

Frugivorous birds' assemblages in neotropical forest: the relevance of landscape elements

Ensamble de aves frugívoras en una selva neotropical: la relevancia de los elementos del paisaje

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ABSTRACT

Many of Mexico's mature tropical forests are immersed in a complex landscape with agricultural fields, second-growth vegetation, and forest fragments; assemblages of frugivorous birds vary in these different landscape elements. We studied assemblages of birds feeding on fruits of three tree species in continuous forest, vegetation corridors, isolated forest fragments, and secondary vegetation. Through direct observation of focal trees and documentation of frugivorous feeding activities, we use effective species numbers and Non-Metric Multidimensional Scaling to describe the variation of habitat use patterns between assemblages. We recorded 1162 individuals of 57 bird species feeding on ripe fruits of *Nectandra salicifolia*, *Dendropanax arboreus*, and *Bursera simaruba*. Thirty-two species fed on isolated fragments and corridors of vegetation; our analysis grouped these two landscape elements by their species composition, representing 64.6% of all recorded individuals. The composition of the assemblages was influenced by the availability of fruits; *Bursera simaruba* exhibited a prolonged fruiting period and attracted a wider range of consumer species. Although the number of species varied slightly between different elements of the landscape, the importance of corridors and isolated forest fragments was key to the connectivity between bird and tree populations. At the geographic scale of this study, the transformation of the area does not reduce the diversity of frugivorous bird assemblages, as a result of the connectivity between the different elements of the landscape.

Keywords: bird community, frugivorous assemblages, plant-bird interactions, transformed habitat, tropical landscape.

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RESUMEN

Muchos de los bosques tropicales maduros de México están inmersos en un paisaje complejo con campos agrícolas, vegetación secundaria y fragmentos boscosos; los ensambles de aves frugívoras varían en estos diferentes elementos del paisaje. Estudiamos ensambles de aves que se alimentan de frutos de tres especies arbóreas en bosque continuo, corredores de vegetación, fragmentos de bosque aislados y vegetación secundaria. A través de observación directa de árboles focales y la documentación de las actividades de alimentación de las aves frugívoras, usamos el número de especies efectivas y el Escalamiento Multidimensional No Métrico para describir la variación de los patrones de uso del hábitat entre ensambles. Registramos 1162 individuos de 57 especies de aves alimentándose de frutos maduros de *Nectandra salicifolia*, *Dendropanax arboreus* y *Bursera simaruba*. Treinta y dos especies se alimentaron en fragmentos aislados y corredores de vegetación; nuestro análisis agrupó estos dos elementos del paisaje por su composición de especies, representando 64.6% de todos los individuos registrados. La composición de los ensambles estuvo influenciada por la disponibilidad de frutos; *Bursera simaruba* exhibió un período de fructificación prolongado y atrajo una amplia gama de especies consumidoras. Aunque el número de especies varió ligeramente entre diferentes elementos del paisaje, la importancia de corredores y fragmentos de bosque aislados fue clave para la conectividad entre poblaciones de aves y árboles. A la escala geográfica de este estudio, la transformación del área no reduce la diversidad de los ensambles de aves frugívoras, como resultado de la conectividad entre los diferentes elementos del paisaje.

Palabras clave: comunidad de aves, ensamble de frugívoros, hábitat transformado, interacciones planta-ave, paisaje tropical

INTRODUCTION

Forests in Mexico are transformed at an alarming rate to different land uses by anthropogenic activities to satisfy different human needs (Sánchez-Colón *et al.* 2009). Despite forest conservation efforts, they are now mostly restricted to federal, state, municipality, private, or social protected areas, and are immersed in a complex mosaic of patches of secondary forest, agricultural fields, or cattle lands (Bezaury-Creel and Gutiérrez 2009).

Fragmentation processes could have negative or positive effects on biodiversity (Fahrig 2017), and in similar ways, biological processes and interspecific interactions might be affected by landscape changes. The impact of habitat fragmentation on biodiversity remains a contentious topic of debate. Kattan and Alvarez (1996) proposed that fragmentation can exert negative effects on the physical environment, which in turn could have repercussion on the biology of the species and biological interactions. As an example, the reproduction of flowering plants could be negatively affected (Cordeiro and Howe 2003, Tylianakis *et al.* 2008, Hagen *et al.* 2012), as the quality and quanti-

ty of pollen received by flowers might decrease (Aguilar *et al.* 2006), or frugivorous bird assemblages' composition might change drastically (Galetti *et al.* 2003, Pizo and dos Santos 2011) modifying consumption of fruits and seed dispersal patterns, that could promote the decline in the reproduction of flowering plants and the recruitment of new individuals (Cordeiro and Howe 2003, Tylianakis *et al.* 2008, Hagen *et al.* 2012). These changes can ultimately influence the distribution and abundance of the original flora and fauna species.

