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PATRONES DE CO-OCURRENCIA, ELECCIÓN DE HÁBITAT Y COMUNICACIÓN HETEROESPECÍFICA DENTRO DE BANDADAS MIXTAS DE AVES

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

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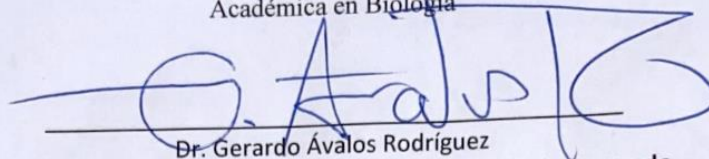Ciudad Universitaria Rodrigo Facio, Costa Rica

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DEDICATORIA Y AGRADECIMIENTOS

Deseo dedicar esta tesis a mi mamá, Lorely, por los incontables momentos en que me ha apoyado, dado consejo y acompañado con todo el cariño y amor. También a mi papá, Elías, por su soporte en estos años de tesis y haberme acompañado en los días de campo.

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Esta Tesis fue aceptada por la Comisión del Programa de Estudios de Posgrado en Biología de la Universidad de Costa Rica, como requisito parcial para optar al grado y título de Maestría Académica en Biología
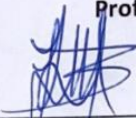
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RESUMEN

Las bandadas mixtas son uno de los sistemas más extendidos e interactivamente dinámicos en la Tierra, pero los factores que median su cohesión aún no se comprenden del todo. Su estudio a través de un enfoque evolutivo podría darnos una idea de cómo son seleccionados ciertos rasgos específicos de las especies en niveles evolutivos más altos, como en el contexto de una bandada mixta. Nuestros objetivos se centraron en estudiar qué especies mantienen la composición de la bandada y cómo lo hacen a través de sus interacciones con otras especies y el entorno en el que se encuentran. Descubrimos que el establecimiento de la bandada no es un proceso estático y que los roles de las especies en las bandadas pueden cambiar (de líder a seguidor), en relación con la presencia y abundancia de otras especies y el entorno en que la bandada se encuentre. Las bandadas mixtas en las tierras altas de Costa Rica son tan dinámicas que ocurren en todos los hábitats presentes en el área de estudio, pero su composición tiende a variar mucho por factores intrínsecos como las interacciones con los demás miembros de la bandada o extrínsecos como el poder formar parte de una bandada en cierto hábitat. Así mismo la evidencia espectral de color sugiere que las bandadas de tierras altas de Costa Rica no han sufrido los efectos evolutivos a nivel de grupo sino posiblemente a nivel de comunidad de aves en general.

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INTRODUCCIÓN GENERAL

Grupos Mixtos de Animales

Las asociaciones heteroespecíficas generalmente surgen cuando individuos de diferentes especies, al interactuar entre si, se benefician por la formación de grupos (Stensland et al., 2003; Farine et al., 2014; Swift et al., 2018). Los beneficios de los individuos o especies que integran estas asociaciones heteroespecíficas son un mejor aprovechamiento del tiempo de forrajeo, detección de depredadores, mayor posibilidad de acceder a hábitats con mejor calidad, y mejorar la defensa de nidos (Farine et al., 2015; Swift et al., 2018). Agregarse en grupos se da tanto por efectos propios del tamaño del grupo (Morse, 1970), como por las características inherentes a cada especie en cuanto a la información que transmiten y reciben por los otros individuos (Goodale et al., 2010; Swift et al., 2018). Dentro de los grupos se producen diferentes tipos de información a nivel intraespecífico, como llamadas, o señales en plumajes, que son aprovechadas por las otras especies miembros del grupo, creando un flujo de información pasiva entre ellos (Goodale et al., 2010; Beauchamp & Goodale, 2011, Croft et al., 2011; Pagani-Nuñez et al., 2018). Un flujo de información pasiva es aquella información que es recibida e interpretada por un receptor, que no es por el cual la información se emitió en primera instancia o al menos no fue emitida exclusivamente hacia el. Se debe profundizar en comprender las dinámicas que rigen la composición (especies e individuos) de los grupos mixtos tomando en cuenta las señales pasivas, como la coloración del plumaje, o la complejidad del hábitat y la fenología de las especies en un sitio (Goodale et al., 2010; Croft et al., 2011; Pagani-Nuñez et al., 2018). Por lo tanto, un enfoque que incluya tanto al ensamblaje de grupos mixtos, así como a las interacciones sociales (factores intrínsecos) y con el medio (factores extrínsecos), brindaría un panorama más amplio de los patrones que rigen la formación de grupos mixtos. Este enfoque representa un panorama más amplio para entender las dinámicas de grupos mixtos y no solo bajo ciertas condiciones como lo han hecho estudios anteriores que se han centrado en describir los patrones de composición y los beneficios de formar grupos mixtos únicamente.

Los grupos mixtos son comunes en muchos ambientes y hábitats (Arbelaéz-Cortéz et al., 2011; Stensland et al., 2003), y se han reportado en diferentes taxa, desde peces, hasta mamíferos e insectos (Stensland et al., 2003; Goodale et al., 2010; Smith et al., 2018). Por ejemplo, en una comunidad de peces de varios lagos de Inglaterra se estudió el nivel de asociación interespecífico entre las especies nativas y *Leucaspius delineatus* una especie de pez invasora (Beyer et al., 2010). Encontraron que la especie invasora formó asociaciones más fuertes con las especies nativas que en aquellas asociaciones formadas exclusivamente por especies nativas (Beyer et al., 2010). Esto se debe al hecho de que la especie invasora disminuye la depredación al asociarse con especies de fenotipo similar y previene ataques de depredadores atraídos por individuos sobresalientes en un grupo (Beyer et al., 2010).

También varias especies de ungulados (e.g. zebras y gazelas) africanos tienden a agregarse cerca de las manadas migratorias de ñus (*Chonocheates gnou*), cuando llegan a sus territorios, más de lo esperado por azar (Sinclair, 1985). Estas asociaciones con las grandes manadas de ñus producen un efecto de dilución, debido a la gran cantidad de individuos, que disminuye la depredación de las especies que se unen (Sinclair, 1985). Estas agregaciones surgen a pesar de la presión por recursos alimenticios, ya que todas las especies involucradas comparten alrededor del 80 % de la dieta (Sinclair, 1985).

Bandadas Mixtas de Aves

Es en aves donde la formación de grupos heteroespecíficos está más ampliamente distribuida, a nivel geográfico y taxonómico, se han reportado desde los trópicos hasta la Taiga, y desde ambientes boscosos hasta costeros, además de que la composición de especies cambia según la localidad (Morse, 1970; Greenberg, 2001; Cordeiro et al., 2015). A estos grupos de aves cuya formación depende de respuestas positivas entre miembros de la misma o de diferente especie se les llama bandadas mixtas (Morse, 1970; Gram, 1998; Farley et al., 2008; Harrison & Whitehouse, 2011). En los bosques tropicales son una de las organizaciones sociales de aves más comúnmente encontradas (Goodale & Beauchamp, 2010) y por las condiciones ambientales que ahí se dan se mantienen todo el año (Powell, 1985; Gram, 1998). Estas condiciones contrastan con sitios templados, como los bosques del noreste de Estados Unidos, donde el tamaño y composición de bandadas mixtas lideradas por carboneros (Paridae: *Baeolophus* sp.; *Parus* sp.)

está limitada a la época no reproductiva (Morse, 1970; Pagani-Nuñez et al., 2018; Swift et al., 2018).

Las bandadas mixtas de aves están ensambladas principalmente por un grupo nuclear de especies al cual se unen ocasionalmente otras especies por razones como el traslape de territorios durante el paso de las bandadas (Morse, 1970; Gram, 1998; Goodale & Beauchamp, 2010; Cordeiro et al., 2014; Pagani-Nuñez et al., 2018). El grupo nuclear lo conforman especies líderes (Morse, 1970; Pagani-Nuñez et al., 2018) que son importantes en la formación y cohesión (permanencia de la unión de individuos en el tiempo) de las bandadas (Morse, 1970; Pagani-Nuñez et al., 2018). Las especies satélites comúnmente son las que siguen a las líderes, y presentan menor número de individuos por especies; se dice que son estas especies las que mayor beneficio obtienen en cuanto al acceso a recursos y protección de depredares producto de la información que generan las especies líderes (Morse, 1970; Goodale et al., 2017; Pagani-Nuñez et al., 2018).

Las bandadas mixtas de aves han sido ampliamente estudiadas en diferentes regiones geográficas. Sin embargo, dichas investigaciones se han centrado mayoritariamente en evaluar las relaciones competitivas de las especies que las forman (Morse, 1970; Sridhar et al., 2009; Arbelaéz-Cortez et al., 2011), las ventajas que confieren sobre el forrajeo (Morse, 1970; Sridhar et al., 2009), y la disminución del riesgo de depredación (Morse, 1970; Sridhar et al., 2009; Harrison & Whitehouse, 2011; Colorado & Rodewald, 2015). Los procesos que rigen su composición (especies e individuos), establecimiento y cohesión, siguen siendo poco conocidos (Greenberg, 2001; Colorado & Rodewald, 2015). Por ejemplo, se ha encontrado que la vocalización de especies líderes puede influir en la formación de bandadas mixtas (Chaves-Campos, 2003) y que incluso la tasa de vocalización puede influir sobre la cohesión y el mantenimiento de las bandadas (Pagani-Nuñez et al., 2018). Pero, hay otros rasgos dentro de los miembros de las bandadas que no se han explorado, tales como las interacciones entre los taxa de las bandadas (ej., patrones de co-ocurrencia; Barberán et al., 2012), la influencia del hábitat en la dinámica de las bandadas mixtas, o el papel de la coloración del plumaje en el establecimiento y cohesión de las bandadas (Graves & Gotelli, 1993; Greenberg, 2001; Goodale et al., 2010; Colorado & Rodewald, 2015).

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CAPÍTULO 1

Color insights in mixed-species flocks from Costa Rican highlands: Revisiting social mimicry hypothesis

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Abstract: Mixed-species flocks' cohesion underlying factors are not well understood yet. Their comprehension through an evolutionary approach might give us insights into how species specific traits could be selected at higher levels, such as in a mixed flock interactive context. Moynihan's social mimicry hypothesis states that birds in mixed-species flocks may present a convergence in coloration, which will make them less conspicuous compared to other bird species, as a way to compensate the flock acoustic conspicuousness. Our objective was to test Moynihan's social mimicry hypothesis in mixed-species flocks from Costa Rican highlands by comparing species that form mixed-species flocks to those that do not. We measured plumage reflectance in 20 flocking and 20 non-flocking species that are phylogenetically close to the flocking species. In each species we measured 8 body parts (crown, nape, mantle, rump, breast, sides, and dorsal side of external rectrices and primaries) of 6 adult individuals (3 per sex) using reflectance spectrophotometry. We used a tetrahedral colorspace visual model and alpha shapes to calculate color volumes and compare plumage patches among species. The color spectral data evidence suggest that social mimicry has not been an important selective factor in promoting formation of mixed-species flocks in Costa Rican highlands, because the color volumes occupied

by flocking species is not different from that of the flocking species. Both the diverse evolutionary origin of Costa Rica's endemic species and their isolation have likely been important in the composition of mixed-species flocks, rather than social mimicry.

Key words: group traits, highland evolution, evolutionary dynamics, plumage coloration, vision

Introduction

Mixed-species assemblages occur in a wide range of taxa (Goodale et al., 2017) and generally arise when their members benefit by forming groups (Stensland et al., 2003; Farine et al., 2014; Swift et al., 2018). Examples include fish shoals in cold waters in England reefs (e.g.,10 sp, Beyer et al., 2010), mammal herds in Africa savannas (e.g., 8 sp, Sinclair, 1985), and birds in the Amazon (e.g., 21 sp, Cordeiro et al., 2015) and North America (e.g., 5 sp, Morse, 1970). In all assemblages, the overall benefits are similar for individual members: better access to resources and reduced predation risk (Goodale et al., 2020). However, the benefits to individuals or species are unequal (Aplin et al., 2014, Krams et al., 2020). Conflict between species or individuals can results in hierarchies and/or interactions affecting the benefits for all individuals in the assemblage (Martínez et al., 2017). In some specific cases, benefits may be reduced to the extend where some members may incur fitness costs. This has been demonstrated to occur, for example, in Fork-tailed Drongos (*Dicrurus adsimilis*) that produce deceptive alarm calls used to kleptoparatize members of the mixed-flock (Babblers and meerkats). When these deceptive calls are produced too often, they become ineffective and target flock members do not abandon their food items or do not respond at all; incurring in fitness loses (Flower, 2011).

Some behaviors, like eavesdropping, may reduce the fitness of some members of the flock while benefiting others (Goodale et al., 2010; Swift et al., 2018). Eavesdropping is the use of information intended for others to one's own benefit (Magrath et al., 2015), which usually has positive implications for the individuals intercepting the information (Pollock et al., 2017).

Heterospecific eavesdropping is key in mixed-species flock establishment because it allows flock members to gather beneficial information about potential predators or foraging sites with a low cost compared with intraspecific eavesdropping (Pollock et al., 2017). This is because members of flocks use different information modalities for eavesdropping. For instance, some bird species learn calls that other species use to indicate the presence of army ant swarms (Chaves-Campos, 2003; Pagani-Nuñez et al., 2018), or mammals that may interpret that Plains zebras' stripes (*Equus quagga*) are a cue for gathering in African savannas (Ireland & Ruxton, 2017). As such, visual cues specifically help to discriminate individuals from their own and other species, detect predators, and mediate interactions between species (Muñoz-Ramírez et al., 2017). Therefore, coloration and patterns may provide important signals for communication and recognition among members of mixed-species assemblages.

