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Diversidad de Semillas Dispersadas por Aves del Interior del Bosque Tropical Amazónico de Yasuní

Disertación previa a la obtención del título de Licenciada en Ciencias Biológicas

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Certifico que la Disertación de Licenciatura en Ciencias Biológicas del Sr. Juan Francisco Herrera Cueva ha sido concluida de conformidad con las normas establecidas; por lo tanto, puede ser presentada para la calificación correspondiente.

Dr. Renato Valencia

Director de la Disertación

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A mi familia: Rebeca, César, Camilo, Carla y Edu

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1 RESUMEN

La ornitozoocoria juega un papel fundamental en la estructura y funcionamiento de los bosques tropicales megadiversos. Este es el caso de los bosques amazónicos del Parque Nacional Yasuní, donde conviven en promedio 670 especies de árboles y arbustos por hectárea y se han registrado más de 200 especies de aves frugívoras dentro del parque, dónde la dispersión de semillas es crucial. El presente estudio analizó la diversidad de semillas dispersadas por aves frugívoras que habitan el interior del bosque de *terra firme* entre hábitats (valles y colinas) y entre estaciones (de mayor y menor precipitación). Se encontró que cada ave puede dispersar en promedio 1,41 ± SD 0,85 especies de semillas por deposición. Los patrones de dispersión en valle o colina variaron con la estacionalidad. En la colina, durante la estación menos lluviosa, se encontró 115 % más especies de aves frugívoras que en el valle, mientras la estación lluviosa fue 30 % menos diversa en aves frugívoras. Igualmente, las semillas dispersadas diversificaron en la estación menos lluviosa fueron 2,2 veces más diversas que durante la estación de lluvias, donde se dio la dominancia de la planta *Clidemia dimorfica*. Las aves de la familia Pipridae dispersaron el 81 % de las especies de semillas registradas, siendo dominante *Lepidothrix coronata*. También, las bayas de Melastomataceae y Araceae fueron la dieta más frecuente (74 %). La repartición de nichos dietarios entre aves frugívoras evidencia una red compleja de interacciones que facilita la coexistencia de cientos de aves y especies de plantas en áreas relativamente pequeñas.

PALABRAS CLAVE: Dinámica de bosque, Dispersión de semillas, Diversidad Beta, Endozoocoria, Estacionalidad, Frugívoro, Ornitocoria,

2 ABSTRACT

Ornithochory plays a key role in the structure and functionality of megadiverse tropical forests. In the Ecuadorian Amazonian tropical forest, in Yasuní National Park, where 670 tree and bush species coexist per hectare alongside more than 200 species of frugivorous birds, seed dispersion by birds is crucial to the ecosystem. This study analyzed the diversity of seeds dispersed by frugivorous birds from the understory of *terra firme* forest between habitats (bottomlands and ridges) and seasons (rainy and less rainy). We found that birds dispersed on average 1.41± SD 0.85 seed species per fecal sample. The dispersion patterns changed between bottomlands and ridges with seasonality. In the ridges during the less rainy season, we found 115 % more frugivorous bird species than the bottomlands, while the rainy season had 30 % less frugivore diversity. Similarly, seed species dispersed by birds diversified during the less rainy season, being 2.2 times more diverse than the rainy season, where *Clidemia dimorfica* seeds dominated. The Pipridae family were key seed dispersers with eight species which dispersed 81 % of seed species, *Lepidothrix coronata* dominated both habitats and seasons. Also, berries from Melastomataceae (with 3 genera) and Araceae (with 2 genera) were the most common source of food (74 % of the diet). The frugivorous bird dietary niche was distributed on a complex interaction web which facilitates the coexistence of hundreds of plants and birds in a relatively small area.

KEYWORDS: Beta Diversity, Endozoochory, Forest dynamic, Frugivory, Ornithocohory, Seed dispersion, Seasonality.

3 MANUSCRITO PARA PUBLICACIÓN

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TÍTULO

Diversity of Seeds Dispersed by Birds of the Interior of the Amazon Rain Forest of Yasuní.

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1. INTRODUCTION

Megadiverse tropical forests are shaped by tangled interaction webs that constantly change with natural selection pressures, where seed dispersion through vertebrates' guts, known as endozoochory, dominates (Karubian, et al., 2012). Endozoochory, as other symbiotic relationships, is defined by genetic and habitat diversity, also demography patterns of plants and their dispersers (Gotelli, 2008). In general, seeds dispersed away from their mother tree have better chances to germinate and survive, because of a negative density dependence (Wright, 2002), where distance from conspecifics aids in avoiding diseases, allelopathy, and intraspecific competition, this idea was first postulated by Janzen (1970) and Connell (1971). Besides this, endozoochory frequently in the tropics reaches longer distances than pollination helping to reduce inbreeding within populations (Westcott & Graham, 2000).

In the tropics, endozoochory relates to fleshy fruit availability from woody plants and epiphytes, mainly dispersed by birds (Datta & Rawat 2008). Hence, evolution process complexes in The Amazon Rainforest are most diverse in communities where birds and plants interact with each other (Karubian, et al., 2012). In Yasuní National Park (YNP) researchers have registered the greatest diversity of tree and bush species per unit area of the world: where on average, in just one hectare of *terra firme* 644 species can be found (Valencia et al., 2004 b.). As for frugivorous birds, in YNP 222 species (36.4 % of the Ecuadorian Amazon richness) have been registered, with 26 families that consume fruits, and Thraupidae as the most diverse - with 45 different species (Freile, et al. 2018; Schulenberg, et al. 2020). Frugivorous bird diversity is constantly coevolving with plant dispersion strategies, such as phenology, plant habit, and fruit type (Karubian, et al., 2012). Consequently, selection is bidirectional, being influenced by both dispersers and by the plants they disperse (Almeida-Neto, et al. 2008). Fruits, as an abundant and accessible food source, have shaped a tangled interaction web of endozoochory (Martinez, 2020).

External factors have also shaped the niche partitioning of birds and plants through different habitat structure and seasonality, which affects plant phenology (Hamjah, 2014). Habitat division and seasonality effects over seed dispersion are poorly understood in most ecosystems (Moermond & Denslow, 1985), which is also the case of Amazon rainforest, where these effects have complex patterns and the largest amount of seed dispersion interactions (Morton, 1973; Valencia et al., 2004 b; Freile, et al. 2018).

YNP is dominated by *terra firme,* well-drained forest, that has two very distinguishable topographic habitats: ridges and wet bottomlands (Almeida-Neto et al., 2008). Previous studies have shown that there is a significant difference in flora composition, structure, and functionality between these habitats (John, et al,2007; Duque et al. 2017). Both habitats only share, at similar densities, 25.0% of plant species, where 50.0% are shared species but much more common in one habitat, and 25.0% are specialist species for one habitat (Valencia et al. 2004 a). Regarding functionality, plant species have developed different strategies by habitat, for example, the average leaf area differs significantly between the two distinct habitats (Kraft et al. 2008). As for structure, these habitats differ as well, where ridges accumulate 50.0 % more biomass than bottomlands (Valencia et al. 2009). This suggests that habitat partitioning enhances high plant richness with low dominance (Wright, 2002). Interestingly, habitat partitioning can be concomitant for frugivorous birds, as found by Blake (2007), inside this forest.

Fruits and insects are main food sources for birds (Poulin, Lefebvre & McNeil,1994), meaning that fructification seasons strongly shape the behaviors of birds (Ridgely & Greenfield, 2001). Furthermore, fructification can be related with precipitation regimes (Hamann, 2004) therefore also influencing bird behavior. For example, a study inside Mata Atlántica forest, in Brazil, found that more habitat humidity means more endozoochory (Almeida-Neto et al., 2008). Other factors that influence fruit production and endozoochory are soil conditions, such as water, nutrients, organic matter and microorganism availability; geology and topography; also, anthropogenic influences, including deforestation, enrichment and degradation of soil, and species introduction (Dent & Estrada-Villegas, 2021).

