



SEASONAL VARIATION IN BIRD ASSEMBLAGE COMPOSITION IN A DRY FOREST OF SOUTHWESTERN MEXICO

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Abstract · Tropical dry forests are characterized by a marked seasonality throughout the year. The response of bird assemblages and species abundance to the seasonal changes of dry forests, as evidenced by bird feeding habits, can contribute to a greater understanding of the ecological processes in this ecosystem. In this study, we estimated variations in richness, abundance and composition of bird assemblages as well as their main feeding habits during two seasons of the year (dry and rainy) in a tropical dry forest in southwestern Mexico. Visual and auditory sampling was performed from February 2010 to February 2011 with a fixed-radius point count method (123 point counts distributed across nine transects). A total of 82 bird species belonging to 28 families were recorded in the study area. Although we found more species and a higher abundance in the dry season than in the rainy season, only the abundance of insectivorous-frugivorous and omnivorous birds was significantly higher. According to an ordination analysis, the composition and abundance of bird assemblage changed seasonally. A total of 21 resident birds were found in the dry season (March–June). Some omnivorous and granivorous birds, such as Streak-backed Oriole (*Icterus pustulatus*) and Black-chested Sparrow (*Peucaea humeralis*), were the most abundant species in both seasons. Other species, such as Western Kingbird (*Tyrannus verticalis*) and Golden-cheeked Woodpecker (*Melanerpes chrysogenys*), both insectivorous-frugivorous, were also abundant in two seasons. The greater diversity of avian feeding guilds in the dry season could be influenced by the reproductive activity that occur during this season and by the presence of *Bursera* fruits, as confirmed in other studies.

Resumen · Variación estacional en la composición de ensambles de aves en un bosque tropical seco del suroeste de México

Los bosques tropicales secos se caracterizan por una marcada estacionalidad climática a lo largo del año. Comprender la respuesta de los ensambles de aves y la abundancia de las especies de acuerdo a sus hábitos de alimentación, respecto a los cambios estacionales en el bosque seco, contribuye al conocimiento de los procesos ecológicos en este ecosistema. En este estudio, estimamos la variación de la riqueza, abundancia y composición de las aves y sus tipos de dieta en dos estaciones del año (secas y lluvias) en un bosque tropical seco al suroeste de México. Se realizaron muestreos visuales y auditivos durante un año (febrero de 2010 a febrero de 2011), con el uso de puntos de conteo de radio fijo (123 puntos distribuidos en nueve transectos). Se registró un total de 82 especies de aves que pertenecen a 28 familias. La estación seca presentó mayor riqueza de especies y abundancia de aves que la estación lluviosa, pero solo la abundancia de las aves insectívoro-frugívoras y omnívoras fue significativamente mayor en la estación seca. De acuerdo al análisis de ordenación, la composición y abundancia del ensamble de aves cambió estacionalmente. Se encontró un total de 21 aves residentes en los meses secos del año, que corresponde a la temporada reproductiva (marzo–junio). Algunas aves omnívoras y granívoras como la calandria dorso rayado (*Icterus pustulatus*) y el zacatonero pecho negro (*Peucaea humeralis*) fueron las más abundantes en ambas temporadas. Otras especies como tirano pálido (*Tyrannus verticalis*) y carpintero enmascarado (*Melanerpes chrysogenys*), ambas insectívoro-frugívoras, también fueron abundantes en las dos estaciones. La mayor diversidad de gremios alimenticios de las aves en la estación seca podría estar influenciada por las actividades reproductivas que transcurren durante esta temporada, y por la presencia de frutos de *Bursera* spp., como se ha observado en otros estudios.

Key words: Balsas basin · Feeding habits · Mexico · Tropical dry forest · Weather seasonality

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INTRODUCTION

Tropical dry forests (TDF) are characterized by their marked seasonality. The dry season can last between 4–7 months, a period with less than 100 mm of rain (Dirzo et al. 2011). In response to seasonal changes, organisms may experience physiological stress (Ceccon et al. 2006). Consequently, the structure of ecological communities in TDF varies with respect to season and temporal changes in the availability of resources (e.g., flowers, fruits and arthropods; Loiselle & Blake 1991, Tvardiková 2010, Modena et al. 2013, Falcão et al. 2014). These dynamics have been little studied in different animal groups in these ecosystems (Wall et al. 2011), particularly in bird communities (Loiselle & Blake 1992, Smith et al. 2001, Carnicier et al. 2009, Chazdon et al. 2011, Pineda-Diez et al. 2012, Burgess & Maron 2016).