Fahrig (2017) found that most of responses exhibited by frugivorous bird assemblages in relation to habitat fragmentation were actually positive. These responses were attributed to increased functional connectivity, habitat diversity positive edge effect, stability of predator-prey systems, reduced competition, spreading of risk and landscape complementation. However, Fletcher *et al.* (2018) pointed out that Fahrig (2017) review does not provide reliable evidence or sufficient context to dismiss the negative effects of habitat fragmentation, mainly based on three reasons: a) omission of key literature, b) biased weighting

of findings, and c) lack of widespread refutation of negative habitat fragmentation.

Regardless of the debate on habitat fragmentation on biodiversity, we know that the responses of frugivorous bird assemblages to new features of the landscapes are variable. For example, some species are more adaptable and flexible and can move among continuous forests and forest patches, reducing the fragmentation effects in the medium-long-term maintaining population genetic flow (Graham *et al.* 2002, Galetti *et al.* 2003, Emer *et al.* 2020). However, more specialized species are more restricted to mature forests and become more vulnerable, leading to local and irreversible extirpation after deforestation (Cordeiro and Howe 2003, Emer *et al.* 2020). Although fragmentation negatively impacts bird communities, the presence of fruit-bearing trees in the different landscape elements contributes to the maintenance of frugivorous bird assemblages (Luck and Daily 2003, Farwig *et al.* 2006).

To understand how bird assemblages are affected, it is critical to understand the patterns of habitat use and the extant interactions among bird and plant species in fragmented landscapes, which eventually might determine seed dispersal dynamics in the landscape (Ortiz-Pulido *et al.* 2000, Graham *et al.* 2002, Githiru *et al.* 2002, Farwig *et al.* 2006, Figuroa-E *et al.* 2009, Pizo and dos Santos 2011), and therefore, the environmental services provided. In tropical environments, however, these studies have been scarce due partly to the diversity and complexity of interacting species (Lefevre *et al.* 2012).

This study examines bird-frugivorous assemblages within a partially modified tropical forest near Calakmul Biosphere Reserve, Campeche, Mexico. We evaluated species richness, diversity, and abundance of frugivorous bird assemblages using three tropical trees present in continuous forest, vegetation corridors, isolated forest fragments, and 20-year-old second-growth vegetation.

MATERIALS AND METHODS

Study Site: This study was conducted at Calakmul municipality near the central-eastern part of Calakmul Biosphere Reserve, Campeche, Mexico. The sampling site was located in the ejido “20 de Noviembre”, an area of roughly 24 km² (18°25’, 18°29’ N; -89°17’, -89°19’ W, Fig. 1). The region is characterized by a warm-sub humid climate, with a range of 1100-1500 mm annual mean rainfall, mainly in summer, mostly covered by semi-evergreen forests with complex floristic composition (dominant species are *Mannikara zapota* (L.) P. Royen and *Brosimum alicastrum* Sw, Martínez *et al.* 2001). We focused only on three tree species because they were present at all sites and provided fruits for birds to feed on: *Nectandra salicifolia* (Kunth) Ness, *Dendropanax arboreus* (L.) Decne. and Planch., and *Bursera simaruba* (L.) Sarg.

Human activities in the region have changed land use patterns, producing a mosaic landscape containing relatively well-preserved forests within agricultural areas, pastures, and second-growth vegetation at different successional stages. We selected 25 sites (Fig. 1) that comprise four landscape elements: a) large areas of continuous forest (ten sites of ten ha on average, CF hereafter), b) isolated forest remnants that are primary forest patches surrounded by pastures (six sites of 0.4 ha in average, Frag hereafter), c) vegetation corridors constituted by patches of trees connecting original forested areas (eight sites covering 1.7 ha total, Corr. hereafter), and d) second-growth vegetation established after the removal of understory shrub and herbaceous vegetation 20 years ago for the cleaning of the “Okol Uitz” archaeological site (one site of 6 ha, SV hereafter); there were no replicas of this landscape element available in the area.

