



# Seasonal dynamics of flock interaction networks across a human-modified landscape in lowland Amazonian rain forest

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**Abstract.** Although lowland tropical rain forests were once widely believed to be the archetype of stability, seasonal variation exists. In these environments, seasonality is defined by rainfall, leading to a predictable pattern of biotic and abiotic changes. Only the full annual cycle reveals niche breadth, yet most studies of tropical organisms ignore seasonality, thereby underestimating realized conditions. If human-modified habitats display more seasonal stress than intact habitats, then ignoring seasonality will have particularly important repercussions for conservation. We examined the seasonal dynamics of Amazonian mixed-species flocks, an important species interaction network, across three habitats with increasing human disturbance. We quantified seasonal space use, species richness and attendance, and four ecological network metrics for flocks in primary forest, small forest fragments, and regenerating secondary forest in central Amazonia. Our results indicate that, even in intact, lowland rain forest, mixed-species flocks exhibit seasonal differences. During the dry season, flocks included more species, generally ranged over larger areas, and displayed network structures that were less complex and less cohesive. We speculate that—because most flocking species nest during the dry season, a time of reduced arthropod abundance—flocks are simultaneously constrained by these two competing pressures. Moreover, these seasonal differences were most pronounced in forest fragments and secondary forest, habitats that are less buffered from the changing seasons. Our results suggest that seasonality influences the conservation value of human-modified habitats, raising important questions about how rain forest organisms will cope with an increasingly unstable climate.

*Key words:* Amazon; deforestation; ecological networks; forest fragmentation; mixed-species flocks; Neotropics; seasonality; species interaction networks.

## INTRODUCTION

Although the tropics were once widely regarded to be aseasonal, it has long been recognized that seasonal variation exists (Dobzhansky 1950). The understory of lowland tropical rain forests is especially stable, with minimal seasonal fluctuations in light, humidity, and temperature (Chazdon and Fetcher 1984, Pollock et al. 2014). This constancy is also evident in the virtually unchanging photoperiod at a near-equatorial site, north of Manaus, Brazil (2° S), which only varies by 17 minutes throughout the year (data *available online*).<sup>4</sup> Consequently, this relative invariance led to the idea that tropical organisms at low elevations are evolutionarily adapted to a stable climate and will thus tolerate a

relatively narrow range of microclimatic conditions (Janzen 1967). However, even in lowland rain forest, seasonal changes do occur, delineated by seasonal variation in rainfall.

In addition to the amount of precipitation, tropical lowland rain forests, although regionally variable, experience other predictable biotic and abiotic changes during the wet and dry seasons. Maximum temperatures coincide with minimum relative humidity in the dry season (Windsor 1990). Therefore, daily fluctuations in temperature and relative humidity increase during the dry season (Pollock et al. 2014). Solar radiation also increases in the dry season because of reduced cloud cover (Wright and van Schaik 1994, Graham et al. 2003). This peak of irradiance may ultimately drive many of the annual tree phenologies in tropical forests, resulting in leaf, flower, and then fruit production that follow peak dry season radiation (Wright and van Schaik 1994, Wright and Calderón 2006, Myneni et al. 2007, Wright and Calderón 2018, Aleixo 2019). Throughout the tropics, pre-flush leaf fall is also more

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concentrated during the dry season, perhaps as a preemptive mechanism to avert the potential of future water stress (reviewed in Wright and Cornejo 1990, Lopes et al. 2016). Scaling up, treefalls also exhibit seasonality, occurring most often during the wet season (Brokaw 1982, Aleixo et al. 2019). Altogether, these changes indicate that there is a characteristic rhythm to the seasons even in relatively stable lowland rain forest. Even so, most studies in the humid tropics either restrict sampling effort to a single season (Pollock et al. 2017; Rutt et al. 2019; Stouffer et al. 2020) or ignore seasonality altogether. Furthermore, disturbance can impair the ability of forests to buffer against natural climatic variation (Ewers and Banks-Leite 2013, González del Pliego et al. 2016, Senior et al. 2017), leaving human-modified habitats more susceptible to the effects of seasonality.

Due to their historically stable environments, tropical organisms might be the most sensitive to disturbance and climate change (Deutsch et al. 2008, Betts et al. 2019), yet we know little about how these organisms respond to seasonality in the humid rain forest, a biome widely recognized for its complexity and unparalleled biodiversity. We know even less about how seasonality affects the intricate web of species interactions in the tropics. Amazonian mixed-species flocks represent an ideal interaction network to explore this question, as these species-rich assemblages appear to represent the apex of stability and complexity for avian multispecies interactions (Munn and Terborgh 1979). Together, a group of flock obligates gather at a predictable site each morning and co-defend a jointly held territory throughout the year, with gathering sites and territorial boundaries both remaining fixed over time, even for decades (Jullien and Thiollay 1998, Martínez and Gomez 2013). These approximately 10 species of obligate flock-followers forage together throughout the day and are joined by dozens of other insectivorous species (Munn and Terborgh 1979, Munn 1985, Jullien and Thiollay 1998). Collectively, in the *terra firme* forests of central Amazonia, we have recorded 105 resident species participating in mixed-species flocks, which represent 36% of the core forest avifauna (Rutt et al. 2017, Rutt et al. 2020; C. L. Rutt, unpublished data). Therefore, these flocks play a central role for avian diversity in Amazonia. Further, because these flocks display year-round residency and include few migrants, they are a model system to evaluate the effect of changing environmental conditions in lowland Amazonian rain forest.

