



## BIRD COMMUNITIES RESPOND TO THE SEASONAL FRUIT AND FLOWER AVAILABILITY IN A FRAGMENTED TROPICAL ANDEAN LANDSCAPE

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**Abstract** · Fire is one of the main causes of fragmentation in tropical Andean forests. Fragmentation can influence plant reproductive phenology, which in turn affects bird communities. In the Bolivian Yungas, we investigated how the seasonal availability of fruits and flowers affects bird richness, abundance and bird community composition in forest edges and adjacent bracken (*Pteridium* ferns) dominated areas. We captured birds with mist nets at eight sites during the dry, transition and wet seasons, and recorded fruit and flower availability through phenological observations and plant collections. We examined variation in species richness and abundance using generalized linear mixed-effects models, and bird species composition in each season using multivariate analyses. Fruit availability was higher in the transition and wet seasons, and lowest in the dry season, while flower availability did not differ among seasons. Bird species richness and abundance were significantly higher in bracken areas, although there was significantly lower fruit availability than at the forest edge, and these were mainly generalist bird species that may be tolerant to disturbance. Total bird abundance increased with higher fruit availability in both habitats, and with flower availability at the forest edge. Bird species composition differed between forest edges and bracken areas in the transition and the wet seasons, being influenced by fruiting and flowering phenology in the dry and transition seasons, and elevation in all seasons. Our results show the varying seasonal influence of plant reproductive phenology on avian communities of disturbed habitats, although other large scale factors associated with fragmentation may also shape bird communities.

### Resumen · Las comunidades de aves responden a la disponibilidad estacional de frutos y flores en un paisaje andino tropical fragmentado

El fuego es una de las causas principales de fragmentación en bosques tropicales andinos. La fragmentación influye la fenología reproductiva de las plantas, que en su caso afecta a las comunidades de aves. En los Yungas de Bolivia, investigamos cómo la disponibilidad de frutos y flores estacional afecta la riqueza de especies, la abundancia y la composición de las comunidades en bordes de bosque y en áreas adyacentes áreas dominadas por bracken (helechos *Pteridium*). Capturamos aves con redes niebla en ocho sitios durante las épocas seca, de transición y húmeda; y registramos la disponibilidad de frutos y flores a través de observaciones fenológicas y colecciones de plantas. Examinamos la variación en riqueza y abundancia de especies usando modelos lineales generalizados de efecto mixto, y examinamos la variación en la composición de especies para cada estación análisis multivariados. La disponibilidad de frutos fue mayor en las estaciones de transición y húmeda, y fue menor en la estación seca. Por otro lado, la disponibilidad de flores no varió entre estaciones. La riqueza y abundancia de aves fueron mayores en áreas de bracken, mayor en la estación de transición y menor en la estación húmeda. Las especies de aves generalistas pueden beneficiarse de la deforestación. La abundancia total de aves incrementó con mayor disponibilidad de frutos. La composición de aves fue diferente entre bordes de bosque y áreas con bracken en las estaciones de transición y húmeda. La fenología de frutos y flores explicó la variación en composición de especies en las estaciones secas y de transición; la elevación fue importante en todas las estaciones. Otros factores a gran escala, quizás relacionados con la fragmentación, también pueden estar dando forma a las comunidades de aves.

**Key words:** Bolivia · bracken · foraging guild · *Pteridium* · reproductive phenology · Yungas

## INTRODUCTION

The increasing fragmentation of tropical forests has strong implications on biodiversity. One of the most important features of fragmentation is the increase of edge habitats, where originally forested habitats are adjacent to deforested areas (Haddad et al. 2015, Liu et al. 2019, Menezes Pinto et al. 2021, Razafindratsima et al. 2021, Chaves et al. 2022, Purificação et al. 2020). In the Andean tropical montane regions, one of the main causes of the increasing fragmentation are uncontrolled human-induced fires (Saavedra et al. 2014). After fire, bracken fern (*Pteridium esculentum* subsp. *arachnoideum*) colonizes the area and dominates the plant community around forests for a long time (Marrs et al. 2000). Forest regeneration is hindered and slow in these bracken-dominated habitats, mostly because forest-tree seeds hardly arrive and establish (Gallegos et al. 2016, Hartig & Beck 2003).

