ACTA
AMAZONICA

http://dx.doi.org/10.1590/1809-4392202000732

ORIGINAL ARTICLE

Niche differentiation mechanisms among canopy frugivores and zoochoric trees in the northeastern extreme of the Amazon

Felipe TODESCHINI[1], José Julio de TOLEDO[1], Luis Miguel ROSALINO[2], Renato Richard HILÁRIO[1,2]*

[1] Universidade Federal do Amapá (UNIFAP), Programa de Pós-Graduação em Biodiversidade Tropical, Rod. JK, km 2, Jardim Marco Zero, 68903-419, Macapá, Amapá, Brazil

[2] Universidade de Lisboa, Faculdade de Ciências, cE3c - Centre for Ecology, Evolution and Environmental Changes, Campo Grande, 1749-016, Lisboa, Portugal

* Corresponding author: renatohilario@gmail.com; https://orcid.org/0000-0002-0346-0921

ABSTRACT

Frugivores and zoocoric trees represent an important proportion of tropical rainforest biodiversity. As niche differences favor species coexistence, we aimed to evaluate morphological and temporal niche segregation mechanisms among zoochoric trees and canopy frugivores in a tropical rainforest in the northeastern extreme of the Brazilian Amazon. We tested the effects of fruit morphology, tree size, frugivore body size and time of day on fruit consumption. We recorded the frugivore species that fed on 72 trees (44 species, 22 genera) and whether these frugivores swallowed the seeds. We monitored trees only once from 07:00 to 17:00 h between January and September 2017. We observed fruit consumption in 20 of the 72 trees. Seventy-three frugivore individuals from 22 species visited the trees. Heavier fruits were consumed by larger frugivores, while seed size was inversely correlated with frugivore size. Narrower fruits and fruits with smaller seeds had greater probability of having their seeds ingested, and larger frugivores were more prone to ingest seeds. Trees bearing fruits with smaller seeds were visited by a greater number of frugivores. Taxonomic groups differed in the time of arrival at fruiting trees. None of the evaluated variables (fruit weight and size, and seed size) affected the richness of frugivores that visited the trees. We concluded that, in the studied forest, fruit morphology (weight, size and seed size) is a niche segregation mechanism among zoochoric trees, while body size and time of day are niche segregation mechanisms among frugivores.

KEYWORDS: Amapá National Forest, frugivory, phenology, seed dispersal, tropical rainforest

Mecanismos de diferenciação de nicho entre frugívoros de copa e árvores zoocóricas no extremo nordeste da Amazônia brasileira

RESUMO

Frugívoros e árvores zoocóricas representam uma proporção relevante da biodiversidade de florestas tropicais. Uma vez que a diferenciação de nicho favorece a coexistência das espécies, nós objetivamos investigar mecanismos morfológicos e temporais de segregação de nicho entre árvores zoocóricas e frugívoros de copa em uma floresta tropical no extremo nordeste da Amazônia brasileira. Testamos os efeitos da morfologia dos frutos, tamanho das árvores, tamanho corporal dos frugívoros e hora do dia sobre o consumo de frutos. Registramos as espécies de frugívoros que se alimentaram em 72 árvores (pertencentes a 44 espécies e 22 gêneros) e se esses frugívoros ingeriam sementes. Monitoramos cada árvore apenas uma vez, de 07:00 a 17:00 h, entre janeiro e setembro de 2017 e observamos o consumo de frutos em 20 das 72 árvores. Setenta e três indivíduos de frugívoros, pertencentes a 22 espécies, visitaram as árvores. Frutos mais pesados foram consumidos por frugívoros maiores, enquanto o tamanho das sementes foi inversamente correlacionado ao tamanho dos frugívoros. Frutos menores e com sementes menores tiveram uma maior probabilidade de ter suas sementes ingeridas, e frugívoros maiores apresentaram maior tendência a ingerir as sementes. Árvores com frutos com sementes menores foram visitadas por um maior número de indivíduos de frugívoros. Os grupos taxonômicos de frugívoros diferiram no tempo de chegada às árvores. Nenhuma das variáveis analisadas (peso e tamanho dos frutos e tamanho das sementes) afetou a riqueza de frugívoros que visitaram as árvores. Concluímos que, na floresta estudada, a morfologia dos frutos (tamanho, peso e tamanho das sementes) é um mecanismo de segregação entre árvores zoocóricas, enquanto tamanho corporal e horário do dia são mecanismos de segregação entre frugívoros.

PALAVRAS-CHAVE: Floresta Nacional do Amapá, frugivoria, fenologia, dispersão de sementes, floresta tropical úmida

CITE AS: Todeschini, F.; Toledo, J.J.; L.; Rosalino, M.; Hilário, R.R. 2020. Niche differentiation mechanisms among canopy frugivores and zoochoric trees in the northeastern extreme of the Amazon. Acta Amazonica 50: 263-272.

INTRODUCTION

Frugivory is an important ecological interaction in which animals gain food while plants may have their seeds dispersed. This relationship is critical in tropical forests, where between 62.1% and 93.5% of woody species are dependent on animals for seed dispersal (Jordano 2000). Many frugivores ingest seeds together with the fruit pulp, and then defecate the intact seeds (Jordano 2000; Fricke *et al.* 2013). Passage through the gut of a frugivore often increases seed germinability (Traveset *et al.* 2007; Rosalino *et al.* 2010; Jordaan *et al.* 2011). Furthermore, seed dispersers take the seeds away from the parent tree, reducing competition among seedlings and attack by pathogens and predators (Warren and Giladi 2014).

Birds and mammals are the main tropical frugivores and seed dispersers (Herrera 2002; Chen and Moles 2015) and may feed on up to 75% of the fruit species throughout the tropics (Uriarte *et al.* 2011; Bello *et al.* 2015). Between 25% and 35% of Neotropical birds are frugivores (Pizo and Galetti 2000). Among mammals, primates are the main arboreal frugivores (Fleming and Kress 2011), and seed dispersal by primates is important since they can swallow larger seeds than most birds and bats (Gardner et al. 2019).

Niche differentiation favors species coexistence (Chesson 2000; Chase and Leibold 2003), and strategies of both frugivores and zoochoric trees to increase niche segregation with their competitors may affect how they interact with each other (i.e. different plant species should attract different frugivores, and different frugivores may feed on different plant species). However, there is also convergence in fruit and frugivore traits in response to evolutionary selective pressures (Lomáscolo *et al.* 2010; Dehling *et al.* 2016), creating redundancy in the seed dispersal interaction (Zamora 2000). The evolutionary patterns shaped by frugivory and seed dispersal may be complex, since successful germination and plant establishment sometimes depend on secondary dispersal by ants, beetles or rodents (Vander Wall and Longland 2004; Camargo *et al.* 2019), which may also shape fruit traits (Vander Wall and Longland 2004).

Plants may segregate spatially, so that each species performs with optimal fitness in a different environment (Svenning 2001; Kraft *et al.* 2008), or in a different vertical stratum (Silvertown 2004). Niche segregation can also be temporal, when different species produce flowers and fruits at different times of the year (Günter *et al.* 2008; Munguía-Rosas *et al.* 2011), or morphological, when plants produce morphologically different fruits and flowers to attract different frugivores and pollinators (Flörchinger *et al.* 2010; Dehling *et al.* 2016). These niche differentiation mechanisms can directly affect frugivory, since plant phenology, spatial distribution, nutritional content, and fruit morphology determine frugivore feeding choices (Leiner *et al.* 2009; Flörchinger *et al.* 2010; Dehling *et al.* 2016).

Frugivorous animals also display niche differentiation, which may be spatial, when species occupy different vegetation types or different vertical strata (Poulsen *et al.* 2002; Bersacola et al. 2015), or morphological/behavioral, when species feed on fruits with distinct colors, shapes, and sizes (Flörchinger *et al.* 2010; Dehling *et al.* 2016). For example, gape size limits the size of fruit that a frugivore can ingest (Moran and Catterall 2010; Burns 2013; Galetti *et al.* 2013). There may also be temporal niche segregation among frugivores, as when nocturnal and diurnal frugivores feed on the same fruits in different periods of the day (Mello *et al.* 2011).