Two main hypotheses have been formulated to explain the range of colors/patterns found in bird species that form heterospecific flocks. The social mimicry hypothesis theorizes that darker and duller plumages in birds may promote aggregation and cohesion of heterospecifics because their visual conspicuity is reduced, which counteracts their vocal conspicuity (Moynihan 1968). The economy of signals hypothesis may also benefit plumage convergence among flocking species, because it is more likely that individuals eavesdrop information from single color traits than from several different color traits with redundant information (Moynihan, 1968; Diamond, 1987; Greenberg, 2001; Harrison & Whitehouse, 2011). These two hypotheses (Moynihan 1960, 1968) are not mutually exclusive, but complementary. Even though the social mimicry and economy of signals approach seems likely in mixed-species flocks, it does not appear to be the case at least in tropical highland bird communities (Hilty et al., 1986; Stiles & Skutch, 1989; Ridgeley & Greenfield, 2001; Schulenberg et al., 2010), perhaps because these hypotheses fail to take into consideration factors external to the mixed-flock itself, such as predator pressure or microhabitat usage that may also influence the evolution of plumage traits. Furthermore, the phylogenetic relationships of the studied species in a region may cause false positives for the mimicry and economy of signals hypotheses. Closely related species are more likely to present similar plumage coloration because of the phylogenetic factor (e.g. shorebirds) and not because of external evolutionary pressures.

In the context of mixed-species flocks, coloration contrasting the background may influence the ability to locate flock members or promote the discrimination among members of the group (Moynihan, 1968; Greenberg, 2001). For instance, the contrasting coloration of the crown, breast and rump may mediate the number of interactions, dominance, and cohesion among members of monospecific flocks of finches. When these patches are altered in finches, the perception of the altered individuals change, because they become visually alien to the flock, which results in aggression (Watt et al., 1998). Other patches that may be involved in cohesion are the rectrices and primaries, because they are regions associated with flight take-offs and may serve as a social signaling of fast and intermittent movement behaviors (Moynihan, 1960, Baker & Parker, 1979). The background or habitat where a bird species occurs influence the conspicuity of these visual signals and may affect the degree in which the signals are effectively transmitted and perceived by other individuals (Uy & Stein, 2007).

Other than a mechanism promoting the formation of mixed-species flocks, social mimicry has been proposed to facilitate competition avoidance, gain access to resources, and predator avoidance (Prum, 2014). For example, in the woodpecker family (Picidae) some species are very similar in plumage patterns to the human eye (Miller et al., 2019). This system of species was assessed worldwide and found that a big portion of the woodpecker species similarity was explained by the geographic overlap of the distributions and not by shared ancestry, habitat or climate factors (Miller et al., 2019). Neotropical highland bird communities are a good model to test the social mimicry hypothesis (Moynihan, 1968) because mixed-species flocks congregate year-round, primarily by resident species (Powell, 1979, 1985; Stiles & Skutch 1989). This means that these species regularly interact the better part of their lifespan and, as a community, use all the forest strata, from understory to canopy, for foraging and movement (Powell, 1985). Indeed, assemblages composed of understory specialists and canopy specialists can potentially coexist and make use of all microhabitats, i.e., tree trunks, tree branches, bromeliads in branches, mosses, vines, and the ground. If there are some plumage traits that may have been selected as grouping traits in bird plumages at the flock level, the evidence might be present in Neotropical highland mixed-species flocks. This is likely because it is within this region that, even across habitats and seasons, mixed-species flocks share the highest level of cohesiveness compared to other sites where mixed-species flocks occur.

Our objective was to test Moynihan's social mimicry hypothesis in mixed-species flocks from Costa Rican highlands by comparing species that form mixed-species flocks to those that do not. If Moynihan's social mimicry hypothesis details a mechanism leading to mixed-species assemblage formation, we predict that plumage colors from flocking species would be more similar to one another relative to the non-flocking species. This will be the first step in finding quantitative and objective evidence-based data on bird´s perception of color for Moynihan's social mimicry hypothesis (1968). Alternatively, if we find that social mimicry hypothesis is not an underlying factor driving mixed-species flock establishment, we may find a different scenario where the evolutionary pressure that is promoting convergence in plumages is the habitat and not the flock. Under this scenario, we will expect that species that present convergent plumage traits would be the majority in the bird community, regardless of their flocking behavior. Under the last scenario social mimicry hypothesis itself would be rejected, but any other form of mimicry is still possible but at the community level and not at the mixed-species flock level.

Methods

Study group

The Costa Rican highland bird community is relatively small compared to the lowlands. It is composed of around 90 species overall (Stiles & Skutch, 1989, Sandoval & Sánchez, 2020), from which nearly half of the species are endemic to the highlands of Costa Rica and western Panama (Barrantes et al., 2011). Highland mixed-species flocks in Costa Rica are not limited to a single group of birds (i.e. tanagers or furnarids), but a large variety of species from different families like Passerellidae, Thraupidae, Furnaridae, and Troglodytidae (Powell, 1979; Muñoz et al., *in prep*). We have recorded 34 species forming mixed-species flocks in this habitat type (Muñoz et al., *in prep*), and each flock is composed of 5 species and 11 individuals on average (Powell, 1979, 1985, Muñoz et al., *capítulo 2*). Costa Rican highland mixed-species flocks are also highly dynamic, usually led by the Sooty-capped Chlorospingus (*Chlorospingus pileatus*) or the Spangle-cheeked Tanager (*Tangara dowii)*, and followed by species like the Ruddy

Treerunner (*Margarornin rubiginosus*), Yellow-thighed Brushfinch (*Atlapetes tibialis*) and the Black and Yellow Silky-flycatcher (*Phainoptila melanoxantha*) (Table 1; Muñoz et al., *capítulo 2*).

To test the hypothesis that social mimicry influenced the formation of assemblages in the Costa Rican highland bird community, we determined if the flocking species are more similar among themselves than to the non-flocking species. We accomplished this by comparing the colors displayed by species that form mixed-species flocks, and closely related species found in highlands but that do not form mixed flocks. The selection of species included in the non-flocking group was performed by selecting the most closely related species, based on current phylogeny, which occurs in the study area (same genus when possible or family when none co-existed). For example, the Mountain Thrush (*Turdus plebejus*) and the Spotted Barbtail (*Premnoplex brunnescens*) are flocking species, so we chose as non-flocking species the Clay-colored Thrush (*Turdus plebejus*) and the Spot-crowned Woodcreeper (*Lepidocolaptes affinis*) which are from the same genus and family respectively (Table 1). In cases for which more than one species of the same genus fell under the selection criteria for non-flocking species, we included both species (i.e. Black-billed and Orange-billed Nightingale-thrush, Table 1).

Data collection

We conducted this study using museum specimens of flocking and non-flocking species in Costa Rican highlands (n = 36 species, SM1). We did a qualitative assessment of the overall plumage condition of the specimens and excluded specimens with damaged feathers or with color degradation. We selected six specimens per species, three per sex, because many species present dichromatism (differences in color related to the sex), even cryptic dichromatism (variations in each sex undetectable by the human eye). We selected only skins of adult birds, because usually juveniles differ in plumage coloration from adults and their presence in mixed-species bird flocks is occasional (Berner & Grubb, 1985; Develey & Stouffer, 2001). We measured the coloration of 199 specimens (3 specimens per sex available for most; Table 1). We targeted specific feather patches (crown, nape, mantle, rump, breast, sides, and dorsal side of rectrices and primaries), which have been reported to promote flocking behavior or used by

flocking species to locate and recognize other individuals (Guhl & Ortman, 1953; Moynihan, 1960; Baker & Parker, 1979; Watt et al., 1998).

Color measurement

We quantified plumage reflectance as the proportion of light reflected in relation to a pure white standard (WS-2, Ocean Insight). From each body part, we took five reflectance measurements, which we averaged for analyses. Between each measurement of the same patch, we moved the sample probe at least 3 mm, keeping a perpendicular position against the plumage by using a rubber stopper (Andersson & Prager, 2006). For species that presented a contrasting plumage pattern or spots over 3 mm wide (e.g. *Premnoplex brunnescens* breast), we recorded two separate sets of measurements for the region, one focusing on the spots and the other focusing on the dominant plumage coloration. The coloration of those patterns, or the patterns themselves, could be a heterospecific cue for other species for recognition (Stoddard & Prumm, 2008). All data are made available upon request, and will be deposited and available on the spectral data repository Nature's Palette (Bitton et al. in prep) once launched (expected January 2022).

Statistical analyses

We performed all spectral analyses using the package "pavo" version 2.0 (Maia et al., 2013, 2019) implemented in R (R Core Team, 2020). We first averaged the five measurements per patch per individual and removed all electrical noise using a LOESS-smoothing function (Maia et al., 2013, 2019). We calculated the xyz coordinates of all sampled species by body parts (flocking and non-flocking species) in avian tetrahedral colorspace. These coordinates were used to assess the colorspace volume of the flocking and non-flocking groups of species using two approaches, convex hull and alpha shapes (Gruson, 2020). The xyz coordinates were calculated using generic UV sensitive and non-UV sensitive tetrahedral colorspace visual models (Endler & Mielke, 2005). We used this model of colour perception because it is a generalization of how tetrachromatic birds perceive colours (Stoddard & Prum, 2008) without requiring species-

specific information (e.g., receptor-noise limited model; Vorobyev & Osorio, 1998). In addition, our research questions addresses the bird community and not the individual perception of colors by each species.

For each of the eight selected patches we calculated the observed differences between the volume of colors displayed by the flocking and non-flocking groups of species using two methods, convex hulls and alpha shapes (Gruson, 2020) for the two visual systems (UV sensitive and UV insensitive), generating 32 plumage color volume scores. We compared these scores to null distributions generated through a randomization process. Each of the 32 null distributions were the product of 1000 iterations which consisted of randomly assigning a category (flocking and non-flocking) to each of the species from the xyz coordinates pool, calculating a volume for each group, and calculating the difference between the two. Finally, we wanted to determine if the flocking species where more similar among themselves than non-flocking species. For this, we calculated the color volume for each study species using the spectral data of all patches from six individuals by species and using alpha-shapes (Gruson, 2020). Then we calculated the mean difference in color volume of each flocking species against all other flocking species and compared it against the non-flocking species color-volume differences. We did this using two-sample T-tests and F-tests of equality of variances.

Results

We did not find any evidence to support Moynihan's social mimicry hypothesis in the highland bird community of Costa Rica. If social mimicry was a factor in the development of the grouping, we would have expected to find flocking species to be more similar with reduced color volumes. We compared our observed values to null distributions generated by a randomization process and none of the patches showed a biologically relevant difference in coloration when compared with values expected by chance (Fig.1). The results were consistent across all the output null distributions using all the approaches available to the date (convex-hull and alpha shapes). Similarly, we did not find significant differences when comparing flocking and non-flocking species color volumes mean differences (t = 0, d.f. = 29.5, p = 1) nor variances ($F_{1,17}$ = 0.44, d.f. = 17, p = 0.95). Thus, contrary to our predictions, flocking and non-flocking species

occupy the same spectrum in the color-space and in similar proportions. Most of the output null distributions presented a normal distribution (Fig. 1, Fig. 2, SM), but some presented a bi-modal (rump and primaries) or uniform distributions (flanks). Rump and primaries are body areas with little variance in colors, but when the colors vary it is contrasting, e.g., white and black tips on the primaries. This could led to obtain a bi-modal distribution on these patches. Similarly, flanks do not vary much, and when it does is subtle (orange and yellowish coloration), leading to a uniform distribution.

Even though we did not find supporting evidence for social mimicry, some patches differed between flocking and non-flocking species, though these differences were not significant. These include differences in color volumes for the nape (convex hull-UV sensitive only, p = 0.17) and the flanks (UV and non-UV sensitive) when using both convex hull (p = 0.13 and p = 0.11 respectively) and alpha-shapes (p = 0.15 and p = 0.17 respectively; Fig 1, Fig. 2, SM). Only the nape patch differed between flocking species and non-flocking counterparts, when the color volume was calculated using alpha-shapes and a UV-sensitive visual model (Table 1, Fig.1B). In all of these cases, the color volume occupied by the flocking species was smaller than that of the non-flocking species.

Discussion

The spectral data evidence that we present from flocking and non-flocking species suggest that social mimicry has not been an important selective factor in promoting formation of mixed-species flocks in Costa Rican highlands. The composition of highland Costa Rican bird communities has some peculiarities that could influence the composition of mixed-species flocks. Around 30 % of Costa Rican highland bird species are endemic, to the highlands of Costa Rica and western Panama, and with a diverse and unrelated ancestry (Barrantes, 2009, Barrantes et al., 2011). The high endemism in these highlands is a consequence of isolation on mountain peaks since the Pleistocene, and 50 % of these endemic species are regular participants of mixed flocks (Muñoz et al., *in prep*). The isolation of these bird species in relatively small areas has

undoubtedly imposed frequent interactions among them in a relatively stable climatic environment since the Pleistocene (Barrantes, 2009; Barrantes et al., 2011). Therefore, both the diverse evolutionary origin of the endemic species and their isolation have likely been important factors in the composition of mixed-species flocks. This is in contrast to original context of the social mimicry hypothesis, which has been suggested to be an important evolutionary factor driving the composition of mixed-species flocks in other environments (Beauchamp & Goodale, 2011). Groupings on oceanic islands, such as he brown and black New Guinean bird flocks for example, may be particularly appropriate to test the effect of either isolation and diverse evolutionary origin, or social mimicry on composition of mixed-species flocks (Moynihan, 1968; Diamond, 1981, 1987).