Data Collection: We studied 129 trees of three fruit-bearing tree species distributed among the four landscape elements (Table 1). Fieldwork was carried out from Septem-

Table 1. The distribution of the trees on four landscape elements at Calakmul

Species tree	Continuous forest	Isolated Forest remnants	Vegetation corridors	Second-growth vegetation	Total
<i>Nectandra salicifolia</i>	20	14	13	4	51
<i>Dendropanax arboreus</i>	2	0	7	6	15
<i>Bursera simaruba</i>	24	17	14	8	63

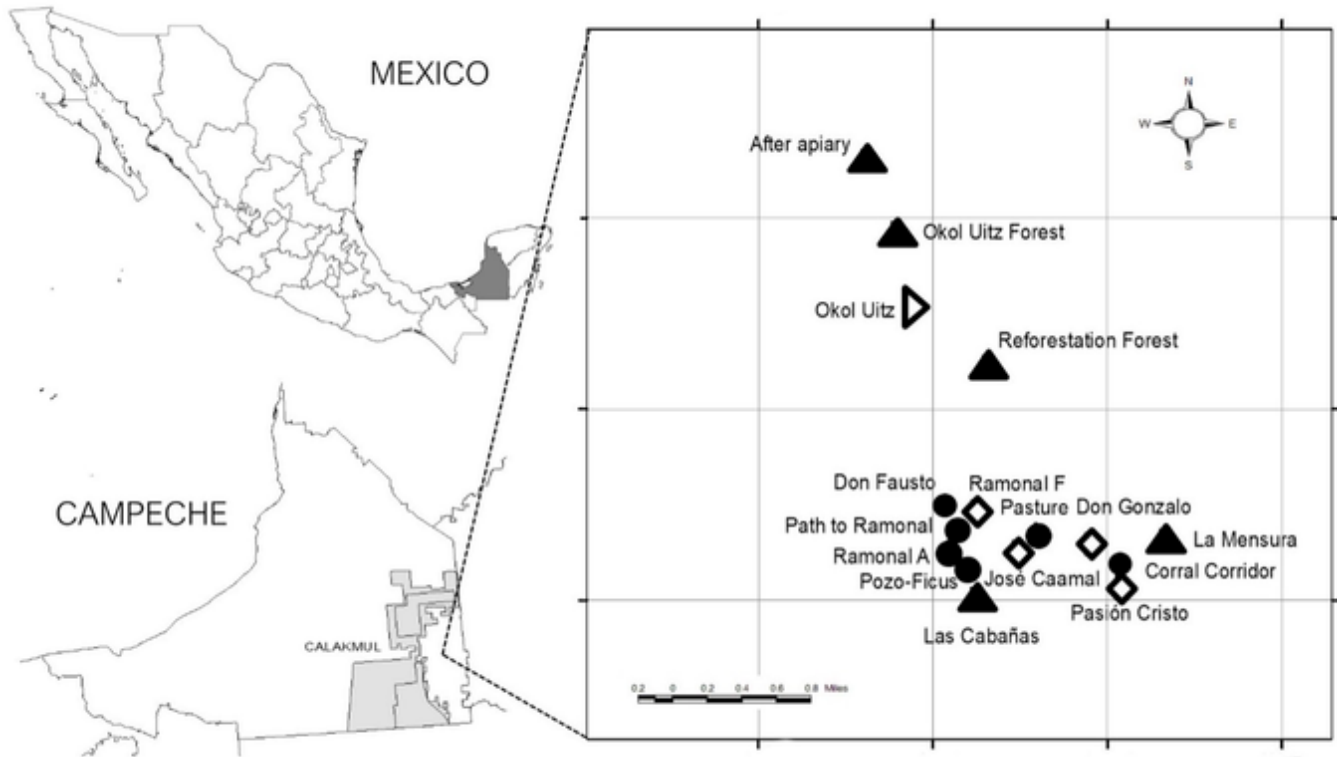


Figure 1. Location of the study area and sampling sites.

▲ Continuous forest; ◇ Isolated forest remnants; ● Vegetation corridors; ▷ Second-growth vegetation

ber to April when ripe fruits were available to birds. Observations were done focally on trees, between 0600 h and 1100 h, for half-hour periods accounting for roughly 500 hours in total. All birds feeding in a focal tree were registered and identified to species level (a code constructed with the first two letters of the genus and the species name was assigned to each of them; [Supplementary material 1](#)). We determined the residency status of the bird species according to our observations and published accounts ([Berglanga *et al.* 2019](#)). We also considered foraging behavior; if the bird swallowed or carried the fruit was counted as a potential disperser, but when the bird squeezed or punctured the fruit, the species was considered a predator.