In the Neotropics, some studies have confirmed that bird communities change in response to seasonal fluctuations. For example, in some TDFs in Central and South America, both richness and abundance of frugivorous, insectivorous, and nectarivorous birds increase during the rainy season (Loiselle & Blake 1992, Corcuera 2001, Riehl & Adelson 2008, Tinoco 2009). In contrast, in the biotic province of the Balsas basin in southwestern Mexico, richness and abundance of the bird community increase in the dry season (Almazán-Núñez et al. 2015). These differences between unique spatial contexts of Neotropical dry forest are influenced by the availability of food resources. For example, TDFs in southwestern Mexico are co-dominated by *Bursera* species, a tree genus that produces fruits mainly during the dry season and whose center of diversification and endemism is found within this region (Rzedowski et al. 2005, De-Nova et al. 2012). During the dry season, the fruits of these trees represent an abundant food resource for frugivores as well as some insectivores and granivores, that supply their diet with these fruits when their main food source decreases (Ramos-Ordoñez & Arizmendi 2011; Almazán-Núñez et al. 2015, 2016).

The aim of this study was to compare the seasonal differences in composition, abundance, and diversity of bird communities and their feeding habits in a TDF of southwestern Mexico. We also analyzed the monthly distribution of the bird assemblage. Given that TDFs in the Neotropics are among the ecosystems most affected by deforestation and other human perturbations (Dirzo et al. 2011), it is important to understand the seasonal variation in the assemblages of birds to guide successful conservation efforts. Therefore, this study has the potential to aid the implementation of conservation and management strategies for birds and for TDFs through assessing the response of species to temporal changes in the resources (Harvey et al. 2008). In addition, this study can serve as a basis for future ecological and biological studies in the area.

METHODS

Study area. This study was conducted in the town of Xochipala, Guerrero, southwestern Mexico (1000 m a.s.l., 18°03'46.65"–17°42'11.14"N, 99°36'36.50"–99°35'30.46"W) (Figure 1). The main vegetation type is tropical dry forest in various successional stages as a result of past and present agricultural activities (Almazán-Núñez et al. 2012). The climate is semi-arid with an annual average temperature of 23.9 °C and 684 mm of rainfall. The area presents a very marked seasonality: The dry season lasts from November to May, and the rainy season lasts from June to October. The dominant plant species are *Bursera longipes*, *B. aptera*, *B. morelensis* (Burseraceae), *Acacia cochliacantha*, *Gliricidia sepium*, *Lysiloma tergemina*, *Mimosa goldmanii*, *M. polyantha*, and *Senna wislizeni* (Fabaceae) (Almazán-Núñez et al. 2012).

Bird surveys. Monthly bird observations were carried out over a one-year period from February 2010 to February 2011. A total of nine transects were established throughout the study area. The transects were spaced at least 1 km from one another to cover a large geographical area (34.4 ha). In each transect, we used 11–15 fixed-radius, 10-minute point counts with a 30-m radius (0.28 ha), as recommended for TDF (Hutto et al. 1986, Bibby et al. 2000). The points were separated by at least 200 m to ensure data independence. Each transect was visited five times during the dry season and three times during the rainy season (72 total visits to all transects). Our sampling effort for the dry season was larger because it lasts longer (7 months) than the rainy season (5 months). An average of five transects were sampled during each visit. The overall abundance of each species was calculated as the average number of records from each point count, including all visits and seasons of year. Abundance was also calculated on a monthly and seasonal basis. Observations were made during peak hours of bird activity in the morning (06:30–11:00 h) and late afternoon (16:30–19:00 h). Aerial birds (swifts), nocturnal birds and some birds of prey, such as vultures and large raptors, were excluded from the analyses because the count method is not suitable to assess their relative abundance (Hutto et al. 1986). To assess foraging preferences, we conducted foraging observations and consulted the scientific literature (e.g., Arizmendi et al. 2002, Nova-Muñoz et al. 2011, Lopes et al. 2016). Accordingly, the birds were grouped in the following categories: carnivores, omnivores, nectarivores, frugivores, granivores, and insectivores. Species with mixed feeding habits (e.g., insectivore-frugivores) were also considered when this behavior was observed in the field. The scientific nomenclature and systematic arrangement followed the guidelines of AOS (www.americanornithology.org) and its most recent update (Chesser et al. 2017).

Data analysis. The sampling efficiency was evaluated with the Chao 2 richness estimator with EstimateS v.