For mixed-species flocks that assemble year-round, the two primary, but non-mutually exclusive, hypotheses proposed to explain seasonality are the timing of breeding for flock members and the potential fluctuation in their arthropod prey (Davis 1946, Fogden 1972, Powell 1985, Devey and Peres 2000, Greenberg 2000). During the breeding season, the logistics of building nests, incubating eggs, and feeding nestlings may constrict species-specific movements and limit species and individuals from participating in flocks (Powell 1985, Greenberg

2000). This would lead us to predict that, while flock members are breeding, flocks should be diminished in both size and space. Alternatively, when resource availability is low, the foraging benefits of joining flocks should increase (Morse 1970, Clark and Mangel 1984), leading to larger flocks with more interspecific interactions and larger home ranges. Because we know that both of these competing hypotheses might affect mixed-species flocks, we will simultaneously consider the seasonality of flocks alongside the seasonality of their reproductive activity and resource availability.

Further, we examine seasonal dynamics of flocks across three habitats following increasing human pressure: no disturbance (primary forest), fragmentation (small forest fragments), and deforestation (secondary forest). In all habitats, we quantify seasonal core area and home range size, species richness and attendance, and four metrics of ecological networks. We predict that within-year changes in abiotic conditions will indirectly affect flocks, trickling down to alter both individual species and the emergent properties of the flocks they comprise. During the period of reduced arthropod abundance, we hypothesize that flocks will expand home range size, include more species with higher attendance rates, become more cohesive, and increase the frequency of interspecific interactions. Alternatively, we predict that the breeding season will shrink the sizes of flock home ranges, reduce species richness, decrease attendance rates, and weaken the resulting networks. Depending upon which set of predictions predominate and whether these two periods temporally overlap will determine what we can infer about the underlying causality of any seasonal dynamics in mixed-species flocks. Furthermore, we predict that any seasonal differences in primary forest will be exacerbated in more heavily disturbed habitats, resulting in a greater seasonal disparity within secondary forest and forest fragments.

## METHODS

### *Study area*

We explored the seasonal dynamics of Amazonian mixed-species flocks at the Biological Dynamics of Forest Fragments Project (2°20' S, 60° W), ~80 km north of Manaus, Amazonas, Brazil. This large-scale landscape experiment was initiated in the late 1970s and early 1980s to study the effects of fragmentation prior to the clearing of three ~15,000-ha cattle ranches. However, the ranches were soon abandoned or operated at low production levels, leaving a patchwork of regenerating secondary growth and degraded forest fragments in a region dominated by continuous primary *terra firme* forest.

### *Defining seasonality by rainfall*

Across many years, rainfall seasonality at Manaus is typically split between two roughly equal components,

with rains generally increasing in October and peaking in March and April before subsiding in June (Stouffer et al. 2013). On the outskirts of Manaus (Reserva Ducke), 50 yr of precipitation data reveal that average annual rainfall is 2.5 m/yr, 68% of which falls between December and May (L. A. Candido, *personal communication*). However, because the onset of rains is variable and can trigger or coincide with leaf production and insect abundance in the tropics (Fogden 1972, Wolda 1978, 1988, Kishimoto-Yamada and Itioka 2015), we wanted to empirically define the onset of the wet season during our sampling period (September 2015–October 2017). To determine these dry-to-wet season transitions, we followed Li and Fu (2004) and Fu et al. (2013). We first acquired hourly precipitation data from the K34 micrometeorological tower (51.4 m) on the ZF-2 road (2°36' S, 60°12' W), which is approximately 40 km southwest of our study sites. Using 2 yr of complete data (2016–2017), we determined the mean daily rain rate (5.93 mm/d). We then averaged daily rainfall by 5-d periods (pentads) and compared these results to the mean rate. We defined the onset of the wet season when six of the subsequent eight pentads first exceeded the mean rain rate. This approach indicated that our two wet seasons began on 23 February 2016 and 29 November 2016 (Fig. 1a). Because we were less concerned with the arrival of the more temporally predictable dry season (Marengo et al. 2001), we considered the wet season to conclude with the transitional month of June. Using this seasonal delineation, we also plotted the maximum daily temperature in the understory (at a height of 5.2 m), which we similarly averaged across the same pentads (Fig. 1b). During this span, maximum daily highs averaged 28.8°C in the wet season and 30.9°C in the dry season.