This study aimed to ask three questions (a) How does the species richness and community composition vary between (i)ridge and valley habitat, and (ii) rainy and less rainy season? Regarding on understory bird species, understory frugivorous bird species and seeds dispersed by understory bird species. (b) How does the interactions between understory frugivorous birds and seeds dispersed vary between habitats and over seasons? (c) How does the species richness and community composition of seeds dispersed by understory frugivorous bird species vary by plant habit?

We predict that (a)Species richness and community compositions will be different between habitats and over seasons, with large beta diversities, as found in plant composition (b) Interactions between understory frugivorous birds and seeds dispersed will be molded by habitat and weather conditions, with more humidity in habitat and season there will be more abundance of seeds dispersed. (c) Generalist birds and seeds will be predominant and present indifferently through seasons and habitats, specialists will be scarce and specifics to habitat and seasons.

2. METHODS

2.1 Study site

The study site was located 1 km from Yasuní Scientific Station (YSS), in the northwest area of Yasuni National Park. Much of the Park is covered in mature lowland *terra firme* rain forest, with a canopy mostly 15-30 m tall and some emergent trees, understory is opened, but thick when light gaps appear. Most of soils are clayey and acidic, with low variation along YNP (Valencia, et al. 2004 a).

Within YNP*,* a 50-ha forest dynamics plot (0°41’0.5” S 76°23’58.9” W, southwest corner) was established in 1994 to study long term population demography (Valencia, et al. 2004 b.). The plot is composed of two main topographic habitat types (Valencia, et al. 2004 b): bottomlands (wet flats, crossed by creeks); and ridges (with steep slopes and high crests). Elevation in the plot varies between 215 and 247 MAMSL. Mean annual precipitation at the site is 3047 mm (Naranjo, 2014); More rain falls from May to October than December to April, but there is no month regularly with less precipitation than 100 mm (Naranjo, 2014). Mean monthly temperature is 24.6 °C and mean monthly relative humidity is 86.8 %.

2.2 Sampling protocol

We sampled in both the less rainy season (February 2021, precipitation = 97.7 mm) and the rainy season (July 2021, precipitation = 264.6 mm) (unpublished data from YSS) in the periphery of the 50-ha plot. In each season, the bird community was sampled using mist nets located in the forest understory. The nets were aligned in five lineal transects, with a combined length of 120 m: ten mist nets of 12 × 2.5 m, for a total trapping area of 300 m^2. We established two transects in ridge habitat, two in bottomland habitat, and one transect that consist of half ridge and half bottomland, following Valencia et al. (2004b). We geo-localized mist nets by mapping the 50-ha plot, which were open individually for 12 hours. In total, 1200 net-hours were sampled, with 600 net-hours in each habitat (Ralph, 1997).

Bird capture care and management followed Ralph (1997). Each frugivorous or omnivorous bird captured was photographed and kept in a cloth bag, with a paper bag inside to collect feces, for a maximum of sixty minutes. If any bird showed signs of stress, we released it (Ralph, 1997). No bird died during the study. More than 50 % of target birds defecated in the net. Defecation samples were taken from paper bags or from leaf litter with entomology forceps or a razor. Samples were placed in Eppendorf tubes and labeled with the field number related to the captured bird. We registered date, hour, mist net, sex, age, and transect of each capture (Ralph, 1997). Fecal samples were frozen at -17°C.

In the laboratory, we separated feces into four categories: entomological remains, fruit pulp, vegetal remains (category joined to fruit pulp in posterior analyses) and seeds (Burns and Naoki, 2004). After this process, the remains were re-frozen to keep fresh for identification and safe from fungi and bacteria.

To identify seeds in the fecal samples, we used the local seed collections and the assistance of the parataxonomist associated with a long-term seed rain monitoring project at YSS. This project monitors dispersed seeds captured in 200 seed traps distributed throughout the 50-ha plot every 15 days, since the year 2000 (Metz et al. 2010; Valencia, pers. com.). This project has data for 1600 species (or morphospecies) of tree and liana seeds. As result of this support, Unidentified seeds that were morphologically similar were grouped in morphotypes, with nomenclature of the lowest taxonomical level (family or genus level), followed by “sp” and serial number started in 1 for each taxonomic group considered as different species (Martin y Barkley. 1961). Each seed species or morphospecies was photographed as a record of seeds dispersed by birds (Martin y Barkley, 1961).

Finally, we dehydrated fecal remains for 48 hours in a food dehydrator at 40°C. Then, we weighed each sample independently in an analytic balance with 0.0001 g precision.

2.3 Data analysis

We classified captured bird species into five dietary niche categories, based on their diet: insectivorous, frugivorous, nectarivorous, ictivorous or omnivorous, based on Freile, et al. (2018) and Ridgely & Greenfield (2001). We determined the frequencies of dietary niches in both seasons and habitats. Similarly, collected seeds were assigned a fruit type and plant habit, based on Tropicos data base (2022). The fecal remains analyses focused on bird diversity and seed diversity relationships across seasons and habitats.

We quantified the weight of seed and other fecal remains by bird sample to establish dietary preferences. We compared differences in the number, individual weight and total weight of seeds in the fecal samples (including fecal samples from frugivorous birds lacking seeds) using ANOVA.

We calculated the alpha and beta diversity of dispersed seeds, frugivorous birds, and non-frugivorous birds captured. Using INEXT online, (Chao & Hsieh, 2016, accessed 2022-01-15), we calculated rarefied estimates of alpha and beta diversity (95 % confidence interval and 100 bootstraps replications) and estimated Simpson’s and Shannon’s index and their effective numbers. If necessary, we interpolated the values between habitats and between seasons to match sample coverage (Chao &

Jost, 2012). To examine alpha diversity, we built the sample-size-based rarefaction and extrapolation sampling curve and the sample completeness curve for frugivorous birds and seeds (Chao & Hsieh, 2016). For beta diversity, we employed the Sørensen community coefficient, to establish species shared between habitats and seasons (Lilleskov, et al. 2004).

We identified dietary preferences and niches of the captured bird species (frugivorous vs. omnivorous and generalist vs. specialist). Using the Sørensen community coefficient we built a dietary overlap matrix for frugivorous birds. Using the R software bipartite package (Dormann, Gruber & Fründ, 2008), we built ecological dispersion webs between bird species and genus-level seed taxa. From these webs, we established nestedness (when a specialist consumes a subset of the generalist diet) and web symmetry (when specialists were dispersed just by specialists).

3. RESULTS

3.1 Bird diversity

Over the two seasons and two habitats of the study we captured a total of 329 individual birds from 62 species, 56 genera and 16 families. The most common specie was *Lepidothrix coronata,* with 43 captures. The most common family was Thamnophilidae with 99 captures. Many species were rare: 22 species were captured as singletons.

Species richness was uniform between seasons, with 48 species captured in both. Species richness was also similar between habitats, with 46 species captured in bottomland habitat and 47 captured in ridge habitat. Across both seasons 71% of species were shared, and across habitats 67% of species were shared (Table 1). The majority of captured birds were insectivorous (52 %), followed by frugivorous species (32 %; Figure S1). In the bottomland habitat, 16 % more individuals were capture than in ridge habitat, largely driven by omnivorous and ictivorous birds (Figure S1).

Based on rarefaction, we estimated that our sampling effort was suitable, capturing 88 % of bird diversity by habitat and season. We found more homogeneous abundances in ridge habitat (Shannon exponential = 31.8) than bottomland habitat (28.6) whereas there was more homogeneity in the rainy season (Shannon exponential = 33.4) than less rainy season (30.2) (Table 1). Our sampling effort of frugivorous birds, by season and habitat, was also equally suitable, as the sample completeness curve approached the asymptote (Figure 1, b and d).

Nevertheless, a number of species were missed in both habitats and less rainy season samples. On the contrary, rainy season samples did not predict the same lack in sampling.