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Forest fragmentation affects ecological processes that are essential for ecosystem functioning, such as seed dispersal and pollination, which are the most vulnerable processes in the life cycle of plants (Neuschulz et al. 2016). In tropical forests, these processes are extremely important for biodiversity maintenance and are predominantly animal-mediated (Bascompte & Jordano 2007). Several studies suggest that seeds of over 75% of tree species in tropical humid forests are dispersed by animals, especially birds (Howe & Smallwood 1982, Muller-Landau & Hardesty 2009, Markl et al. 2012, Traveset et al. 2014), and that about 90% of angiosperm plants in tropical forests are pollinated by animals, many of which are vertebrates (Ollerton et al. 2011, Vizentin-Bugoni et al. 2018). Forest fragmentation can not only affect bird species richness, but also the composition of bird species assemblages (Laurance et al. 2011, Bovo et al. 2018), leading to changes in seed dispersal and pollination in which birds are involved (Sekercioglu 2006, Muller-Landau & Hardesty 2009, Traveset et al. 2014, Menezes et al. 2016, Pelayo et al. 2021). Therefore, understanding some of the factors that influence bird species' persistence is critical to maintaining ecosystem functioning. In this sense, resource availability — determined by plant reproductive phenology (i.e., timing of flower and fruit production; Pothasin et al. 2016)— influences the abundance and diversity of pollinator and frugivorous birds (Benavidez et al. 2023, Gonçalves da Silva et al. 2020), and thus the structure of seed dispersal and pollination interaction networks (Aguirre et al. 2011, García et al. 2011, Gonzalez & Loiselle 2016, Morente-López et al. 2018, Pelayo et al. 2021, Ramos-Robles et al. 2018). It is crucial to understand the role of phenology on these interacting ecological communities, especially for their conservation under rapid global changes (Encinas-Viso et al. 2012).

Here, we use edges of forest remnants in a bracken-dominated landscape to examine how a bird community is affected by the seasonal and habitat variation in fruit and flower availability. Specifically, we ask how the variation in fruit and flower resources during three seasons (dry, transition and wet seasons) and in two habitats (forest edge and the adjacent bracken-dominated areas) affect richness, abundance (recorded during this study) and composition of bird communities. We predicted that bird species richness and abundance would be higher in bracken areas (Gallegos et al. 2024) and during the transition season, as it is the birds' breeding season. We predicted that bird species composition would be different in each season, and would respond to fruit and flower availability.

## METHODS

**Study area.** Our study was conducted in the tropical Andes of La Paz, in the Sud Yungas province (16°24'37"S, 67°31'37"W) northwest of the town of Chulumani, in montane areas within a range of 1900 to 2300 m a.s.l. (Figure S1). We included and compared two habitats: forest edges and the surrounding bracken-dominated areas (hereafter called bracken areas). The forests in this area have been highly fragmented by human-induced fires and coca crops, and only two large continuous forest remnants remain (Figure S1). These forests are surrounded by bracken areas: fire-disturbed vegetation dominated by the fern *Pteridium esculentum* subsp. *arachnoideum* (bracken) and predominantly wind-dispersed successional shrubs (e.g., mostly Asteraceae and Melastomataceae species; Lippok et al. 2013), but also some bird-dispersed plants such as *Myrsine coriacea*, *Morella pubescens*, and numerous species of Ericaceae and Melastomataceae (López et al., unpublished data). On the other hand, the vegetation at forest edges is characterized by the presence of pioneer plant species such as *Myrsine coriacea* and *Cecropia elongata*, and a high abundance of species in the following most representative families dispersed by birds: Clusiaceae (e.g., *Clusia trochiformis*, *C. sphaerocarpa*), Euphorbiaceae (e.g., *Alchornea brittonii*, *A. grandiflora*,

Melastomataceae (e.g., *Miconia calvescens*, *M. cordata*), Lauraceae (e.g., *Nectandra acutifolia*), Myrtaceae (e.g., *Myrcia paiva*, *Eugenia* spp.), Phyllanthaceae (e.g., *Hieronyma moritziana*, *H. oblonga*), Rubiaceae (e.g., *Palicourea* cf. *grandiflora*, *Psychotria carthagenensis*) (Lippok et al. 2014). Plant families with flowers visited and pollinated by birds are, for example: Campanulaceae (e.g., *Siphocampylus* spp.), Heliconiaceae (e.g., *Heliconia* spp.), and Rubiaceae (e.g., *Palicourea* cf. *grandiflora*) (Boehm et al. 2018, Lippok et al. 2014).

The wet season in this area goes between late November to April, the dry season from mid-April to August, and a transition season from late August to November (Saavedra et al. 2014, Molina-Carpio et al. 2019). The mean annual temperature is 19.5°C, and the mean annual precipitation is ca. 1,500 mm (Molina-Carpio et al. 2019).