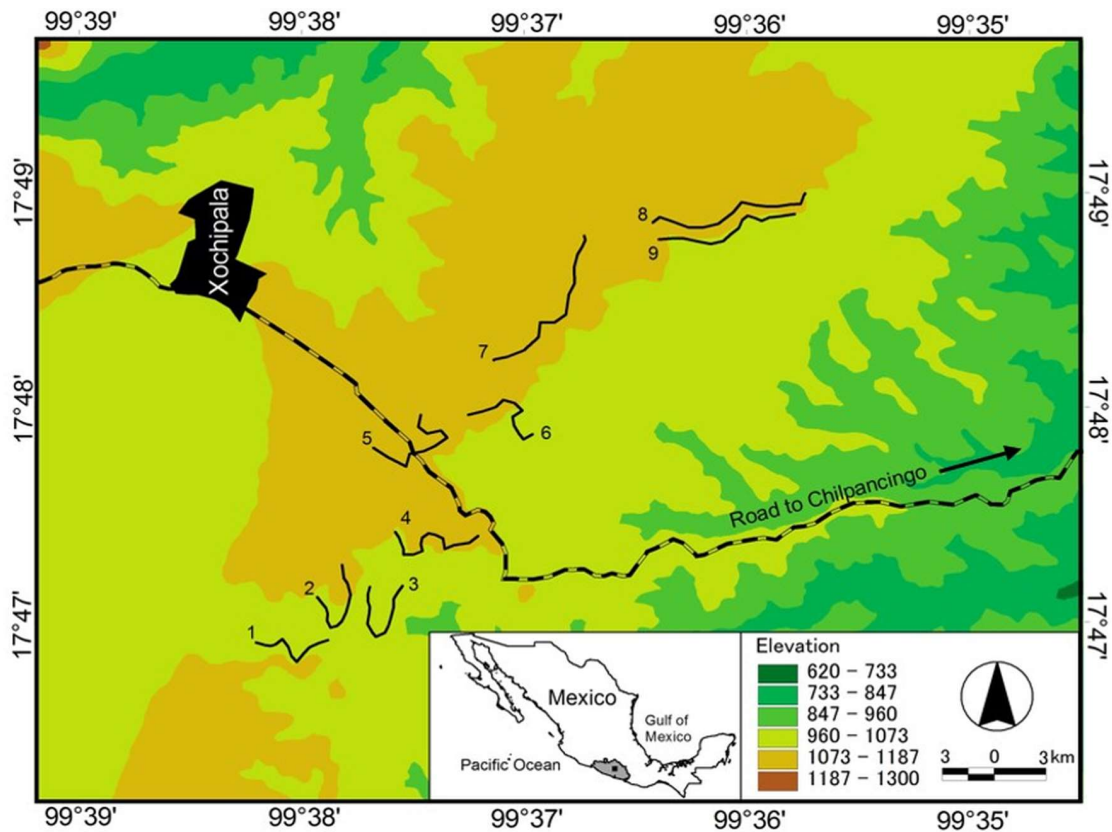


Figure 1. Geographical location of the study area in a tropical dry forest of southwestern Mexico. The numbered lines represent the observation transects using the point-count method.

9.0 (Colwell 2013). This estimator has been shown to be reliable for relatively small sampling units (i.e., circular plots; Hortal et al. 2006). In addition, this method is less dependent on sampling intensity than other estimators (Colwell & Coddington 1994, Hortal et al. 2006). Because the sampling effort was different between the two seasons of the year (5 visits during the dry season and 3 during the rainy season), species richness was compared by calculating the effective numbers of species per season based on the sample coverage (Jost 2006), which is the probability that the next recorded organism will be of the same species as the previously recorded one. This analysis was performed in the iNEXT program using both interpolations (rarefaction) and extrapolations of the observed data (Hsieh et al. 2016). To calculate the number of effective species, which is the number of species of equal abundance expected in a community, three levels of diversity (0D , 1D , and 2D , respectively) were calculated. The first index corresponds to species richness and does not consider abundance (0D). The second index weights species according to observed abundances (1D). The third index (2D) gives more weight to dominant species (Jost 2006, Moreno et al. 2011).

The species abundance among feeding guilds for each season of the year (dry and rainy) was compared with rank-abundance curves using log₁₀ data on the proportion of each species (p_i). Data were sorted according to the most abundant species

(James & Rathbun 1981, Feinsinger 2001). A one-way ANOVA was also used to assess differences in the average abundance of bird feeding guilds between seasons. These statistical analyses were performed in the SPSS v. 20.0 software (SPSS 2011), and differences were considered significant at $P \leq 0.05$.