Understanding niche segregation mechanisms may contribute to explain the high biodiversity in tropical forests, which are the most biodiverse environments globally (Lewis *et al.* 2015). Nevertheless, most studies investigating frugivory-related niche segregation have focused only on a few pairs of species (Russo 2003; McConkey *et al.* 2014; Moreira *et al.* 2017; Pegman *et al.* 2017), which is insufficient to understand niche segregation patterns at the community level. In addition, temporal niche segregation between frugivores is poorly understood. Therefore, the aim of this study was to fill these information gaps by evaluating how fruit, seed, and tree characteristics affect fruit consumption by canopy frugivores, and how the attributes of these frugivores are related to fruit consumption in a Neotropical rainforest. We expected that frugivore body size is related to the traits of the fruits they consume, and to whether they swallow the seeds or not. In turn, we expected that fruit traits and tree size are related to the probability of the fruit and its seeds being ingested, and affect the richness and abundance of frugivores that feed on them. Finally, we predicted that the prevalence of ripe fruit in the forest affects the visitation of the trees by frugivores, and that different taxonomic groups of frugivores will differ in the time of arrival at the fruiting trees. Our hypotheses and their underlying reasoning are explained in more detail in Table 1.

MATERIAL AND METHODS

Study site

The study was performed during a 10-month period (November 2016 to September 2017) in the Amapá National Forest (ANF), located in the northeastern extreme of the Brazilian Amazon, in the Guiana Shield region. ANF is a protected area consisting of 459,867 ha of mostly pristine evergreen forests (ICMBio 2014) surrounded by two additional protected areas, the Amapá State Forest and Mountains of Tumucumaque National Park (ICMBio 2014). Fieldwork was authorized by Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO license # 49776–2). Information about arboreal frugivores in ANF is still scarce, but previous inventories reported 110 and 14 of, at least partially frugivorous species of birds and arboreal/

Table 1. Hypotheses established for the evaluation of the relation among zoochoric trees and canopy frugivores in Amapá National Forest (Amapá, Brazil) and their underlying reasoning.

Hypotheses	Reasoning
H1 - Larger frugivores will consume heavier and larger fruits, and fruits with larger seeds.	Larger frugivores are stronger (Sekar and Sucumar 2013) and have larger gape sizes (Moran and Catterall 2010; Burns 2013; Galetti *et al.* 2013) allowing them to cope with heavier and larger fruits, and with fruits with larger seeds.
H2 - Larger frugivores will prefer to feed on larger trees (larger DBH).	Larger trees bear higher fruit abundance (Chapman *et al.* 1992), supplying more efficiently the higher energetic demand of larger frugivores (Hawes and Peres 2014).
H3 - Larger frugivores will swallow the seeds more frequently than smaller ones.	Gape size, which is related to frugivore size, limits the size of seeds that can be swollen by frugivores (Moran and Catterall 2010; Galetti *et al.* 2013).
H4 - Smaller fruits will have their seeds swallowed more frequently than larger fruits.	Given the limiting effect of gape size in the ingestion of fruits (Moran and Catterall 2010; Burns 2013), more frugivores should be able to swallow the smaller fruits as a whole (Jordano 2000; Muñoz *et al*. 2016).
H5 - Fruits with smaller seeds will have their seeds swallowed more frequently than fruits with larger seeds.	Larger seeds occupy more space within the frugivore gut (Jordano 2000), limiting the ingestion of fruit pulp. Thus, frugivores must avoid ingesting larger seeds.
H6 - The richness and abundance of frugivores that visit a given fruit tree will be related to fruit traits, such as size, weight, as well as seed size.	Fruit size and weight, as well as seed size may constrain the consumption of such fruits by some frugivore species (Moran and Catterall 2010; Galetti *et al.* 2013; Blendinger *et al.* 2016).
H7 - Larger trees will attract a large number of frugivore individuals and species.	Larger trees may be more conspicuous and produce higher fruit abundance (Chapman *et al.* 1992).
H8 - Frugivore richness and abundance in the focal trees will be higher in months with lower prevalence of ripe fruits.	Frugivores will concentrate their feeding in the few trees bearing fruits in months with low fruit prevalence (Stevenson *et al*. 2000, Saracco *et al*. 2005).
H9 - Taxonomic groups will differ in the time of arrival in the fruiting tree.	Taxonomic groups differ regarding predation risk, and physiological constraints that may influence the time of activity onset (Taufique *et al*. 2006; Saggese *et al.* 2011).

scansorial mammals, respectively (Sick 1997; Reis *et al.* 2006; Supplementary Material, Table S1).

The climate in ANF is classified as Af (tropical forest climate) according to Köppen's classification (ICMBio 2014). Maximum and minimum temperatures are approximately 32°C and 22°C, respectively. Average annual rainfall is 2284 mm, concentrated between December and July, with a dry season from August to mid-December, yet rainfall is typically above 60 mm even in the driest months (ICMBio 2014).

Sampling design

A 5 × 5-km grid of trails of the Research Program on Biodiversity (PPBio) (https://ppbio.inpa.gov.br/en/home) is located in the southern region of the ANF (Figure 1), and includes 30 standardized sampling plots (40 × 250 m) (ICMBio 2014). Our study was performed in five of these plots (Figure 1). We identified the zoochoric trees [>10 cm DBH (diameter at breast height)] in the plots and recorded their DBH, since it is correlated with fruit production (Chapman *et al*. 1992). The trees were identified by an experienced parataxonomist following Byng *et al.* (2016). Although 59.5% of the trees in the plots were zoochoric, most of the zoochoric species had only one or two individuals in the study plots. Therefore, we initially selected 942 trees belonging to species that had three or more individual trees in the five plots, to allow for at least 30 hours of observation for each species. The 942 trees were monitored monthly from November 2016 to September 2017 to register whether they bore ripe fruits.

We used the focal-tree method (Galetti *et al.* 2013) to record vertebrate frugivore species feeding on each tree and whether the frugivore species typically swallowed or discarded the seeds of the focal tree. Each month, we selected four to 10 trees bearing ripe fruits over at least 30% of their canopies to monitor frugivore visits, totaling 72 trees, pertaining to 44 species and 22 genera. To keep independence among samples, each focal tree was monitored only once throughout the study, at a time when it was bearing fruit. By sampling each tree only once, we avoided the bias associated with pseudoreplication of repeated monitorings of the same tree. Ideally, we aimed to select focal individuals of the same species, to avoid increased variability associated with distinct species. However, due to the limited availability of conspecific fruit-bearing trees, in some cases we had to select focal individuals of different congeneric species. Although the variation in fruit traits (e.g. size) across species is often higher than variation within species (Mubo *et al*. 2004), this was not the case for most of the genera in this study, with the exception of *Protium* (data available at: https://ppbiodata.inpa.gov.br/metacatui/#view/PPBioAmOc.229.4). Although acknowledging this limitation, we used congeneric trees to allow the inclusion of this genus in our study (otherwise it would have to be excluded), because

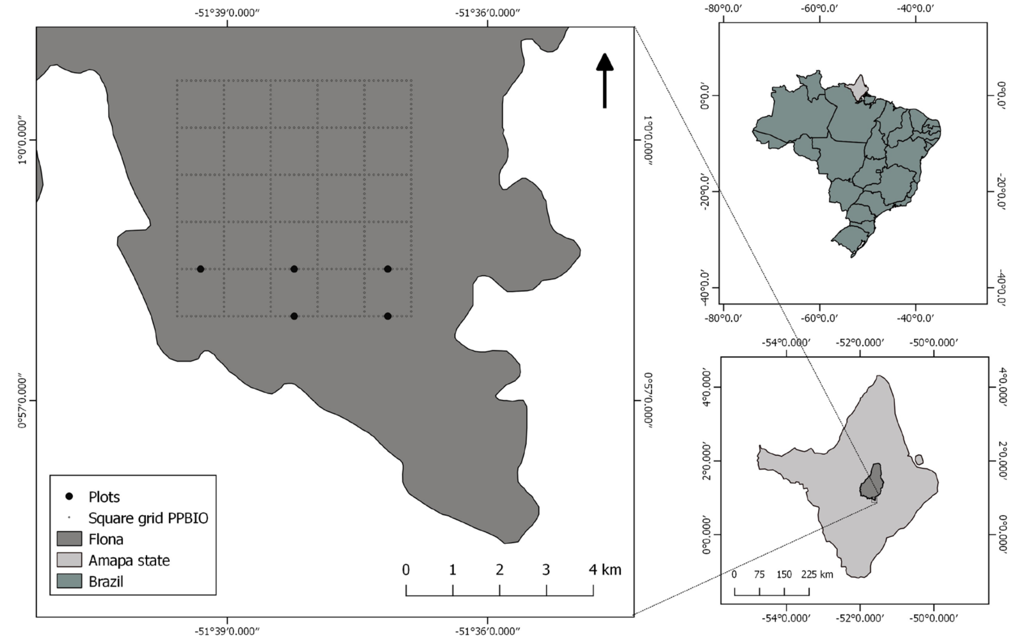

Figure 1. Location of Amapá state in Brazil, of the Amapá National Forest (ANF) (Flona in the figure legend) in Amapá, and of the 5x5-km trail grid and the five sampling plots within ANF. (Map: Bayron R. Calle Rendón).

field data clearly showed that this genus is a food resource for the animal species at the study site.