**Bird surveys.** We conducted bird surveys in eight sites on the edges of the two main forest relicts (Figure S1). At each site, birds were captured using eight mist nets (9 x 2.5 m, 36-mm mesh) set at about 0.5 m from the ground. Four mist nets were located in the forest edge at 20 m from the forest margin, and four in the bracken areas at ca. 20 m from and parallel to the forest margin. We captured birds during the transition (August–November 2020), wet (December 2020–March 2021), and dry seasons (May–June 2021). We visited each of the eight sites once per season. During each visit, we opened mist nets from 06:30 to 18:30 h for 2–3 days (ca. 126–170 net-hours per season; one mist net open for one hour equals one net-hour, Blake & Loiselle 2009). Our total sampling effort was 3608 net-hours.

All species captured were assigned to one of the following foraging guilds: frugivores, insectivores, nectarivores, and omnivores (based on Herzog et al. 2016, Billerman et al. 2022). We registered the total species richness and counted the number of individuals in this study (hereafter abundance) for each bird species at each habitat and site.

**Data on fruiting and flowering plants.** To obtain data on the fruiting and flowering plants available to birds, we conducted monthly plant phenological observations at different sites in the study area, particularly at the edges of the two large forest relicts (Figure S1), and collected plants at the study sites (Table S1). We compiled a total list of plant species available to birds, with presence or absence of ripe fruits and flowers per month. We recorded phenology of a total of 143 plant species, of which 118 species had fruits available to birds, and 39 species had flowers available to birds (see Table S1). In this list, we assigned a primary habitat affinity to each plant species, Forest or Bracken. Plant habitat affinity was based on plant abundance, expert knowledge (S. Gallegos and C. López), and literature review (e.g., Killeen et al. 1993). Phenology data was compiled into one variable, which consisted on the total numbers of plant species with ripe fruits (sppFr) and flowers (sppFl) in each site per month (i.e., considering the month in which we conducted bird captures at each site), per season, and per habitat (based on habitat affinity).

**Statistical analyses.** Using generalized linear models (GLM), we examined differences in fruit and flower availability, with season and habitat as fixed effects, considering a Poisson distribution of errors (link log) in the *lme4* package (Bates et al. 2014). Differences were tested using the *Anova* function of the package *car* (Fox & Weisberg 2019).

To examine the variation in total bird species richness and abundance in response to the availability of plant species bearing fruits and flowers, we used generalized linear mixed-effects models (GLMM) performed with the *lme4* package (Bates et al. 2014), using a Poisson distribution (log link). Fixed

effects were season, habitat and fruiting and flowering plant richness (sppFr, sppFl). Site was the random effect to account for the nested structure of our sampling design. We report the most parsimonious model as determined by the lowest Akaike Information Criterion score (AICc) corrected for small sample size. All deviations from homoscedasticity were visually checked with residual plots in the *DHARMA* package (Hartig 2022). We also compared each best model with a null model and calculated p-values from log-likelihood ratio tests (LRT). Model fit calculations and comparisons were conducted using the package *MuMin* (Barton 2022).

To examine the effects of habitat on bird community composition in each season, we used a nonparametric permutation test (perMANOVA with the *adonis2* function in the *vegan* package). To examine the effect of fruiting and flowering plant availability on the composition of bird communities in each season, we used canonical correspondence analysis in the *vegan* package (Oksanen et al. 2022). The environmental variables we used for each CCA were sppFr, sppFl, and elevation; the variation in elevation among sites was only 1900–2300 m a.s.l., but we considered it as a variable because bird species composition can change substantially even with 500 meters of elevation (Blake & Loiselle 2000). All analyses were performed in R v. 4.2.0 (R Core Team 2022).

