1
Leptotila verreauxi	1	0	0	0	0	0	1
Mackenziaena severa	0	0	0	1	0	0	1
Phyllomyias fasciatus	1	0	0	0	0	0	1
Sporophila sp.	0	0	0	0	1	0	1
Taraba major	0	0	0	0	0	1	1
Thalurania glaucopis	0	0	0	0	1	0	1
Turdus amaurochalinus	0	0	1	0	0	0	1
Turdus leucomelas	0	0	0	0	0	1	1
Xenops rutilans	0	0	0	0	1	0	1

(22), *Conopophaga lineata* (19), *Tiaris fuliginosus* (16), *Habia rubica* (14), *Platyrinchus mystaceus* (14), *Myiothlypis flaveola* (14) and *Lathrotriccus euleri* (13) (Table 2).

Insectivorous birds had the largest number of captured species (n=23), followed by omnivorous species (n=9), frugivorous species (n=3), granivorous species (n=2) and nectarivorous (n=1) species (Figure 3).

Of the birds captured in the largest numbers (n>14), only *Habia rubica* completes its diet with fruits and may be a dispersing species in the gaps, since the largest number of captures (57.2%) occurred in these environments.

Based on the birds recorded according to the mist net method, the capture frequency of each species could also be obtained (Table 3).

The three highly common species were: *Basileuterus culicivorus* (100%), *Conopophaga lineata* (83.3%) and *Sittasomus griseicapillus* (75%). On the other hand, species like *Cyanocorax chrysops*, *Dysithamnus mentalis*, *Lepdocolaptes angustirostris*, *Leptotila verreauxi*, *Mackenziaena severa*, *Myiarchus swainsoni*, *Phyllomyias fasciatus*, *Sporophila* sp., *Taraba major*, *Thalurania glaucopis*, *Thlypopsis sordida*, *Turdus amaurochalinus*, *Turdus leucomelas* and *Xenops rutilans* were uncommon

Table 3: Occurrence frequency of the species captured at "Mata da Bica". Where the capture frequency classes are: Uncommon (8.3 to 33.3 %), Common (41.66 to 66.6 %) and Highly Common (75 to 100 %).

	Rank of Occurence Frequency		
	Uncommon (8.3 to 33.3%)	Common (41.66 to 66.6%)	Highly Common (75 to 100%)
Relative abundance	63.1	28.9	7.9
Number of species	24	11	3

Table 4. Richness of species, number of captures and characteristics of the gaps located at "Mata da Bica". Where size classes are: S = small, M = medium, L = large.

Gap	Area (m²)	Size class	Number of species	Number of captures	Light intensity (Lux)
1	183.4	P	11	28	900
2	207.23	P	8	12	910
1	263.34	M	12	21	1703
2	321.34	M	12	28	1501
1	458.52	G	20	43	1387.5
2	638.57	G	8	9	1178

in the area, and were captured in only one campaign.

Although there were no significant differences in both the number of captured species (H = 1.5; p = 0.4724) and their abundance (H = 0.071; p = 1.0) for the different size classes, one of the large gaps (LG1) showed greater species richness (20) and greater abundance of captured species (43), followed by medium gaps with 12 species each (Table 4).

The presence of bamboos of the genus *Chusquea* sp. under regeneration in LG1 provided the birds with resting sites and shelter and may have influenced the number of captures in this gap. The latter showed a significant difference, when its abundance was separately compared to that of the understory (t = 5.930; p = 0.004; D.F. = 4; CI = 95%).

As to the total number of birds captured in gap and understory environments, no statistical differences were found between the two environments ($F_{[1.11]}$ = 0.499; p = 0.495).

There was great similarity in the composition of species that frequent the gaps, which suggests that their size does not influences the species composition of birds using them (Figure 4).

Only one species, *Automolus leucophthalmus* (n=3), was captured only in the understory.

We observed that the number of individuals captured was lower in the month of August (n = 16), for the winter, along with lower activity of birds. The highest number of individuals captured occurred during the months of December and March (n = 23) (Figure 5).