The 72 focal trees were monitored from January to September 2017, as we could not arrive at the focal trees early in the morning during the late dry season due to the low level of the river used to access the grid, which prevented navigation among surfaced rocks before dawn. We selected the focal trees so that a minimum of three and a maximum of six trees were monitored for each genus (Supplementary Material, Table S2). We observed the focal trees from 07:00 to 17:00h (sunrise varied from 6:04 to 6:35 h and sunset, from 18:11 to 18:41 h). It was not possible to start monitoring earlier in the morning due to fog. Trees were observed with 10 × 42 binoculars. Only two observers stayed near the focal tree, in a position from where they could observe the whole tree canopy. The observers adopted a discreet posture, wore camouflage, and avoided making any sound to minimize any disturbance to the frugivores. We did not register terrestrial and/or nocturnal frugivores. We recorded the length of each feeding bout, i.e. the time between the moment that each frugivore individual or group started feeding on the fruiting tree, and the moment it/they stopped feeding or left the tree (we assume no registration bias occurred as we never observed more than one species visiting the monitored tree at the same time). We used a field guide (Sigrist 2013) to identify bird species and obtain their body length. The body length of primates was obtained from Bicca-Marques *et al.* (2006).

For each focal tree, we collected fallen ripe fruits (average = 3.6 fruits per tree; standard deviation = 2.9; range = 1 to 14) to measure fruit characteristics. Considering the low level of frugivory in the study site, we assume that fallen fruits may represent the average fruit traits of each tree. We used a caliper to record fruit length and width and calculated a fruit size index by multiplying fruit length by width. Fruit weight was measured with spring scales. We calculated a seed-size index by multiplying seed length by width. The smallest seeds were considered as having a size of 0.01 cm, the smallest division of the caliper. Fruit and seed traits were averaged over the focal trees of the same species (Supplementary Material, Table S2).

Statistical analyses

To examine the mechanisms of niche segregation between frugivores and trees, we evaluated the factors that affect four dependent variables: frugivore size (average species body length), whether the seeds were swallowed or not by the frugivore species, species richness, and abundance of frugivore individuals visiting each tree. We ran generalized linear models in a multi-model inference approach in the "MuMIn" package (Barton 2009) of the R software version 3.6.3 (R Core Team 2019). We created four full models (one for each dependent variable; Supplementary Material, Table S3), including the independent variables that we hypothesized could affect the dependent variables. We then tested every possible combination of independent variables and ranked the models based on their AICc (Akaike's Information Criterion corrected for small samples). ΔAICc values (the difference between the AICc of a given model and the AICc of the most parsimonious model) were used to calculate Akaike weights, which were then used to average the models and calculate importance values for each independent variable (Burnham and Anderson 2004). We only considered those models with a ΔAICc ≤ 2.0. Variables were considered important when their importance value was > 4.0 (Burnham 2015). Prior to the analyses, all continuous variables were standardized to zero mean and unit variance. Since some independent variables could be correlated, we calculated Variance Inflation Factors (VIF) with the "car" package (Fox and Weisberg 2011), using the R software, and excluded those models in which collinearity could represent a problem (at least one VIF > 3.0; Quinn and Keough 2002). Therefore, the model averaging approach was carried out only with collinearity-free models. The sampling units of these analyses were the feeding bouts (dependent variables: frugivore size and whether the seed was swallowed or not) or the focal trees (dependent variables: frugivore richness and abundance). We also tested if the time of arrival at the feeding tree (continuous dependent variable) differed between taxonomic groups (independent variable) through an ANOVA with Tukey's post-hoc test. Given the low number of visits for some taxonomic groups, we grouped all non-passerine birds into one category, and compared them to Passeriformes and Primates.

RESULTS

Seventy-three frugivore individuals visited the focal trees during the study. The number of frugivore individuals presented a bimodal temporal pattern, with peaks in January (17 individual frugivores) and July (20 individual frugivores) (Figure 2). The highest number of species visiting the focal trees was recorded in August and September (Figure 2). Twenty-two species (20 bird and two primate species) were recorded consuming fruit of 20 (27.8%) of the 72 focal trees (Supplementary Material, Tables S2 and S4).

Frugivores observed in this study consumed only ripe fruits. The frequency of trees bearing ripe fruit was low between January and March (approximately 4%) and tended to increase throughout the study period, reaching 18% in August and September (Figure 2). Out of the 942 trees of zoochoric species monitored monthly, we did not detect fruit-bearing in 51% (n = 472) over the course of the study. Coinciding with fruit availability, frugivory was more prevalent in August and September, when we observed fruit consumption in 40% of the focal trees.

Fruit weight, as well as seed size, were important to explain the size of the frugivores that visited the focal trees. Heavier fruits were consumed by larger frugivores, whereas seed size was inversely correlated with frugivore size (Table 2). Fruit dimension and frugivore size were important for predicting whether the seeds were swallowed or not (Table 2). Larger frugivores ingested seeds more frequently than smaller ones. Moreover, seeds of narrower and lighter fruits were also ingested more frequently. None of the independent variables tested were important for predicting the number of frugivore species that fed on the focal trees (Supplementary Material, Table S5). Nevertheless, the number of individual frugivores recorded in the focal trees was negatively related to the seed's smallest dimension (Table 2; Supplementary Material, Table S6).

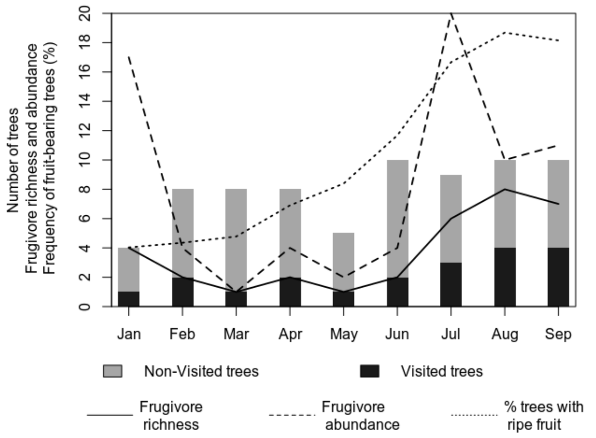

Figure 2. Monthly variation in the number of focal trees, fruit availability, and frugivore visitation in the five sampling plots during the study in Amapá National Forest (Amapá, Brazil). Bars show the number of focal trees monitored each month (visited and non-visited by frugivores). Lines show frugivore species richness (solid line), and individual abundance (dashed line) observed in the monitored trees, and the percentage of trees bearing ripe fruit in the sampling plots (dotted line).

Regarding temporal niche segregation between taxonomic groups, primates arrived later at the trees to forage compared to Psittaciformes and Piciformes ($F_{4,39} = 3.771$; $p = 0.011$), i.e. primates visited the fruiting trees in average 4.5 hours later then Psittaciformes and Piciformes. Most (65.8%) of the observed frugivores visited the monitored trees in the morning.

DISCUSSION

Niche segregation among frugivores

We showed that fruit traits influence which frugivores will feed on them, and affect the probability of fruits and seeds being ingested by frugivores, thus affecting seed dispersal patterns. Body size was among the most important niche segregation factors among frugivores, with larger frugivores feeding on heavier fruits due to their greater strength and larger gape (partially corroborating H1). Body size is correlated with gape size in birds, which limits the maximum fruit size that birds can swallow whole (Moran and Catterall 2010). However, sometimes frugivores can handle the fruits to eat them piecemeal, and primates and psittacids can feed on fruits much larger than their gapes (Oliveira *et al*. 2011; Baños-Villaba 2017). Indeed, this was the case of the two small psittacids (*Brotogeris chrysoptera* and *Touit huetii*) in our study, which fed on fruits larger than their gapes, by eating the pulp but not ingesting the seeds. Therefore, the relationship

Table 2. Model-averaging results based on Akaike weights of the models with ΔAICc (difference between the AICc of a given model and the AICc of the most parsimonious model) ≤ 2.0. Variables were considered important for predicting frugivore size, whether the seed was swollen or not, and frugivore abundance when they presented an importance value > 0.4. Coefficients, standard errors, and *P*-values were conditionally averaged. Coef = coefficient; Imp = variable importance; na = not applicable; DBH = tree diameter at breast height; abs = variable absent from the models with ΔAICc ≤ 2.0. The models used in the model averaging are presented in Supplementary Material, Table S6.