3.2 Diversity of frugivorous birds

Of the 62 bird species captured, 19 species in eight families were frugivorous or omnivorous and dispersed seeds. The family Pipridae (manakins) was the richest with eight species and included the dominant bird captured in both habitats and seasons, *Lepidothrix coronata* (41 % of all frugivorous birds captured). In contrast, 31 % of frugivorous bird species were singletons for the study (Figure 3). Exactly, 25.0 % of birds captured were juveniles or immatures (56 % of them consumed also arthropods), 44 % were male and 31% were female.

The 59 % of frugivorous bird species have shared habitats; In Contrast, birds such as *Mionectes oleagineus* (Tyrannidae), *Cyanoloxia rothschildii* (Cardinalidae) y *Euphonia xanthogaster* (Fringilidae) preferred bottomlands (where 87.5 %, 66.0 % y 75.0 % of species captures, respectively, occurred). *Machaeropterus striolatus* and *Cryptopipo holochlora* (Pipridae) were only captured in ridges, while *Ceratopipra erythrocephala* (Pipridae) was captured two times more frequently in ridges (Figure 3).

A whole 69 % of frugivorous bird species were found in both seasons; the only bird captured in one specific space and time was *Tyranneutes stolzmanni* (Pipridae) captured only in bottomlands during the rainy season. *Dixiphia pipra* (Pipridae) was two times more abundant in the rainy season, while *Chiroxiphia pareola* (Pipridae; Figure 3) was six times more abundant in the less rainy season. Therefore, the rainy season was 30% less diverse than the less rainy season (e-Simpson: 4.30 vs. 5.60).

In rarefaction analysis, bottomlands during the rainy season had 66.0 % more evenness and diversity compared to ridges of the same season. However, ridges, during the less rainy season had 115.0 % more evenness and diversity than bottomlands of the same season.

3.2 Seed transport capacity

Birds on average transported 1.41 ± SD 0.85 seed species per fecal sample. Also, per fecal sample one bird had transported 17.7 ±SD 24.2 seeds. There were wide variations seasonally and spatially, however, they were not significant (Table 2).

Seed fecal sample dry weight significantly varied per habitat (Table 2 and Figure 4). Meaning that seed dry mass was heavier in bottomlands compared to ridges, this pattern remained seasonally. Seeds transported from the whole sample set had a dry mass of 2.92 g; Only one sample of *Psychotria* (Rubiaceae) was not a fecal sample, as it was regurgitated by *Ceratopipra erythrocephala* (Pipridae).

3.3 Seed diversity

We identified 1570 individual seeds belonging to 89 plant (morpho)species, in 18 genera, and 14 families. We identified 12 % of seeds to species level, 86 % to genus and only 2 % to family level. Besides that, berries fruit type (74 %) and bushes habit (61 %) dominated the plants dispersed (Table 3). Melastomataceae was the most common family consumed by understory birds with 36 species or morphospecies from three genera. During the study 83 % of seed species were singletons. However, in the rainy season *Clidemia dimorphica* seeds dominated the sample (Figure 3), captured 14 times in seven bird species. Only 11 % of seed species shared seasons, and just 16 % shared habitats (Table 1).

Based on rarefaction, we concluded that sample effort was not suitable, as we collected by habitat just 35 % of seed diversity and by season just 38 %. This means 3.5 times more species are expected by habitat and season, approximately, but with a sample effort of more than 500 collected samples (Figure 2). Globally, analyzing seed diversity by extrapolation we estimated 300 seed species effectively dispersed by understory birds that can be captured by mist nets, but with a sample effort of 900 samples (Figure 2). Bottomlands had 16.0 % more homogeneous abundance than ridges (e-Shannon: 37.7 vs. 32.2), while seasonally, the less rainy season was 2.2 times more diverse than the rainy season (e-Simpson: 31.5 vs. 14.1; Table 1), this seasonal diversity even increased in ridges.

Anthurium seeds (Araceae) were only found, with three species, in ridges during the less rainy season. But as the rains arrived, two seed species of this genus were only found in bottomlands, with *A. signatum* as 86.0 % of the genus captures. Similarly, 70.8 % of *Philodendron* seeds (Araceae) were found in bottomlands, but invaded ridges with the rains (Figure 5).

Important seasonal segregation happened between seed genera. The less rainy season had 15 genera, though nine genera were found during the rainy season, with variations in dominance patterns. It should be noted that *Psychotria* (Rubiaceae) and *Tetracera* genus (Dilleniaceae) were specialists to the bottomlands and the rainy season; finally, *Rollinia* (Annonaceae) was found in the bottomlands during the less rainy season (Figure 3).

3.4 Bird-seed relation

Pipridae species showed generalist diet preferences, transporting 84.2 % of seed species. However, *C. pareola* and *D. pipra* showed specialization on berries from

Melastomataceae (66.6 % and 58.3 % of their respective seed ingestion). Similarly, *L. coronata* preferred *Philodendron* (30.0 % of seeds consumed). On the other hand, *Tyranneutes stoltmanni* was a generalist, feeding on six plant genera with no strong preferences (Figure 6).

Non-Pipridae birds were also seed specialists. *Geotrygon montana* (Columbidae) and *C. rothschildii* (Cardinalidae) feed on Melastomataceae berries. Meanwhile, *M. oleagineus* (Tyrannidae) feed on six plant genera, with no particular preferences for them (Figure 6).

E. xanthogaster (Fringilidae) specialized its diet on Araceae fruits (75.0 % of seeds consumed), following *Anthurium* fructification, demonstrated by the fact that 80.0% of this bird's captures happened in ridges during the less rainy season, but it completely moved to the bottomlands during the rains. For their part, *L. coronata,* during the less rainy season, was captured almost twice as many times in the bottomlands than the ridges, where *Philodendron* predominantly fruited.

L. coronata and *D. pipra* caused asymmetry on interaction webs. Both of them shared fruit diets with 66.6 % of frugivorous birds. *D. pipra* transported 22.4 % of the total seed species collected. While, *L. coronata* transported 42.6 %. As well, *Ceratopipra erythrocephala* transported 10.1 % of seed species collected and overlapped diets with 26.6 % of frugivorous bird species. Despite this asymmetry, nestedness of this web was not comprehensive, because several fruit food sources were exclusive to specialist birds (Figure 6).

4. DISCUSSION

4.1 Bird diversity

Compared to the YNP comprehensive bird species list, we captured 10.5 % of the possible bird diversity (Freile, et al. 2018). This diversity between habitats shared a similar percentage of beta diversity estimated for the region based on previous studies of The Ecuadorian Amazon [β_{sim}= 0.150-0.422; Melo et al. (2009)]. Also, frugivorous birds shared habitat as expected by this beta diversity estimation. However, it is important to note that Melo et al (2009) covered general bird diversity in the area and not only *terra firme* understory diversity. Even though habitats were contiguous and interspersed (Valencia et al. 2004), shared bird species were higher than expected in similar YNP forest study. Though such study area was separated by 1.5 km, 87 % of bird species shared habitats. This is likely due to the fact that the study effort was greater and used bird observation and not mist nets, explaining higher percentage of shared species (Blake, 2007). Blake (2007) also found *L. coronata,* dominance in habitats and seasons, as found in our study.

4.2 Seed diversity

According to Valencia et al. (2004 b), in the same forest and study area, trees and shrubberies had different composition between bottomlands and ridges, sharing only 27 % of species. As a result, habitat vegetation inside the 50-ha plot had a Sørensen dissimilarity index of 73 %. In our study, seeds dispersed by birds registered a Sørensen dissimilarity index of 83.7 %, showing higher habitat specialization of plants dispersed by birds, as found by Legendre (2014), or the need for more sampling effort.

From all the seeds dispersed by birds in this study, 83.1 % were singletons. In another study inside YNP, done with understory piprids, almost 50.0 % of plant species dispersed were singletons, as their sample size was larger (Loiselle et al., 2007). However, this suggests that the seed diversity consumed by birds in the understory comes from a vast group of vascular plants. With greater sampling effort one could hope to capture around 20 % of seed species offered in the 50-ha plot (1600 species or morphospecies; Metz et al. 2010).