The distribution of species throughout the year was analyzed with a correspondence analysis (CA; ter Braak & Verdonshot 1995). For this analysis, the abundance of each species was used, but species with less than three records were eliminated, as very low numbers can reflect random observations (ter Braak 1986). This analysis was performed using the CANOCO v. 4.5 and CANODRAW statistical packages (ter Braak & Smilauer 2002).

RESULTS

Richness and abundance of the bird community between seasons. We found 82 bird species belonging to 28 families (Appendix S1). More species were recorded in the dry season than in the rainy season (Figure 2). The sampling efficiencies during the dry and rainy seasons were 88% and 86%, respectively, according to the Chao 2 estimator.

Of the 76 species recorded during the dry season, 43% were recorded exclusively during this period, and 12% in the rainy season (of a total of 49 species; Appendix S1). More resident and migratory species were recorded in the dry season (56 and 20 species,

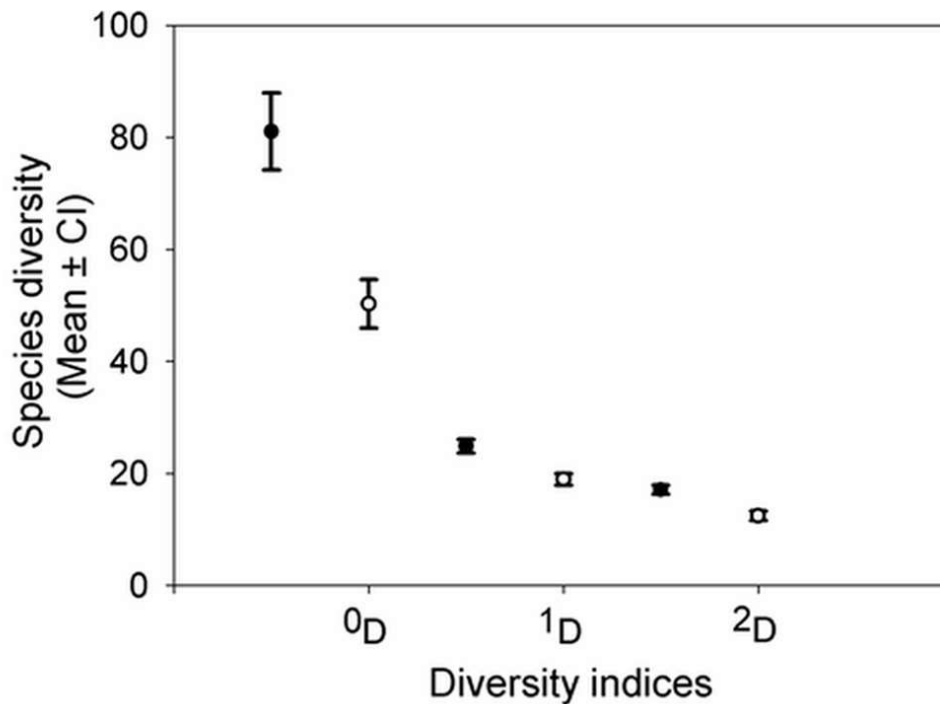


Figure 2. Comparison of bird species richness (0D) and diversity (1D and 2D) between the dry (black circle) and rainy (white circle) seasons given a sample coverage of 0.992 for a tropical dry forest located in southwestern Mexico. Confidence intervals were set at 95%.

respectively), than in the rainy season (20 and 14 species; Appendix S1). The bird community of the dry season was more diverse than that of the rainy season according to 1D and 2D (Figure 2).

Feeding guilds between seasons. The abundance of insectivore-frugivores (ANOVA $F_{1,86} = 15.38$, $P < 0001$) and omnivores (ANOVA $F_{1,86} = 8.04$, $P = 0.006$) was higher during the dry season (Figure 3). The relative abundances of each species by feeding guilds also varied between seasons (Figure 4).

Seasonal distribution of the birds. The first and second axes of the ordination explained 30% and 31% of the variance (eigenvalues: 0.476 and 0.33, respectively). The analysis showed that the distribution of the bird assemblage changed gradually throughout the year and coincided with the main climatic seasons (Figure 5a). For example, the months of October and November form a group defined by the transition between the rainy and the dry season. A second group was defined by the months of December to February, which are dry with lower temperatures, and the months of March to early June, which are equally dry but experience an increase in temperature. Another distinct group was evident during the months of July to September, which are the rainiest months of the year (Figure 5a). Twenty percent of the resident insectivores and 16% of the granivores were associated with the rainy months (July–September; Figure 5b). Resident species, such as Inca Dove (*Columbina inca*), Streak-backed Oriole (*Icterus pus-tulatus*), White-tipped Dove (*Leptotila verreauxi*),

Golden-cheeked Woodpecker (*Melanerpes chrysogenys*), and West Mexican Chachalaca (*Ortalis polio-cephala*), were present throughout the year but were more abundant in the driest months (March to May). Meanwhile, American Kestrel (*Falco sparverius*), Nashville Warbler (*Oreothlypis ruficapilla*), Western Tanager (*Piranga ludoviciana*), and Western Kingbird (*Tyrannus verticalis*) were migratory species associated with October and November (Figure 5a–b), the transitional period between the dry and the rainy season.