Independent variables	Frugivore size			Seed swallowed or not			Frugivore abundance		
	Coef ± SE	p	Imp	Coef ± SE	p	Imp	Coef ± SE	p	Imp
Fruit weight	0.635 ± 0.141	<0.001	1.00	-1.053 ± 0.588	0.083	0.90	abs	abs	abs
Seed size	-0.387 ± 0.112	<0.001	1.00	-1.988 ± 1.444	0.182	0.20	abs	abs	abs
Fruit size	abs	abs	abs	-2.417 ± 0.940	0.013	0.24	-0.212 ± 0.222	0.375	0.17
Seed smallest dimension	abs	abs	abs	-0.866 ± 0.606	0.166	0.41	-0.631 ± 0.215	0.006	1.00
DBH	0.136 ± 0.113	0.240	0.38	na	na	na	0.137 ± 0.154	0.409	0.16
Fruit smallest dimension	abs	abs	abs	-2.037 ± 0.817	0.015	0.76	abs	abs	abs
Frugivore size	na	na	na	1.605 ± 0.553	0.005	1.00	na	na	na
Ripe fruit prevalence	na	na	na	na	na	na	0.184 ± 0.143	0.231	0.24

of frugivore size and the size of the fruits they can ingest may be dependent on the behaviour of the taxonomic group. We were not able to evaluate this relationship within taxonomic groups due to sample size.

Larger frugivores also consumed fruits with smaller seeds and swallow the seeds more frequently than smaller frugivores, a result that partially contradicts H1, but supports H3. This pattern is probably linked with the fact that they swallow the whole fruit instead of discarding the seeds (Jordano 2000; Jordano and Schupp 2000), and that frugivores maximize the pulp:seed ratio, preferring large fruits with small seeds (Blendinger *et al*. 2016). Also, although many studies detected a positive relationship between frugivore size and the seed size they ingest (e.g. Moran and Catterall 2010; Burns 2013; Galetti *et al*. 2013), a recent study with a larger data set actually revealed a negative relationship, which confirms our findings (Chen and Moles 2015). By ingesting seeds more frequently, larger frugivores disperse the seeds of a larger array of plants than smaller ones (Moran and Catterall 2010; Chen and Moles 2015). Larger body sizes may be advantageous for gape-constrained frugivores, allowing them to feed on a wider range of fruits (Moran and Catterall 2010; Chen and Moles 2015; this study). Conversely, larger frugivores also have a higher energetic demand, which poses a challenge, especially during periods of fruit scarcity, when they must rely on alternative food sources (Hawes and Peres 2014). Nonetheless, larger frugivores, such as ramphastids and primates, accounted for 38% of the feeding bouts in our study, highlighting the role of these groups in the maintenance and structuring of biodiversity in tropical forests.

In addition to morphology, timing was also a niche segregation dimension among frugivores in our study. Birds visited fruiting trees earlier than primates during the day, obtaining a competitive advantage (supporting H9). Indeed, most frugivory occurs in the morning, when frugivores feed on the fruits that ripened overnight (Daily and Ehrlich 1994; Graham *et al.* 2002). Besides food availability and environmental factors (Bruni *et al.* 2014), an animal's activity onset also depends on physiological factors (Taufique *et al.* 2016) and predation risk (Saggese *et al.* 2011), which may explain the differences between primates and birds.

Time is also a niche segregation factor between diurnal and nocturnal frugivores, although we were not able to analyze the latter in this study. Nocturnal canopy frugivores at our study site include bats, marsupials, and kinkajous (IEPA/CI 2006), and the amount of fruit consumed by these frugivores during the night may affect the scale of the advantage of birds in consuming fruit earlier in the morning, in spite of their arriving earlier to feed than primates. However, the fruit consumed by nocturnal and diurnal frugivores generally differ morphologically and chemically (Korine *et al*. 2000; Albuquerque *et al*. 2006), and a limited proportion of the plants are exploited by both diurnal and nocturnal frugivores (Mello *et al*. 2011). Considering this, our conclusions are, therefore, limited to diurnal canopy frugivores.

Niche segregation among trees

Fruit morphology influences seed dispersal (Galetti *et al.* 2013), which is an important niche dimension related to plant reproductive success. We found that fruit morphology (weight and seed size) is a niche segregation mechanism among zoochoric trees at ANF, a pattern that corroborates our hypotheses H1, H4, H5 and H6. Trees may influence the size of frugivores that visit them through the weight of the fruit and the size of the seeds. By influencing the size of the frugivores, trees may also influence seed dispersal distance, since larger dispersers are often involved in greater seed dispersal distances (Jordano *et al.* 2007; Wotton and Kelly 2012). Producing smaller fruits can also maximize seed ingestion and, consequently, dispersal.

The number of frugivores that visit trees may also be increased through seed size (H6). The increased visitation of trees with small seeds may have been related to a frugivore preference for feeding on fruits that maximize the pulp:seed ratio. Large seeds occupy greater volumes in the gut, limiting the amount of pulp that a frugivore can ingest and digest, and/or speeding up gut transit time, which reduces fruit digestibility (Jordano 2000). Besides morphological aspects of fruits and seeds, there are other ways in which plants can influence fruit selection by frugivores, such as the nutritional content of the fruits, olfactory cues, and timing of fructification (Cazetta *et al*. 2008; Leiner *et al*. 2009), which were not evaluated in our study.

Comparison with previous studies

Most studies evaluating frugivory consider only relatively few species (Russo 2003; McConkey *et al.* 2014; Moreira *et al.* 2017; Pegman *et al.* 2017), which limits the understanding of frugivory intensity throughout entire biological communities, particularly in the highly diverse tropical forests. Two exceptions are studies that registered a high intensity of frugivory at the community level in tropical rainforests in Kenya (Kakamega Forest - KF) (Flörchinger *et al.* 2010) and the Colombian Amazon in the Tinigua National Park – TNP (Stevenson *et al.* 2015). We observed a lower level of visitation by frugivores in our focal trees than that reported by the latter studies. Sampling effort was equivalent in the three studies, yet the number of frugivores recorded per hour of monitoring was much higher in Kenya and Colombia. Therefore, sampling effort cannot explain our lower figures. In addition, the proportion of zoochoric trees bearing fruits throughout the year does not seem to vary significantly between ANF and TNP (Stevenson 2004). We did not find any comparable data on fruit availability in the KF. Frugivore densities may explain the differences between ANF and the other sites. However, although the density of spider monkeys (*Ateles* spp.) is lower in ANF than in TNP (Stevenson 1996; Michalski *et al.* 2017), no comparable information exists on the densities of other frugivores. Although low densities of frugivores may explain the low level of frugivory in ANF, this hypothesis remains to be tested.

The study at KF also examined niche segregation factors at the community level (Flörchinger *et al.* 2010). Although these authors investigated different factors and used a different analytical approach, some comparison can still be made between both studies. Plant height, fruit crop mass, fruit size, and fruit color affected which frugivores visited each tree in KF. Other two studies used different approaches and found that frugivore size and fruit size affected fruit consumption positively and negatively, respectively, in the Andean forests of Colombia (Muñoz *et al*. 2016), and that frugivore traits, such as size, are related to plant traits, such as plant height and fruit size in the Andean forests of Peru (Dehling *et al.* 2016). Thus, all these studies agree with our findings that tree size and fruit morphology are niche segregation mechanisms among zoochoric trees, and that body size is a niche segregation mechanism among frugivores. In addition, our study also showed that the time of day in which frugivores feed is a niche segregation mechanism among diurnal canopy frugivores.

CONCLUSIONS

We found that body size is a niche segregation factor among vertebrate canopy frugivores in Amapá National Forest, being related to the size and weight of the fruit consumed, and seed ingestion, which is essential for seed dispersal. Frugivores also differed in the time of day they visited fruiting trees, which may represent an advantage to birds, which visit the trees earlier than primates. Plant traits, such as fruit weight and seed size, also influenced which frugivore species and the abundance of individuals that visit a given fruiting tree, with potential consequences for the success of seed dispersal. Despite the high number of focal trees sampled in this study, the low level of visitation by frugivores at ANF resulted in a small sample size. This small sample size prevented more complex analyses, such as ecological networks, and may have prevented the detection of some relationships among variables. Nevertheless, our results corroborate most of our hypotheses and seem to be robust, both statistically and in view of their ecological sense. At our study site, frugivore size, time of day of tree visitation by frugivores, and plant traits seem to be important niche segregation mechanisms, which may also be crucial determinants in other Amazonian biological communities.

ACKNOWLEDGMENTS

We are thankful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES (Brazil) for the scholarships to FT and RRH (Process # 88881.314420/2019-01). This study was carried out with the support of Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (Brazil) (Process # 447432/2014-1). LMR was financially supported by Centro de Ecologia, Evolução e Alterações Ambientais – cE3c (Portugal) (Process # UID/BIA/00329/2019) and Fundação para a Ciência e a Tecnologia – FCT/MCTES (Portugal) through national funds, and co-funding by FEDER, within the PT2020 Partnership Agreement and Compete 2020. We are grateful to Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (Brazil) for the permit and all the ANF staff for their support in fieldwork. We also thank Universidade Federal do Amapá for help with transportation. Finally, we are grateful to two anonymous reviewers, who contributed with valuable suggestions on an earlier version of the manuscript.