Predation pressure has been considered an underlying factor for the evolution of social mimicry (Moynihan, 1968; Barnard, 1979) and also for mixed-species flocking behavior (Goodale et al., 2020). In Costa Rican highlands, according to eBird occurrences (ebird.org), the overall presence of potential predators is lower than in the rest of the country. Therefore, the reduced predation pressure on Costa Rican highland bird communities may have favored acoustic communication (loud and noisy flocks) over visual communication, e.g., social mimicry. However, quantitatively measures of predation have yet to be obtained. A study by Pomara et al. (2003) has shown that not all species in mixed flocks respond equally to the presence of predators, suggesting that predation pressure may influence flock composition. It showed, for example, that only one in four species of warblers in Panamanian coffee fields spent less time alert for predators and more time foraging when part of a mixed-species flocks (Pomara et al., 2003).

If social mimicry had been important in the evolution and composition of Costa Rican highland mixed-species flocks, the assembling species would have more similar visual cues among themselves independent of the phylogenetic relation (Moynihan, 1960, 1968). In this study we focused on potential visual cues coming from the plumage in general, but we did not consider the pattern or arrangements of colors on the birds' bodies. Plumage patterns, as well as their colors and behaviors associated to those pattern patches, may give a broader view of how visual cues may affect flocking behavior among on different species (Negro et al., 2020). Visual cues displayed through plumage patterns could act at a different interaction scale. Rather than

mediate communication among all members of a flock, patterns may facilitate interactions between pairs of species. No studies have yet tested this idea.

Our results also included a trend whereby the nape and flanks were nearly different between flocking and non-flocking species. We do not perceive this as evidence for social mimicry being present in mixed-species flocks. In the case of the nape, these differences are better explained by a strong and unknown selection force for UV plumages in one or two of the analyzed species, because the difference was only present when the model was sensitive to UV. In the case of the flanks, if social mimicry caused the differences, we would expect that the same would happen in more exposed areas like the mantle or the rump and that is not the case. We would expect the flanks to be relevant for communication if these mixed-species flocks flew over longer distances. On the contrary, these flocks move from one perch to another, hiding their flanks. Another scenario that needs to be tested is the focus point of the flock members when moving. If flock members focus more on individuals by their side than in front, this would suggest that signals on the flanks of the usual leader species may influence grouping on mixed-species flocks.

Direct evidence for the role of social mimicry on birds mixed-species flocks or other groups is lacking, and though some systems seem to present obvious mimicry to the human eye, it may not be the case for birds. Birds differ in the density and type of photoreceptors when compared to humans (Stoddard & Prum, 2008). For instance, it has been proposed that small flycatchers mimic larger non-closely related species, e.g., Great Kiskadee and Broad-billed flycatcher (Tello et al., 2009; Prum, 2014). These flycatchers seem to have quite similar yellow plumages and brownish wings, but when reflectance was analyzed the authors found that the colors were dissimilar enough for a bird to distinguish from one another (Meneses-Giorgi & Cadena, 2020). On the contrary, reflectance measurements on *Ceroglossus* ground beetles have showed primary evidence for Mullerian mimicry among sympatric beetle species (Muñoz et al., 2016). Studying plumage reflectance on flocking and non-flocking species is a first step to understanding different ways social mimicry can influence flocking bird composition. However, closer inspection of, for instance, pairs of species within flocks with similar plumage pattern may reveal other information of the effect of mimicry on the evolution and formation of mixed-species flocks.

Acknowledgements

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Tables

Table 1. List of species from the highlands of Costa Rica that either form, or do not form, mixed species flocks which were included in this study and do not form part of mixed-species flocks

Flocking species	Non-flocking species
Collared Trogon - *Trogon collaris* N=4	Resplendent Quetzal - *Pharomachrus mocinno* N=2
Hairy Woodpecker - *Dryobates villosus* N=6	Hoffmann´s Woodpecker - *Melanerpes hoffmannii* N=6
Ruddy Treerunner - *Margarornis rubiginosus* N=6	Red-faced Spinetail - *Cranioleuca erythrops* N=6
Streak-breasted Treehunter - *Thripadectes rufobrunneus* N=6	Spot-crowned Woodcreeper - *Lepidocolaptes affinis* N=6
Spotted Barbtail - *Premnoplex brunnescens* N=6	Silvery-fronted Tapaculo - *Scytalopus argentifrons* N=4
Mountain Elaenia - *Ealaenia frantzii* N=6	Yellow-bellied Elaenia - *Elaenia flavogaster* N=6
Olive-striped Flycather - *Mionectes olivaceus* N=3	Social flycatcher - *Tyrannus melancholicus* N=6
White-throated spadebill - *Platyrinchus mystaceus* N=4	Black-capped flycatcher - *Empidonax atriceps* N=5
Gray-breasted Wood-wren - *Henichorhina leucophrys* N=6	Black-faced Solitaire - *Myadestes melanops* N=6
Mountain Thrush - *Turdus plebejus* N=6	Clay-colored Thrush - *Turdus grayi* N=6
Black and Yellow Silky-flycatcher - *Phainoptila melanoxantha* N=6	Long-tailed Silky-flycatcher - *Ptiliogonys caudatus* N=6
Black-cheeked Warbler - *Basileuterus melanogenys* N=6	Wrentrhush - *Zeledonia Coronata* N=6
Collared Redstar - *Myioborus torquatus* N=6	Northern Emerald Toucanet - *Aulacorhynchus prasinus* N=6
Spangle-cheeked Warbler - *Tangara dowii* N=6	Blue-gray Tanager - *Thraupis episcopus* N=6
Yellow-thighed Brushfinch - *Atlapetes tibialis* N=5	Rufous-collared Sparrow - *Zonotrichia capensis* N=6
Golden-browed Chlorophonia - *Chlorophonia calllophrys* N=6	Prong-billed - *Semnornis frantzii* N=4
Common Chlorospingus - *Chlorospingus flavopectus* N=6	Black-billed Nightingale-thrush - *Catharus graciliristris* N=6
Sooty-capped Chlorospingus - *Chlorospingus pileatus* N=6	Orange-billed Nithingale-thrush - *Catharus frantzii* N=6

Figures

Figure 1. Color volumes calculated using alpha-shapes and a UV-sensitive model. Red lines mark where the observed values of overlap fall for a two-tailed test on a null distribution for A) Crown, B) Nape, C) Mantle, and D) Rump. Blue represent the color volume occupied by flocking species, while red the non-flocking species.

Figure 2. Color volumes calculated using alpha-shapes and a UV-sensitive model. Red lines mark where the observed values of overlap fall for a two-tailed test on a null distribution for A) Breast, B) Flanks, C) Rectrices, and D) Primaries. Blue represent the color volume occupied by flocking species, while red the non-flocking species.