Data Analyses: We used two diversity measures to describe the frugivorous-bird assemblages: a) diversity of order 0 (0D), which represents bird species richness, and b) diversity of order 1 (1D), in which species are weighted according to their relative abundance without favoring rare or common species ([Pineda and Verdú 2013](#)); due to the known sensitivity of the Shannon diversity index to rare species, we used the number of effective species or the exponential of

Shannon entropy index H' ([Moreno *et al.* 2011](#)). The indices estimation was done in the PAST software package ([Hammer *et al.* 2001](#)). To evaluate the frugivorous-birds richness, we used rarefaction with an 84 % interval confidence, taking into account the same number of individuals and standardized data ([MacGregor-Fors and Payton 2013](#)); this was done in the EstimateS software package ([Colwell 2021](#)).

We evaluated beta diversity using complementarity as a measure of the dissimilarity between the species recorded in each one of the landscape elements. The above was done by using the formula: $C = [(S_j + S_k) - 2 V_{jk} / (S_j + S_k) - V_{jk}] * 100$ expressed as a percentage, where S_j and S_k are the numbers of species on sites j and k , respectively, and V_{jk} is the number of species common to both sites ([Colwell and Coddington 1994](#)).

Differences in the composition and abundance of species among the landscape elements were analyzed with a Non-Metric Multidimensional Scaling (NMDS) ordination. A matrix of specific composition and relative abundance of taxa was used to test differences in habitat use

by bird assemblages; we also generated a matrix of consumed fruits and the specific composition to assess their use by bird species. Based on the abundance of birds, the Bray-Curtis coefficient was used to perform NMDS and a similarity profile (SIMPROF) test. The NDMS analysis was used to graphically display the similarity among observations regarding species composition and abundance of birds feeding on the tree fruits. All similarity measures and ordination techniques were computed with the Primer-6 software package (Clarke and Gorley 2006).

RESULTS

Landscape-level. We tallied 1162 records of individuals consuming fruits in four landscape elements in Calakmul. A total of 57 frugivorous bird species were recorded during 185 days of fieldwork, some being obligated [e.g., *Trogon melanocephalus* Gould, 1836, *Ramphatos sulfuratus* R. Lesson, 1830] or opportunistic [e.g., *Setophaga magnolia* (A. Wilson, 1811), *Megarynchus pitangua* (L., 1766)]. Forty-five species (79 %) were categorized as potential dispersers, eleven species (19.3 %) were predatory, and *Pionus senilis* (Spix, 1824) acted in both ways, as disperser and predator, feeding on fruits and consuming seeds (1.7 %). In terms of their residence status, 41 species were permanent residents, twelve species were migratory, two species were summer residents, and two additional species were transient migrants (Supplementary material 1).

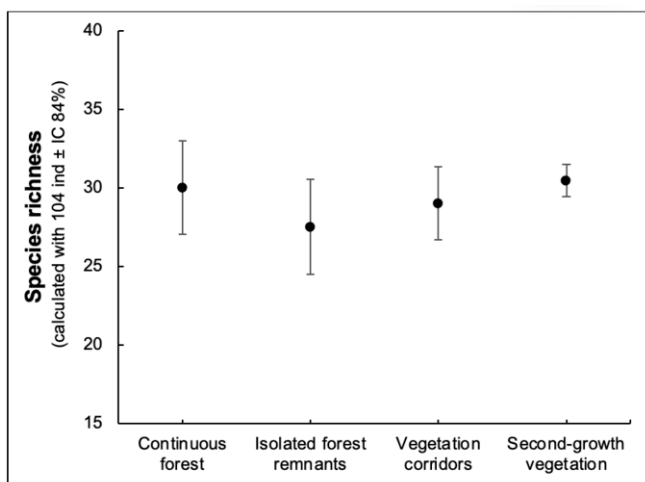


Figure 2. Estimates of richness of frugivorous birds between different fragments at Calakmul estimated by rarefaction with lower individuals (Second-growth vegetation).

Table 2. True diversity measures estimated for four elements of the landscape at Calakmul.