## RESULTS

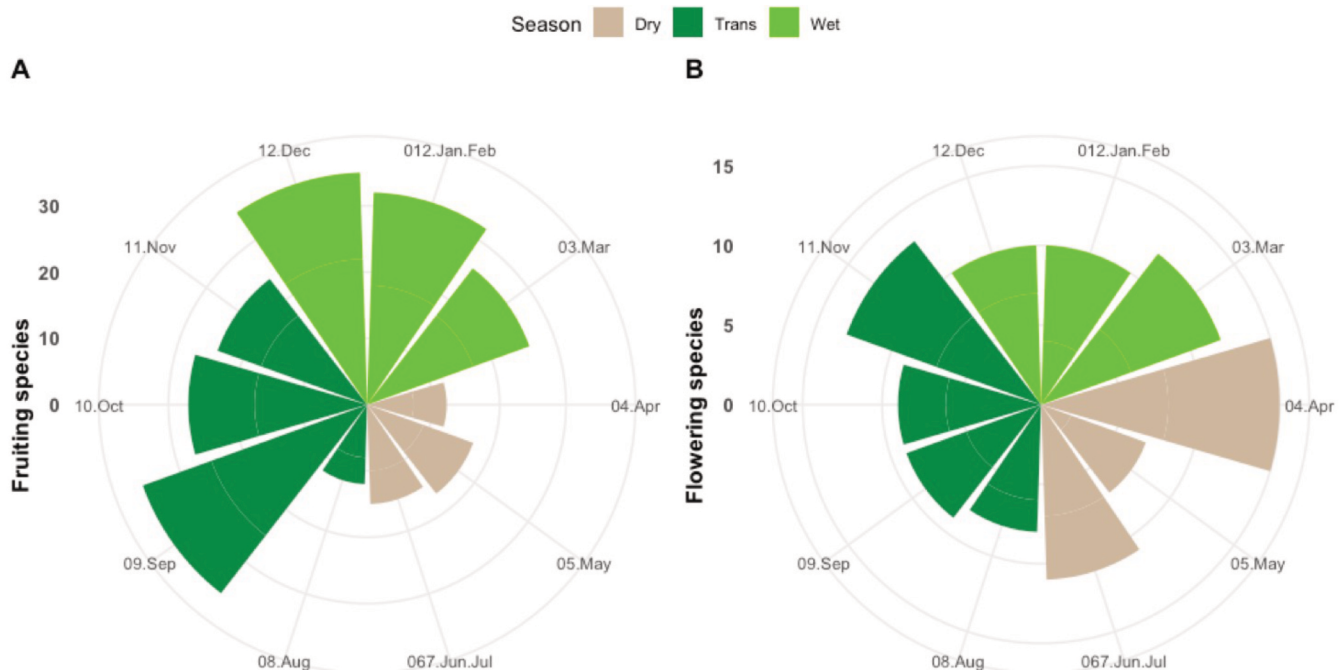
**Fruit and flower availability.** Fruit availability was higher during the transition and wet seasons, and lowest in the dry season ( $\chi^2 = 18.29$ ,  $p < 0.001$ ; Figure 1A, Table S1); flower availability did not differ among seasons ( $\chi^2 = 0.288$ ,  $P = 0.865$ ; Figure 1B). The distribution of fruit data was unimodal, with greater fruiting richness in the transition months, whereas flowering data had two peaks, one in April during the dry season and one in November during the transition season (Figure S2). Fruit availability was significantly higher at the forest edge than in bracken areas ( $\chi^2 = 17.57$ ,  $P < 0.001$ ); flower availability did not differ between habitats ( $\chi^2 = 1.387$ ,  $P = 0.238$ ).

**Bird species richness and number of individuals in relation to fruit and flower availability.** We captured a total of 311 birds

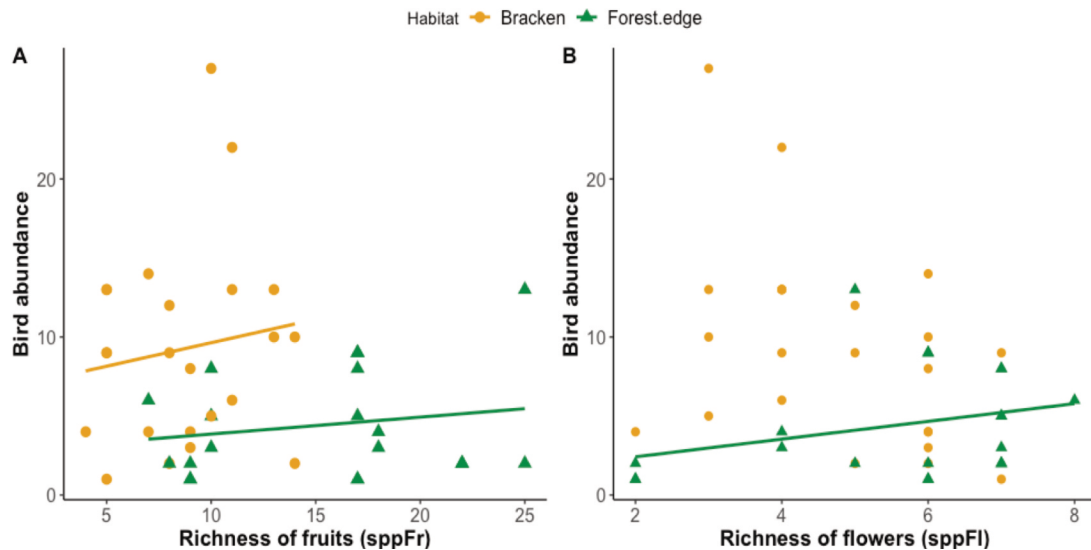
belonging to 74 species (Table S2). Of these, 16 were frugivorous, 18 nectarivorous, 31 insectivorous, and eight omnivorous. Due to small sample size, granivorous species (e.g., *Spinus xanthogastrus* or *Catamblyrhynchus diadema*) were included in the omnivorous foraging guild (Table S2). Bracken areas had significantly higher species richness ( $\chi^2 = 24.37$ ,  $P < 0.001$ ) and abundance ( $\chi^2 = 42.60$ ,  $P < 0.001$ ) than forest edge areas. Bird species richness did not differ among seasons ( $\chi^2 = 5.73$ ,  $P = 0.056$ ), but bird abundance was significantly higher in the transition season ( $\chi^2 = 12.90$ ,  $P < 0.001$ ).