Supplementary Material. 1. Color volumes calculated using convex hull and a UV-sensitive model. Red lines mark where the observed values of overlap fall for a two-tailed test on a null distribution for A) Crown, B) Nape, C) Mantle, and D) Rump. Blue represent the color volume occupied by flocking species, while red the non-flocking species.
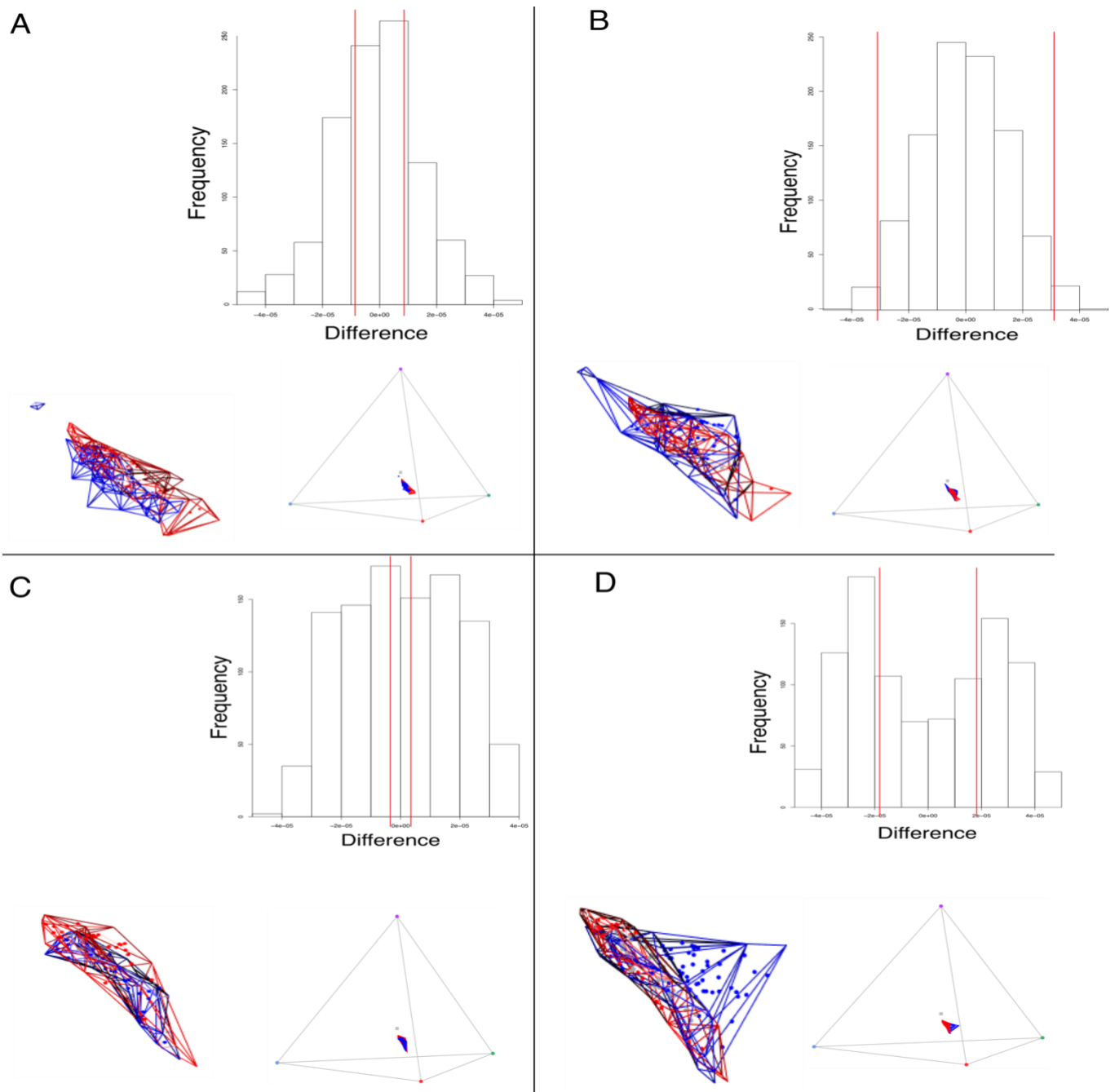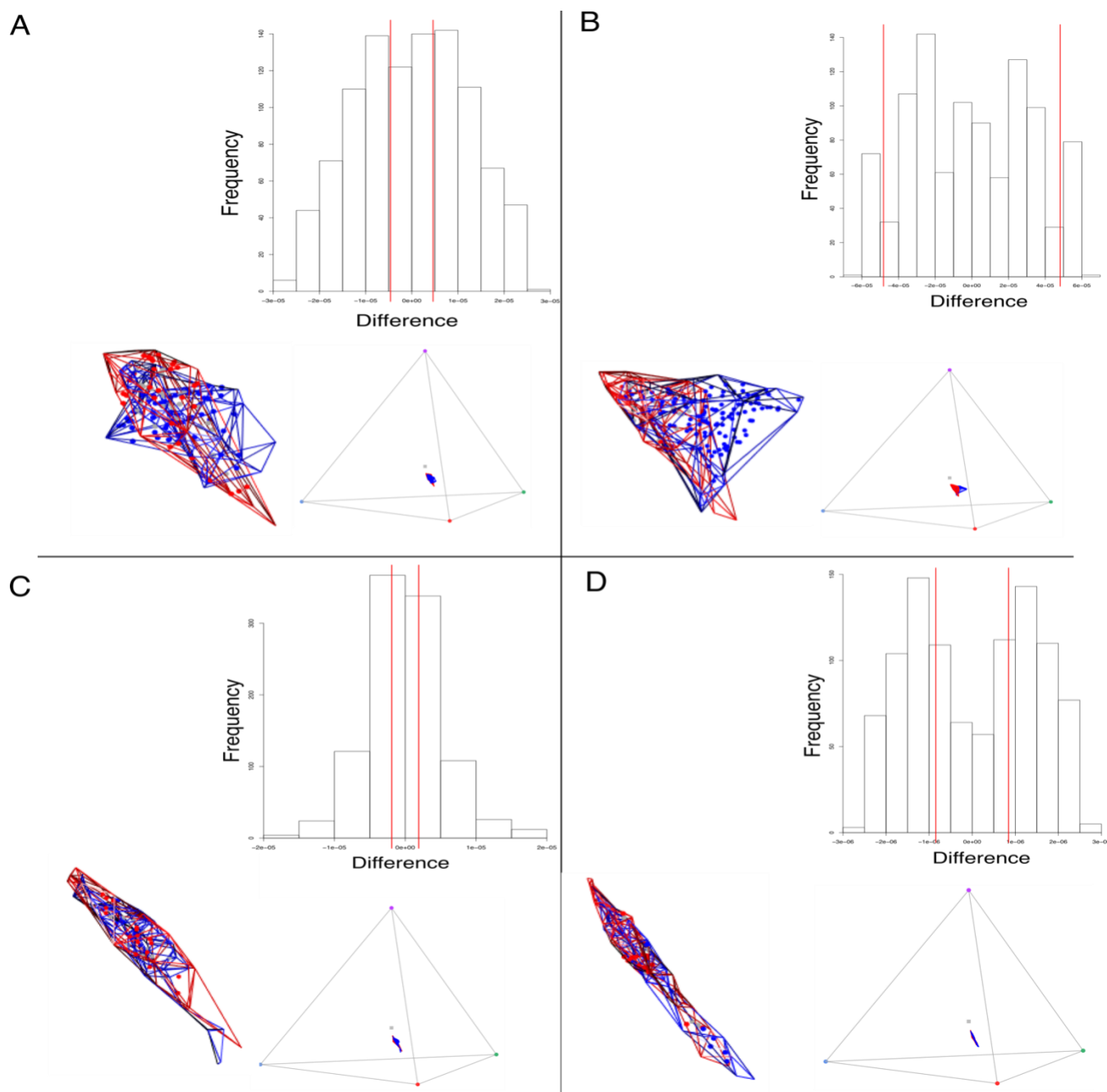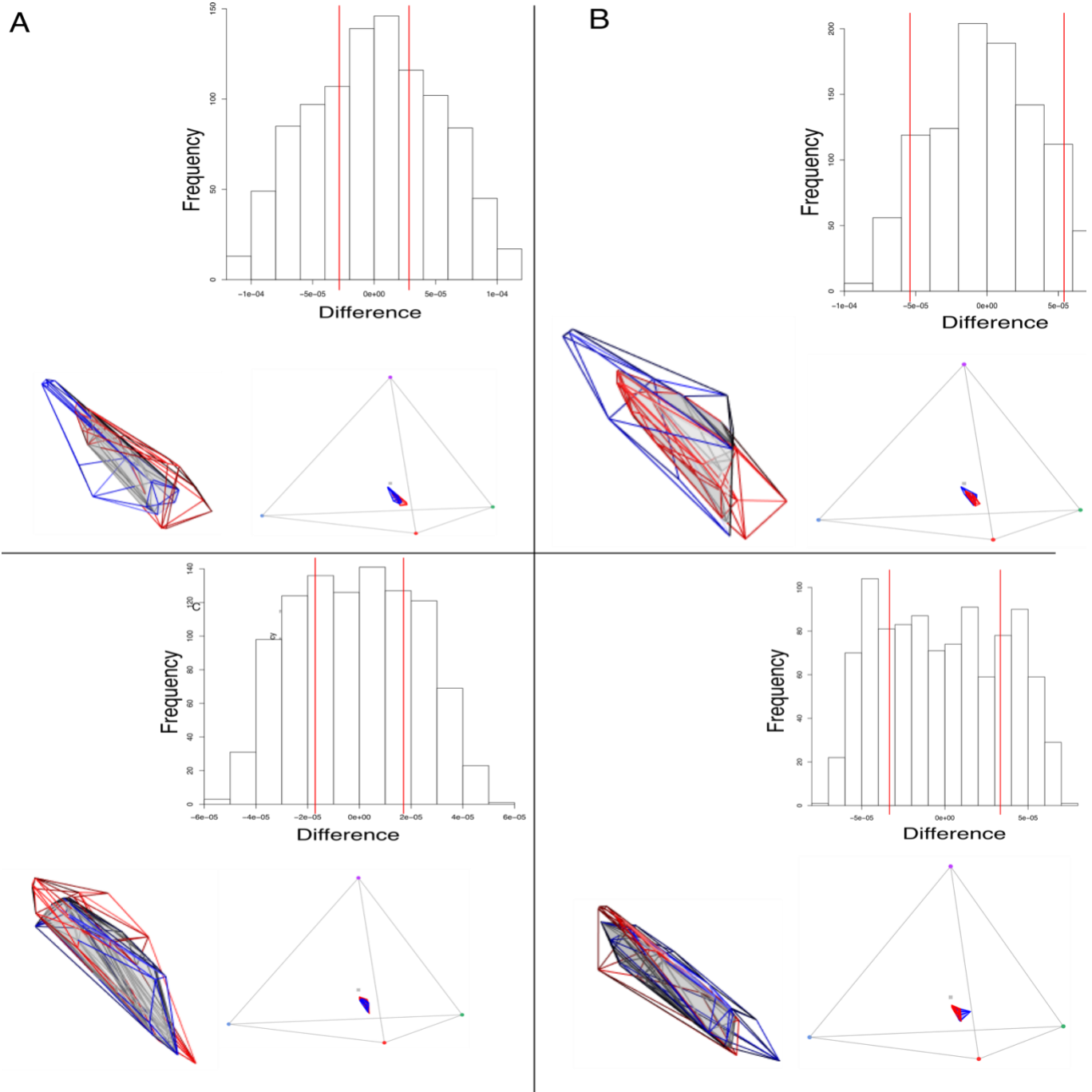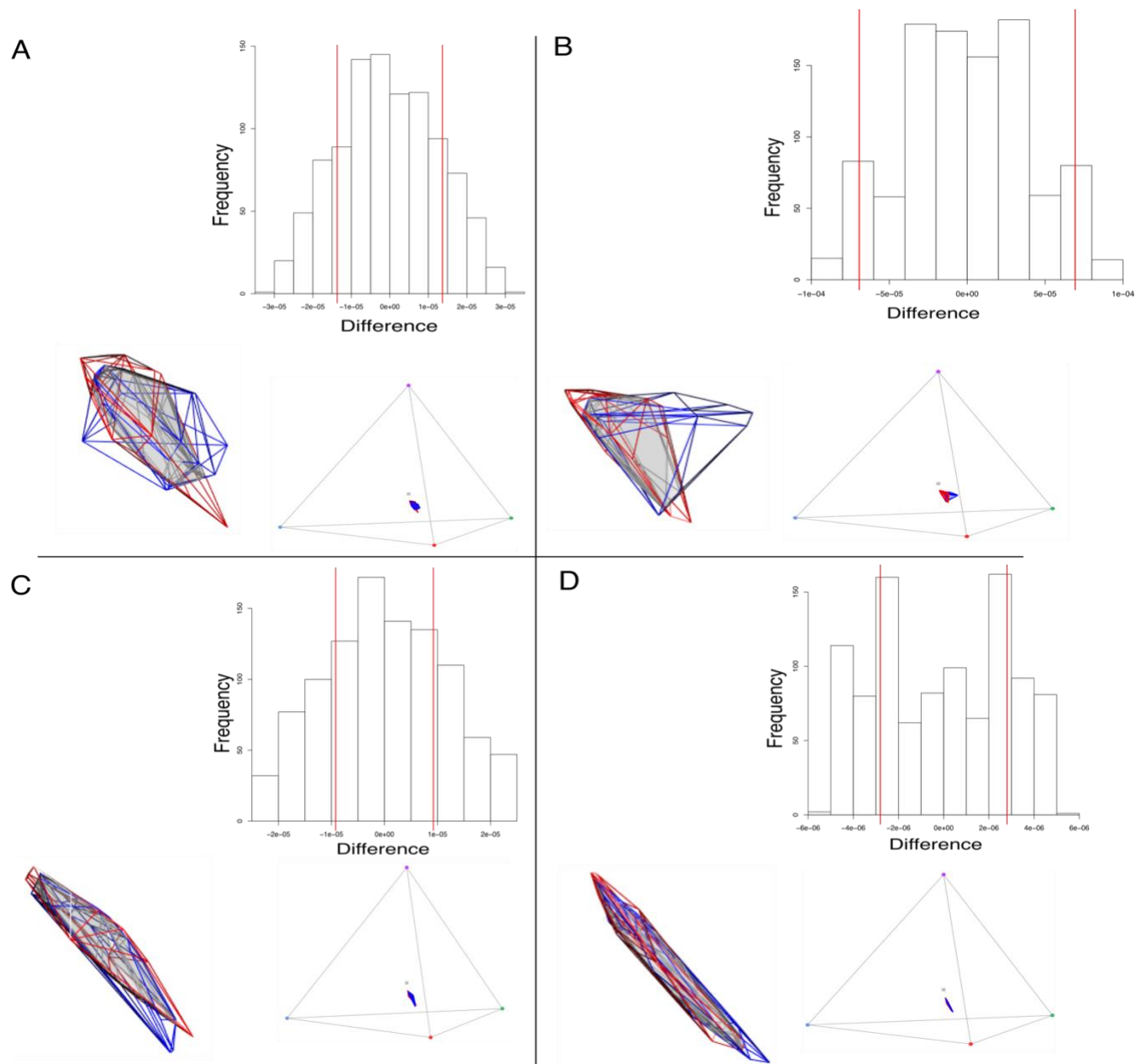
Supplementary Material. 2. Color volumes calculated using alpha-shapes and a UV-sensitive model. Red lines mark where the observed values of overlap fall for a two-tailed test on a null distribution for A) Breast, B) Flanks, C) Rectrices, and D) Primaries. Blue represent the color volume occupied by flocking species, while red the non-flocking species.

CAPÍTULO 2

Interaction behavior dynamics and co-occurrence patterns of mixed-species bird flocks: a social network approach

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Abstract: Mixed-species flocks are one of the most widespread and interactively dynamic systems on Earth. Mixed-species flocks rely on constant interactions among members to shape its composition and keep cohesiveness. However, details on how the behavior of species shape flock composition through interactions with others is not understood yet. We studied which species keep flock composition and how they do it through their interactions. We recorded one year of flock composition and interactive behaviors among members (follow, forage and attack) at a Costa Rican highland forest. We conducted social networks based on the field interactions recorded. We found that flock establishment is not a static process, and that species roles in flocks may change (leader to follower), related to the occurrence and abundance of other species. Some species presence might condition the occurrence and interactions of another species. Like the Sooty-capped Chlorospingus that often turn into a follower when Spangle-cheeked Tanager is abundant. This settles in-depth evidence to our assumption that certain species combinations may repel, facilitate, or modify the behavior of others inside the flock.

Key words: Animal groups, *Chlorospingus pileatus*, Tropical avifauna, interactive behavior

Mixed-groups occur in a wide range of animal taxa, from mammals to insects and from land to the ocean (Goodale et al. 2017). A recent review on this topic proposes a framework for understanding their composition and interactions (Goodale et al. 2020). This framework states that interactions in mixed-species groups range from supplementary, when the interactions occur on groups of individuals of the same or similar species, closely related phylogenetically (e.g. fish shoals, Hoare et al. 2000), to complementary, when group members are different and each species plays a role in the group (e.g. some mixed bird flocks, Morse 1970) (Goodale et al. 2020). Therefore, the members of mixed-species groups may obtain different benefits from joining. In birds, members of mixed-species foraging flocks often increase their fitness, because being part of these flocks increase foraging efficiency and reduce predation risk (Goodale et al. 2020; Krams et al. 2020). The establishment and cohesion of many bird flocks rely heavily on the vocalizations of leader species (Chaves-Campos 2003; but see Farine et al. 2014), and even the rate of those vocalizations could be relevant to determine the cohesiveness of mixed-species flocks (Pagani-Nuñez et al. 2018). But other factors that are also likely important in the formation and cohesion of mixed flocks, such as direct or indirect interactions among species, known as co-occurrence patterns, are poorly studied across taxa and environments (Graves and Gotelli 1993; Greenberg 2001; Goodale et al. 2010; Colorado and Rodewald, 2015).

Understanding how mixed-species flocks are formed and remain cohesive would shed light on the mechanisms that maintain the stability of such a dynamic system, with multiple multispecies interactions, and the flock itself interacting with environmental variation. One approach to study mixed-species flocks' composition, establishment, and their cohesiveness in a particular bird community is through the general model of community assembly rules (Diamond 1975). This model fits well the study of mixed-species flocks because: (1) if all the potential interactions among species are considered, just some of them would occur in nature; and (2) the interactions or species combinations that occur in nature limit or prevent the formation of other associations of species. So that the co-occurrence patterns will influence the richness and abundance of species within mixed-species flocks, as the individuals that are part of these flocks interact (positively or negatively) with each other (Graves and Gotelli 1993). In this sense, mixed-species flocks in a particular space could be considered as islands that can be colonized by some, but not all, species of the total avifauna (Harrison and Whitehouse 2011). These

associations and interactions can be statistically analyzed via social networks based on the interactions that occur within the flock (Farine 2013; Farine and Whitehead 2015).