#### *Flock-following data collection*

We sampled 12 Amazonian mixed-species flocks for 15 months across three treatments: 30–35 yr-old secondary forest (five flocks), 13.2-ha and 14.1-ha forest fragments (two flocks), and primary forest (five flocks). We will hereafter collectively refer to forest fragments and regenerating secondary forest as disturbed habitat. After defining the onset of the wet season in 2016, this resulted in 4 months of wet season sampling (March–June 2016) and 11 months of dry season sampling (September 2015–February 2016, July–August 2016, and August–October 2017; see Fig. 1). Based upon our extensive experience with this system, we established a list of 103 flocking species (Appendix S1: Table S1) and excluded all other birds incidentally registered with flocks. To focus on the resident bird community, we excluded three boreal migrants (*Vireo olivaceus*, *Setophaga fusca*, and *S. striata*) that were rarely detected (a total of five times). C. L. Rutt followed each of these 12 flocks on foot once a month for at least 3 h and binned species composition by 30-minute time blocks. Additionally, while following directly behind the flock, C. L. Rutt also recorded flock spatial positions

every 30 s using a handheld GPS unit. For more specific details about subsetting and data quality control, please see section 2.2 in Rutt et al. (2020).

#### *Analysis*

*Space use.*—With the spatial point data, we estimated the size of core areas (50% quantile) and home ranges (95%) using the ‘ctmm’ package (Fleming and Calabrese 2019) in R (2019). This package produces autocorrelated kernel density estimates by accounting for the autocorrelation structure of the data and allowing for the best-fit continuous time movement model to differ for each flock. For these finely sampled data, all best-fit models incorporated an Ornstein-Uhlenbeck Foraging (OUF) process, which identifies range residency while accounting for position and velocity autocorrelation (Calabrese et al. 2016). We generated these core areas and home ranges twice for each flock, once during the wet season and again during the dry season. We then ran generalized linear models (GLM) in base R to analyze whether a change in space use could be explained by the fixed effects of season (wet vs. dry), treatment (secondary forest, fragments, and primary forest), and the interaction of season and treatment. After examining fit statistics, specifically measures of overdispersion, we selected a normal error distribution for core area and a quasi-Poisson error distribution with a log link function for home range. To interpret model results, we used estimated marginal means (Searle et al. 1980; hereafter EMM) in the package emmeans (Lenth 2019) for all pairwise comparisons and, in the case of the quasi-Poisson model, to additionally back-transform responses from the log scale. Lastly, we report the effective sample size ( $\hat{N}_{\text{area}}$ ) for each flock, which is the number of independent locations that remain for home range estimation after accounting for autocorrelation.

*Species attendance.*—To determine whether there was a seasonal change in species-specific attendance rates, we considered all treatments together. We began by deriving the proportion of 30-minute time blocks that each species was present during both the wet and the dry season. Because species attendance rates range from 0 (absent in a given season) to 1 (always present), we chose the quasi-binomial error distribution to model this interval [0,1]. We then ran a GLM with a logit link function to compare species-specific attendance rates across seasons, after which we back-transformed the slope to the response scale using the inverse logit function. Using a test of a specific slope (a single *t* test where the null hypothesis is a value other than 0), we then contrasted the empirical slope of this relationship to 1, which is the theoretical slope of the line that represents no seasonal difference. If the *P* value was less than 0.05, then we considered this statistical evidence for a seasonal difference in attendance rates.