DISCUSSION

Richness, diversity, and abundance of birds between dry and rainy seasons. The abundance, diversity, and number of bird species were higher in the dry season. The higher richness in the dry months was explained by the presence of at least 10 Neotropical migratory birds that were not recorded in the rainy season (e.g., Lucy's Warbler *Oreothlypis luciae*, Cedar Waxwing *Bombycilla cedrorum*, Ash-throated Flycatcher *Myiarchus cinerascens*, Yellow-rumped Warbler *Setophaga coronata*, and Clay-colored Sparrow *Spizella pallida*). These species arrive at the tropical environments of southwestern Mexico late in the year (between November and December) in contrast to other migratory species, which usually arrive during the middle of the rainy season (e.g., *Falco sparverius* and Blue-gray Gnatcatcher *Poliophtila caerulea*) and may also be present during the dry season (Howell & Webb 1995, MacGregor-Fors & Schondube 2011). The distribution of birds may be more or less random

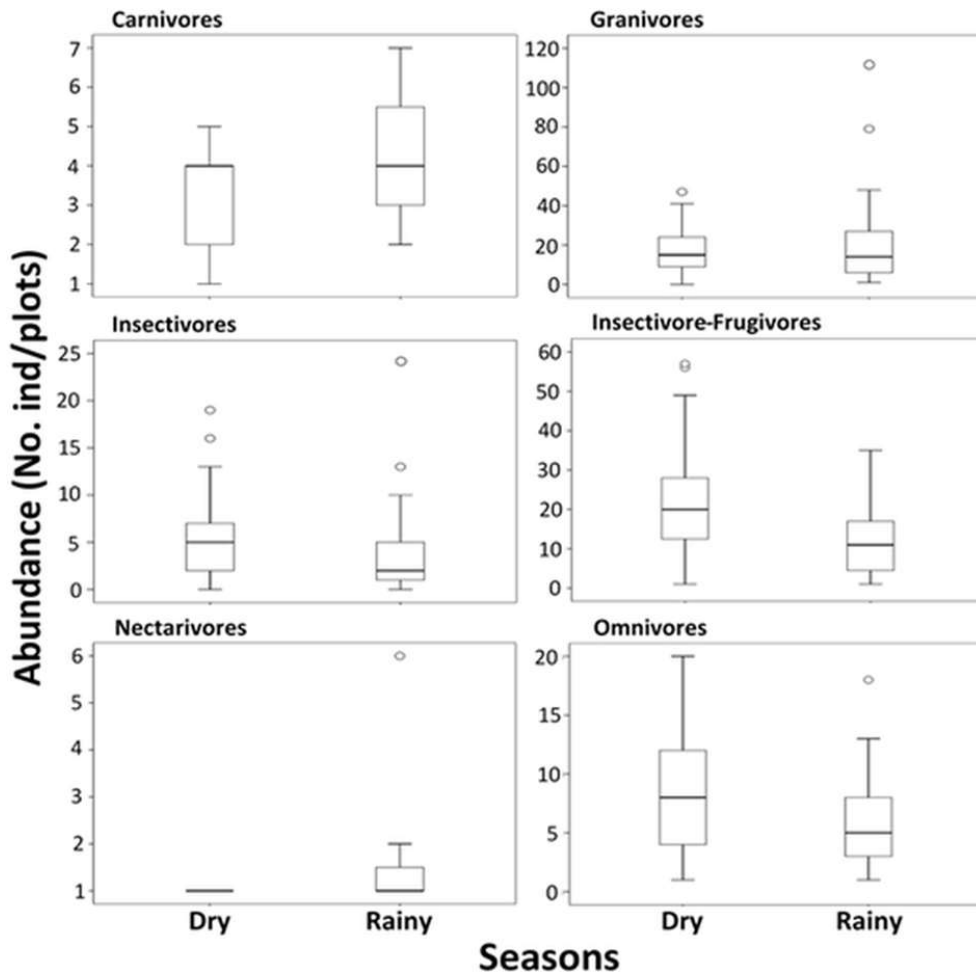


Figure 3. Bird abundance according to feeding guilds between the dry and the rainy season of a TDF in southwestern Mexico. The horizontal line inside each box shows the median abundance, and the horizontal lines enclosing the rectangle indicate the upper and lower quartiles. The whiskers represent the maximum and minimum values of the sample. The extreme values (*outliers*) are depicted as circles.