The dynamics of mixed-species flocks tend to be more complex when the number of individuals and species increase (Zuluaga and Rodewald 2015). In tropical forests, mixed-species flocks are composed of a large number of species and individuals per species (Goodale and Beauchamp 2010), so that their dynamics is more complex than flocks in other ecosystems. Tropical mixed-species flocks in highland forests occur year-round with some temporal fluctuations in their composition (Powell 1979; 1985). These flocks include a set of nuclear species, from which at least one of them tend to be more abundant (Goodale and Beauchamp 2010), and, within the flocks individuals, are in a constant activity, e.g., foraging, serving as sentinels, or mobbing intruders (Powell 1985). Considering the interactions that occur within highland tropical bird flocks, they are ideal to study Diamond's community assembly rules (Diamond 1975) through social networks because the level of interactions between individuals is high and is maintained year-round. Another characteristic of highland mixed-species flocks is that birds use numerous microhabitats present along all forest strata (e.g., tree trunks, branches, understory bushes, Moynihan 1962; Powell 1985), which may enhance the interactions among flocking microhabitat-specialist species (Remsen and Parker 1984). Our objective is to identify the co-occurrence and interaction patterns within mixed-species flocks of a Costa Rican highland forest. If highland bird assembly pattern is linear (leader-follower) as some studies had indicated in general for mixed-species flock systems (Morse 1970; Greenberg 2001), we would expect to find a mixed-species flock social network with a unique central species that is followed by all others. But, if the pattern is not linear, we would expect to find a complex arrangement of species interactions, in which several species are likely to be followed when moving, but some others are likely to be followed when, for instance, they are involved in foraging.

Methods

Study area

We conducted this study in the high land forest of Braulio Carrillo National Park, Heredia Costa Rica (10°05' N, 84°04' W; 2100 m a.s.l.). The study area includes different habitats such as Oak forest (*Quercus* sp.), peat bogs, and secondary growth areas. The avifauna at this elevation is less diverse than that at lowlands (8 vs 21 species per flock on average, Powell 1985; Cordeiro et al. 2015), which makes the record of individuals' interactions within flocks more feasible at highlands.

Mixed-species flock and interactions

We searched for flocks twice a week from March to December of 2019, from 0600-1100 h, during birds' activity peak, along a 5.5 km transect that covers different habitats (Oak Forest, peat bogs, and secondary growth areas), and interchanged the starting point between consecutive samplings to avoid potential bias of bird detection associated to particular habitats. Once we encountered a mixed-species flock we followed it for at least 10 min and in the first 2 min we recorded all species and individuals that were part of the flock. Then we chose a focal individual and recorded its interactions with conspecific and heterospecific individuals for 1 min (foraging with, following, or attacking other members of the flock). In general, the first focal individual sampled in each mixed-species flock was the first we spot and follow, then we chose another one of a different species. We defined an interaction when the presence or action of an individual is directed affects the behavior of another (or several) individual in the flock, as proposed by Whitehead (2008) and Farine et al. (2012). After ending the observation period for the first focal individual, we chose another of a different species and repeated the process. We tried to observe individuals of all the species that formed part of each flock, to avoid overrepresentation on the interactions recorded of the most abundant species (e.g., *Chlorospingus pileatus*- Sooty-capped Chlorospingus). However, when we detected a species that was not a common participant of mixed flocks we made an effort to record as many of its interactions as possible, such that we could evaluate its role in the flock. After observing a flock, we walked at least 100 m to start searching for the next mixed-species flock. If the last observed flock moved in the same direction we walked, we wait until we stop perceiving visually and acoustically the birds of that particular flock to re-start searching for another flock.

Analyses

To analyze the interaction of species within mixed-species flocks we built two types of networks. The first is based on the co-occurrences of species following the "gambit of the group" approach (Franks et al. 2010). This approach requires the construction of a co-occurrence interaction network based on flock by species matrices using sampling periods (Farine 2013). The second type of network requires an edge list (Farine 2013), based on forage, follow, and attack interactions. We were not able to build networks based on the "attack" behavior, because these interactions were scarce so that the sample size was insufficient. We conducted all analyses using the package "asnipe", "igraph" and "sna" (Csardi and Nepusz 2006; Farine 2013; Butts 2008; 2016) implemented in R (R Core team 2021). For the analyses we used only the species that were present in at least 5 % of the mixed-species flocks; this is the minimum number of flocks require to build an informative social network.

We calculated the weighted degree (centrality measure of the strength of association) of the co-occurrence and interaction networks (observed values) and compared them against null distributions of 1000 permuted networks (Farine 2013). With this procedure we determined if flocks experienced an overall change in their level of gregariousness (co-occurrence networks) or interspecies interactive behavior (interaction networks) between the first and second half of the year. We calculated the difference of the mean weighted degree of the actual networks (first and second half) and compared it with a null distribution. For this null distribution, we permuted 1000 mixed-species flocks and calculated their mean weighted degree, and then calculated the difference of the mean weighted degree of the permuted networks. Finally, to determine if some specific species change their role or interactive behavior inside the mixed-species flocks we compared the weighted degree of each of the species against a null distribution based on that species weighted degree from 1000 permuted networks. We conducted this species-specific analysis on the Spangle-cheeked Tanager (*Tangara dowii*), Sooty-capped Chlorospingus (*Chlorospingus pileatus*), Common Chlorospingus (*Chlorospingus flavopectus*), Black-cheeked Warbler (*Basileuterus melanogenys*), Collared Redstar (*Myioborus torquatus*), Yellow-thighed Brushfinch (*Atlapetes tibialis*), Ruddy Treerunner (*Margarornis rubiginosus*), and Buffy

Tuftedcheek (*Pseudocolaptes lawrencii*). We chose this set of species because they were the most central and abundant species in the mixed-species flocks that we studied.

Results

We recorded a total of 139 mixed-species flocks, composed on average by 11 individuals of 5 species. During the first half of the year we sampled 86 mixed-species flocks and 53 during the second half of the year. We registered 34 species forming mixed-species flocks, from which 17 species (50 %) were seen in 5 % or more of the mixed-species flocks and therefore used on the analyses (Table 1). A similar pattern was observed when we filtered the species for the first (17 species) and the second half (19 species) of the year (Table 1).

We found that species co-occurrences and their level of association on mixed-species flocks (weighted degree) were higher than that expected by chance ($P < 0.001$, Figure 1. Mixed-species flocks from the first half of the year had the same level of co-occurrence and association, based on the mean weighted degree, as mixed-species flocks from the second half of the year ($P = 0.1$, Figure 1, Figure S1). Even though the overall mixed-species flocks' mean weighted degree did not change through the year, some species did change their level of centrality and interaction within the flocks. The Spangle-cheeked Tanager ($P = 0.06$) and the Common Chlorospingus ($P = 0.06$) increased their centrality within the mixed-species flocks (Figure 1). Spangle-cheeked Tanager ($P < 0.001$), Yellow-thighed Brushfinch ($P < 0.001$), Ruddy Treerunner ($P < 0.001$), and Common Chlorospingus ($P < 0.001$) were followed more frequently within mixed-flocks in the second half of the year (Figure 2). We also found that the Sooty-capped Chlorospingus, the species with the highest weighted degree, diminished its centrality in the second half of the year ($P < 0.001$, Figure 1).

We found that Sooty-capped Chlorospingus and the Ruddy Treerunner (Figure 1-3) were central in all mixed-species flocks, regardless of the interaction analyzed. Hence, they were found in all flocks, followed, and searched for other species to forage nearby them (Figure 1-3). In addition to those species that presented a high centrality (based on co-occurrence), some

species were also followed by others within flocks, such as the Spangle-cheeked Tanager and the Yellow-thighed Brushfinch (Figure 2.). Despite that species had a similar pattern of association in social networks (Figure 2,3), some species that were not followed (e.g., Collared Redstar, Yellow-thighed Brushfinch, and the Black-cheeked Warbler; Figure 3) often were searched by other species for foraging.

We also found that some species serve as links for other species to join the mixed-species flocks. The majority of the usual follower species almost exclusively follow the Sooty-capped Chlorospingus, which was the usual leader, but some species tend to follow more than one species inside mixed-species flocks (Figure 2). We recorded the Black-cheeked Warbler, Collared Redstar, and the Yellow-thighed Brushfinch following the Ruddy Treerunner and the Spangle-cheeked Tanager (Figure 2). Even more specialized associations were observed in the Buffy Tuftedcheek and Spotted Barbtail which almost exclusively followed and foraged nearby Ruddy Treerunners, despite that Sooty-capped Chlorospingus was leading the mixed-species flocks (Figure 2,3).

Discussion

We found that interactions among birds of Costa Rican highland mixed-species flocks are dynamic, but at the same time stable through time. Such interactions were even more stable than other Costa Rican mixed-species flocks which showed an increase in size and gregariousness towards the second half of the year (Powell 1979). We discovered that the role of some species is interchangeable depending on each species-specific behavior and time of the year. We also uncovered different patterns of association when, in addition to species co-occurrences, we recorded specific interactive behaviors within mixed-species flocks.

The Sooty-capped Chlorospingus was the most frequent leader in the mixed-species flocks in the study area, but Spangle-cheeked Tanager and Yellow-thighed Brushfinch lead several flocks. We speculate that the fact that these two species led some flocks is directly related to some of their biological features. The Spangle-cheeked Tanager migrates altitudinally

within the country (Wolf 1976), thus it is not always present in the study area or is not sufficiently abundant to form part of mixed flocks. During the second half of the year this species became more common in the area and in mixed-species flocks as well, when we observed other species following it, included the Sooty-capped Chlorospingus. On the contrary, the Yellow-thighed Brushfinch is present year-round in the area, but its gregariousness varies over time. We recorded species following the Yellow-thighed Brushfinch only during a short period (end of June to the beginning of August) when this species formed familiar groups of 4 to 6 individuals by the end of its breeding season (Stiles and Skutch 1989).

Gregariousness could then vary within a species, conditioned by the period of the year and the place where individuals of that species occur. A combination of specific conditions for certain species may induce species to change their role in the flocks, e.g., change from followers to leaders facilitating mixed-species flock establishment. This change in role is presumably a "flock decision" based on the behavioral traits of leader species and flock composition, rather than a decision of the leader species (Hutto 1988; Farine 2021). Particularly because within mixed flocks the benefit/cost relationship is expected to be similar if the species is a follower or a leader. In addition, under certain conditions the benefits of being in a mixed flock may not be so different from the benefits obtained by being in an intra-specific flock (Goodale et al. 2017), and in such cases, the establishment of mixed flocks may be determined by other species following the mono-specific flock.

The interactions and co-occurrences in mixed-species flocks of Common Chlorospingus also became stronger during the second half of the year (Figure 1,2). This species is an abundant resident of the area but is more abundant at lower elevations (Stiles and Skutch 1989). However, recent changes in the landscape, due to changes in land use and climate change (Jetz et al. 2007; Bateman et al. 2016), may have induced this species to move uplift part of the year, likely searching for better weather conditions or food resources. This species partially shifts its diet when form part of mixed flocks (Valburg 1992), so it may have access to a different set of food items when form part of mixed flocks at higher elevations. Another possibility is that the Common Chlorospingus moves altitudinally on a seasonal basis as does the Spangle-cheeked Tanager, but on a smaller scale, incrementing its relative abundance in the study area during the second half of the year.

When specific interactions inside flocks are considered, we found that the most common leader species is not followed equally nor exclusively by the rest of the mixed-species flock attendants. Instead, flock attendants tend to follow more than one species inside the same flock. We also found that on some occasions a flock attendant does not follow the leader at all. This situation may occur when a particular species only becomes part of a mixed-flock when another particular species is present in the flock to follow it or forage nearby. In our study, this may be happening with woodcreepers. The Ruddy Treerunner, which is the most abundant woodcreeper in the area and the second most common species in mixed-flocks, may be producing some cues that facilitate others (i.e., Buffy Tuftedcheek and Spotted Barbtail) to join the flocks. We also observed the Streak-breasted Threehunter (*Thripadectes rufobrunneus*) following exclusively the Ruddy Treeruner within the flocks, though it was not included in the analyses due to insufficient occurrences in the mixed-flocks. The influence of cues produced by species in mixed flocks to induce other species to join a flock has also been reported in mixed-species flocks from Panamanian lowlands (Martínez et al. 2018). These authors found that some species that first behaved as eavesdroppers, were later eavesdropped on after joining the mixed-species flock, indicating that for some species to join a flock is conditioned by the presence of one or some particular species in the flock (Martínez et al. 2018). However, additional information, particularly using playbacks, is needed to test the role of species vocalizations on the decision some species made to either join or not a mixed-species flock.

The interaction rules prevailing in Costa Rican highland mixed-species flocks follow a classic checkerboard co-occurrence pattern (Diamond 1975; Graves and Gotelli 1993; Gotelli et al. 1997). According to this pattern, if a set of species are present in the flock (a checker) several other species would join it (adjacent checkers), but at the same time they limit the inclusion of other species, as expected by the community assembly rules (Diamond 1975). In addition, the number of species that can potentially join a flock, does not exclusively depend on the composition, nor the abundance of the species in the flock, but some other factors. Some of these factors are related to fluctuation in the level of gregariousness of the species across the year, the abundancy of the species in the area, and the species behavior within the mixed flocks that may also change through time. The clearest example is a species with the role of a leader at some specific time, could turned into a follower at other time.

In sum, Costa Rican highland mixed-species flocks are dynamic, rather than static systems. The species within mixed-flocks from the highlands of Costa Rica vary over the year in their interactions (co-occurrences, follow, and forage). Further, these mixed-species flocks are not linear, because they have multiple leader species and their roles inside mixed-species flocks are interchangeable. Additionally, the dynamics within mixed-species flocks are complex: some species follow other species to forage closer, others just to travel together, and even other species follow others that could play the role of leaders and resource finders in the flock.