Fonseca (2005), studying phenology and key-species of "Mata da Bica" , noted the existence of two distinct periods, one during the months of January, February, March and April, and another in the months of May, June, July, August, September and October. The latter group coincided with both a time of fruit shortage in the community and the lower species richness of birds observed in our study.
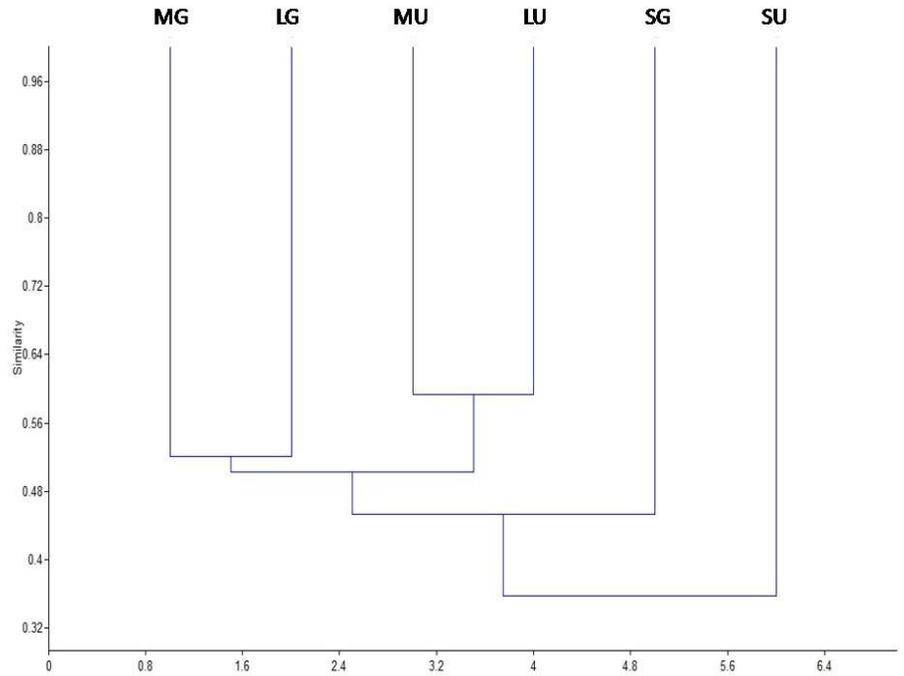

Figure 4. Cluster Analysis, using the Jaccard index for the three size classes of the studied gaps: SG = small gap; MG = medium gap; LG= large gap; SU= understory adjacent to the small gap; MU= understory adjacent to the medium gap; LU = understory adjacent to the large gap.
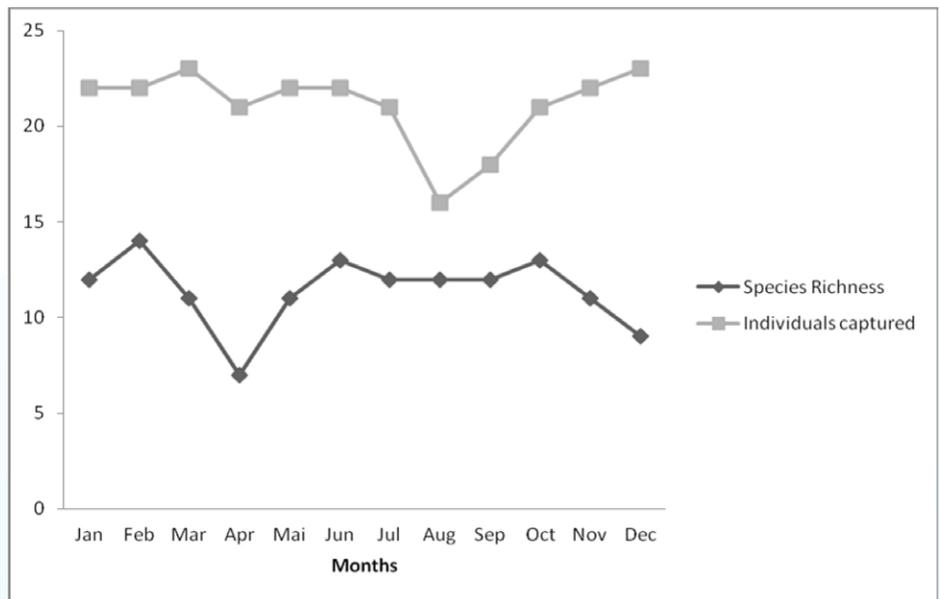

Figure 5: Richness of bird species and number of individuals captured on the Edgárdia's Farm, during one year of study, Botucatu, Sao Paulo, Brazil.

Discussion

The number of species recorded in the present study was highly similar to that found in a previous study carried out at the same fragment, which recorded 40 species using the same method (Fonseca 2005). Among the species recorded by this capture method, *Corythopis delalandi*, *Cyanocorax chrysops*, *Lepdocolaptes angustirostris*, *Mackenziaena severa*, *Phyllomyias fasciatus*, *Taraba major* and *Xenops rutilans* had not been recorded for "Mata da Bica" by Fonseca (2005). In the present study, however, there was no record of endangered species such as *Sporophila angolensis* (Linnaeus, 1766), *Spinus magellanicus* (Vieillot, 1805) and *Cyanoloxia brisonii* (Lichtenstein, 1823), which were found by the above-mentioned authors.