Shrub species that produce berries are the main food source for understory birds. So, unsurprisingly, dominant seeds were from the berry of the bush *C. dimorfica* and other berry producer species of the epiphyte genus *Philodendron.* Therefore, the seed diversity found was as expected, in accordance to Loiselle et al. (2007) who found *Philodendron, Clidemia, Cecropia, Anthurium* and other genera dominant in piprid diet. Definitively, all the dispersed fruits were fleshy, reducing the fruit food source to only two thirds of plant diversity, those which produce fleshy fruits in tropical forests (Wheelwright, 1988).

4.3 Seed transport capacity

In the present study, we registered eight piprid species which dispersed 81.3 % of seed species. According to Karubian et al. (2012), in the Western Amazon more than five piprid species can be found, differing with Costa Rica where on average only two species can be found. Therefore, the Pipridae family is a key seed disperser in the Ecuadorian Amazon, as also found by Loiselle et al. (2007).

The least overlapped niche belongs to the bird *M. oleaginous.* that carried six seed genera, half of which were only found in this species samples, and all the species carried by *M. oleaginous* were unique in the sample. Westcott y Graham (2000), found that *M. oleagineus* consume the *Miconia* and *Psychotria* genus, but these genera were not eaten by this bird in our study. In conclusion, the evidence shows both a very diverse and very specialized bird diet.

Some birds have a highly specialized diet, such as *E. xanthogaster* that transported 75 % of Araceae, and though it has a known relation with Melastomataceae berries (Kessler-Rios y Kattan, 2012), no such plant was transported by this bird during the study. This resulted in this bird sharing as maximum of 14 % of its diet with *Dixiphia pipra.* Such specialist birds play a key role of mutual dependence with the seeds that they disperse (Hilty, 2020).

Dixiphia pipra, Lepidothrix coronata and *Ceratopipra erythrocephala* can be considered key dispersers in the study area, as concluded by Loiselle et al. (2007) inside a *terra firme* forest of YNP. These birds shared the majority of their seed species diet percentage with other understory birds, which aids in strengthening ecosystem resilience, where healthy populations of these birds mean better effectiveness in seed dispersion for important seed species, in both habitats and seasons. Despite this, according to Blake (2007), *D. pipra* and *C. erythrocephala* preferred ridge habitats, we only observed this pattern with *C. erythorcephala.*

4.4 Climatic and geographic effects over seed dispersion

Level of rainfall was related with plant fructification and frugivorous bird diversity. YSS had 2.7 times more precipitation during the rainy season (July, 2021: 264.6 mm) than the less rainy season (February, 2021: 97.7 mm). However, there are no clear seasonal phenological patterns in the study ecosystem (Bradley et al., 2011). Furthermore, understanding fructification patterns per habitat and season is a multifaceted and intricate process, that requires genus and species level studies, and has several knowledge gaps: soil nutrients and water availability patterns, weather factors, inter and intraspecific competition, biomass productivity, etc. (Laurance et al. 1999; Grubb & Coomes. 1997; Willson et al.1989).

Based on literature two main factors proved to be predominant in defining fructification in the study area. Firstly, sun radiation and its annual cycle defined phenology in *terra firme* forests¸ including Yasuní (Bradley et al.,2011). In such ecosystems, more radiation improves photosynthesis, as well photosynthetic tissue development, however it does not stimulate floriation and fructification (Bradley et al.,2011; Jones, Kimball & Nemani, 2014). Secondly, soil and weather conditions that cause humidity can improve fruit production. Almeida-Neto et al. (2008) suggested that humidity significantly increased endozoochory between localities. They supported the idea with the hypothesis of metabolic cost proposed by Willson et al (1989) who argued that soil humidity and fertility enhance fleshy fruit production, which is metabolically expensive. However, Araujo (1970) found in an area of the Brazilian Amazon a small peak of fructification during the less rainy season, similarly to ours.

Frugivorous bird diversity through the less rainy season increased mainly in the ridge habitat. Birds clearly move into these areas at this time because of food resource availability, in the form of ripe fruits that were more diverse in the same season and habitat (Ridgely & Greenfield, 2001). Ridges have more biomass and tree density, meaning more shade (Valencia et al. 2009), which leads to the fact that the increase of solar radiation in the less rainy season could be insignificant in the ridges in terms of humidity, meaning fructification can actually improve during this time (Bradley et al.,2011; Almeida-Neto et al. 2008).

Frugivorous birds were less diverse, but more concentrated, in the rainy season in the bottomlands. Likewise, dispersed plant species were two times less diverse when the rains arrived, principally caused by the dominance of *C. dimorfica*. Such condition could be caused by the huge increase of water availability, further intensified in the bottomlands (Valencia et al. 2004 a; Naranjo, 2014). Garcia, Barros & Lemos-Filho, (2009) recognized more fructification at the start of the rainy season in a study region in the Brazilian Amazon Forest, contrary to the fructification peak during the less rainy season proposed by Araujo (1970). However, Morellato, Camargo & Gressler (2013) conclude that rainfall enhances fast fruit production mainly by herbs and bushes, that became more abundant during the rains. So, less seed diversity and frugivorous bird conglomeration in Yasuní bottomlands during the rainy season could be caused by predominance of fast-growing fleshy fruits, whose massive abundance masked true seed diversity in the dispersion sample. This dominance also reduced bird diversity by only attracting birds interested in this abundant but less diverse set of fruits, such as *T. stolzmanni* who clearly preferred this habitat and season.

Most of fruit production dispersed by birds, spatially and seasonally, had a partial synchrony in their phenology. These results did not agree with the highlighted asynchrony proposed by Jones, Kimball & Nemani (2014) though this could be partially due to the fact that they added canopy plants in their study. Furthermore, according to Poulin, Wright, Lefebvre & Calderon (1999), occasional inter and intraspecific synchronies of fructifications can lead to the conglomeration of disperser vectors and enhance dispersion.

4.5 Seed mass habitat variation

Seed mass was three times greater in bottomlands than ridges (Table 2). As phenology process, seed size, and mass variation is a multifaceted and intricated analysis, with several knowledge gaps in Amazon region (Parolin & Junk, 2000; Foster & Janson, 1985; Grubb & Coomes, 1997) the exact drivers behind this difference are difficult to determine, however soil nutrients are a good candidate for the cause. For example, tropical African seeds proved to be bigger because of poor soil nutrients, since, in order to compensate for this, the mother plant provides more nutrients, increasing seed biomass (Hladik & Miquel, 1990). This same pattern is also found in New Zeeland grass species (Lee & Fenner. 1989). Alternatively, Grubb & Coomes (1997), in the same region of our study, had found a complete lack of big seeds in Brazilian Caatinga habitats with poor soil nutrients when comparing to better nurtured ecosystems. Analysis of soil in Amazon ridge habitat near YNP showed significantly poorer soil nutrients than the nutrients rich bottomlands (Laurance et al. 1999). In conclusion, our findings support a similar pattern to the Brazilian Cattinga, where large seeds are absent in more nutrient-poor habitats.

On the other hand, Foster & Janson (1985) identified solar radiation as key factor in Amazonian seed mass variation, where bigger seeds germinate with low solar radiation below canopy. Also, Valencia et al. (2009) defined the ridge habitats with more tree density, meaning with more shade. In contrast, the bottomland habitats allow more solar radiation in the understory. Possibly, bottomland seeds take advantage of the solar radiation that reaches the ground to germinate below canopy with moderate shade condition, something that is impossible in the dark ridges.

4.6 Seasonal dispersion movements

The Araceae family had conspicuous movements in their dispersion through habitat types. Herbs, principally epiphytes, produced fleshy fruits all year round, but usually increase their production in rainy seasons (Acosta-Mercado. 1996; Willson et a. 1989). *A. signatum* fulfilled this pattern, which produced fruits in both seasons, but exploded production with the rains. On the contrary, habitat seasonal movement fructification has not been reported previously in scientific literature and its causes could be related to phenological, climatic and nutritional factors, among others (Bradley et al., 2011; Jones, Kimball & Nemani. 2014; Garcia, Barros & Lemos-Filho, 2009).