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Tables

Table 1. List of species included in the analyses and their occurrence frequency in mixed-species flocks.

Species	Analyses included	Occurrence Freq.
Black-cheeked Warbler	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.40
Golden-browed Chlorophonia	All-occ,Fh-occ,Sh-occ,Fh-f,Fo	0.15
Common Chlorospingus	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.19
Sooty-capped Chlorospingus	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.88
Slatty Flowerpiercer	All-occ,Fh-occ,Sh-occ,Fh-f	0.12
Mountain Elaenia	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Fo	0.22
Yellowish Flycatcher	Sh-occ	0.02
Grey-breasted Woodwren	All-occ,Fh-occ,Sh-occ,Sh-f	0.33
Ruddy Treerunner	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.76
Collared Redstar	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.44
Flame-throated Warbler	All-occ,Fh-occ,Sh-occ	0.06
Black and Yellow Silky-flycatcher	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.15
Spotted Barbtail	All-occ, Sh-occ,Sh-f	0.06
Hairy woodpecker	Fh-occ	0.03
Yellow-thighed Brushfinch	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Fo	0.48
Buffy-tuftedcheek	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.14
Spangle-cheeked Tanager	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.24

Mountain Thrush	All-occ,Fh-occ,Sh-occ,Fh-f,Sh-f	0.27
Yellow-winged Vireo	All-occ,Fh-occ,Sh-occ,All-f,Fh-f,Sh-f,Fo	0.16
Prong-billed Barbet	Sh-occ	0.03

All: All year, **Fh:** First half, **Sh:** Second half, **occ:** Occurrence, **f:** follow, **Fo:** Forage

Figures
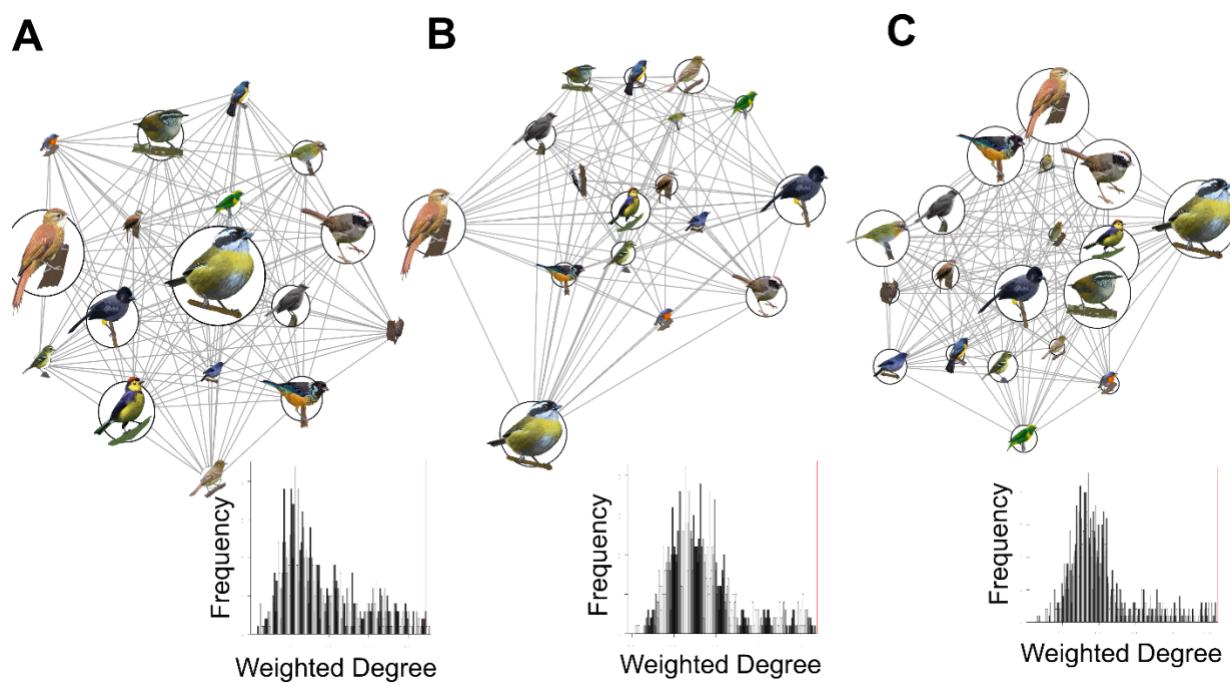
Figure 1. Mixed-species flock networks based on co-occurrences. A) All year, B) First half of the year, and C) Second half of the year.
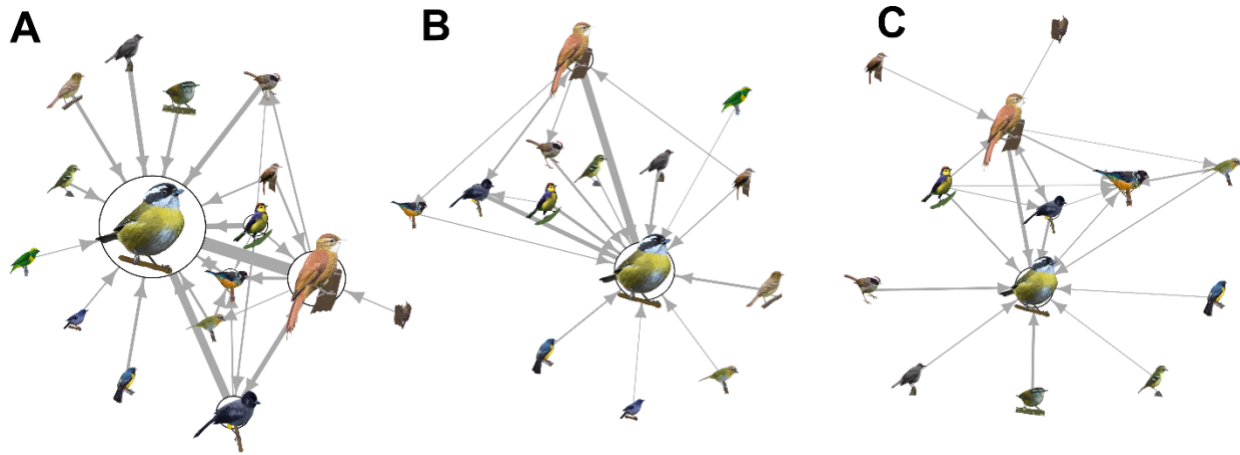
Figure 2. Mixed-species flock networks based on which species follow who. A) All year, B) First half of the year, and C) Second half of the year.
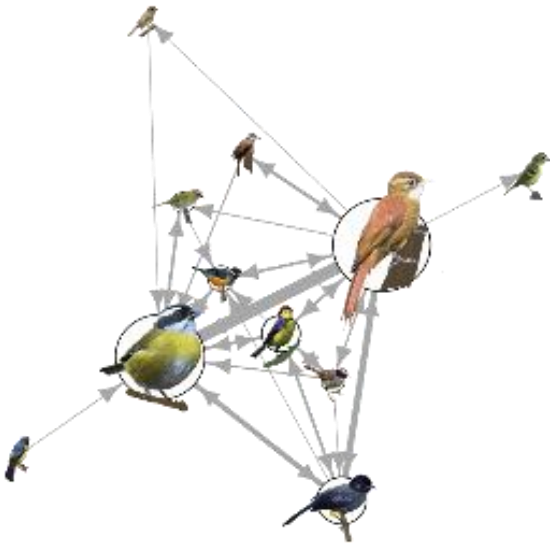
Figure 3. Figure 3. Mixed-species flock network based on which species forage nearby who.

Co-occurrences weigthed degree first and second half difference $P = 0.103$

Probability (y-axis)

Weighted degree difference (x-axis)
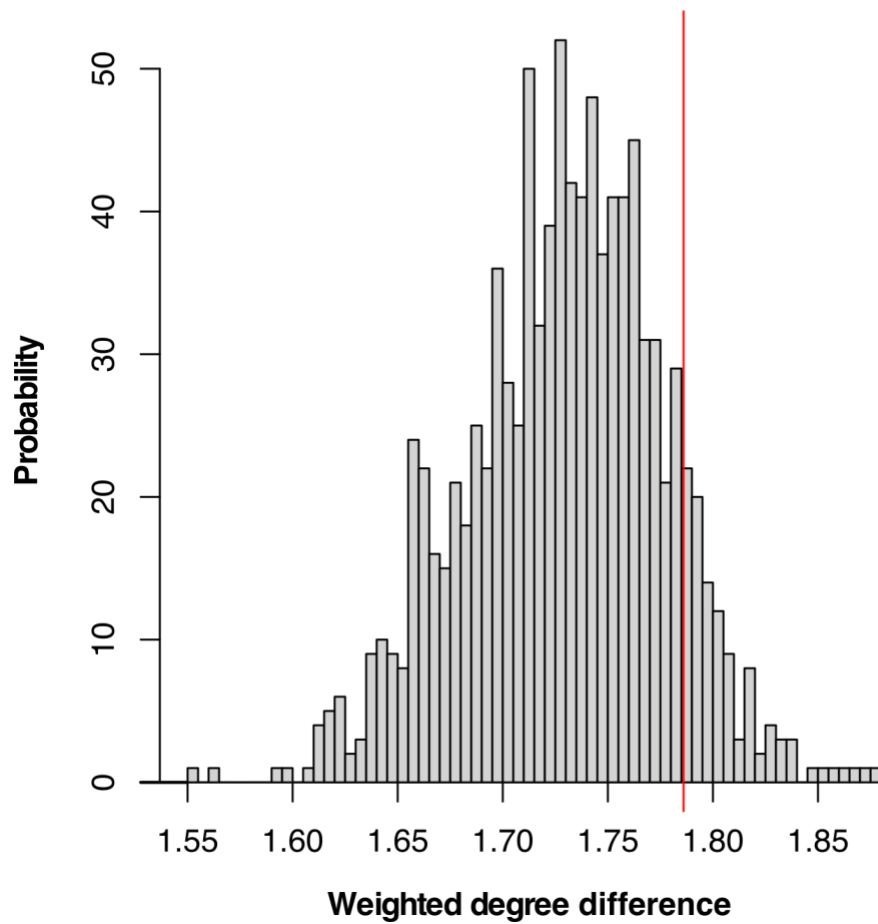
Supplementary Material 1. Observed value of weighted degree of the difference from the second and first half of the year.

CAPÍTULO 3

Variations in mixed-species flock composition and interactions correlate to differences in habitat complexity

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Abstract: Species assemblages in different environments are highly mediated by the habitat structure and the resources available. In the case of mixed-species bird flocks, the habitat structure, in some specific and already studied systems, can determine their presence. Mixed-species flock presence in those scenarios are limited mostly by the restrictions in the mobility of the flocks through the landscape, vanishing them from certain areas. The purpose of this study was to determine how the variations in habitat structure relates to the composition and occurrence of mixed-species flocks in a highland of Costa Rica. We did this by measuring habitat structure traits (canopy height, understory cover, canopy cover, diameter at breast height and leaf area index) in 16 plots that covered all the different habitats present in the area. We also conducted mixed-species flock surveys and gather data on species, individuals and their occurrence points to relate them to the habitat traits. We found that mixed-species flocks are present in all the study area, but its composition varies greatly related to the habitat where they were present. Also, the reason they are present is because the mixed-species flock core species are present in all the habitats, but some of their potential members are not.

Introduction

Habitat complexity, defined as the physical structure of the habitat (Carter et al., 2018), affects species assembly and their interactions within a community: from parasite-host to food webs and predator-prey interactions (Kovalenko & Thomaz, 2012; Carter et al., 2018; Staniczenko et al., 2019). This complexity can either enhance the interspecies interactions by boosting the number of species or individuals that can occur in the habitat by providing enough resources for sustaining a large flock of individuals of different species (Maldonado-Coelho & Marini, 2000; 2004). For example, lower complexity of habitat of oysters and their predators produced a disruption in the predator-prey interaction, but not in the whole trophic cascade (Grabowski, 2004). When community interactions are assessed, the individual and habitat structure variation are often ignored and assumed as homogenous, leading to incomplete insights or unrealistic interpretations (Carter et al., 2018). Therefore, variation must be taken into consideration because heterogeneity is key to understand the drivers of complex communities (Carter et al., 2018; Gibert & Brassil, 2014, Mokross et al., 2018). This is particularly of relevance when addressing bird communities, that not only use habitat structure differently, but also tend to form complex interspecies associations like mixed-species flocks within this type of habitats (Jones & Robinson, 2021).

Mixed-species flocks of birds are one of the most common and interactive group systems in nature (Morse, 1970; Goodale et al., 2020); and those flocks are dynamic assemblages that depend on positive and negative interactions (Goodale et al., 2020). How they are established, stay cohesive, and interact intra-specifically (Jones et al., 2020) are a central issues in community ecology. Among the most common reported interactions within mixed-species flocks are behavioral interactions (Morse, 1970), role turn-overs (Farine, 2021), and species facilitation to join the mixed-species (Martínez et al., 2018; Muñoz et al., in prep.). Other interactions could occur when the relative population of a species increases in the area, which leads to a turn-over of some species roles. For example, when *Atlpetes tibialis* turns into a gregarious species outside of the breeding season and becomes a leader species in the mixed-species flocks. Facilitation occurs when members of the flock display behaviors that trigger flocking, like specific vocalizations (Pagani-Nuñez et al., 2018), but also a product of external factors like habitat complexity (Goodale et al., 2010; Croft et al., 2011).