Less specialized frugivorous species like *Ramphastos toco* can be commonly found in altered areas, suffering less fragmentation effects (Aleixo & Vielliard 1995). Since they highly favor fruits, move over wide areas, and are large, which contributes to the dispersion of *Trichilia catigua* A. Juss., *T. clausenii* C. DC., *T. pallida* Swartz and *T. elegans* A. Juss. in the studied fragment, groups of *Ramphastos toco* have been found feeding on these trees. In Ecuador, Poulsen (1994) noted that frugivorous species more frequently move among forest spots, compared to insectivorous and omnivorous species.

On the other hand, frugivorous species may be affected because the local production of fruits can be low in some seasons of the year (Willis 1979, Antunes 2005), which may be the cause of the low richness of captured frugivorous species. There was lack of fruits from July to November (Fonseca 2005). The fruits are highly variable in time and space and frugivorous species consequently move over wide areas following their availability (Loiselle & Blake 1993).

In the present study, *Basileuterus culicivorus* (37), *Sittasomus griseicapillus* (22) and *Conopophaga lineata* (19) had high capture abundances, which occurred in all environments, since they are generalist insectivorous species capable of living on the forest edges and more easily survive in disturbed environments, facilitating their finding even in smaller forest fragments (Almeida 1982).

During the sampling, we also noted the occurrence of *Ramphocelus carbo* and *Turdus albicollis* in gap environments; since these species live on the edges of forests and in brushwoods (Da Silva *et al.* 1996) or are the first colonizers of new gaps (Charles-Dominique 1986), they may be important dispersing agents in these environments.

The habitats of closed forest, gap and forest edge also differ as to the vegetation composition and structure and consequently as to the composition of bird species (Schemske & Brokaw 1981).

Studying the abundance of resources with the use of gaps by the birds, Blake and Hoppes (1986) did not find significant differences in species richness and capture abundance but observed a positive relationship between the low abundance of specialist frugivorous species and the density of plant covering above the soil.

In this study conducted at "Mata da Bica", the vegetation structure is more closely associated with the abundance of birds than with the availability of prey and fruits, as also found by Manhães & Dias (2011).

Chiroxiphia caudata was present in eight captures, all in large gaps or adjacent areas. This species is common in the edges of secondary forests, as well as in gaps of humid forests, predominantly feeds on fruits and may be an effective dispersing agent of plant species (Sigrist 2006). Other authors have associated the presence of frugivorous species in these areas with a larger and longer production of fruits (Schemske & Brokaw 1981; Levey 1988b, 1990). For McArthur (1964 *and* Lopes 2000), the covering corresponding to the herbaceous, shrub and arboreal vegetation determines the diversity of birds. Thus, each species has its preferred characteristics of vegetation at each level.

The rate of capture increased between September and December, coinciding with birds' breeding seasons, when the exploitation of food resources increases (Jordano 2014). In the tropics, animal-seed dispersal is more common during wet season, relating to the timing of plant fruiting (Howe & Smallwood 1982, Fleming *et al.* 1987, Wunderle 1997).

We observed a decrease abundance in capture rates in April (Autumn), when the weather is drier in the region, and a lower species richness and abundance of individuals caught in gaps in August, that is, in late winter, in southeastern Brazil, when the resources are scarce (Fonseca 2005) and the birds have low activity.

At local scales, both spatial (e.g., variation in habitat) and temporal (e.g., seasonal or annual variation in environmental conditions such as rainfall) factors influence the structure and composition of tropical communities (Blake & Loiselle 2009, 2016).

Among the frugivorous vertebrates that contribute most to the natural regeneration of the gaps in forests are birds and bats. Because they have the habit of defecating while they are perched, birds tend to deposit more seeds on the periphery of these new open spaces, where the availability of perches is greater, whereas bats defecate in flight, spreading propagules more within the center of gaps, generally more clear of obstacles to their displacement. Thus, seeds of several species of pioneer plants, for example, *Piper amalago*, can reach the gaps starting the local succession. Birds and other frugivores commonly create foci of seed densities under perching sites (Gorchov *et al.* 1993, Duncan & Chapman 1999, Arteaga *et al.* 2006, Blendinger *et al.* 2011, Carlo & Tewksbury 2014, Athiê & Dias 2016).

Viswanathan *et al.* (2015) examined patterns of seed rain and found a clumped spatial distribution of seeds, which may be a consequence of indirect interspecific interactions between plant species dispersed by birds.

The course of directed dispersal is important since dispersal into the vicinity of a gap may increase the chances of eventual seedling establishment and reproduction relative to dispersal into a gap or the understory. Seeds deposited near gaps are likely to be exposed by new treefalls relatively quickly because gaps tend to expand; trees exposed around their edges are more likely to topple than trees buffered by forest on all side (Hartshorn 1978).