Spatial asynchrony of peak fructifications between genera was conspicuous, for example the habitat where *Anthurium* fructified*, Philodendron* avoided fruit production, and vice versa. Furthermore, spatial and temporal segregation among competitor seeds of vector dispersals had been registered previously by Warren, Giladi, & Bradford (2014). Hypothetically, both genus of Araceae avoid dispersal vector competition, splitting fructification spatially. Along with this, *Anthurium* fruit production was followed by *E. xanthogaster* and separately *L. coronata* followed *Philodendron* through habitats, but both dispersers occasionally consumed the other Araceae genus. Such preferences demonstrate a coevolutive relation between seed genera and their dispersers, as previously observed by Kessler-Rios & Kattan, (2012) in *E. xanthogaster* and Loiselle et al. (2007) in *L. coronata.* Additionally, dietary preferences caused behavior variations in function of fruit production, in more extreme coevolutive relations with fruit production, birds could develop nomadism (Karubian et al. 2012; Rey. 1995). Definitively, fruit production triggered competition among plants that mold behavior and localization of all the frugivorous birds which compete with each other.

D. pipra preferred the rainy season just as *C. dimorphica* fructification, suggesting this bird followed the fructification of this abundant shrub, but consumed other plants as well, this bird is known to consume several seed species (Kessler-Rios and Kattan, 2012; Loiselle et al. 2007), as also found by our study. Although their dispersion relations are wide and complex, this preference of *C. dimorphica* fructification peaks is novel, and in our data showed a preference of the Melastomataceae family *for D. pipra*.

Bird and plant coevolutive dispersion relations trigger codependence. However, in megadiverse ecosystems as *terra firme* of Yasuní, there is no important symmetric interactions between fruits and birds. Likewise, nestedness tends to be high, because of the huge availability of fruit and equally huge dispersers demand. In *terra firme it* is not profitable to feed on only one plant species with all the diversity that is available. This idea is supported by the pattern previously observed by Loiselle et al. (2007) who identified a 0.93 % of niche overlap between piprids in a YNP forest.

4.3 Dietary evolutive traits

In the 50-ha plot of YSS seed dispersion made up 42.56 % of the mass transported in the gut of birds (Figure 4) and all the seeds were uninjured and presumably fertile. Passeriform and Columbiform birds had a bill morphology designed to swallow the entire fruit pulp with the seeds inside and safe, but, big seeds tend to be regurgitated and not defecated (Loiselle et al. 2007; Naoki. 2003).

One exception to this is the Thraupidae family which is known to handle the fruit with its bill, disposing of seeds and solid tissues, reducing seed ingestion capability

(Murray, 1988). As a result, from the three tanager samples obtained just 10.58 % of the gut weight was seeds. Furthermore, 86.0 % of the sample from *Tachyphonus surinamus* belong to entomologic remains. Gorchov et al, (1995) had proposed this tanager species as omnivorous, and Naoki (2003) found that in omnivorous tanagers fruits represent more than half of their diet, because they are easier to find; but birds spend more time searching for arthropods, which are hard to find. Consequently, in our study *T. surinamus* seemed to consume fruits as a supplement to a preferential insectivorous diet, which was the classification previously proposed by Terborgh et al, (1990). As well, *Thamnophilus murinus* (Thamnophilidae) had just 1.39 % of its sample gut weight as seed remains, the rest were entomologic remains, suggesting it is an insectivorous bird with occasional seed ingestion (Schulenberg, 1983).

The present study registered 16 frugivorous birds which carried entomologic remains at similar percentage in both seasons and habitats, of which 56 % were immatures or juveniles. According to Morton (1973) an entirely frugivorous diet is extremely rare in nature, because this would mean risk in seasons with fruit shortages and also could mean low fast-growing animal protein for juveniles, slowing down their growth and exposing them to predators. Our analysis, during the study seasons, supports the hypothesis of juveniles need for entomological food sources to grow quickly and avoid predation.

5. CONCLUSIONS

Seed dispersion by endozoochory in understory *terra firme* forest of the western Amazon favors shrubs and epiphytes that produce berries, principally Melastomaceae bushes. This dispersion is done mainly by piprids, dominated by *L. coronata.* Understory seed dispersion of YNP is molded by tangled interactions among habitats, seasonal rainfall, and solar radiation patterns, which determine bird species behavior around localization and diet preferences. Bottomlands provide more seed abundance, but less diversity, especially with the rains, and bigger seeds. While ridges had more fruit diversity dispersed, especially during the less rainy season. Rainfall highly influenced *Clidemia dimorfica* and other fast-growing herbs and shrub fruit abundance, which molded the entire relation dynamic, which is still not yet completely unraveled. However, our findings show important interconnectedness between flora and fauna of the region and with this demonstrate that potential changes in forest structure and dynamic caused by climate change and habitat degradation could trigger significant changes in plant and bird species composition and ecology.

6. TABLES

Table 1. *Birds, frugivorous birds, and seed diversity*. (λ: Simpson Index; H': Shannon Index (*:Indicates interpolation of index to confront same estimated sample coverage obtained in INext Online); Abbreviatures: Bot: Bottomland; Rid: Ridge; LS: Less rainy season; RS: Rainy season; Glo: Global).

a) Captures	Birds					Frugivorous and Omnivorous Birds					Seeds				
	Bot	Rid	LS	RS	Glo	Bot	Rid	LS	RS	Glo	Bot	Rid	LS	RS	Glo
No. captures	152	178	172	157	329	57	46	56	47	103	77	55	64	68	132
No. species	46	47	48	48	62	14	13	16	13	19	56	42	48	45	89
λ	0.04	0.04	0.05	0.04	0.04	0.20	0.23	0.23	0.17*	0.21	0.03*	0.03	0.03	0.07*	0.02
Reciprocal (λ)	21.6	22.1	19.9	24.0	NA	4.26	4.77	4.30	5.60*	NA	29.0*	32.7	31.5	14.1*	NA
H	3.35	3.46	3.40	3.50	3.57	1.99	1.89	2.05	2.04*	2.11	3.62*	3.47	3.70	3.10*	4.17
Exponential (H)	28.6	31.8	30.2	33.4	35.7	7.4	6.65	7.78	7.74*	8.3	37.7*	32.1	40.6	22.3*	65
Beta Sørensen	67%		71%		NA	59%		69%		NA	16%		11%		NA
Completeness	88%		88%		94%	88%		86%		93%	35%		38%		45%

Table 2. Means by fecal sample and P value of ANOVA test by set (*: significant P value, α = 0.05)

	Bottomland	Ridge	Less rainy	Rainy	Global
Seeds per fecal sample	14.15	19.96	11.16	22.07	17.71
DF	Between groups	Within groups	Between groups	Within groups	
	1	60	1	60	
SS	Between groups	Within groups	Between groups	Within groups	
	522.56	610.12	1836.79	588.22	
Fvalue	0.85		3,12		
Pvalue	0.35		0.08		----
Seed species per fecal sample	1.47	1.38	1.41	1.45	1.41
DF	Between groups	Within groups	Between groups	Within groups	
	1	60	1	60	
SS	Between groups	Within groups	Between groups	Within groups	
	0.12	1.04	0.02	1.04	
Fvalue	0,12		0.02		
PValue	0.72		0.87		---
Seed weight per fecal sample	0.020	0.0071	0.0117	0.0140	0.0137
DF	Between groups	Within groups	Between groups	Within groups	
	1	69	1	60	
SS	Between groups	Within groups	Between groups	Within groups	
	0.003	0.0002	0.0000807	0.00026	
Fvalue	14.12		0.30		
PValue	0.00035*		0.58		

Table 3. Total seed number distribution by plant habit and fruit type. Eight fruit types and four plant habits were found.

	Tree	Shrub	Herb	Liana
Achene	9	-	-	-
Berry	-	63	35	-
Capsule	-	-	1	-
Drupe	5	3	1	-
Schizocarp	-	9	-	-
Follicle	-	-	-	3
Legume	-	-	1	-
Sincarp	2	-	-	-

7. FIGURES

Figure 1.