Habitat complexity may facilitate flocking behavior in different ways. For instance, specific habitat traits (e.g., background conspicuousness) influence signal transmission and its interpretation by conspecifics and heterospecifics (Uy & Stein, 2007). Moreover, habitat structure traits, like forest height and area size, influence the gregariousness of mixed-species flocks (Mokross et al., 2014), because it may physically limit the number and identity of species joining a flock and by influencing the cost-benefit tradeoff for the potential flock members. For example, the lack of larger trees limits the occurrence of woodcreepers that need them to forage or to support a territory (Maldonado-Coelho & Marini, 2000; Darrah & Smith, 2013), or the lack of dense understory limits the occurrence of wrens and antbirds that rarely move in open areas (Mokross et al., 2018). There are other aspects regarding forest structure that might affect mixed-species flock composition (Hutto, 1988; Kotogama & Goodale, 2004), which have not totally been considered yet like resource availability (e.g., fruits or flowers), shelter (e.g., abundance of trees and size), or specialized foraging structures (e.g., dense understory, canopy cover). Changes in these habitat complexity traits may trigger composition effects over the mixed-species flock structure. Reduced availability of understory resources may lead to lessening the complexity of mixed-species flocks based on an overall decreased foraging efficiency of bird species (Hutto, 1988). In addition, a complex habitat structure, higher canopy and cover, may put at the disposition of bird species more usable habitat space when moving on a mixed-species flock (Mokross et al., 2014). As well, changes in the habitat complexity could be seen by a higher or lower understory cover, which also limits the species that could potentially join the mixed-species flock by not finding a suitable forest cover for them (Rutt et al., 2020).

Habitat complexity varies significantly not only at a big scale, but also over short distances within the same area (Rutt et al., 2020) and this will affect directly the composition and level of association of mixed-species flocks. Therefore, our objective is to describe the relation between the composition and occurrence sites of mixed-species flocks with the habitat complexity (structure and phenology) of a highland forest. We expect that in a more complex habitat we will find mixed-species flocks with more individuals per species and more species. Because, more complex habitat structure areas provide a wider range of resources like shelter, foraging substrates, food or movement space we hypothesize that habitat complexity may facilitate interactions between heterospecifics. Costa Rican highlands are suitable to answer this question because they present mixed-species flocks all year round with its members interacting

among them at all times (Powell, 1979, 1985). In addition, tropical mixed-species flocks tend to use all forest structures present in its habitat, like branches, trunks, mosses, understory cover, and treetops (Powell, 1985).

Methods

Study area

We conducted this study in the highland area of the Braulio Carrillo National Park in Heredia, Costa Rica (10°05' N, 84°04' W; 2100 m a.s.l.) from March to December 2019. The study area was composed of a mixture of secondary and old-growth oak forest, as well as several disturbed areas with pastures, peat bogs, isolated trees, bushes, forest edges, and natural bamboos. These features make this land a heterogeneous landscape for mixed-species flocks to occur year-round.

Habitat complexity

To measure habitat complexity traits, we selected 16 plots of 10x10 m distributed across the study area to cover all the habitat types present (Fig. 1). Half of the 16 plots were located near transects where mixed-species flocks were sampled and the remaining plots were located at least 200 m away from the transects. We placed the plots semi-randomly, by a distance criteria from each other (at least 200 m) and also by placing with the purpose of catching the variances related to habitat types present in the study area (peatbogs, old-growth oak forest, etc…). At each of these plots we measured the diameter at breast height (DBH) from all the trees (> 10 cm), and canopy height in three different points of the plot (the center and two of the sides). At each plot we selected four 1x1 m sub-plots where we measured the understory cover as the percentage of cover. Finally, we measured the leaf area index using five photos per plot following Martin (2015). We took the photos using a Canon SL1 camera and an 18-55 mm lens, four photos were directed at each of the cardinal points at a 45 degrees angle and the fifth photo was at a 90

degrees angle towards the canopy. Using the data gathered from all the 16 plots we interpolated, using the inverse distance weight method, to the rest of the un-sampled area using QGIS (QGIS development team, 2021). This created a different layer per trait that covered all the study area.

Spatial modeling of mixed-species flocks occurrences

We searched for mixed-species flocks twice per week from 0600-1100 h during the birds' peak activity along a 5.5 km transect (Fig. 1). We swapped the starting point each day to diminish a potential bias related to the time and place of the samples. We recorded the number of individuals every time we encountered a flock and for a subsequent prediod of 10 min. We also recorded the flocks' geographical position when first found and at the end of the 10 min sampling period, using a GPS (Garmin 64s). Each mixed-species flock sampled and georeferenced was used as an occurrence at the beginning and at the end of the sampling period. Before the use of the mixed-species flock occurrences, we filtered the occurrences to be 10 m or more apart from each other. We used 10 m as a threshold because the predictor layers that we used were interpolated to present 10x10 m pixels. Using QGIS and land cover layers we classified the site where each mixed-species flock occurred, as pastures/peatbogs, old-growth forest, forestall plantation, secondary forest or unknown (classified as clouds in the layer). To determine the suitability of the different habitat structures in the study area for the occurrence of mixed-species flocks we built three false color map models using the kernel density estimation in QGIS (QGIS.org, 2021) and the filtered flock occurrences. We built these models for the large mixed-species flocks (> 7 species or > 12 ind), the smallest mixed-species flocks (< 4 species or < 8 ind), and for averaged-sized mixed-species flocks (5-6 species or 9-11 ind)

Non-metric multidimensional scaling (NMDS)

As a complementary analysis, to determine if a specific composition of mixed-species flocks (large, average, or small flocks as described above) were more with specific habitat structure traits we conducted a Non-metric Multidimensional Scaling analysis (NMDS). We used each of the mixed-species flock filtered occurrences as specific points over the habitat structure

layers in QGIS to extract the variables associated with the occurrences. After this procedure we ended with a dataframe where each row was a mixed-species flock and each column a variable (flock type, average tree DBH, average number of trees, average canopy height, understory cover, and leaf area index). With this multivariate table we conducted the NMDS (1500 iterations) analysis in R (R Core team, 2021).

Results

Smaller mixed-species flocks occurred in similar quantities in each of the five habitats (Table 1, Fig. 1). Average-sized mixed-species flocks were more common in old-growth and forestplantation than in the other three habitats (Table 1, Fig. 2). Large mixed-species flocks were more common at forest plantations and pasture/peatbogs habitats (Table 1, Fig. 3). Smaller mixed-species flocks were composed of similar average number of individuals per species than the other two flock sizes, but the proportion of each species inside the smaller mixed-flock was higher, relative to average and large sized mixed-species flocks (Table 2). Almost all species present on small-sized mixed-species flocks were also present on average and large sized mixed-species flocks, but not the other way (Table 2).

Smaller mixed-species flocks did not appear to be particularly associated with any specific habitat trait (Fig. 1). Even though mixed-species flocks do not disappear in any specific habitat, variations in composition were recorded over short distances (e.g., <1 km). The changes in mixed-species flocks composition seem to be partially associated with habitat structure traits, because some traits seem to facilitate certain types of mixed-species flocks, while others does not appear to influence them (Fig.1). The habitat structure trait that seems to be less associated with mixed-species flock composition is tree DBH (Fig.1E). Tree DBH seems to be less associated with mixed-species flock composition because this trait did not vary much throughout the study area, while flock composition models did vary. On the contrary, the number and height of trees present in an area, regardless of their DBH, facilitate the occurrence of average and large-sized mixed-species flocks (Fig. 1B-C). The area were the number of trees and their height is the biggest in the study area corresponds also to the highest concentration of occurrences of average and large-sized mixed-species flocks.

When addressing the NMDS results, we corroborated that small flocks are not directly associated with any particular habitat trait studied (Fig. 2). On the contrary, large and average-sized mixed-species flocks seem to be more dependent on the number of trees present, leaf area index, and understory coverage (Fig. 2). Also, to a lesser extent, large DBH and higher canopy seem to influence, by increasing, the presence of average and large mixed-species flocks (Fig. 2). Even though, bigger DBH, a large number of trees, large understory coverage, more canopy cover, and canopy height seem to facilitate the occurrence of mixed-species flocks in a particular area, some average-sized mixed-species, but no large-sized flocks, were recorded in areas with little to no understory coverage, an open and low canopy, fewer and and thinner trees.

Discussion

We found that forest plantations and old-growth forests may provide more microhabitats compared to the disturbed areas, for bird species to occur in mixed-species flock, specially understory species (Zuluaga & Rodewald, 2015). Therefore, we found average and large-sized flocks more commonly in the most complex habitats (Table 1). Small sized mixed-species flocks occurred equally in all types of habitat structures, because the core species that composed Costa Rican highland mixed-species flocks occur all over the study site (disturbed areas, old and secondary growth forest), and are not limited by habitat structure (Barrantes et al., 2011; ebird.org), which is detailed below. In terms of habitat structure functionality, changes from old-growth forest to forest plantation does not represented a big change in structure, because the forest cover and tree density remain similar. However, as was expected the vegetation structure in open and disturbed areas change significantly in comparison to other habitats because the forest cover was minimal and not that high. Nonetheless we recorded a fair amount of occurences of large-sized flocks in open disturbed areas. The large-sized flocks recorded in open areasgained their size by adding more individuals of the same species and not by adding more individuals of different species. Because species that tend to inhabit open areas are used to be more numerous as well (Blake & Loiselle, 2001) which ends in more potential members of a mixed-species flock.

Highland mixed-species flocks at Costa Rica cannot be split into understory and canopy mixed-species flocks as in lowlands (Munn, 1985), because in Costa Rican highlands forest

strata are not well defined as in lowlands. This is caused by a lower canopy that maintains understory and canopy bird species closer to each other when moving in the flocks (Powell, 1985). For example, the Grey-breasted Wood-wren (*Henichorhina leucophrys*),an understory species, move closer to the ground in the same flock as the Spangle-cheeked Tanager (*Tangara dowii*) that is a subcanopy-canopy species (Muñoz et al., *in prep*). The flock core species (i.e., Sooty-capped Chlorospingus, Ruddy Treerunner, and Yellow-thighed Brushfinch, Muñoz et al., in prep.) occurred all over the study area outside of flocks because they are not specialized in any vegetation type (Stiles, 1985). The core species of theses flocks also tend to forage on substrates such as isolated trees, forest edges and mature forest, which occur all over the study site. So, this may be the reason why abrupt changes in habitat structure over short distances (e.g., change from old-growth forest or forest plantation to open areas) only affected the number of species in the mixed-species flocks. Because more dependent forest species (e.g., woodcreepers, tapaculo, wood-wren) would abandon the flock (Rutt et al., 2020), but the core species would continue foraging together across habitat structures. In other environments, like Amazonian lowlands, abrupt changes of the habitat structure limit the movement of mixed-species flock in general, because their core species are more forest dependent than Costa Rican highland species (Rutt et al., 2020). Our results re-confirmed the idea that mixed-species flock ocurrence is mediated by both the interactions of the species with the habitat and with the other flocking species (Latta & Wunderle, 1996).

Nonetheless, more complex habitat structures facilitated larger mixed-species flocks, because it allowed species with different microhabitat use, like understory specialists, intergrate the flock (Zuluaga & Rodewald, 2015). But, quantify the difference in available microhabitats among forest structure need to be done in most tropical forest (Guariguata & Kattan, 2002). Our result disagree with a study on mixed-species flocks composition related to habitat complexity in another tropical forest, which demonstrated that complexity (more individuals and species) of flocks increased on advanced forest successional stages (Zhang et al., 2013). The study system we addressed behaved differently, with the largest mixed-species flocks occurring on both old forest plantations and peatbogs (Table 1). The majority of ocurrences, regardless of their complexity, were recorded on intermediate successional habitat structure following a similar pattern to the intermediate disturbance hypothesis of Connell (1978).

We conclude that the presence of mixed-species flocks as a whole was not limited by forest structures in the study area, but their sizes and composition was. Forest structures with more potential microhabitats for species to forage might potentiate the occurrence of mixed-species flocks on an area. There was a set of species that join mixed-species flocks that stayed the same all forest types and flock sizes that could be the reason why these flocks are present through all the study area. For future directions might be interesting to look the specif interactions of species inside mixed-species flocks by forest type and flock size, because those interactions could be modified due to a lack of microhabitats or also a lack of a flocking species on a certain area (Zhang et al., 2013).

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Tables

Table 1. Proportion of mixed-spcecies flock occurrence relative to habitat type

Habitat Type	Small (%)	Average (%)	Large (%)
Pasture/Peatbogs	20.8	15.7	34
Old-growth	23.1	27.8	14.9
Forest Plantation	19.8	32.5	40.4
Secondary Forest	15.4	7.2	2.1
Unknown	20.8	16.9	8.5

Table 2. Species that occur inside mixed-species flocks from the highlands of Costa Rica and their relative abundance, proportion of occurrence inside flocks and average proportion that represent inside the mixed-species flocks.