	Continuous forest	Forest remnants	Vegetation corridors	Second-growth vegetation
0D	38	36	41	31
1D	19.5	19.4	24.9	21.6
No. Ind.	305	363	390	104

The total number of frugivorous bird species per site varied from 31 to 41; bird-frugivorous richness (0D) was higher in vegetation corridors than in the continuous forest, as well as in second-growth vegetation (Table 2), which is also true for the diversity of order 1 (1D). Concerning diversity of order 1, the second highest diversity was observed in second-growth vegetation (Table 2), despite the lesser number of individuals recorded. However, as seen with rarefaction (Fig. 2), bird-frugivorous assemblages are statistically similar; no differences in richness were found among the four landscape elements.

Vegetation corridors and remnants of isolated forests shared the largest number of bird-frugivorous species and, as a whole, included most of the individuals (64.8 %) (Table 2). Complementarity ranged from 28.9 % to 56.3 %; continuous forest and second-growth vegetation have the higher complementarity, sharing 21 of the 57 species of frugivorous birds, while corridors and forest remnants had the lowest complementarity values, sharing 32 of the 57 species (Table 3).

The ordination analysis separates sampling sites into three significantly different groups (stress=0.12, Fig. 3). The first cluster comprises only continuous forest sites, with 20 species feeding almost exclusively on *Bursera*, and seven exclusive species. The second cluster included isolated forest remnants and vegetation corridors, with 30 species that mostly consumed *Bursera* fruits. Forty-six species were included in the third cluster, which encompasses sites of the four landscape elements; roughly 66 % of the birds feeding on *Bursera*, 23 % on *Nectandra*, and 11 % consuming *Dendropanax* fruits. The second and third clusters share twelve bird species.

Frugivorous bird assemblages. Overall, the bird-frugivorous assemblage using *Bursera* fruits is the