Species richness of frugivorous bird species captured in mist nets around the Yasuni forest dynamics plot in 2021. Sample-size based rarefaction and extrapolation sample curve by a) habitat and c) season. Sample completeness curve by b) habitat and d) season. Build in INEXT online, developed by Chao & Hsieh (2016).

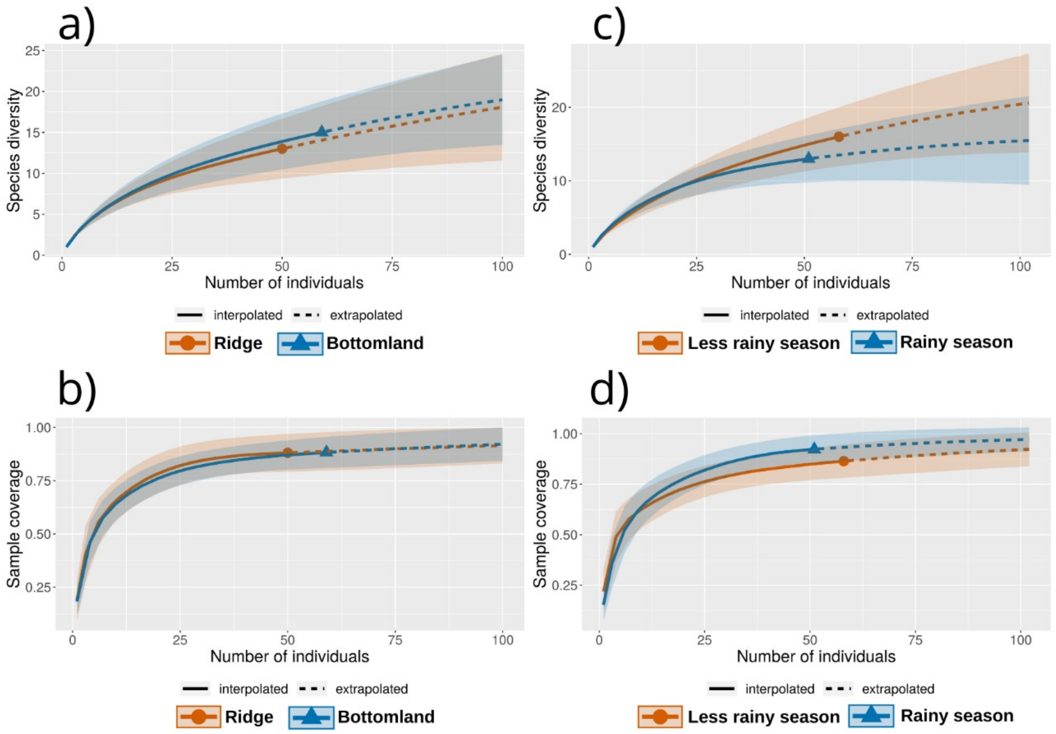


Figure 2.

Species richness of seeds dispersed by frugivorous birds captured in mist nets around the Yasuni forest dynamics plot in 2021. Sample-size based rarefaction and extrapolation sample curve by a) habitat and c) season. Sample completeness curve by b) habitat and d) season. Build in INEXT online, developed by Chao & Hsieh (2016).

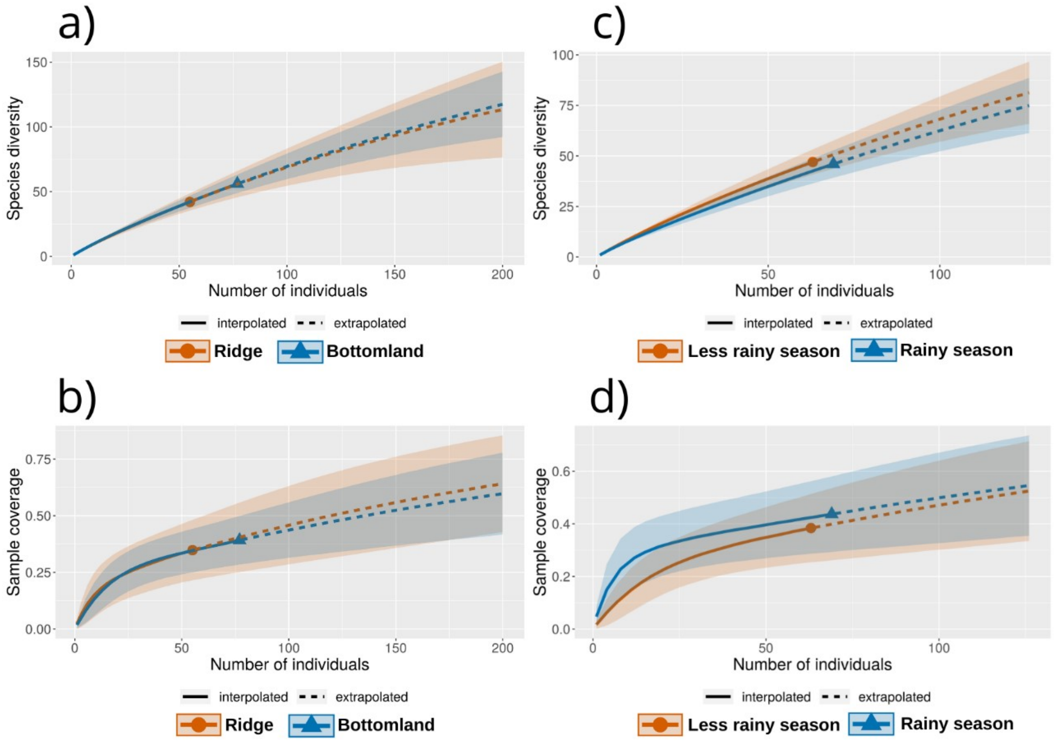


Figure 3.

Bird species abundances at a) ridges (salmon color) and bottomlands (turquoise) and c) Less rainy season (rose) and rainy season (light blue). Seed genus abundances at b) habitat and d) season; obtained by net number of captures (Species and genus abbreviatures: Table S1).