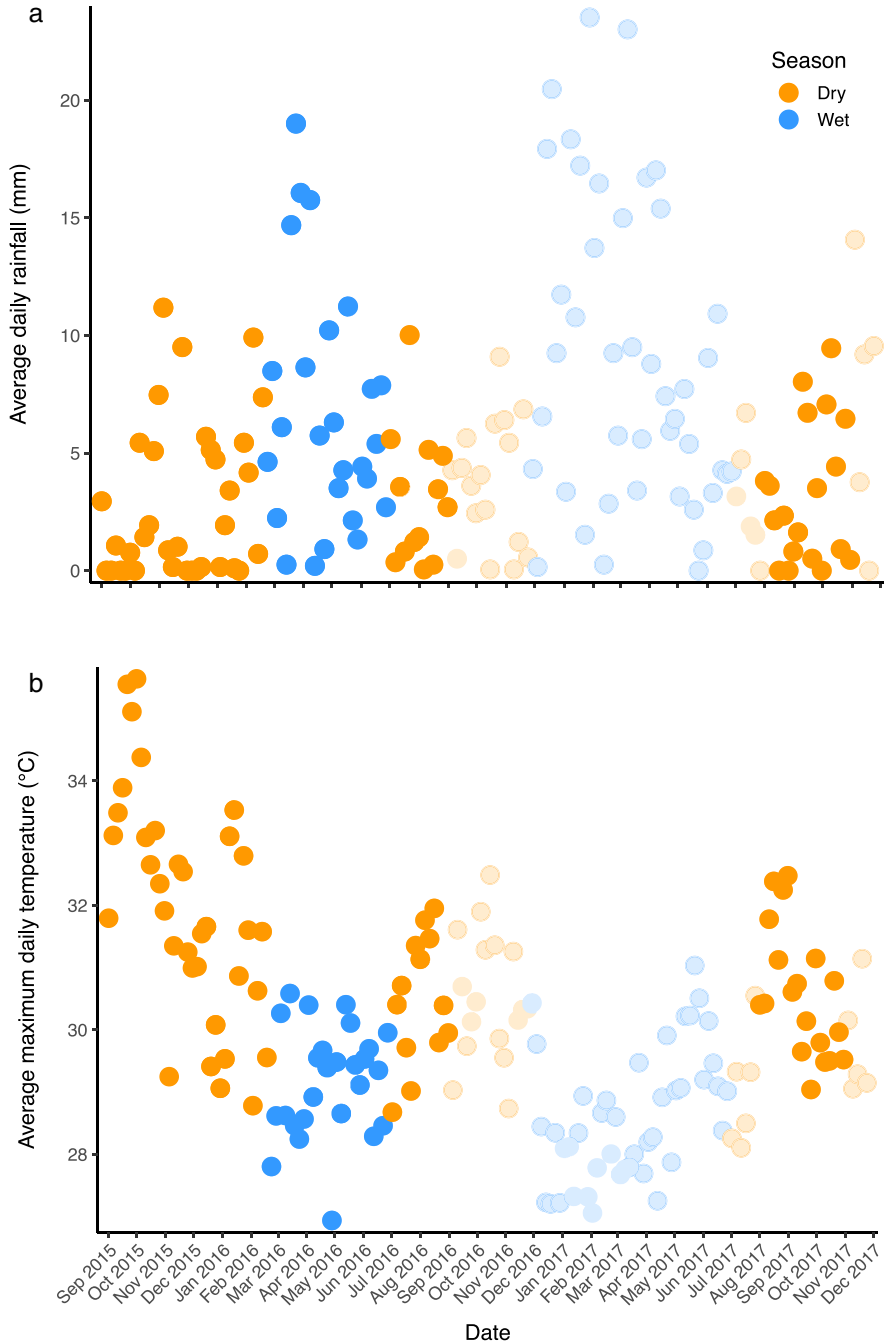


FIG. 1. Seasonal daily (a) rainfall and (b) maximum temperatures near the Biological Dynamics of Forest Fragments Project, averaged across 5-d intervals (pentads) between September 2015 and December 2017. These rainfall data were used to empirically define the onset of two wet seasons: 23 February 2016 and 29 November 2016. Mixed-species flocks were sampled across 15 of these months (shown with opaque points), which resulted in 4 months of wet season sampling (blue) and 11 months of dry season sampling (orange). All other months, when flock-following sampling did not occur, are illustrated with transparent points.

*Constructing networks of species co-occurrences.*—To describe flock properties that emerge from these complex interspecific associations, we built unipartite, undirected networks of species co-occurrences. Following

Mokross et al. (2014), we considered all flocking species that co-occurred in a single 30-minute time block to be associating reciprocally with one another; defining interspecific associations in this way (i.e., by group

membership) is termed the “gambit of the group” (Whitehead and Dufault 1999). For all species (nodes), we then weighted interspecific associations (edges, or links between species) by the frequency of pairwise interactions, which we derived using the simple ratio index (see Appendix S1: Fig. S1 for an illustrative representation of a flock network). This association index calculates the cumulative number of time blocks that two species co-occurred, divided by the total number of times in which one or both species were present with the flock. Proportions range between 0 (two species that never co-occurred) and 1 (two species that were always together in the flock). We constructed and primarily analyzed networks using the *igraph* (Csárdi 2019) and *asnipe* (Farine 2019) packages. Note that these ecological networks are complementary to social networks, except that nodes represent species instead of individuals.

*Species richness and network analyses.*—We then used these observed networks to explore whether there were seasonal changes in the size (i.e., species richness) or emergent properties of the flocks, downstream effects that might be more complex or nuanced than species attendance or species richness. We accomplished this by partitioning each flock network into seasonal time slices, or time-aggregated networks, resulting in a total of 24 networks (i.e., 12 flocks  $\times$  2 seasons). Although a single observer followed all flocks in the same, standardized way, unequal sampling effort between seasons, roughly three times more sampling for flocks in the dry season, could introduce sampling effects into the network comparisons. For instance, more species, and thus more connections, might emerge as an artifact of a greater number of opportunities to detect those species. Therefore, to remove the potential for sampling effects, we generated 1,000 seasonal networks for every flock, but limited the better-sampled dry season data ( $\geq 33$  h) to have only as many subsamples as the wet season (12 h for all flocks). To create each of these networks, we randomly subsampled (with replacement) 24 30-minute time blocks for each flock across seasons. We also bootstrapped the sampling data for the wet season, which ensured equal effort across seasons and allowed us to estimate uncertainty for all species richness and network metrics.

For each subsampled network, we calculated five metrics at both the species and flock level, largely following Mokross et al. (2014) and Zhou et al. (2019): (1) species richness, (2) mean normalized degree, (3) mean weighted degree, (4) skewness, and (5) the global clustering coefficient (hereafter, clustering). Degree is the sum of the number of interspecific connections for a given species, which we normalized by dividing by the number of available species ( $n - 1$ ), before averaging to obtain a single overall estimate for the network. Weighted degree is similar but sums the frequency of interspecific associations (edge weights) for each species, which we again averaged.