at the landscape (Hutto 1998, Gillespie & Walter 2001) or be influenced by extrinsic factors, such as the physiognomy of vegetation. However, at local scales habitat use depends on intrinsic factors, such as food availability and plant composition (Hutto 1985, Peck 1989, Hewson et al. 2011). In addition, a higher number of resident species was found during the dry season. This result may be explained by the temporary changes in the detectability of species, which could have influenced the abundance patterns of certain species. For example, in the study area, the main breeding activities of birds occur during the dry season coinciding with flowering and fruiting (mainly of *Bursera* trees), so birds are often more active and therefore more conspicuous and/or territorial (Langen & Berg 2016). This allows a higher number of resident birds to be recorded, as have been found in others dry forest of western Mexico (Renton et al. 2018). On the other hand, the greater abundance of birds in the dry season can also be explained by the arrival of migratory birds that are usually gregarious and ubiquitous like *Tyrannus verticalis* and Cassin's Kingbird (*T. vociferans*). Some resident raptors, such

as Crested Caracara (*Caracara cheriway*) and Ferruginous Pygmy-Owl (*Glaucidium brasilianum*), were observed to only use the habitat during the dry season for perching or searching for food. Canopy conditions in TDFs are more open during the dry season because of the defoliation of most plants. In this scenario, some raptors and other species can probably move spatially to optimize their search for resources. Therefore, open habitats can favor foraging activities (Otieno et al. 2011), as observed in other dry forests (Vega-Rivera et al. 2010).

Interestingly, the resident flycatchers *Myiarchus tuberculifer* and *M. nuttingi* were also exclusively observed during the dry season and were only seen eating *Bursera* spp. fruits. Other studies have emphasized the close mutualistic relationship between *Bursera* species and flycatchers of the genus *Myiarchus* (Almazán-Núñez et al. 2015, 2016). These species also eat high densities of arthropods in the rainy season (Vega-Rivera et al. 2010). However, during the rainy season, flycatchers likely move to other local sites in search of additional resources that are not available in the study area.