REFERENCES

Albuquerque, L.B.; Velázquez, A.; Mayorga-Saucedo, R. 2006. Solanaceae composition, pollination and seed dispersal syndromes in Mexican Mountain Cloud Forest. *Acta Botanica Brasilica*, 20: 599-613.

Baños-Villalba, A.; Blanco, G.; Díaz-Luque, J.A.; Dénes, F.V.; Hiraldo, F; Tella, J.L. 2017. Seed dispersal by macaws shapes the landscape of an Amazonian ecosystem. *Scientific Reports*, 7: 1-12.

Barton, K. 2009. MuMIn: multi-model inference. R package version 1.0.0.

Bello, C.; Galetti, M.; Pizo, M.A.; Magnago, L.F.S.; Rocha, M.F.; Lima, R.A.; Jordano, P. 2015. Defaunation affects carbon storage in tropical forests. *Science Advances*, 1: e1501105.

Bersacola, E.; Svensson, M.S.; Bearder, S.K. 2015. Niche partitioning and environmental factors affecting abundance of strepsirrhines in Angola. *American Journal of Primatology*, 77: 1179-1192.

Bicca-Marques, J.C.; Silva, V.M.; Gomes, D. 2006. Ordem Primates. In: Reis, N.R.; Peracchi, A.L.; Pedro, W.A.; Lima, I.P. (Ed.). *Mamíferos do Brasil*. Edifurb/UEL, Londrina, p.107–150.

Blendinger, P.G.; Martín, E.; Osinaga, A.O.; Ruggera, R.A.; Aráoz, E. 2016. Fruit selection by Andean forest birds: influence of fruit functional traits and their temporal variation. *Biotropica*, 48: 677-686.

Bruni, A.; Mennill, D.J.; Foote, J.R. 2014. Dawn chorus start time variation in a temperate bird community: relationships with seasonality, weather, and ambient light. *Journal of Ornithology*, 155: 877-890.

Burnham, K.P. 2015. Multimodel Inference: Understanding AIC relative variable importance values. (https://sites.warnercnr.colostate.edu/kenburnham/wp-content/uploads/sites/25/2016/08/VARIMP.pdf). Accessed on 19 Oct 2019.

Burnham, K.P.; Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33: 261–304.

Burns, K.C. 2013. What causes size coupling in fruit–frugivore interaction webs? *Ecology*, 94: 295-300.

Byng, J.W.; Chase, M.W.; Christenhusz, M.J.M.; Fay, M.F.; Judd, W.S.; Mabberley, D.J.; Sennikov, A.N.; Soltis, D.E.; Soltis, P.S.; Stevens, P.F. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181: 1–20.

Camargo, P.H.; Rodrigues, S.B.; Piratelli, A.J.; Oliveira, P.S.; Christianini, A.V. 2019. Interhabitat variation in diplochory: Seed dispersal effectiveness by birds and ants differs between tropical forest and savanna. *Perspectives in Plant Ecology, Evolution and Systematics*, 38: 48-57.

Cazetta, E.; Schaefer, H.M.; Galetti, M. 2008. Does attraction to frugivores or defense against pathogens shape fruit pulp composition? *Oecologia*, 155: 277-286.

Chapman, C.A.; Chapman, L.J.; Wangham, R.; Hunt, K.; Gebo, D.; Gardner, L. 1992. Estimators of fruit abundance of tropical trees. *Biotropica*, 24: 527–531.

Chase, J.M.; Leibold, M.A. 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, 212p.

Chen, S.C.; Moles, A.T. 2015. A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. *Global Ecology and Biogeography*, 24: 1269-1280.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31: 343–366.

Daily, G.C.; Ehrlich, P.R. 1994. Influence of social status on individual foraging and community structure in a bird guild. *Oecologia*, 100: 153-165.

Dehling, D.M.; Jordano, P.; Schaefer, H.M.; Böhning-Gaese, K. Schleuning, M. 2016. Morphology predicts species functional roles and their degree of specialization in plant–frugivore interactions. *Proceedings of the Royal Society B*, 283: 20152444.

Fleming, T.H.; Kress, W.J. 2011. A brief history of fruits and frugivores. *Acta Oecologica*, 37: 521–530.

Flörchinger, M.; Braun, J.; Böhning-Gaese, K.; Schaefer, H.M. 2010. Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. *Oecologia*, 164: 151–161.

Fox, J.; Weisberg, S. 2011. *An R companion to applied regression*. Sage Publications, Los Angeles, 608p.

Fricke, E.C.; Simon, M.J.; Reagan, K.M.; Levey, D.J.; Riffell, J.A.; Carlo, T.A.; Tewksbury, J.J. 2013. When condition trumps location: seed consumption by fruiteating birds removes pathogens and predator attractants. *Ecology Letters*, 16: 1031e1036.

Galetti, M.; Guevara, R.; Côrtes, M.C.; Fadini, R.; Von Matter, S.; Leite, A.B.; *et al.* 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, 340: 1086–1090.

Gardner, C.J.; Bicknell, J.E.; Baldwin-Cantello, W.; Struebig, M.J.; Davies, Z.G. 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. *Nature Communications*, 10: 1-7.

Graham, C.; Martínez-Leyva, J.E.; Cruz-Paredes, L. 2002. Use of fruiting trees by birds in continuous forest and riparian forest remnants in Los Tuxtlas, Veracruz, Mexico. *Biotropica*, 34: 589-597.

Günter, S.; Stimm, B.; Cabrera, M.; Diaz, M.L.; Lojan, M.; Ordoñez, E.; Richter, M.; Weber, M. 2008. Tree phenology in montane forests of southern Ecuador can be explained by precipitation, radiation and photoperiodic control. *Journal of Tropical Ecology*, 24: 247–258.

Hawes, J.E.; Peres, C.A. 2014. Ecological correlates of trophic status and frugivory in neotropical primates. *Oikos*, 123: 365–377.

Herrera, C.M. 2002. Seed dispersal by vertebrates. In: Herrera, C.M.; Pellmyr, O. (Ed.). *Plant–Animal Interactions: an Evolutionary Approach*. Blackwell, Oxford, p.185-208.

ICMBio. 2014. *Plano de Manejo da Floresta Nacional do Amapá, Volume I-Diagnóstico*. ICMBio, Macapá, 222p.

IEPA/CI. 2006. *Inventários Biológicos na Floresta Nacional do Amapá – Expedições I e II*. Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá-IEPA/Conservação Internacional, Macapá. Unpublished technical report. 128p

Jordaan, L.A.; Johnson, S.D.; Downs, C.T. 2011. The role of avian frugivores in germination of seeds of feshyfruited invasive alien plants. *Biological Invasions*, 13: 1917–1930.

Jordano, P. 2000. Fruits and frugivory. In: Fenner, M. (Ed.). *Seeds: the Ecology of Regeneration in Plant Communities*. CABI Publishing, Wallingford, p.125-166.

Jordano, P.; Garcia, C.; Godoy, J.A.; García-Castaño, J.L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences USA*, 104: 3278–3282.

Jordano, P.; Schupp, E.W. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, 70: 591-615.

Korine, C.; Kalko, E.K.; Herre, E.A. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia*, 123: 560-568.

Kraft, N.J.B.; Valencia, R.; Ackerly, D.D. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322: 580–582.

Leiner, N.O.; Nascimento, A.R.; Melo, C. 2009. Plant strategies for seed dispersal in tropical habitats: patterns and implications. In: del Claro, K.; Oliveira, P.S.; Rico-Gray, V. (Ed.). *Tropical Biology and Conservation Management: Natural History of Tropical Plants. v.1.* Eolss Publishers, Oxford, p.155-170.

Lewis, S.L.; Edwards, D.P.; Galbraith, D. 2015. Increasing human dominance of tropical forests. *Science*, 349: 827–832.

Lomáscolo, S.B.; Levey, D.J.; Kimball, R.T.; Bolker, B.M.; Alborn, H.T. 2010. Dispersers shape fruit diversity in Ficus (Moraceae). *Proceedings of the National Academy of Sciences*, 107: 14668–14672.

McConkey, K.R.; Brockelman, W.Y.; Saralamba, C. 2014. Mammalian frugivores with different foraging behavior can show similar seed dispersal effectiveness. *Biotropica*, 46: 647–651.

Mello, M.A.R.; Marquitti, F.M.D.; Guimarães, P.R.; Kalko, E.K.V.; Jordano, P.; Aguiar, M.A.M. 2011. The modularity of seed dispersal: differences in structure and robustness between bat– and bird–fruit networks. *Oecologia*, 167: 131 (doi.org/10.1007/s00442-011-1984-2).