The best models for total bird species richness and abundance included habitat, and fruiting and flowering richness (sppFr and sppFl) (Table S3). Fruit and flower species richness in the bracken area had no significant effect on total bird species richness. We found a positive relationship between bird species richness and flower species richness at the forest edge, where the number of plant species with bird pollinated flowers was higher (LRT:  $\chi^2 = 43.57$ ,  $P < 0.001$ ,  $R^2_c = 0.66$ ; Table S3). Total bird richness and abundance were lower in the forest edge than in the bracken area. Total bird abundance significantly increased with higher richness of fruits (sppFr) in both habitats (Table S3, Figure 2A) and with higher richness of flowers (sppFl) in the forest edge (LRT:  $\chi^2 = 78.78$ ,  $p < 0.001$ ,  $R^2_c = 0.789$ ; Table S3, Figure 2B).

**Bird composition in relation to fruiting and flowering availability in each season.** During the dry season, there was no difference in bird species composition between forest edges and bracken areas (perMANOVA: Pseudo- $F = 1.512$ ,  $df = 1$ ,  $P = 0.051$ ; Figure 3A). Canonical correspondence analysis (CCA) explained 25% of the variance in species composition (CCA Anova: Pseudo- $F = 1.224$ ,  $P = 0.03$ ). Axis 1 ( $\lambda_1 = 0.67$ ) was positively correlated with elevation (0.51) and negatively correlated with richness of fruiting species sppFr (−0.419) and flowering species sppFl (−0.30), representing a gradient of lower richness of fruits/flowers and bracken areas on the right, and higher richness of fruits/flowers and forest edges on the left (Figure 3A). Insectivorous species captured only in forest edges (e.g., *Platyrinchus mystaceus* – PLMY.I; Table S1), nectarivorous species (e.g., *Metallura tyrianthina* – METY.N,



**Figure 1.** Circular plots showing the number of A) fruiting and B) flowering plant species in each season: dry (light brown), transition (dark green) and wet season (light green).



**Figure 2.** Effect of A) richness of fruits (sppFr) and B) richness of flowers (sppFI) on total bird abundance, according to habitat: bracken areas (orange circles) and forest edges (green triangles). Lines represent significant relationships.

*Adelomyia melanogenys* – ADME.N) captured only in bracken areas, and frugivorous species (e.g., *Mionectes striaticollis* – MIST.F, *Elaenia albiceps* – ELAL.F) captured in either of the habitats were separated along this first axis (Figure 3A, Table S2). Axis 2 ( $\lambda_2 = 0.46$ ) was negatively correlated with sppFI ( $-0.88$ ) and sppFr ( $-0.55$ ).

During the transition season, there was a significant difference in species composition between forest edge and bracken areas (perMANOVA: Pseudo- $F = 2.589$ ,  $df = 1$ ,  $P = 0.002$ ; Figure 3B). CCA explained 27% of the variance in species composition (CCA Anova: Pseudo- $F = 1.407$ ,  $P = 0.01$ ). Axis 1 ( $\lambda_1 = 0.55$ ) had a high negative correlation with sppFr ( $-0.95$ ), representing a gradient from forest edge on the left to bracken areas on the right (Figure 3B). Frugivorous species such as *E. albiceps* – ELAL.F, captured only in bracken areas, or species such as *Chiroxiphia boliviana* – CHBO.F or *M. striaticollis* MIST.F, captured only at forest edges, were segregated along this axis (Figure 3B, Table S2). Axis 2 ( $\lambda_2 = 0.46$ ) was negatively correlated with elevation ( $-0.90$ ) and positively correlated with sppFI (0.62), representing a gradient of higher elevation on the bottom and lower on the top (Figure 3B).