At the flock level, we calculated skewness using the moments package (Komsta and Novomestky 2015). This measures the skew of the frequency distribution of all species’ normalized degree values, or the extent to which a network is weighted toward individual species with few connections (positive skew) or many connections (negative skew). Finally, we examined clustering (or global transitivity), which measures the probability that three species (triads) in the network are connected by taking the proportion of closed triads divided by the total number of triads.

To evaluate statistical significance, we fit GLMs with post hoc tests 1,000 times for each of the bootstrapped network metrics. Just as with space use, these GLMs analyzed whether a change in network metrics could be explained by the fixed effects of season (wet vs. dry), treatment (secondary forest, fragments, and primary forest), and the interaction of season and treatment. Best-fitting models for these variables were the Normal (skewness), the inverse normal with a  $1/\mu^2$  link function (mean normalized degree and clustering), the Poisson with a log link function (species richness), and the quasi-Poisson error distribution with a log link function (mean weighted degree). We generated *P* values as the proportion of models where the beta (slope) for each of our parameters was greater or less than zero; if all but 50 models ( $50/1,000 = 0.05$ ) produced positive or negative slopes, we considered that parameter to be significant ( $p_{\text{boot}} \leq 0.05$ ). This approach to hypothesis testing for bootstrapped networks is akin to that discussed for pre-network permutations in social network analyses (Farine and Whitehead 2015, Farine 2017), which similarly randomize the observed data.

## RESULTS

Across seasons, we followed the 12 flocks for a total of 550.5 h (Table 1); however, this effort was disproportionately weighted toward the dry season (406.5 h in the dry season and 144 h in the wet season). Similarly, because of uneven replication among treatments, sampling effort was uneven between fragments and the two continuous habitats. We accompanied flocks for 225 h in primary forest, 225 h in secondary forest, and 100.5 h in fragments. Because of the very small sample size for fragment flocks ( $n = 2$ ), we encourage cautious interpretation of results for this treatment, in particular. Ten species were detected only in the larger dry season sample (Appendix S1: Table S1); however, removal of these 10 species did not qualitatively change any of the subsequent results.

### *Space use*

Although home range size of fragment flocks increased substantially during the dry season (Fig. 2a), only treatment effects in the GLM were statistically significant (likelihood ratio deviance = 7.6,  $P < 0.01$ ).

TABLE 1. Summary of sampling effort, species richness, and space use for mixed-species flocks across two seasons at the Biological Dynamics of Forest Fragments Project

Treatment (flock)	Effort (h)		Species richness†			Core area (ha)			Home range (ha)		$\hat{N}_{\text{area}}‡$		
	Wet	Dry	Wet	Dry		Wet	Dry		Wet	Dry	Wet	Dry	
Secondary forest flocks													
North	12	33	29.0	40.6	↑	3.76	3.55		14.45	12.66	↓	6.4	18.9
South	12	33	32.8	38.3	↑	2.78	3.85	↑	11.04	13.81	↑	8.2	22.4
Stream	12	33	37.5	41.1		3.46	4.44	↑	14.72	17.79	↑	6.9	17.2
Tower	12	33	29.9	36.7	↑	4.06	4.81	↑	14.53	16.89	↑	11.1	17.6
WSW	12	33	25.3	30.0	↑	3.18	2.43	↓	12.21	9.46	↓	8.0	17.7
Fragment flocks													
Colosso 14.1-ha	12	39.5	42.3	48.0	↑	1.55	3.59	↑	6.29	13.25	↑	10.6	29.5
Porto Alegre 13.2-ha	12	37	44.2	52.3	↑	2.35	3.22	↑	9.52	11.57	↑	14.7	27.4
Primary forest flocks													
Chato	12	33	46.0	46.1		4.26	4.17		16.53	16.54		7.6	23.2
Junction	12	33	41.6	54.5	↑	3.07	3.6	↑	11.86	12.22		11.4	26.3
Lanio	12	33	60.7	61.0		4.68	4.57		17.88	18.06		7.5	20.4
Novo	12	33	46.4	53.7	↑	3.93	5.71	↑	14.11	20.56	↑	8.2	18.4
Trilha	12	33	54.4	60.6	↑	4.92	4.25	↓	18.49	14.41	↓	7.0	24.2

Notes: Arrows denote a >10% absolute change in species richness and space use in the dry season. WSW, West-southwest.  
 †Flock species richness is averaged across 1,000 networks, generated by subsampling time blocks to ensure equal effort across seasons.  
 ‡ $\hat{N}_{\text{area}}$  effective sample size, or the equivalent number of statistically independent GPS locations.