Michalski, F.; Michalski, L.J.; Barnett, A.A. 2017. Environmental determinants and use of space by six Neotropical primates in the northern Brazilian Amazon. *Studies on Neotropical Fauna and Environment*, 52: 187–197.

Moran, C.; Catterall, C.P. 2010. Can functional traits predict ecological interactions? A case study using rain forest frugivores and plants in Australia. *Biotropica*, 42: 318-326.

Moreira, J.I.; Riba-Hernández, P.; Lobo, J.A. 2017. Toucans (*Ramphastos ambiguus*) facilitate resilience against seed dispersal limitation to a large-seeded tree (*Virola surinamensis*) in a human-modified landscape. *Biotropica*, 49: 502–510.

Mubo, S.A.; Adeniyi, J.A.; Adeyemi, E. 2004. A morphometric analysis of the genus *Ficus* Linn. (Moraceae). *African Journal of Biotechnology*, 3: 229-235.

Munguía-Rosas, M.A.; Ollerton, J.; Parra-Tabla, V.; De-Nova, J.A. 2011. Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. *Ecology Letters*, 14: 511-521.

Muñoz, M.C.; Schaefer, H.M.; Böhning-Gaese, K.; Schleuning, M. 2017. Importance of animal and plant traits for fruit removal and seedling recruitment in a tropical forest. *Oikos*, 126: 823-832.

Oliveira, L.C.; Neves, L.G.; Raboy, B.E.; Dietz, J.M. 2011. Abundance of jackfruit (*Artocarpus heterophyllus*) affects group characteristics and use of space by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in cabruca agroforest. *Environmental Management*, 48: 248-262.

Pegman, A.P.M.; Perry, G.L.W.; Clout, M.N. 2017. Exploring the interaction of avian frugivory and plant spatial heterogeneity and its effect on seed dispersal kernels using a simulation model. *Ecography*, 40: 1098–1109.

Pizo, M.A.; Galetti, M. 2000. Métodos e perspectivas do estudo da frugivoria e dispersão de sementes por aves. In: Matter, V.S.; Straube, F.C.; Piacentini, V.Q.; Accordi, I.A.; Cândido, J.F.J. (Ed.). *Ornitologia e Conservação: Ciência Aplicada, Técnicas de Pesquisa e Levantamento*. Technical Books Editora Ltda, Rio de Janeiro, p.1–12.

Poulsen, J.R.; Clark, C.J.; Connor, E.F.; Smith, T.B. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, 83: 228–240.

Quinn, G.P.; Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, New York, 537p.

R Core Team. 2019. *R: A language and environment for statistical computing*. Version 3.6.2. R Foundation for Statistical Computing, Vienna.

Reis, N.R.; Peracchi, A.L.; Pedro, W.A. Lima, I.P. 2006. *Mamíferos do Brasil*. Edifurb/UEL, Londrina, 437p.

Rosalino, L.M.; Rosa, S.; Santos-Reis, M. 2010. The role of carnivores as Mediterranean seed dispersers. *Annales Zoologici Fennici*, 47: 195-205.

Russo, S.E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): Implications for selection. *Oecologia*, 136: 80–87.

Saggese, K.; Korner-Nievergelt, F.; Slagsvold, T.; Amrhein, V. 2011. Wild bird feeding delays start of dawn singing in the great tit. *Animal Behaviour*, 81: 361-365.

Saracco, J.F.; Collazo, J.A.; Groom, M.J.; Carlo, T.A. 2005 Crop size and fruit neighborhood effects on bird visitation to fruiting Schefflera morototoni trees in Puerto Rico. *Biotropica*, 37: 81–87.

Sekar, N.; Sukumar, R. 2013. Waiting for Gajah: an elephant mutualist's contingency plan for an endangered megafaunal disperser. *Journal of Ecology*, 101: 1379-1388.

Sick, H. 1997. *Ornitologia Brasileira*. Nova Fronteira, Rio de Janeiro, 862p.

Sigrist, T. 2013. *Avifauna Brasileira: Guia de Campo*. Avis Brasilis Editora, São Paulo, 591p.

Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution*, 19: 605-611.

Stevenson, P.R. 1996. Censos diurnos de mamíferos y algunas aves de gran tamaño en el Parque Nacional Tinigua, Colombia. *Universitas Scientiarum*, 3: 67–81.

Stevenson, P.R. 2004. Phenological patterns of woody vegetation at Tinigua Park, Colombia: methodological comparisons with emphasis on fruit production. *Caldasia*, 26: 125–150.

Stevenson, P.R.; Link, A.; González-Caro, S.; Torres-Jiménez, M.F. 2015. Frugivory in canopy plants in a western Amazonian forest: dispersal systems, phylogenetic ensembles and keystone plants. *PLoS ONE*, 10: e0140751.

Stevenson, P.R.; Quiñones, M.J.; Ahumada, J.A. 2000. Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia 1. *Biotropica*, 32: 533-544.

Svenning, J.C. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). *Botanical Review*, 67: 1–53.

Taufique, S.T.; Jha, N.A.; Kumar, V. 2016. Circadian rhythm determines the timing of activity, and ingestive and grooming behaviours in Indian house crows, *Corvus splendens*. *Current Science*, 110: 897–901.

Traveset, A.; Robertson, A.W.; Rodríguez-Pérez, J. 2007. A review on the role of endozoochory on seed germination. In: Schupp, E.W.; Green, R.J.; Westcott, D.A.; Dennis, A.J. (Ed.). *Seed Dispersal, Theory and its Application in a Changing World*. CAB International, Wallingford, p.78–103.

Uriarte, M.; Anciães, M.; Silva, M.T.B.; Rubim, P.; Johnson, E.; Bruna, E.M. 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. *Ecology*, 92: 924–937.

Vander Wall, S.B.; Longland, W.S. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology & Evolution*, 19: 155-161.

Warren, R.J.; Giladi, I. 2014. Ant-mediated seed dispersal: a few ant species (Hymenoptera: Formicidae) benefit many plants. *Myrmecological News*, 20: 129-140.

Wotton, D.M.; Kelly, D. 2012. Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. *Journal of Biogeography*, 39: 1973-1983.

Zamora, R. 2000. Functional equivalence in plant-animal interactions: ecological and evolutionary consequences. *Oikos*, 88: 442-447.

RECEIVED: 06/03/2020
ACCEPTED: 21/06/2020
ASSOCIATE EDITOR: Paulo E. Bobrowiec

SUPPLEMENTARY MATERIAL (only available in the electronic version)

Todeschini *et al*. Niche differentiation mechanisms among canopy frugivores and zoochoric trees in the northeastern extreme of the Amazon

Table S1. List of diurnal mammal and bird species that include fruits in their diet, with confirmed presence in the Amapá National Forest, Amapá, Brazil. We highlight whether they were observed feeding during the study. We did not include terrestrial birds and mammals (Reis *et al.* 2006; Sick 1997). Body length for mammals is considered without the tail and was obtained from Reis *et al.* (2006), and for birds it includes the tail and was obtained from Sick (1997).