During the wet season, there was a significant difference in species composition between habitats (perMANOVA: Pseudo- $F = 1.837$ ,  $df = 1$ ,  $P = 0.032$ ; Figure 3C). CCA explained 25% of the variation in bird species composition (CCA Anova: Pseudo- $F = 1.249$ ,  $P = 0.07$ ). Axis 1 ( $\lambda_1 = 0.64$ ) was positively correlated with elevation (0.70) and negatively with sppFr ( $-0.67$ ) and sppFI ( $-0.51$ ), representing a gradient from forest edge on the left, and bracken areas on the right (Figure 3C). Frugivorous species captured only in one of the two habitats (e.g., *E. obscura* – ELOB.F in bracken areas or *Turdus amaurochalinus* – TUAM.F and *C. boliviana* – CHBO.F in forest edges) were separated along this axis (Table S2, Figure 3C). Axis 2 ( $\lambda_2 = 0.59$ ) was positively correlated with sppFI (0.63) and sppFr (0.62).

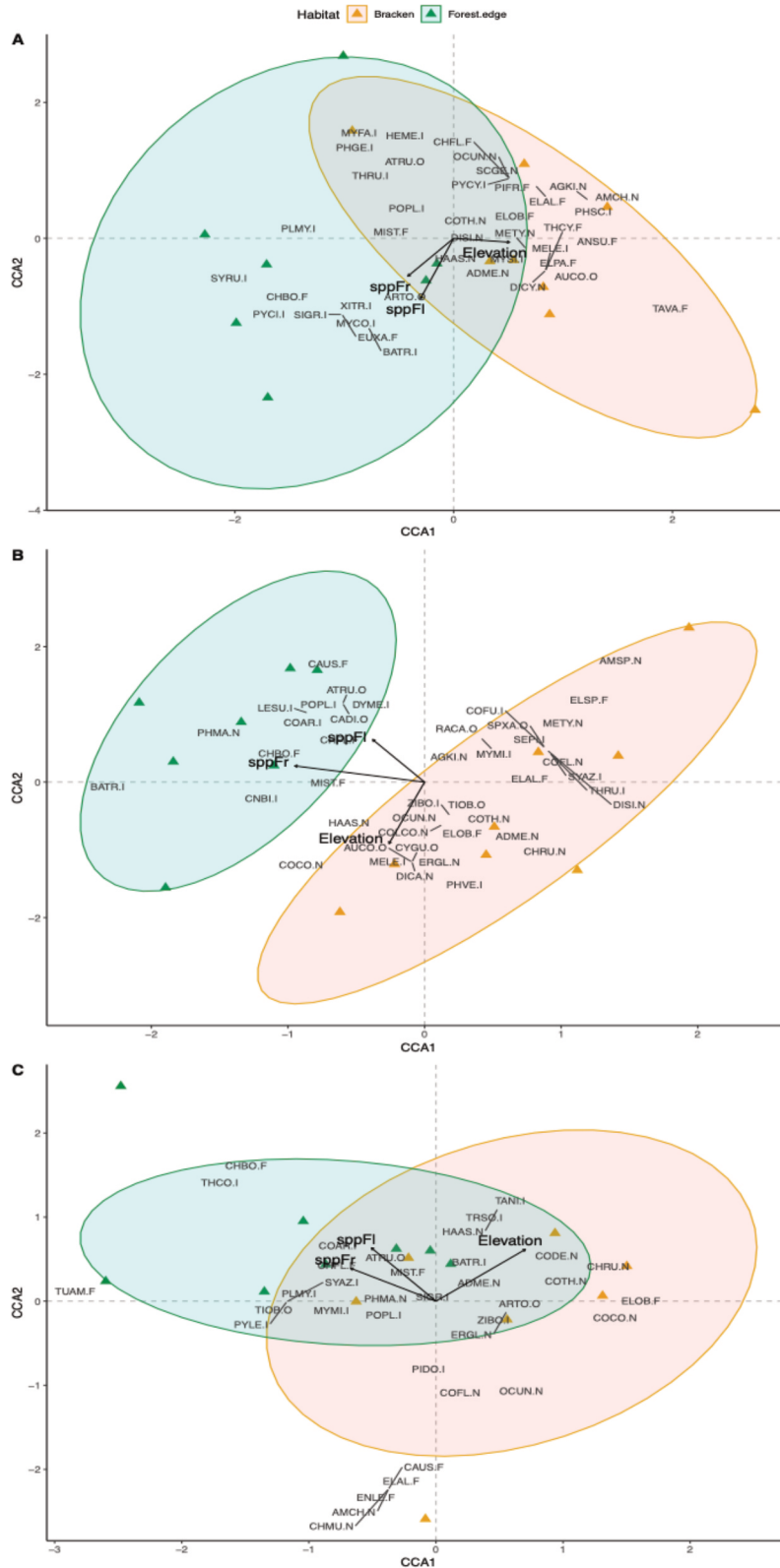
## DISCUSSION

Our results show that bird communities respond to the seasonal variation in plant reproductive phenology. Fruiting plant richness positively influenced total bird abundance but had no effect on bird richness. There was a significant difference in bird composition between bracken and forest edges in the transition and the wet seasons, but not in the dry season. Fruiting and flowering phenology, along with elevation significantly explained the variation in bird species composition during the dry and

transition seasons.

As we predicted, we found that total bird richness and abundance were higher in bracken areas than in forest edges, even though bracken areas had fewer fruiting plants. This could be related to a high diversity of bird generalist species that are able to survive in deforested areas (O’Dea & Whittaker 2007, Gomes et al. 2008, Carlo & Morales 2016, De Souza Leite et al. 2022), and especially generalist frugivorous species (e.g., in the families Thraupidae, Turdidae, Tyrannidae; Carlo et al. 2022), that are common in early and mid-successional stages of forest regeneration (Shankar Raman et al. 1998, Catterall et al. 2012). Generalist species represent 29.7% of all the bird species we recorded, and among frugivorous species, 86.7% are generalist (Table S2). Generalist species can be tolerant to habitat disturbances, as they can forage in early regeneration sites and even in open habitats (Carlo & Morales 2016, Gonçalves da Silva et al. 2020). Some of these generalist species (e.g., *Ramphocelus carbo* – RACA.O) can be very resilient to