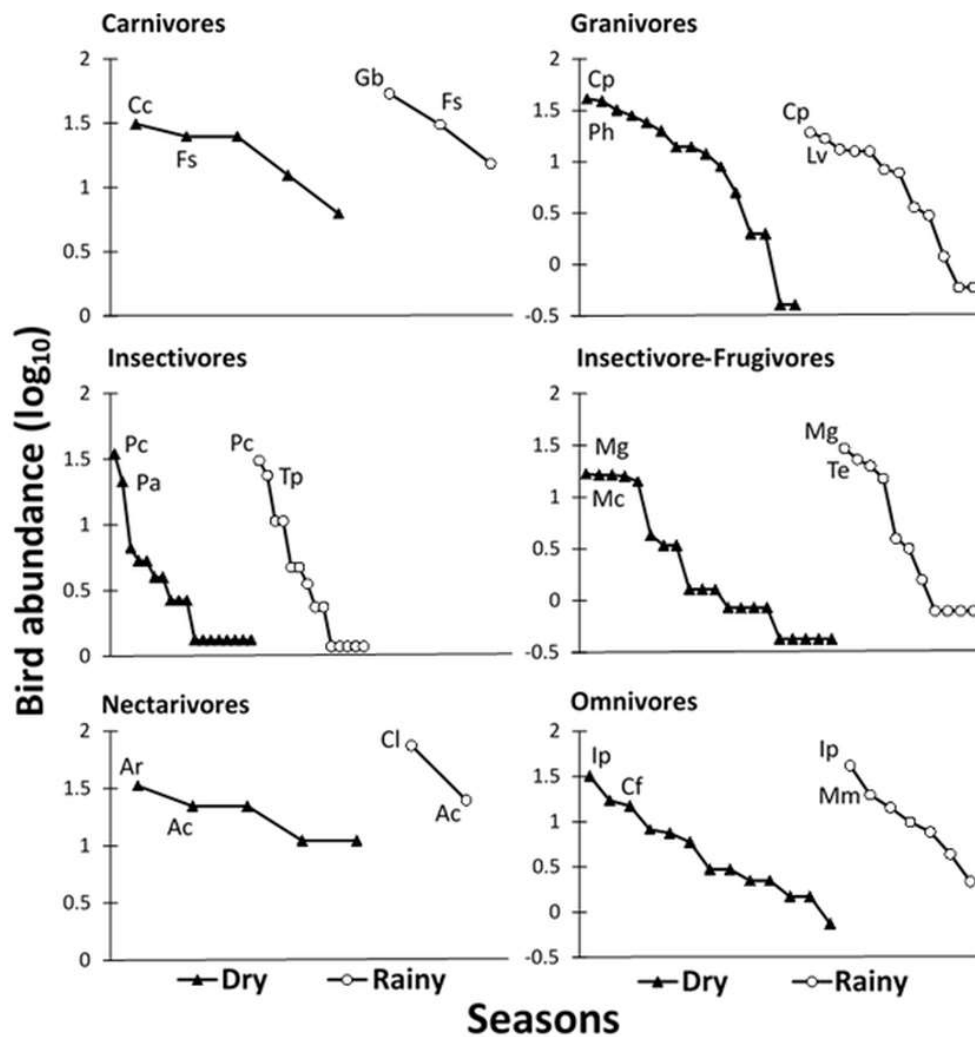


Figure 4. Rank-abundance curves for bird feeding guilds between the dry and the rainy season of a TDF in southwestern Mexico. The code for each species is defined in Appendix S1.

Differences in foraging between seasons. The abundance of insectivorous-frugivorous birds was significantly higher in the dry season. This result differs from several previous studies that reported an increase in the abundance of these birds during the rainy season (e.g., Corcuera 2001, Riehl & Adelson 2008, Tinoco 2009). During the rainy season, greater foliage cover leads to an increase in the abundance of insects (Borghesio & Laiolo 2004, Anjos 2006, de Lima et al. 2012), thus promoting the abundance of insectivorous birds as well. Meanwhile, during the dry season woody vegetation loses its leaves, reducing the habitat for many arthropods (Tovar-Sánchez et al. 2004, Vega-Rivera et al. 2010). Despite the decrease in arthropod density during the dry season, several insectivorous species show plasticity in their diet and eat different resources (e.g., mainly fruits of *Bursera* spp.; Peters et al. 2010, Morales-Betancourt et al. 2012, Mulwa et al. 2012; Almazán-Núñez et al. 2015, 2016).

Although the number of arthropods is higher in the rainy season (Borghesio & Laiolo 2004, Riehl & Adelson 2008), the number of fruits on trees of the

Bursera genus considerably increases in the dry season, and these fruits are used by several insectivorous bird species as a facultative resource (Almazán-Núñez et al. 2015). As a consequence of abrupt changes in the availability of resources at all trophic levels in the two seasons of the year, many birds that inhabit TDF are more generalist in their diet. For example, oriole species (*Icterus wagleri* and *I. pustulatus*) were observed eating different resources per season, including fruits (in the dry season), arthropods (in the rainy season) and flower nectar (at the end of the dry season). Dietary specialists, on the other hand, must move spatially according to the availability and abundance of food resources (Vega-Rivera et al. 2010). For example, *Setophaga coronata*, a typically insectivorous species, was observed removing fruits from *Bursera morelensis*, as did other parulids during the dry season. This diet plasticity has also been reported for mammals in other TDFs (Stoner & Timm 2004).

The abundance of omnivores was also higher in the dry than in the rainy season. This result differs from other studies that reported greater abundance