Neither the effects of season (likelihood ratio deviance = 0.72,  $P = 0.24$ ) nor the interaction of season and treatment were significantly different

(likelihood ratio deviance = 1.45,  $P = 0.25$ ). Across seasons, only the home ranges of fragment flocks differed in marginal means from the other two treatments,

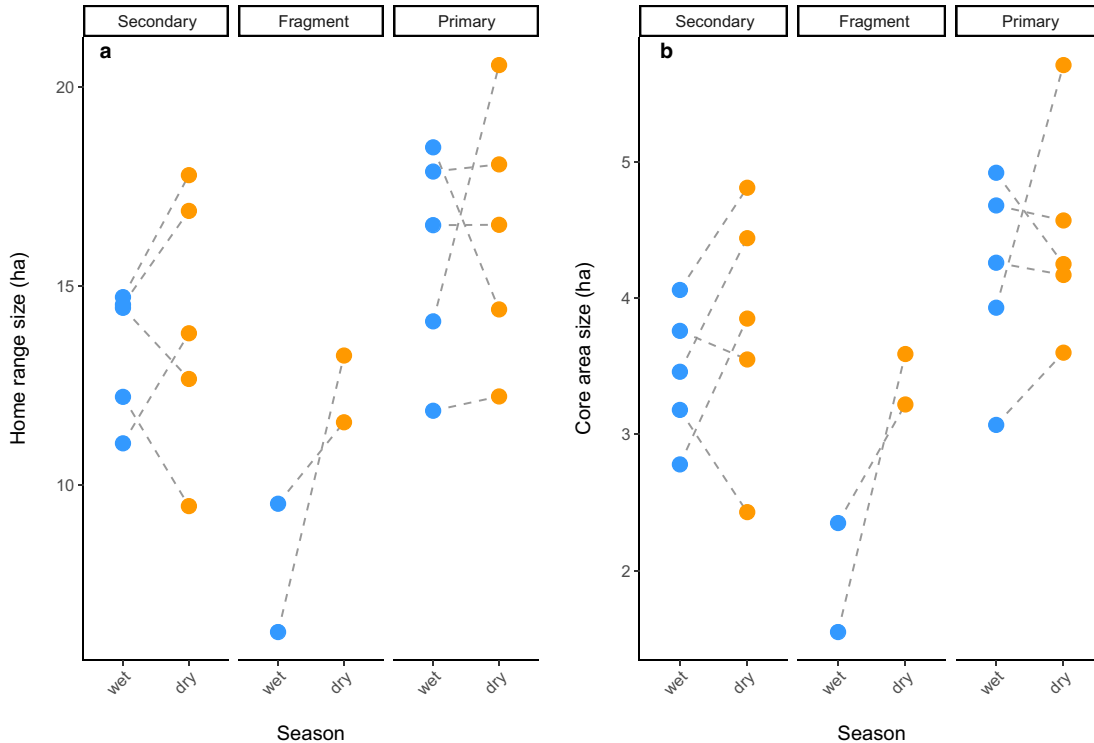


FIG. 2. Stripcharts highlight seasonal shifts and treatment differences in (a) home range and (b) core area size for flocks in forest fragments compared to those in primary and secondary forest. Dashed lines connect values from the same flock across seasons. Blue points refer to the wet season and orange points to the dry season.