Class	Family	Species	Body length (cm)	Observed in the study
Mammalia	Callitrichidae	*Saguinus midas*	38.5	X
Mammalia	Cebidae	*Saimiri sciureus*	25.3	
Mammalia	Cebidae	*Cebus apella*	41.9	
Mammalia	Cebidae	*Cebus olivaceus*	41.9	
Mammalia	Atelidae	*Alouatta seniculus*	52.5	
Mammalia	Atelidae	*Ateles paniscus*	54.0	X
Mammalia	Pitheciidae	*Chiropotes satanas*	40.35	
Mammalia	Pitheciidae	*Pithecia pithecia*	39.0	
Mammalia	Bradypodidae	*Choloepus didactylus*	73.0	
Mammalia	Mustelidae	*Eira barbara*	62.0	
Mammalia	Procyonidae	*Nasua nasua*	52.0	
Mammalia	Procyonidae	*Potus flavus*	59.5	
Mammalia	Sciuridae	*Sciurillus pusilis*	9.8	
Mammalia	Sciuridae	*Sciurus aestuans*	20.0	
Aves	Psittacidae	*Ara ararauna*	80.0	
Aves	Psittacidae	*Ara macao*	89.0	
Aves	Psittacidae	*Ara chloropterus*	90.0	
Aves	Psittacidae	*Forpus sclateri*	12.0	
Aves	Psittacidae	*Brotogeris versicolurus*	21.5	
Aves	Psittacidae	*Brotogeris chrysoptera*	17.5	X
Aves	Psittacidae	*Touit purpuratus*	17.0	X
Aves	Psittacidae	*Pionopsitta barrabandi*	24.0	
Aves	Psittacidae	*Pionopsitta caica*	23.0	
Aves	Psittacidae	*Graydidascalus brachyurus*	22.0	
Aves	Psittacidae	*Pionus menstruus*	27.0	
Aves	Psittacidae	*Pionus fuscus*	26.0	
Aves	Psittacidae	*Amazona amazonica*	34.0	
Aves	Psittacidae	*Amazona farinosa*	40.0	
Aves	Psittacidae	*Deroptyus accipitrinus*	43.0	
Aves	Cracidae	*Ortalis motmot*	49.0	
Aves	Cracidae	*Penelope marail*	64.0	
Aves	Cracidae	*Pipile cumanensis*	74.0	
Aves	Cracidae	*Crax alector*	90.0	
Aves	Odontophoridae	*Odontophorus gujanensis*	26.5	
Aves	Psophiidae	*Psophia crepitans*	48.5	
Aves	Falconidae	*Daptrius ater*	41.0	
Aves	Falconidae	*Ibycter americanus*	54.5	
Aves	Rallidae	*Aramides cajanea*	39.0	
Aves	Rallidae	*Laterallus viridis*	18.0	
Aves	Columbidae	*Patagioenas speciosa*	30.0	
Aves	Columbidae	*Patagioenas cayennensis*	26.0	
Aves	Columbidae	*Patagioenas plumbea*	34.0	
Aves	Columbidae	*Patagioenas subvinacea*	29.0	
Aves	Columbidae	*Leptotila verreauxi*	26.5	
Aves	Columbidae	*Geotrygon montana*	24.0	
Aves	Cuculidae	*Crotophaga ani*	36.0	
Aves	Cuculidae	*Piaya cayana*	47.0	
Aves	Trogonidae	*Trogon viridis*	30.0	
Aves	Trogonidae	*Trogon violaceus*	22.0	
Aves	Trogonidae	*Trogon melanurus*	31.5	X
Aves	Momotidae	*Momotus momota*	44.0	
Aves	Bucconidae	*Bucco tamatia*	17.0	
Aves	Ramphastidae	*Ramphastos tucanus*	55.0	
Aves	Ramphastidae	*Ramphastos vitellinus*	46.0	X
Aves	Ramphastidae	*Selenidera culik*	33.0	
Aves	Ramphastidae	*Pteroglossus viridis*	33.0	X
Aves	Ramphastidae	*Pteroglossus aracari*	43.0	
Aves	Ramphastidae	*Selenidera piperivora*	34.0	X
Aves	Picidae	*Veniliornis passerinus*	15.0	
Aves	Picidae	*Celeus grammicus*	20.0	
Aves	Picidae	*Celeus flavescens*	27.0	
Aves	Picidae	*Dryocopus lineatus*	33.0	
Aves	Picidae	*Campephilus rubricollis*	34.0	
Aves	Picidae	*Piculus flavigula*	19.5	X
Aves	Grallariidae	*Grallaria varia*	19.5	
Aves	Tyrannidae	*Mionectes macconnelli*	11.5	
Aves	Tyrannidae	*Tyrannulus elatus*	10.5	
Aves	Tyrannidae	*Myiopagis gaimardii*	12.5	
Aves	Tyrannidae	*Elaenia flavogaster*	15.0	
Aves	Tyrannidae	*Pitangus sulphuratus*	22.5	
Aves	Tyrannidae	*Tyrannus albogularis*	20.0	
Aves	Tyrannidae	*Tyrannus melancholicus*	21.5	
Aves	Tyrannidae	*Myiarchus ferox*	19.5	
Aves	Tyrannidae	*Attila spadiceus*	17.0	
Aves	Cotingidae	*Phoenicircus carnifex*	21.0	
Aves	Cotingidae	*Cotinga cotinga*	18.0	
Aves	Cotingidae	*Procnias albus*	28.0	
Aves	Cotingidae	*Lipaugus vociferans*	24.0	X
Aves	Cotingidae	*Xipholena punicea*	19.0	
Aves	Cotingidae	*Querula purpurata*	27.0	
Aves	Cotingidae	*Perissocephalus tricolor*	35.0	
Aves	Pipridae	*Corapipo gutturalis*	8.6	
Aves	Pipridae	*Lepidothrix serena*	8.7	
Aves	Pipridae	*Manacus manacus*	11.0	
Aves	Pipridae	*Dixiphia pipra*	10.0	
Aves	Pipridae	*Pipra aureola*	10.5	
Aves	Pipridae	*Pipra erythrocephala*	11.0	

Table S1. Continued

Class	Family	Species	Body length (cm)	Observed in the study
Aves	Tityridae	*Schiffornis turdina*	16.0	
Aves	Tityridae	*Laniocera hypopyrra*	20.7	
Aves	Tityridae	*Tityra cayana*	21.0	
Aves	Corvidae	*Cyanocorax cayanus*	33.0	
Aves	Troglodytidae	*Cyphorhinus arada*	12.6	
Aves	Turdidae	*Turdus leucomelas*	22.0	
Aves	Turdidae	*Turdus fumigatus*	24.0	X
Aves	Turdidae	*Turdus albicollis*	22.0	X
Aves	Coerebidae	*Coereba flaveola*	10.8	
Aves	Thraupidae	*Lamprospiza melanoleuca*	15.5	
Aves	Thraupidae	*Eucometis penicillata*	18.0	
Aves	Thraupidae	*Tachyphonus cristatus*	15.5	
Aves	Thraupidae	*Tachyphonus surinamus*	15.5	
Aves	Thraupidae	*Tachyphonus luctuosus*	12.5	
Aves	Thraupidae	*Tachyphonus rufus*	18.0	X
Aves	Thraupidae	*Tachyphonus phoenicius*	15.5	
Aves	Thraupidae	*Lanio fulvus*	18.0	X
Aves	Thraupidae	*Ramphocelus carbo*	18.0	X

Table S1. Continued.

Class	Family	Species	Body length (cm)	Observed in the study
Aves	Thraupidae	*Thraupis episcopus*	16.5	
Aves	Thraupidae	*Thraupis palmarum*	18.0	
Aves	Thraupidae	*Tangara chilensis*	13.5	
Aves	Thraupidae	*Tangara punctata*	12.0	
Aves	Thraupidae	*Dacnis lineata*	11.5	
Aves	Thraupidae	*Dacnis cayana*	13.0	
Aves	Thraupidae	*Cyanerpes caeruleus*	9.3	
Aves	Thraupidae	*Cyanerpes cyaneus*	11.7	
Aves	Thraupidae	*Chlorophanes spiza*	13.5	
Aves	Cardinalidae	*Saltator grossus*	19.0	X
Aves	Cardinalidae	*Saltator maximus*	19.5	
Aves	Cardinalidae	*Cyanocompsa cyanoides*	19.0	
Aves	Icteridae	*Psarocolius viridis*	43.5	
Aves	Icteridae	*Psarocolius decumanus*	39.5	
Aves	Icteridae	*Cacicus cela*	25.5	
Aves	Icteridae	*Cacicus haemorrhous*	24.5	
Aves	Icteridae	*Cacicus chrysopterus*	20.5	
Aves	Fringillidae	*Euphonia violacea*	9.5	
Aves	Thamnophilidae	*Cymbilaimus lineatus*	18.0	X

Table S2. Tree species that were visited by frugivore mammals and birds in the Amapá National Forest (Amapá, Brazil), their average fruit characteristics, and sample size (i.e. number of measured fruits). N = number of seeds.