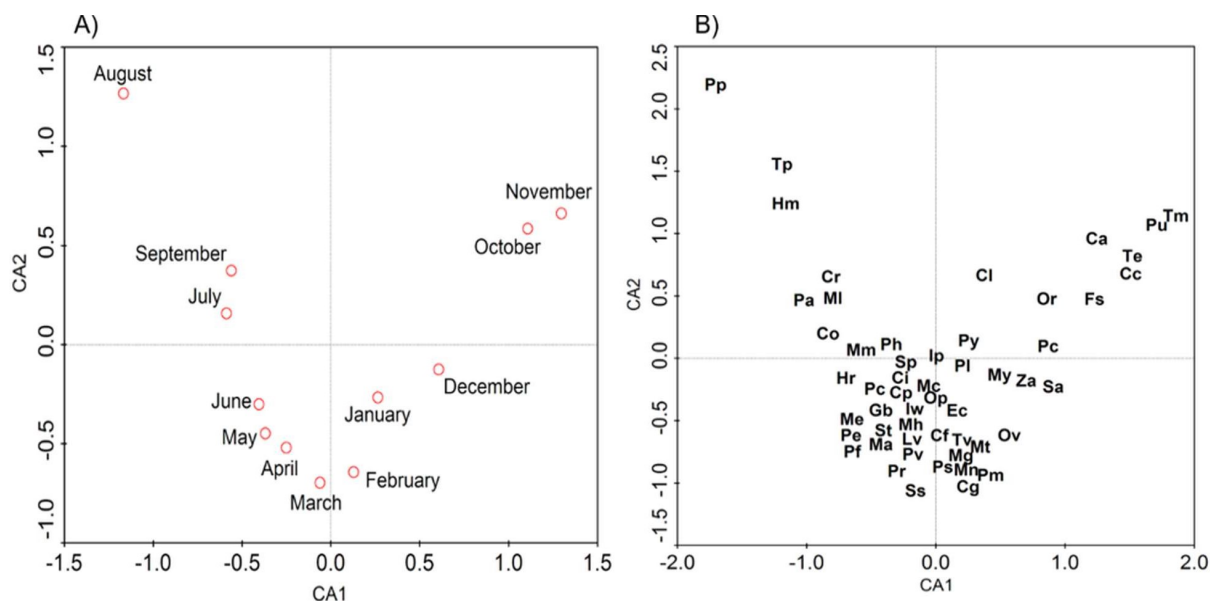


Figure 5. Correspondence analysis (CA) for the abundance of bird species observed during 12 months in a TDF of southwestern Mexico according to (A) months of the year and (B) bird species. The code for each species is defined in Appendix S1.

of omnivorous birds in the rainy season (e.g., Borghesio & Laiolo 2004, Tinoco 2009). In particular, as observed in the ordination analysis some species, such as the White-throated Magpie-Jay (*Calocitta formosa*), were more abundant in the dry season, especially during the breeding months when they are more territorial. Omnivores present a great amplitude in their trophic niche. For this reason, they are little affected when a resource diminishes or becomes scarce during certain seasons of the year. Different studies have demonstrated that omnivorous birds can be present in and adapt to different environments (Godoi et al. 2014, Girma et al. 2016, Katuwal et al. 2016). Moreover, the abundance of granivorous birds was associated with the rainy season, although this difference was not significant, and was also favored by the presence of species from the families Columbidae, Fringillidae, and Passerellidae. This result coincides with that obtained by Tinoco (2009) and Chazdon et al. (2011), who found a greater number of associated granivorous birds during the rainy season in TDFs of Ecuador and Mexico, respectively.

On the other hand, several studies have shown nectarivorous birds to be more abundant in the dry season (e.g., Malizia 2001, Borghesio & Laiolo 2004, Medina-van Berkum et al. 2016). However, in the present study, nectarivorous species also used the habitat in the rainy months when a diverse range of plants produce flowers (Flores & Espejel 1994, Medina-van Berkum et al. 2016).

Overall, the majority of the most abundant species did not vary between the seasons (e.g., Common Ground-Dove *Columbina passerina*, *Polioptila caerulea*, *Melanerpes chrysogenys*, Ruby-throated Hummingbird *Archilochus colubris*, and *Icterus pustulatus*). These birds may be responding to habitat structure and not to climatic conditions since a large num-

ber of these species occupy more than one type of habitat throughout the year (Jetz et al. 2007, Goetz et al. 2014).

In summary, our study yielded pronounced seasonal differences in the distributions of species richness, abundance, and some feeding guilds of birds between the dry and rainy seasons in a TDF in southwestern Mexico. The results of this study revealed that the dry season had a higher bird diversity. The presence of migratory species, reproductive activities, and seasonal changes in the composition and abundance of birds, who are dependent from particular seasonal resources (fruits of *Bursera* spp. in dry season), are the factors that cause seasonal differences in the bird assemblage.

The results of this study have implications for the conservation and management of TDF in the Balsas basin. In particular, TDF ecosystems are among the ecosystems most affected by deforestation and constant land use changes in Mexico (Quesada et al. 2009). Temporal variation in the abundance of a species or a set of species may have different implications for the ability of species to survive after a disturbance or loss of habitat (Loiselle & Blake 1992). In addition, under current climate-change scenarios species' populations may be diminished as a consequence of increasing temperature and decreasing precipitation, which may also result in longer dry seasons (Villers-Ruiz & Trejo 1997, Golicher et al. 2011). In this context, based on ecological niche modeling Prieto-Torres & Rojas-Soto (2016) predicted the future disappearance of TDFs in regions such as the Balsas river basin where our study area is located. As it has been shown that several species could modify their original ranges to occupy new locations as a result of climate changes (Møller et al. 2011), determining the monthly fluctuations in bird composition and abundance can provide a greater

understanding of the adaptability and tolerance of species to particular climate conditions.

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