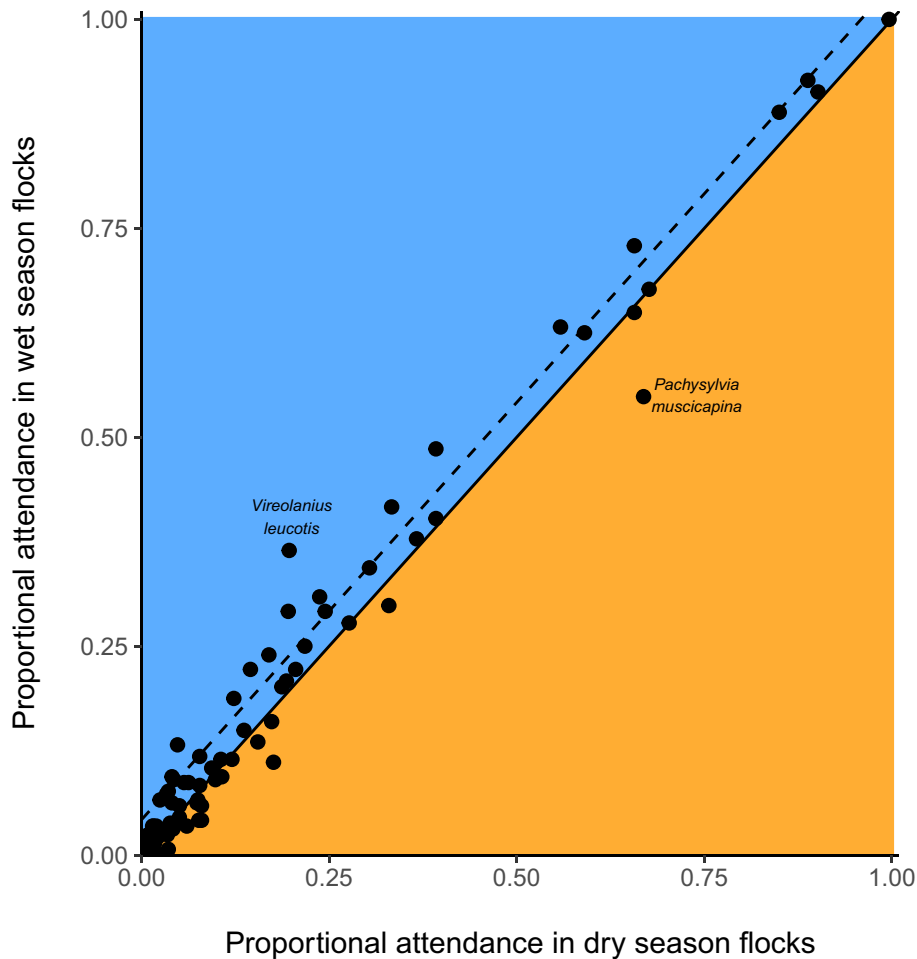


FIG. 3. Across all treatments, species attended flocks at similar rates during the wet (blue) and dry (orange) seasons. The diagonal 1:1 line (solid) represents the theoretical condition of identical attendance rates across seasons. The dashed line depicts the empirical relationship back-transformed from a generalized linear model of the data. A value of 0.25 within a season indicates that a species was present in one-quarter of all 30-minute time blocks. In each season, the two labeled species showed the greatest apparent seasonal difference in flocking preference.

being significantly smaller than those of both secondary forest flocks (EMM 9.9–13.8 = –3.9 ha,  $z$  ratio = –2.51,  $P = 0.03$ ) and primary forest flocks (EMM 9.9–16.1 = –6.2 ha,  $z$  ratio = –3.76,  $P < 0.01$ ). Results for core area size mirrored those of home range size (Fig. 2b). Again, only treatment effects were significantly different in the GLM (likelihood ratio deviance = 7.94,  $P < 0.01$ ). The effects of season (likelihood ratio deviance = 1.6,  $P = 0.08$ ) and the interaction of season and treatment were not significantly different (likelihood ratio deviance = 1.07,  $P = 0.36$ ). Averaging across seasons, only the core area size of fragment flocks, which was again smaller, differed significantly from that of primary forest (EMM 2.68–4.32 = –1.64 ha,  $z$  ratio = –3.86,  $P < 0.01$ ). Taken together across treatments, the size of home ranges and core areas increased by 19% and 22%, respectively, during the dry season, although these shifts were nonsignificant.

#### Species attendance

Across all treatments, we found that seasonal species-specific attendance rates fell very close to the 1:1 line (Fig. 3; see Appendix S1: Fig. S2 for attendance rates separated by treatment). Although species tended to increase flock attendance during the wet season (60/103 species [58%] in the blue polygon; Fig. 3), these shifts were subtle. As such, the back-transformed slope of the empirical line was 0.999 and was therefore statistically indistinguishable from 1 ( $P = 1$ ), indicating no seasonal difference in attendance rates.

#### Species richness and network analyses

Bootstrapped networks revealed that season was a significant predictor for changes in species richness and for all of the species- and flock-level network metrics. Across

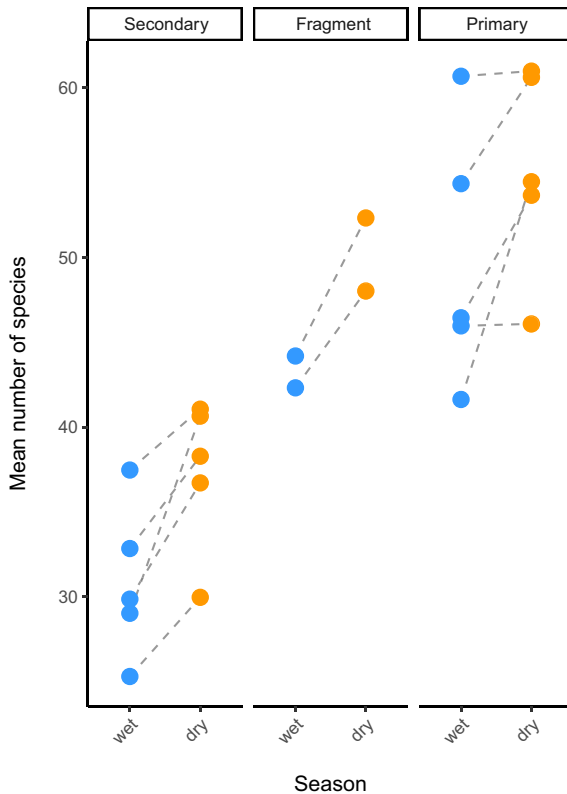


FIG. 4. Mean species richness increased in the dry season (orange) for all flocks in secondary forest, forest fragments, and primary forest. Flock means are derived from 1,000 bootstrapped networks in each season. Dashed lines connect values from the same flock across seasons.