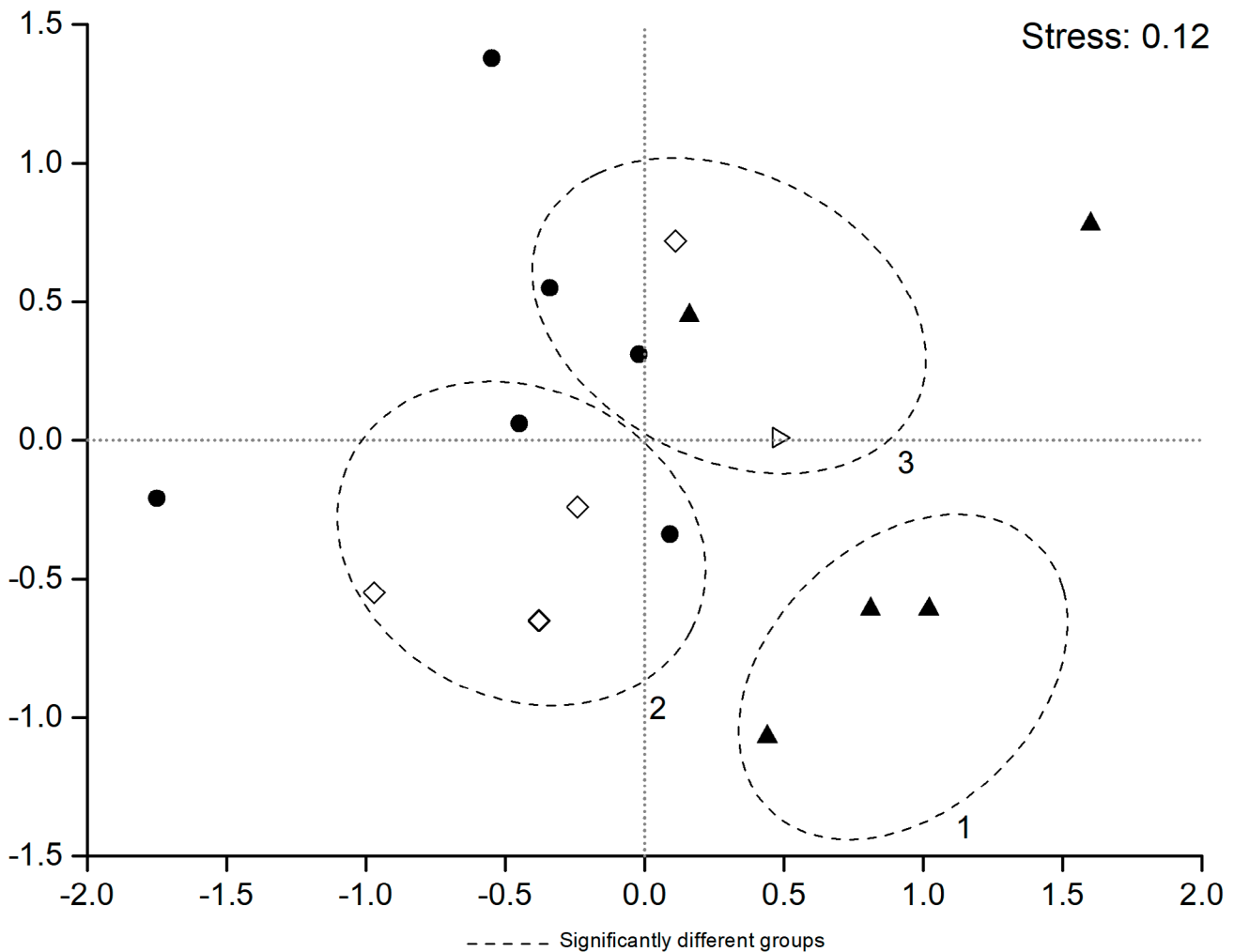


Figure 3. Non-Metric Multidimensional Scaling analysis (NMDS) plot based on bird similarities between sites in Calakmul.

▲ Continuous forest; ◇ Isolated forest remnants; ● Vegetation corridors; ▷ Second-growth vegetation

richest (46 species) than those assemblages feeding on *Dendropanax* and *Nectandra* (27 species each) (Supplementary material 1). Based on the differential usage of fruit species by birds, the frugivorous assemblages are separated onto four significantly different groups (stress=0.02) (Fig. 4). The first group comprises five species that fed mainly on *Dendropanax* fruits; *Dumetella carolinensis* (L., 1766), a migratory species, was the most important consumer of *Dendropanax* fruits. Eleven species that consumed mainly *Nectandra* fruits conformed the second group; as part of it, *Amazona albifrons* (Sparman, 1788), a resident species, is the most frequent consumer (acting as seed predator), followed by *Hylocichla mustelina* (Gmelin, 1789) a disperser migratory species. The third group fed *Bursera* fruits and included 29 species; the primary consumers were the resident *Tityra*

semifasciata (Spix, 1825) and the migratory *Vireo griseus* (Boddaert, 1783). Finally, the fourth group encompassed twelve bird species that fed indistinctly on fruits of the three tree species analyzed.

DISCUSSION

The availability of fruits in a tropical landscape matrix greatly determines the conformation and the dynamics of frugivorous bird assemblages (Luck and Daily 2003, Farwig et al. 2006, McConkey et al. 2012). However, the selection of three tree species that are ubiquitous in all the landscape elements in our design allowed us to observe the differential use of the landscape elements by those bird species.