disturbances such as fire, as it was reported in a study conducted also in Yungas montane forests, located at about 45 km from our study area (Montaño-Centellas & Garitano-Zavala 2015). Also, bracken areas may provide habitat complexity, which means a larger concentration of the required resources (Tschardt et al. 2012), especially for these generalist bird species. However, we recognize that these are ecotonal areas where birds may be continuously moving between forest edges and bracken, and perhaps in the future if we sample birds in each habitat at a farther distance from the forest margin, we might get different results.

Bird abundance did increase with richness of fruiting plants, as found in other studies: in montane tropical forests in the Atlantic rainforest in Brazil (Hasui et al. 2007, Banks-Leite et al. 2010, Gonçalves da Silva et al. 2020), in Mt. Kinabalu in Borneo (Kimura et al. 2001), or in more temperate areas such as some Mediterranean forests in Europe (Carnicer et al. 2009). The highest richness and abundance of birds happened during the transition season, which coincides with the avian breeding season in the tropical Andes, lasting from July–Aug to November (Jankowski 2010, Merkord 2010). On the other hand, the lowest bird richness and abundance, especially of frugivorous birds, were found during the wet season; one reason for this could be that frugivorous birds undertake seasonal and elevational migrations before and after the breeding season (Loiselle & Blake 1991, Kimura et al. 2001, Chaves-Campos 2004, Boyle et al. 2011, Villegas et al. 2016). In



**Figure 3.** CCA ordinations (triplots) of bird communities in each season: A) Dry, B) Transition and C) Wet season. Dark-grey letters correspond to the species, triangles to the sites, and black arrows to the environmental variables. Ellipses of habitats represent 90% of confidence intervals. The environmental variables are: richness of plants with fruits (sppFr), richness of plants with flowers (sppFl) and Elevation. The arrows show the direction (orientation with respect to the axis) and strength (length) of the correlations between environmental variables and bird species composition. The last letter of each species code denotes its foraging guild (see Table S2).

some cases, these movements may be triggered by strong storms, which can reduce fruit availability and foraging opportunities, as has been found in humid montane forests of Costa Rica (Boyle et al. 2010).