Tree species	Botanical family	Visiting frugivore species	Fruit width (cm)	Fruit length (cm)	N seeds per fruit	Seed width (cm)	Seed length (cm)	Sample size
Guatteria sp.	Annonaceae	*Brotogeris chrysoptera* *Lipaugus vociferans*	1.20	1.85	1.0	1.00	1.70	3
Protium nitidifolium (Cuatrec.) Daly	Burseraceae	Bird not identified	2.13	2.86	1.0	1.05	1.50	3
Protium polybotrium (Turcz.) Engl.	Burseraceae	*Turdus fumigatus*	1.30	1.95	10.0	0.01	0.01	4
Buchenavia grandis Ducke	Combretaceae	*Touit purpuratus*	1.85	3.21	1.0	1.01	2.23	4
Hirtella bicornis Mart. & Zucc.	Chrysobalanaceae	*Lanio fulvus* Bird not identified	0.29	1.00	1.0	0.50	0.70	1
Goupia glabra Aubl.	Goupiaceae	*Trogon melanurus*	0.85	0.95	1.0	0.45	0.60	2
Roucheria punctata (Ducke) Ducke	Linaceae	*Brotogeris chrysoptera*	1.81	2.40	1.0	0.52	0.79	14
Miconia cuspidata Mart. ex Naudin	Melastomataceae	Bird not identified *Ramphocelus carbo* *Pteroglossus viridis*	1.20	1.10	>100	0.01	0.01	1
Miconia tomentosa (Rico.) D. Don ex DC.	Melastomataceae	*Pteroglossus viridis* *Mionectes* sp. *Selenidera piperivora* *Myiarchus* sp. *Saguinus midas*	1.15	1.65	>100	0.01	0.01	2
Virola bicuhyba (Schott ex Spreng.) Warb.	Myristicaceae	*Turdus fumigatus* *Ramphastos vitellinus*	1.40	2.40	1.0	0.80	1.20	2
Virola michelii Heckel	Myristicaceae	*Ramphastos vitellinus* *Trogon melanurus* *Turdus albicollis* *Ateles paniscus*	0.90	1.27	1.0	0.50	0.69	4

Table S2. Continued

Tree species	Botanical family	Visiting frugivore species	Fruit width (cm)	Fruit length (cm)	N seeds per fruit	Seed width (cm)	Seed length (cm)	Sample size
Virola michelii Heckel	Myristicaceae	*Ramphastos vitellinus* Bird not identified	1.23	1.70	1.0	0.76	1.27	3
Eugenia sp1	Myrtaceae	Bird not identified *Lanio fulvus* *Saltator grossus*	0.70	0.70	2.5	0.15	0.25	2
Myrcia grandis McVaugh	Myrtaceae	*Turdus* sp. *Cymbilaimus lineatus* *Tachyphonus rufus*	1.00	1.10	1.0	0.86	0.80	3
Neea altissima Poepp. & Endl.	Nyctaginaceae	*Mionectes* sp.	0.43	0.54	1.0	0.19	0.39	4
Manilkara huberi (Ducke) Standl.	Sapotaceae	*Ramphastos vitellinus*	1.79	1.73	1.0	0.65	1.20	8
Micropholis trunciflora Ducke	Sapotaceae	*Turdus fumigatus*	2.09	2.52	1.0	0.92	1.45	2
Pouteria pallens TD Penn.	Sapotaceae	*Touit purpuratus*	3.03	3.12	1.0	2.40	2.88	5
Pourouma tomentosa Mart. ex Miq.	Urticaceae	Piculus flavicula	1.06	1.57	1.0	0.85	1.15	3
Pourouma tomentosa Mart. ex Miq.	Urticaceae	*Trogon melanurus*	1.23	1.70	1.0	0.82	1.10	2

Table S3. Dependent and independent variables included, the correspondent error distribution, and sampling units of the full models to perform the multi-model inference analyses to investigate niche segregation mechanisms among diurnal canopy frugivores and zoochoric trees in the Amapá National Forest (Amapá, Brazil).

Dependent variable	Independent variables	Sampling unit	Error distribution
Frugivore size	Fruit weight + Fruit size + Fruit's smallest dimension + Seed size + Seed smallest dimension + Tree DBH	Each individual/group of frugivore that visited the trees	Gaussian
Seed swallowed or not	Fruit weight + Fruit size + Fruit smallest dimension + Seed size + Seed smallest dimension + Frugivore size	Each individual/group of frugivore that visited the trees	Binomial
Frugivore richness	Fruit weight + Fruit size + Fruit smallest dimension + Seed size + Seed smallest dimension + Tree DBH + Prevalence of ripe fruit in the month	Each visited tree	Poisson
Frugivore abundance	Fruit weight + Fruit size + Fruit smallest dimension + Seed size + Seed smallest dimension + Tree DBH + Prevalence of ripe fruit in the month	Each visited tree	Poisson

Table S4. List of the 72 focal trees monitored in the Amapá National Forest (Amapá, Brazil), with the number of frugivore individuals and species recorded feeding on their fruits. N = number of individuals/species.

Focal tree species	N frugivore individuals	N frugivore species	Month of monitoring
Buchenavia congesta	-	-	June
Buchenavia grandis	2	1	May
Buchenavia grandis	-	-	May
Duroia macrophylla	-	-	February
Duroia macrophylla	-	-	February
Duroia macrophylla	-	-	February
Eugenia cupulata	-	-	September
Eugenia cupulata	-	-	September
Eugenia sp.	4	3	September
Goupia glabra	1	1	March
Goupia glabra	-	-	July
Goupia glabra	-	-	June
Guatteria citriodora	-	-	August
Guatteria hypoglauca	-	-	April
Guatteria olivacea	-	-	March
Guatteria sp.	2	2	April
Hirtella bicornis	3	2	August
Hirtella bicornis	-	-	August
Hirtella rodriguesii	-	-	August
Licania bracteata	-	-	April
Licania bracteata	-	-	April

Table S4. Continued.

Focal tree species	N frugivore individuals	N frugivore species	Month of monitoring
Licania octandra	-	-	May
Manilkara bidentata	-	-	May
Manilkara huberi	-	-	January
Manilkara huberi	3	1	February
Manilkara huberi	-	-	March
Manilkara huberi	-	-	March
Manilkara huberi	-	-	June
Miconia cuspidata	5	3	July
Miconia pyrifolia	-	-	July
Miconia tomentosa	13	5	July
Micropholis guyanensis	-	-	June
Micropholis guyanensis	-	-	July
Micropholis guyanensis	-	-	August
Micropholis trunciflora	1	1	August
Myrcia floribunda	-	-	February
Myrcia grandis	3	3	August
Myrcia grandis	-	-	September
Neea altissima	1	1	February
Neea floribunda	-	-	January
Neea madeirana	-	-	February
Ocotea negrensis	-	-	February
Ocotea percurrens	-	-	June
Ocotea percurrens	-	-	September
Ocotea puberula	-	-	August
Pourouma tomentosa	1	1	September
Pourouma tomentosa	3	1	September

Table S4. Continued.

Focal tree species	N frugivore individuals	N frugivore species	Month of monitoring
Pourouma tomentosa	-	-	September
Pouteria engleri	-	-	August
Pouteria pallens	2	1	June
Pouteria peruviensis	-	-	January
Pouteria peruviensis	-	-	June
Protium nitidifolium	2	1	July
Protium polybotrium	2	1	June
Protium trifoliatum	-	-	June
Roucheria punctata	-	-	March
Roucheria punctata	2	1	April
Roucheria punctata	-	-	April
Sextonia rubra	-	-	July
Sextonia rubra	-	-	July
Sextonia rubra	-	-	July
Siparuna decipiens	-	-	March
Siparuna decipiens	-	-	May
Siparuna monogyna	-	-	September
Siparuna sp.	-	-	March
Theobrama subincanum	-	-	March
Theobrama subincanum	-	-	April
Theobrama subincanum	-	-	April
Theobrama subincanum	-	-	June
Virola bicuhyba	3	2	September
Virola michelli	17	4	January
Virola michelli	3	2	August

Table S5. Model-averaging results based on Akaike weights of the models with ΔAICc (difference between the AICc of a given model and the AICc of the most parsimonious model) ≤ 2.0. None of the dependent variables was considered important for predicting frugivore richness on fruit-bearing trees in the Amapá National Forest (Amapá, Brazil), since they presented importance values < 0.4. Coefficients, standard errors, and ***P***-values were conditionally averaged. DBH = tree diameter at breast height.

Independent variables	Coefficient ± SE	p	Variable Importance
Seed's longest dimension	0.334 ± 0.190	0.100	0.25
Fruit size	-0.327 ± 0.208	0.142	0.20
Fruit's longest dimension	0.262 ± 0.178	0.171	0.15
Seed size	-0.311 ± 0.261	0.265	0.12
DBH	-0.235 ± 0.177	0.217	0.12

Table S6. Models used in model averaging, their AICc and Akaike weights (see model averaging results in Table 2).

Dependent variable	Independent variables	AICc	Akaike weight
Frugivore size	Fruit weight + Seed size	102.71	0.62
	Fruit weight + Seed size + Tree DBH	103.68	0.38
Seed swallowed or not	Frugivore size + Fruit weight + Fruit smallest dimension	41.34	0.26
	Frugivore size + Fruit weight + Fruit smallest dimension + Seed size	41.86	0.20
	Frugivore size + Fruit weight + Fruit smallest dimension + Seed smallest dimension	41.91	0.20
	Frugivore size + Fruit weight + Fruit size	42.78	0.13
	Frugivore size + Fruit weight + Fruit size + Seed smallest dimension	43.08	0.11
	Frugivore size + Seed smallest dimension + Fruit smallest dimension	43.20	0.10
Frugivore abundance	Seed smallest dimension	115.28	0.43
	Seed smallest dimension + Prevalence of ripe fruit in the month	116.44	0.24
	Seed smallest dimension + Fruit size	117.14	0.17
	Seed smallest dimension + Tree DBH	117.27	0.16