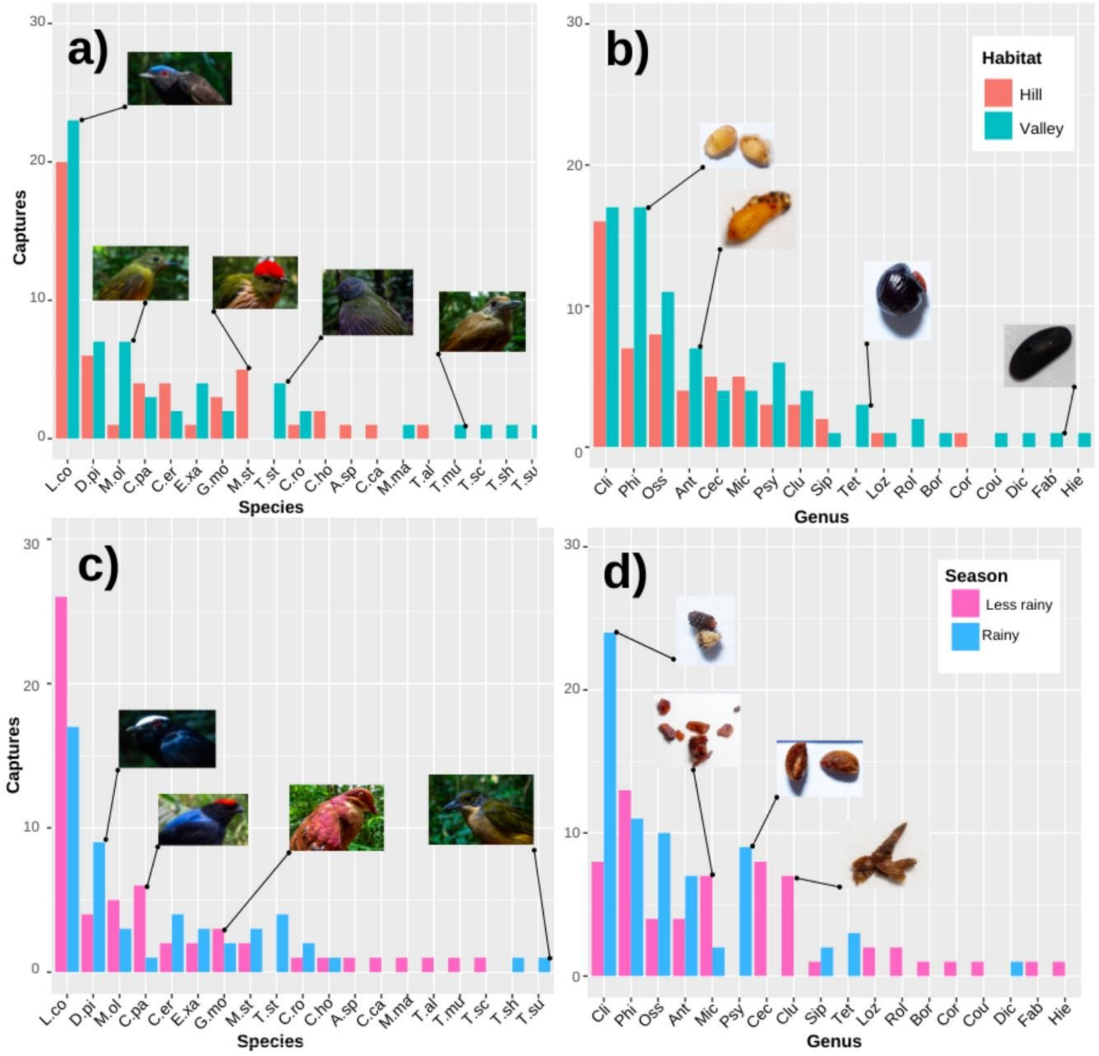


Figure 4.

Weight distribution by fecal remain type among habitats with standard deviation and P value

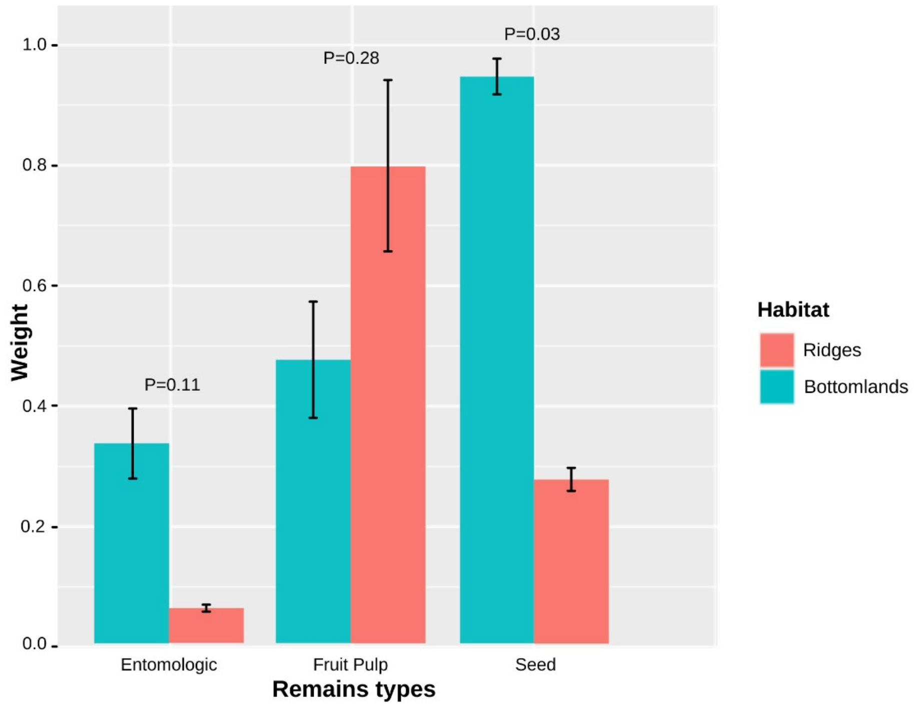


Figure 5.

Seed dispersion frequency of Araceae family genus among habitats and year seasons.

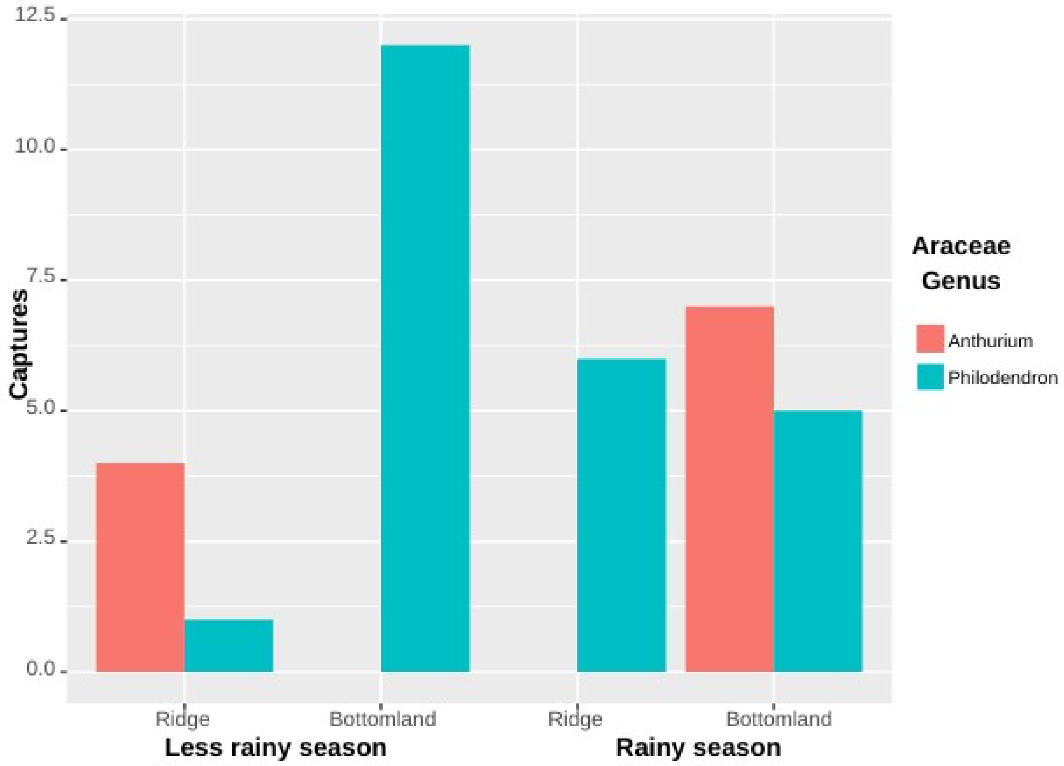
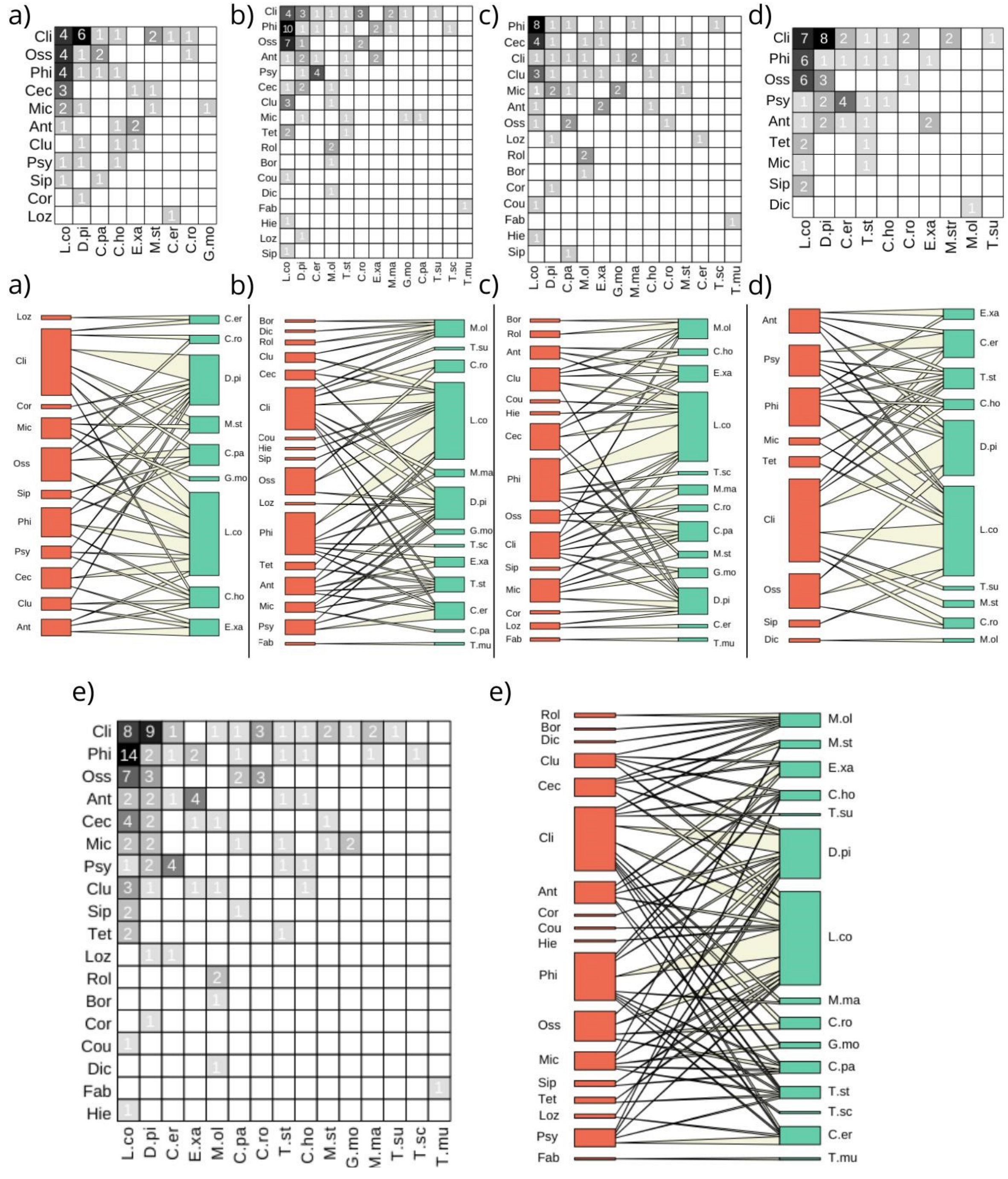