Fruit and flower richness were the main factors explaining

bird species composition, especially in the transition season. In this season, the species correlated with high fruit richness (characteristic of forest edges) are essential frugivorous/disperser species (e.g., *C. boliviana* – CHBO.F, *M. striaticollis* – MIST.F). In fact, in every season there were frugivorous or omnivorous species correlated with fruit species richness, for

example *Arremon torquatus* – ARTO.O in the dry season, or *Chlorospingus flavopectus* – CHFL in the wet season. On the other hand, bird species composition strongly responded to variations in elevation in all seasons, despite the short elevational range (400 m) among our study sites. Further, during the dry and wet seasons, elevation (and its associated factors like temperature or humidity; McCain 2009) was a more important factor than fruit and flower availability in structuring bird species composition. These responses in some cases were guild-specific; for instance, insectivorous species were more common at lower elevations, perhaps because in these areas there are more optimal conditions for the production of their food resources, such as insects (McCain 2009). Conversely, frugivorous and nectarivorous species were uniformly distributed along the elevational gradient in ordination space.

The composition of birds between forest edges and bracken areas did not differ during the dry season, probably due to the lower fruit availability at this time compared to the transition and wet seasons. Some bird species showed habitat exclusivity in each season, however during the dry season, birds were captured in both habitats (e.g., *M. striaticollis* is mostly found in forest edges but it was captured in both habitats during the dry season). Higher fruit availability benefits not only frugivorous species but also other foraging guilds, such as omnivores. Some plants, common to forest edges and second-growth areas (e.g., *Miconia* or *Myrsine*) are good fruit resources for frugivorous birds (Saavedra et al. 2014, Gonçalves da Silva et al. 2020), for omnivorous birds, and could also attract insectivorous birds by attracting insect pollinators (Renner 1989). Plants like many *Miconia* species have a long and asynchronous fruiting period, likely ensuring frugivore fidelity (Vidal et al. 2014), and since they are typical of early stages of succession, they could provide important habitat and fruit resources during times of food shortage in the forest (e.g., during the dry season in our study area) (Blake & Loiselle 2001, Vidal et al. 2014). In periods of food scarcity, birds tend to rely more on each other for foraging, and they may form mixed-species flocks (Saracco et al. 2004, Mangini & Areta 2018, Montaña-Centellas & Jones 2021). In the Atlantic forest of Brazil, Develey & Peres (2000) showed that the number of species attending flocks was related to arthropod availability rather than to fruit availability. Frugivorous birds have the ability to track fruit resources and switch diets in periods of scarcity, for example between fruits and invertebrates or between fruits and flowers (Quiñán et al. 2018); this could be happening in our study area. On the other hand, flower resources tended to have a higher richness during the dry season (although not significantly), which is consistent with other Neotropical forests (Fleming 2005).

Studying fruit and flower phenologies is crucial for understanding animal responses and the potential for ecosystem changes (Morellato et al. 2016, Abernethy et al. 2018). Changes in plant phenologies can have community-wide responses, for instance they can potentially affect other plants through competition or facilitation for seed dispersers and pollinators; moreover, crashes in fruit availability can dramatically affect vertebrate frugivores (Morellato et al. 2016). However, studies on phenology in the tropics are few because these environments were considered aseasonal until recently, phenologies of tropical trees in Central and South America have just started in the 90s, and long-term datasets are scarce (Abernethy et al. 2018). From the few long-term studies that exist, we know that climate change is effecting shifts in phenology (Abernethy et al. 2018). Specifically for our study, we acknowledge that the plant phenology records were not obtained directly in each study site. However, our work experience in the area (i.e., over ten years), allows us to propose that the plant phenology information we present here fairly describes the fruit and flower resources available to birds in each site. We recommend that future studies should thoroughly characterize the plant reproductive phenology in each study site, and should also assess it

throughout the years, for us to better understand how fruit and flower availability affect these bird communities.

Overall, we show that bird communities change spatially (according to habitat) and seasonally in response to the available flowering and fruiting phenology. These influences on bird species composition were more pronounced during the dry and transition seasons. At the small spatial scale of our sites, deforestation may not be as detrimental as expected. At this scale, bracken areas may represent rich and complex habitats with a high concentration of food resources, especially for generalist bird species. In disturbed environments such as this, sensitivity to habitat disturbance may have a more direct effect on bird communities than food availability (Restrepo et al. 1999, Hasui et al. 2007). We suggest that future studies should assess the influence of other large-scale factors related to fragmentation, because they could be contributing in structuring bird communities in this landscape.

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