It is important to consider that mist nets capture mostly understory birds and those of the canopy.

Final considerations

The regeneration process in the areas of the gaps does not depend exclusively on specialized frugivores, usually medium and large, which are often absent, but on a large number of generalist species of secondary environments or forest edges, usually with diets based on fruits and insects, such as, for example, birds of the families Tyrannidae, Turdidae and Thraupidae, (Carvalho 2008), as seen in this study. Birds of these families that eat insects and fruits also tend to disperse seeds to gaps when searching for insects in these environments, indicating that markedly heterogeneous clumped patterns of dispersal are generated during the normal foraging/movement of dispersers, as observed by Viswanathan *et al.* (2015).

The species of birds observed using the gaps are typically generalists. This result was expected, since most of birds that frequent these areas have opportunistic habits, with diets based on insects and fruits, common in forest edges, secondary environments and the gaps.

Morphologically distinct bird species are characterized by differences in movement behavior, home ranges and habitat preferences, and this variability in functional roles might increase the functional complementarity among seed-dispersing species and the maintenance of tropical forests.

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Appendix 1. Species captured at "Mata da Bica", Botucatu-SP.

Táxon	Portuguese Name	English Name
Columbiformes		
Columbidae		
Leptotila verreauxi	juriti-pupu	White-tipped Dove
Apodiformes		
Trochilidae		
Thalurania glaucopis	beija-flor-de-fronte-violeta	Violet-capped Woodnymph

Táxon	Portuguese Name	English Name
Galbuliformes		
Bucconidae		
Malacoptila striata	barbudo-rajado	Crescent-chested Puffbird
Passeriformes		
Thamnophilidae		
Mackenziaena severa	borralhara	Tufted Antshrike
Taraba major	choró-boi	Great Antshrike
Thamnophilus caerulescens	choca-da-mata	Variable Antshrike
Dysithamnus mentalis	choquinha-lisa	Plain Antvireo
Conopophagidae		
Conopophaga lineata	chupa-dente	Rufous Gnateater
Dendrocolaptidae		
Sittasomus griseicapillus	arapaçu-verde	Olivaceous Woodcreeper
Campylorhamphus falcularius	arapaçu-de-bico-torto	Black-billed Scythebill
Lepidocolaptes angustirostris	arapaçu-de-cerrado	Narrow-billed Woodcreeper
Xenopidae		
Xenops rutilans	bico-virado-carijó	Streaked Xenops
Furnariidae		
Automolus leucophthalmus	barranqueiro-de-olho-branco	White-eyed Foliage-gleaner
Synallaxis ruficapilla	pichororé	Rufous-capped Spinetail
Pipridae		
Chiroxiphia caudata	tangará	Swallow-tailed Manakin
Platyrinchidae		
Platyrinchus mystaceus	patinho	White-throated Spadebill
Rhynchocyclidae		
Leptopogon amaurocephalus	cabeçudo	Sepia-capped Flycatcher
Corythopis delalandi	estalador	Southern Antpipit
Tolmomyias sulphurescens	bico-chato-de-orelha-preta	Yellow-olive Flycatcher
Hemitriccus orbitatus	tiririzinho-do-mato	Eye-ringed Tody-Tyrant
Tyrannidae		
Phyllomyias fasciatus	piolhinho	Planalto Tyrannulet
Myiarchus swainsoni	irré	Swainson's Flycatcher
Lathrotriccus euleri	enferrujado	Euler's Flycatcher
Corvidae		
Cyanocorax chrysops	gralha-picaça	Plush-crested Jay
Turdidae		
Turdus leucomelas	sabiá-branco	Pale-breasted Thrush
Turdus rufiventris	sabiá-laranjeira	Rufous-bellied Thrush
Turdus amaurochalinus	sabiá-poca	Creamy-bellied Thrush
Turdus albicollis	sabiá-coleira	White-necked Thrush
Parulidae		
Basileuterus culicivorus	pula-pula	Golden-crowned Warbler
Myiothlypis flaveola	canário-do-mato	Flavescent Warbler
Thraupidae		
Trichothraupis melanops	tiê-de-topete	Black-goggled Tanager
Tachyphonus coronatus	tiê-preto	Ruby-crowned Tanager
Tiaris fuliginosus	cigarra-preta	Sooty Grassquit
Saltator similis	trinca-ferro	Green-winged Saltator
Thlypopsis sordida	saí-canário	Orange-headed Tanager
Sporophila sp.		
Cardinalidae		
Habia rubica	tiê-de-bando	Red-crowned Ant-Tanager