Species	Small			Average			Large		
	Average No. ind/flock	Occurrence (%)	Proportion inside flock (%)	Average No. ind/flock	Occurrence (%)	Proportion inside flock (%)	Average No. ind/flock	Occurrence (%)	Proportion inside flock (%)
Trogon collaris	NA	NA	NA	NA	NA	NA	1.3	10	0.9
Semnornis frantzii	NA	NA	NA	1	2.2	0.2	1.7	10	1.2
Dryobates villosus	NA	NA	NA	1	6.5	0.6	1.5	6.7	0.7
Pachyramphus versicolor	NA	NA	NA	1	4.3	0.4	NA	NA	NA
Platyrinchus mystaceus	NA	NA	NA	1	2.2	0.2	NA	NA	NA
Mionectes olivaceus	1	2	0.3	1	2.2	0.2	NA	NA	NA
Elaenia frantzii	1.1	15.7	2.2	1.5	30.4	4.3	1.4	26.7	2.4
Mitrephanes phaeocercus	NA	NA	NA	2	2.2	0.3	NA	NA	NA
Empidonax flavescens	NA	NA	NA	NA	NA	NA	1.5	6.7	0.5
Pseudocolaptes lawrencii	1	5.9	0.6	1	13	1.2	1.5	26.7	2.3
Thripadectes rufobrunneus	NA	NA	NA	1	2.2	0.2	1	10	0.6
Premnoplex brunnescens	1	2	0.2	1.5	4.3	0.6	1	16.7	0.9
Margarornis rubiginosus	1.8	64.7	14	1.9	80.4	14.1	2.7	90	14
Vireo carmioli	1.3	7.8	1	1	15.2	1.6	1.1	30	2.3
Phainoptila melanoxantha	2	5.9	1.5	1.4	21.7	2.7	1.4	16.7	1.4
Henicorhina leucophrys	1.4	19.6	2.8	1.3	26.1	3.2	1.4	60	4.9
Myadestes melanops	NA	NA	NA	NA	NA	NA	1	3.3	0.2
Turdus plebejus	1.3	15.7	2.9	1.4	28.3	3.6	1.4	46.7	4.2

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Chlorophonia callophrys	1.5	3.9	0.8	1.3	13	1.6	1.4	23.3	2
Chlorospingus pileatus	4.2	82.4	42.6	3.8	91.3	30.6	3.6	93.3	20.4
Chlorospingus flavopectus	2.4	9.8	3.3	1.8	17.4	2.6	2.6	33.3	4.5
Arremon brunneinucha	NA	NA	NA	1	2.2	0.2	NA	NA	NA
Atlapetess tibialis	2.4	41.2	12.5	2.3	43.5	8.8	2.1	70	8.2
Vermivora chrysoptera	NA	NA	NA	NA	NA	NA	1	3.3	0.2
Oreothlypis gutturalis	NA	NA	NA	1.8	8.7	1.2	1.3	13.3	1
Setophaga fusca	NA	NA	NA	2	2.2	0.3	1	3.3	0.2
Setophaga virens	1	2	0.3	NA	NA	NA	NA	NA	NA
Basileuterus melanogenys	2	19.6	5.7	1.8	37	5.9	1.9	73.3	8.7
Cardellina pusilla	NA	NA	NA	NA	NA	NA	1	3.3	0.2
Myioborus torquatus	1.9	17.6	4.3	1.5	54.3	7.4	1.8	66.7	7
Piranga bidentata	NA	NA	NA	1	2.2	0.4	2	6.7	0.7
Pheuticus tibialis	NA	NA	NA	NA	NA	NA	1	3.3	0.2
Tangara dowii	3.5	7.8	3.2	3.5	21.7	6.3	3.3	50	8.5
Diglossa plumbea	1.4	9.8	2	1.3	8.7	1.2	1	26.7	1.7

Figures
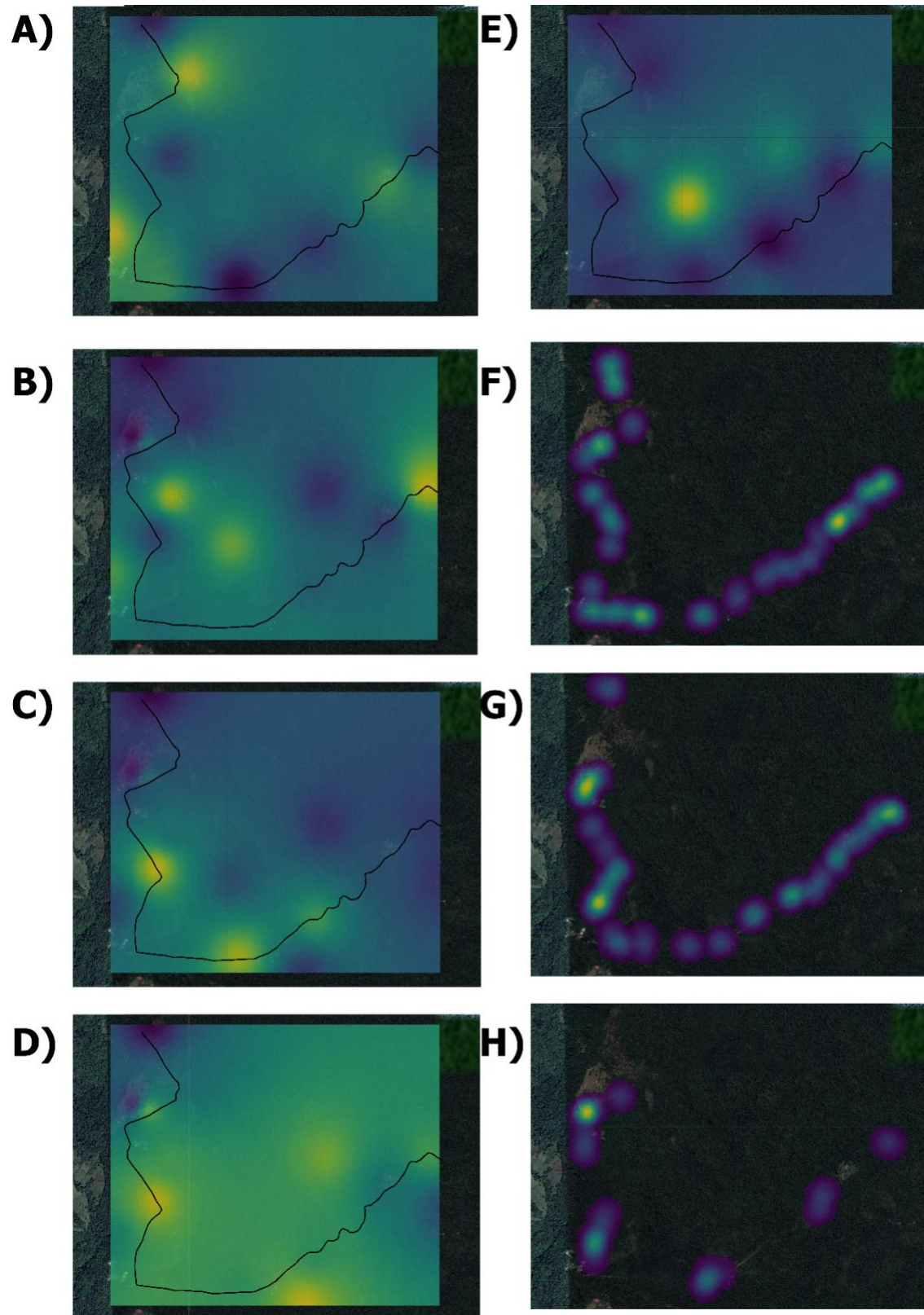
Figure 1. Inverse weighted interpolations of habitat structure variables for the whole area A) Understory cover, B) Tree height, C) Number of trees, D) Leaf area index, and E) Diameter at breast height. Kernel density estimation models for F) Small-sized, G) Average-sized, and H) Large-sized mixed-species flocks. Yellow indicates higher values of the variable, while pruple indicates lower values of the variable.
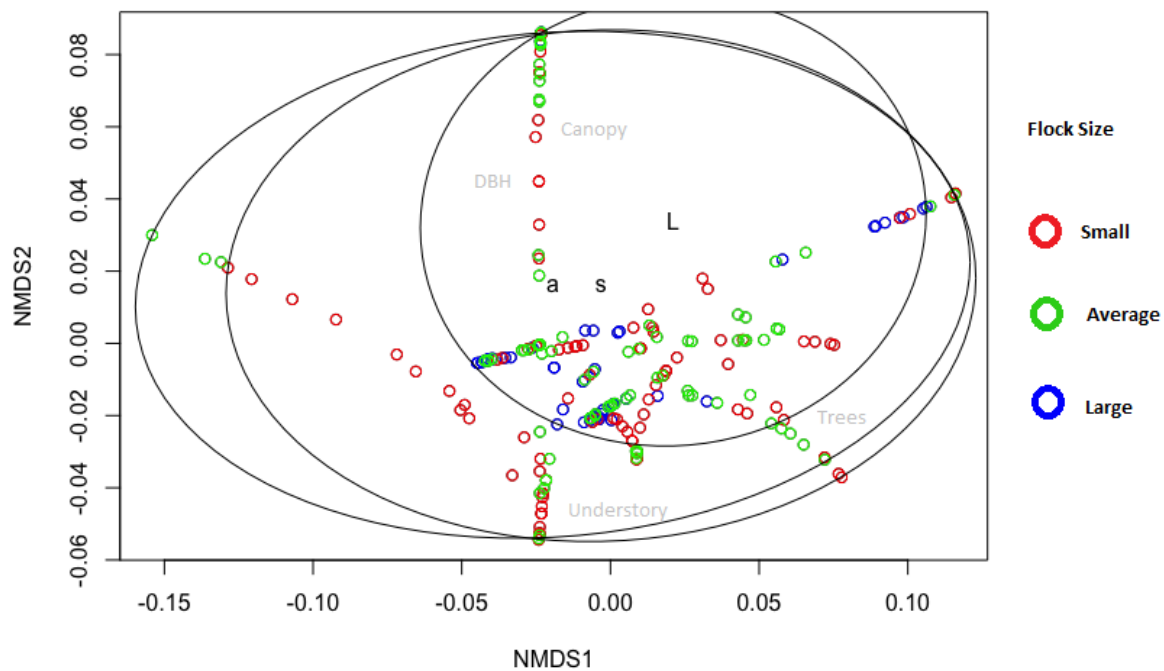

Figure 2. NMDS plot of the multidimensional position of different size mixed-species flocks. Ellipses were calculated with a 0.95 confidence. The inner ellipse correspond to large-sized flocks, the outter ellipse correspond to average-sized flocks and the remaining one to small-sized flocks. Stress value: 0.037.

CONCLUSIONES

Concluímos que las bandadas mixtas de aves de tierras altas del Parque Nacional Braulio Carrillo son un sistema totalmente dinámico, por lo tanto, su composición e interacciones varían por distintos factores. Estos factores son, la estructura del hábitat y la fenología y comportamiento de las especies que forman bandadas mixtas. Sin embargo, encontramos también que la coloración de plumaje no parece ser una señal o rasgo que promueva la asociación de especies distintas de aves para formar bandadas mixtas, a pesar de que en otros escenarios similares la coloración si sea un factor clave para la agrupación de individuos y especies.

A pesar de que las bandadas de tierras altas se pueden encontrar todo el año y en distintos hábitats con rasgos funcionales diferentes, su composición si se cambia. La estructura del hábitat afecta en dos niveles, primero a nivel de las especies que están en los sitios, que potencialmente podrían unirse a las bandadas, y segundo a nivel de grupo principalmente en el tamaño de las bandadas. En hábitats abiertos, como las turberas, hay menos especies que formen bandadas mixtas que en áreas de crecimiento secundario y bosque maduro, lo que hace que el número de especies presente por bandada sea más pequeño, sin embargo, las bandadas pueden llegar a ser grandes en el número de individuos. También, bandadas mixtas con más especies están limitadas a sitios más complejos, es decir con mayor disponibilidad de microhabitats que las especies dentro de las bandadas mixtas pueden utilizar.

En cuanto a la composición de las bandadas mixtas y sus interacciones dentro del grupo, encontramos que las especies varían a lo largo del año en su nivel de interacción y los tipos de interacción (co-ocurrencias, comportamiento de seguimiento y forrajeo). Además, las bandadas mixtas de aves de las tierras altas de Costa Rica no son lineales, ya que tienen múltiples especies líderes y sus roles dentro de las bandadas pueden ser intercambiables. La dinámica dentro de las bandadas mixtas es compleja: algunas especies siguen a otras con el fin de alimentarse cerca de ellas porque posiblemente sean buenas encontrando fuentes de alimento similares. Otras especies solo siguen a otras con el fin de movilizarse a través del hpabitat e incluso otras especies siguen a

otras porque las segundas son potencialmente buenas para desempeñar el papel de líderes y buscadores de recursos al mismo tiempo

Por último, nosotros nos enfocamos en el efecto que la coloración del plumaje podría tener sobre el establecimiento y composición de las bandadas mixtas de aves de tierras altas de Costa Rica. Específicamente nos centramos si las bandadas mixtas de tierras altas presentan evidencia de mimetismo social. Concluimos que el mimetismo social no es un factor que haya moldeado la comunidad de aves que forman bandadas mixtas en las tierras altas de Costa Rica, a pesar de que el mimetismo parecía ser obvio para el ojo humano. Las especies que forman bandadas mixtas y las que no forman bandadas mixtas en las tierras altas de Costa Rica presentan una coloración similar, por lo que una presión evolutiva que promueva la convergencia de los plumajes puede ser el hábitat, que actúa sobre toda la comunidad de aves, y no la bandada como tal.