Figure 6.

Trophic interaction boxes and webs among disperser bird species and dispersed seed genus by habitat (a) ridge and b) bottomland), by season (c) less rainy and d) rainy and e) The global interactions registered. Grey color in boxes represents the number of interactions, labeled in white colored numbers. Web connector lines thickness indicates number of interactions. (Abbreviatures: Table S1)



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10. SUPPORTING INFORMATION

Figura S1. Diet niche comparison among seasons and habitats a) species and b) captures

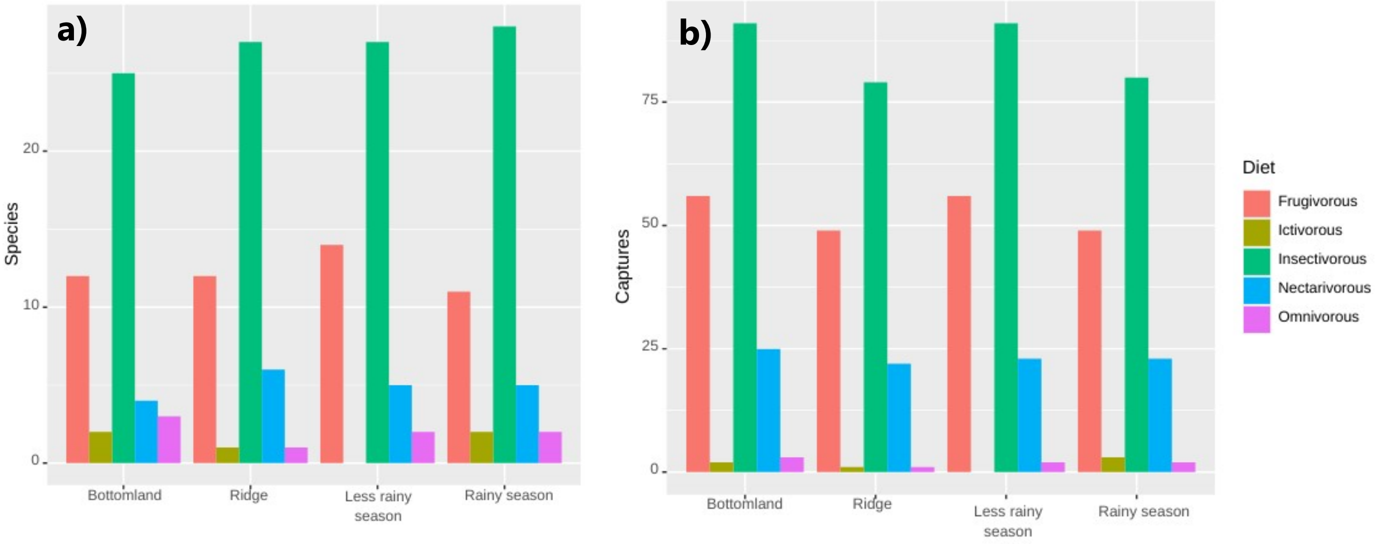

Table S1. Frugivorous bird species and seed genus with its number of species captured, and their respective abbreviatures.

Family	Bird species	Abbreviature	Family	Seed Genus	Abbreviature	Species	Morphospecies
Tyrannidae	Attila spadiceus	Asp	Araceae	Anthurium	Ant	signatum	4
Pipridae	Ceratopipra erythrocephala	C.er	Boraginaceae	Boraginaceae	Bor	-	1
Pipridae	Chiroxiphia pareola	C.pa	Urticaceae	Cecropia	Cec	ficifolia, sciadophylla	2
Pipridae	Cryptopipo holochlora	C.ho	Melastomataceae	Clidemia	Cli	dimorfica	14
Thraupidae	Cyanerpes caeruleus	C.ca	Clusiaceae	Clusia	Clu	-	7
Cardinalidae	Cyanoloxia rothschildii	C.ro	Cordiaceae	Cordia	Cor	-	1
Pipridae	Dixiphia pipra	D.pi	Urticaceae	Coussapoa	Cou	-	1
Fringilidae	Euphonia xanthogaster	Exa	Commelinaceae	Dichorisandra	Dic	-	1
Columbidae	Geotrygon montana	G.mo	Fabaceae	Fabaceae	Fab	-	1
Pipridae	Lepidothrix coronata	L.co	Phyllanthaceae	Heronyma	He	alchornoiedes	-
Pipridae	Machaeropterus striolatus	Mst	Lacistemataceae	Lozania	Loz	klugii	-
Pipridae	Manacus manacus	Mma	Melastomataceae	Miconia	Mic	grandifolia	8
Tyrannidae	Mionectes oleagineus	Mol	Melastomataceae	Ossaea	Oss	-	12
Thraupidae	Tachyphonus surinamus	T.su	Araceae	Philodendron	Phi	platypodium	15
Thraupidae	Tangara schrankii	T.sc	Rubiaceae	Psychotria	Psy	poeppigiana	6
Thamnophilidae	Thamnophilus murinus	T.mu	Annonaceae	Rollinia	Rol	-	2
Thamnophilidae	Thamnophilus schitaceus	T.sh	Siparunaceae	Siparuna	Sip	cuspidata	2
Turdidae	Turdus albicollis	T.al	Dilleniaceae	Tetracera	Tet	wildinogiana	1
Pipridae	Tyranneutes stolzmanni	T.st					

4 INSTRUCCIONES PARA AUTORES