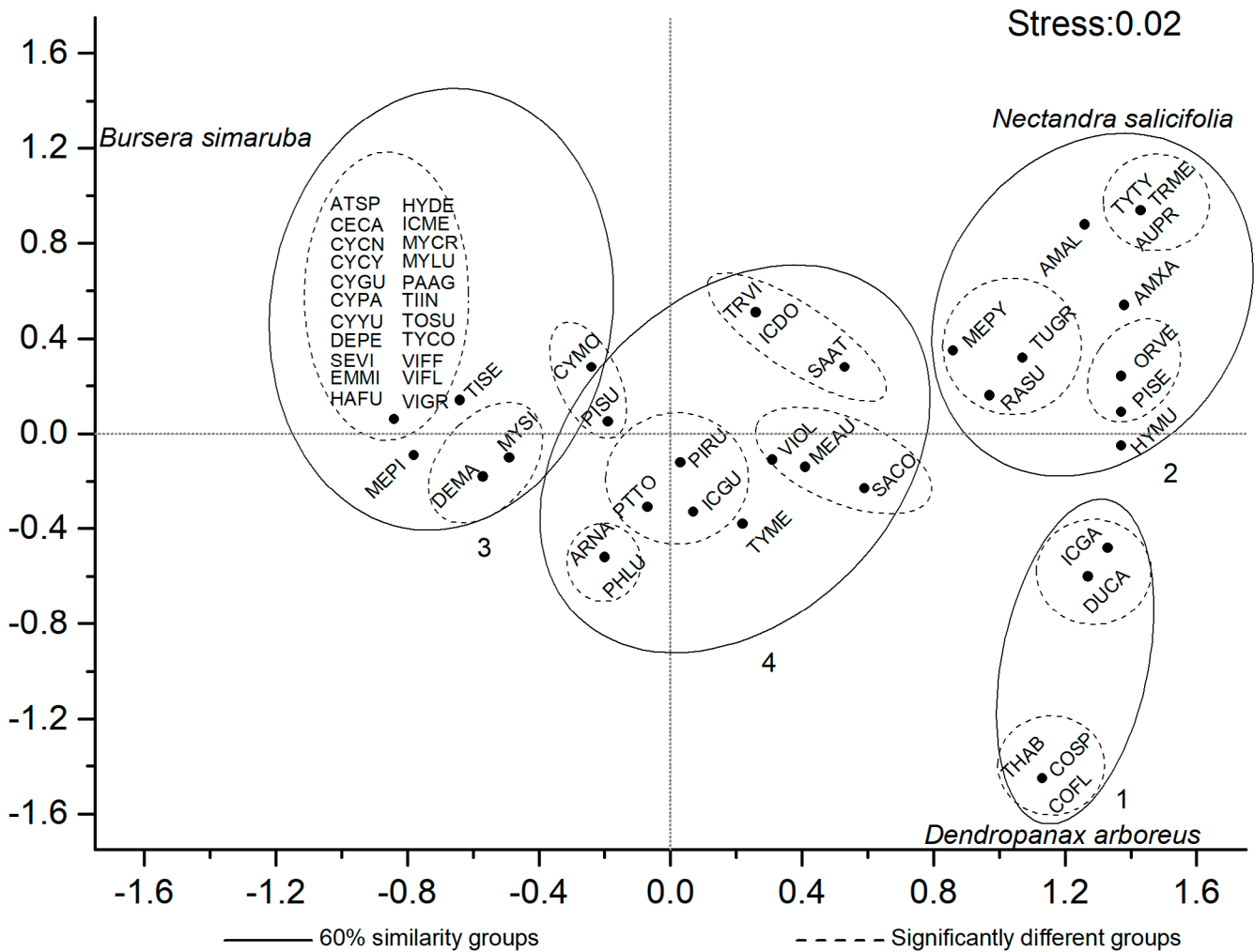


Figure 4. Non-Metric Multidimensional Scaling analysis (NMDS) plot based on preferences of the frugivorous birds at Calakmul.

Our results indicate that vegetation corridors and forest fragments act as feeding sites (64.8 % of the recorded individuals) with the highest richness and diversity of frugivorous bird assemblages in Calakmul. This landscape structure functions as connecting corridors network for birds (Tewksbury et al. 2002, Pizo and dos Santos 2011), acting as stepping-stones favoring the dispersion and movement of animal species (Levey et al. 2005, Hagen et al. 2012) and hence, increasing bird diversity as observed in this work.

Levey et al. (2005) have demonstrated that vegetation corridors substantially increase the movement of birds and seed dispersal between habitat patches. The above provides critical connectivity to forest fragments and continuous forests that allow the movement of sensitive species (Luck and Daily 2003, Pizo and dos Santos 2011), maintaining the integrity of frugivorous bird assemblages.

The integrity of frugivorous bird assemblages is critical in areas with increased changes in land usage, like in Calakmul, because it allows seed dispersal, favoring the genetic flow of tropical plants and the regeneration of forest species within a very heterogeneous landscape (Nason et al. 1997, Vieira and Carvalho 2009, Figuroa-E et al. 2010). Although we do not observe it, we must consider that fragmentation might modify the visitation patterns of frugivorous birds and their effectiveness as dispersers (Graham et al. 2002, Figuroa-E et al. 2009, Pizo and dos Santos 2011).

In the same way, the increased richness and diversity over vegetation corridors and forest fragments could be also a response to vegetation structure. The vertical structure of the vegetation in these landscape elements is characterized by the presence of open spaces in the upper canopy

Table 3. Number of frugivorous birds shared (lower diagonal) and beta diversity (percentage of complementarity, upper diagonal) between different landscape elements.

	CF	Frag	SV	Corr
CF	*	52	56.3	48.1
Frag.	24	*	54.3	28.9
SV	21	31	*	56
Corr.	27	32	22	*

CF = Continuous forest; Frag = Isolated forest remnants; Corr =Vegetation corridors; SV = Second-growth vegetation

and subcanopy (Lynch and Whigham 1984, Watson *et al.* 2004) and contains a considerable abundance or aggregation of resources for birds (Loiselle and Blake 1990, Carlo and Morales 2008); the location of these available food sources makes easier for birds to locate them because they are clumped and are more quickly accessible. Moreover, compared with vegetation corridors of forest fragments, the canopy in the continuous forest is more closed, the areas are more spacious, the trees are dispersed, and the distribution of resources is more heterogeneous; under these circumstances, birds spend more time searching for fruits that might have lower availability (García and Ortíz-Pulido 2004, Carlo and Morales 2008).

Conversely, Gomes *et al.* (2008) suggest differences in the tolerance levels of frugivorous birds to habitat disturbance; larger species are more tolerant to intermediate disturbance and intolerant to severe disturbance. In contrast medium to small-sized frugivorous birds often shows higher tolerance. Although we did not further explore this idea, our results strongly suggest that the composition of the assemblage was determined by the presence of different resources and the preferences and abundances of bird species in habitats which differ in vegetation structure (Watson *et al.* 2004, Alvarez-Alvarez *et al.* 2022) and fruit display (Gutián *et al.* 1992).

Bursera simaruba is a species with a broad distribution across tropical regions. It is generally abundant in primary forests and second-growth vegetation, where it is among the largest tree species and has high fruit productivity; therefore, as in our case, it is frequently visited. *Bursera* fruits were always available and had the most diverse frugivorous bird assemblages during our sampling period. Similar assemblages, also feeding on *Bursera* fruits,

have been reported in Veracruz, Mexico, at La Mancha (27 species) by Ortíz-Pulido *et al.* (2000) and Los Tuxtlas (39 species) by Graham *et al.* (2002), as well as in and Panama (26 species) by Trainer and Will (1984).

Ramos-Robles *et al.* (2018) found *Bursera simaruba* to be one of the most important plants regarding high fruit crops and their use by the most abundant resident bird species in a plant-frugivory network analysis at La Mancha, Veracruz. In our study, *Tityra semifasciata* and *Vireo griseus* strongly preferred *Bursera* fruits; this observation is consistent with Graham *et al.* (2002) results. Regarding *Vireo griseus*, Greenberg *et al.* (1995) suggested that its higher densities were related to higher densities of *Bursera* trees in the Yucatan Peninsula.

In Calakmul, *Nectandra salicifolia* trees were recorded in all landscape elements, but their lipid-rich fruits were available only for a short time (September to October). According to Ramos-Robles *et al.* (2018), *Nectandra* fruits are consumed mainly by migratory birds such as *Dumetella carolinensis* (Ramos-Robles *et al.* 2018); in our study, we observed that their primary consumers and potential dispersers were the migratory birds *Hylocichla mustelina* and *Dumetella carolinensis*, and by *Amazona albifrons*, a seed predator.

Dendropanax arboreus has a widespread distribution in tropical areas of Mexico (Pennington and Sarukhán 2005); it produces abundant fruits between the end of September to the middle of November. However, these trees were uncommon in the study site and were absent in forest fragments. As observed with *Nectandra*, *Dumetella carolinensis* and *Hylocichla mustelina* also were the primary consumers of *Dendropanax*; these observations are consistent with Figuroa-Esquivel and Puebla-O (2009). In the case of *Turdus grayi* Bonaparte, 1838, we observed that the primary consumption is on *Nectandra*; in contrast, Graham *et al.* (2002) found it as the most frequent consumer of *Dendropanax* in Los Tuxtlas. Ramos-Robles *et al.* (2018) suggested that *Dendropanax* fruits are consumed primarily by larger species, but this was not the case in Calakmul, where medium to small species consume this fruit.

Our findings suggest that the tree species might not be drastically affected by changes in the landscape structure. In Calakmul, the transformation of the landscape does not reduce the diversity of fruit-eating bird assemblages, primarily due to connectivity between different landscape

elements, particularly vegetation corridors and forest fragments. However, continuous habitat fragmentation could cause a significant reduction in the number of frugivorous birds that disperse seeds of tropical trees.

Finally, we think that the integrity of frugivorous bird assemblages is critical for maintaining the dynamics of tropical forests, given that most woody plants depend on them for seed dispersal. The structure and function of biotic communities in disturbed ecosystems can be assessed through network analyses of interspecific interactions, which provide the basis for understanding and conserving ecological processes (Ramos-Robles *et al.* 2018, Wang *et al.* 2023). Although we did not explore this approach, it is an opportunity that might prove valuable in future studies.

AUTHOR'S PARTICIPATION

Study Conception EMFE; Formal analysis EMFE and OUHA; Investigation EMFE; Data curation EMFE and OUHA; Writing initial draft EMFE; Writing critical review and commentary of revision OUHA, JFVG, RVF and VHLM; Funding acquisition EMFE.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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