treatments, flocks included, on average, an additional 6.4 species during the dry season than the wet season (46.9–40.5 species, randomized EMM  $\beta_{\text{mean}} = 0.15$ ,  $p_{\text{boot}} < 0.01$ ; Fig. 4), a 16% increase in species richness. This dry season increase in flocking species was significant in all habitats but was proportionately largest in secondary forest and fragments compared to primary forest: secondary forest (37.3–30.9 = 6.4 species [21%], randomized EMM  $\beta_{\text{mean}} = 0.19$ ,  $p_{\text{boot}} < 0.01$ ), fragments (50.2–43.3 = 6.9 species [16%], randomized EMM  $\beta_{\text{mean}} = 0.15$ ,  $p_{\text{boot}} = 0.01$ ), and primary forest (55.2–49.8 = 5.4 species [11%], randomized EMM  $\beta_{\text{mean}} = 0.10$ ,  $p_{\text{boot}} < 0.01$ ). Using the original observed data, we also calculated monthly species richness, which resulted in the counterintuitive finding that, even though more species utilized flocks throughout the course of the dry season, observed flocks contained slightly more species during the wet season (Appendix S1: Fig. S3). Across seasons, primary forest flocks were the most species (randomized EMM 52.4 species,  $p_{\text{boot}} < 0.01$ ), fragment flocks were intermediate (randomized EMM 46.6 species,  $p_{\text{boot}} < 0.01$ ), and secondary forest flocks were the most depauperate (randomized EMM 34.0 species,  $p_{\text{boot}} < 0.01$ ).

Across all treatments, the average flock species was associated with a greater number of species during the

wet season (mean normalized degree; randomized EMM  $\beta_{\text{mean}} = 0.65$ ,  $p_{\text{boot}} < 0.01$ ; Fig. 5a), despite species richness being higher in the dry season. The interaction of season and treatment for mean normalized degree was significant across all treatments, but this wet season increase in interspecific connections was steepest in secondary forest (randomized EMM  $\beta_{\text{mean}} = 0.90$ ,  $p_{\text{boot}} < 0.01$ ) and fragments (randomized EMM  $\beta_{\text{mean}} = 0.61$ ,  $p_{\text{boot}} < 0.01$ ) and lowest in primary forest (randomized EMM  $\beta_{\text{mean}} = 0.44$ ,  $p_{\text{boot}} < 0.01$ ; see also Appendix S1: Fig. S4a). Similarly, the average frequency of interspecific associations (mean weighted degree) was also higher in the wet season (randomized EMM  $\beta_{\text{mean}} = -0.22$ ,  $p_{\text{boot}} < 0.01$ ; Fig. 5b) and the interaction term was significant across all treatments. This increase in the strength of interspecific associations was nearly twice as high in fragments (randomized EMM  $\beta_{\text{mean}} = -0.28$ ,  $p_{\text{boot}} < 0.01$ ) as it was in primary (randomized EMM  $\beta_{\text{mean}} = -0.15$ ,  $p_{\text{boot}} < 0.01$ ) and secondary forest (randomized EMM  $\beta_{\text{mean}} = -0.22$ ,  $p_{\text{boot}} < 0.01$ ; Appendix S1: Fig. S4b). Not only was the mean normalized degree lower in the dry season, but the shape of the distribution changed for species' normalized degree values (skewness). Whereas wet season flocks contained mostly well-connected species (a normalized degree  $\sim 1$  and a negative skew), dry season flocks contained another peak of species with relatively few connections, creating a bimodal distribution and a stronger positive skew (randomized EMM  $\beta_{\text{mean}} = 0.45$ ,  $p_{\text{boot}} < 0.01$ ; Fig. 5c). The interaction term was also significant across all treatments, illustrating a consistent distributional shift during the dry season toward species with fewer connections, but which was most pronounced in disturbed habitats (secondary forest, randomized EMM  $\beta_{\text{mean}} = 0.58$ ,  $p_{\text{boot}} < 0.01$ ; fragments, randomized EMM  $\beta_{\text{mean}} = 0.43$ ,  $p_{\text{boot}} = 0.05$ ) and least so in primary forest (randomized EMM  $\beta_{\text{mean}} = 0.33$ ,  $p_{\text{boot}} = 0.01$ ; Appendix S1: Fig. S4c). Finally, flocks were also more cohesive in the wet season (clustering; randomized EMM  $\beta_{\text{mean}} = 0.27$ ,  $p_{\text{boot}} < 0.01$ ; Fig. 5d). Again, all three interaction terms were significant, with the largest differences in secondary forest (randomized EMM  $\beta_{\text{mean}} = 0.38$ ,  $p_{\text{boot}} < 0.01$ ) and fragments (randomized EMM  $\beta_{\text{mean}} = 0.25$ ,  $p_{\text{boot}} < 0.01$ ) and the smallest differences in primary forest (randomized EMM  $\beta_{\text{mean}} = 0.18$ ,  $p_{\text{boot}} < 0.01$ ; Appendix S1: Fig. S4d).

## DISCUSSION

Our results illustrate that a rich and diverse species interaction network makes seasonal adjustments to periods that are warmer and drier. During the dry season, mixed-species flocks included more species, generally ranged over larger areas, and displayed network structures that were less complex and less cohesive (cf. Jullien and Thiollay 1998). More specifically, the emergent properties of these diminished networks indicate that dry season flocks contained fewer and less frequent



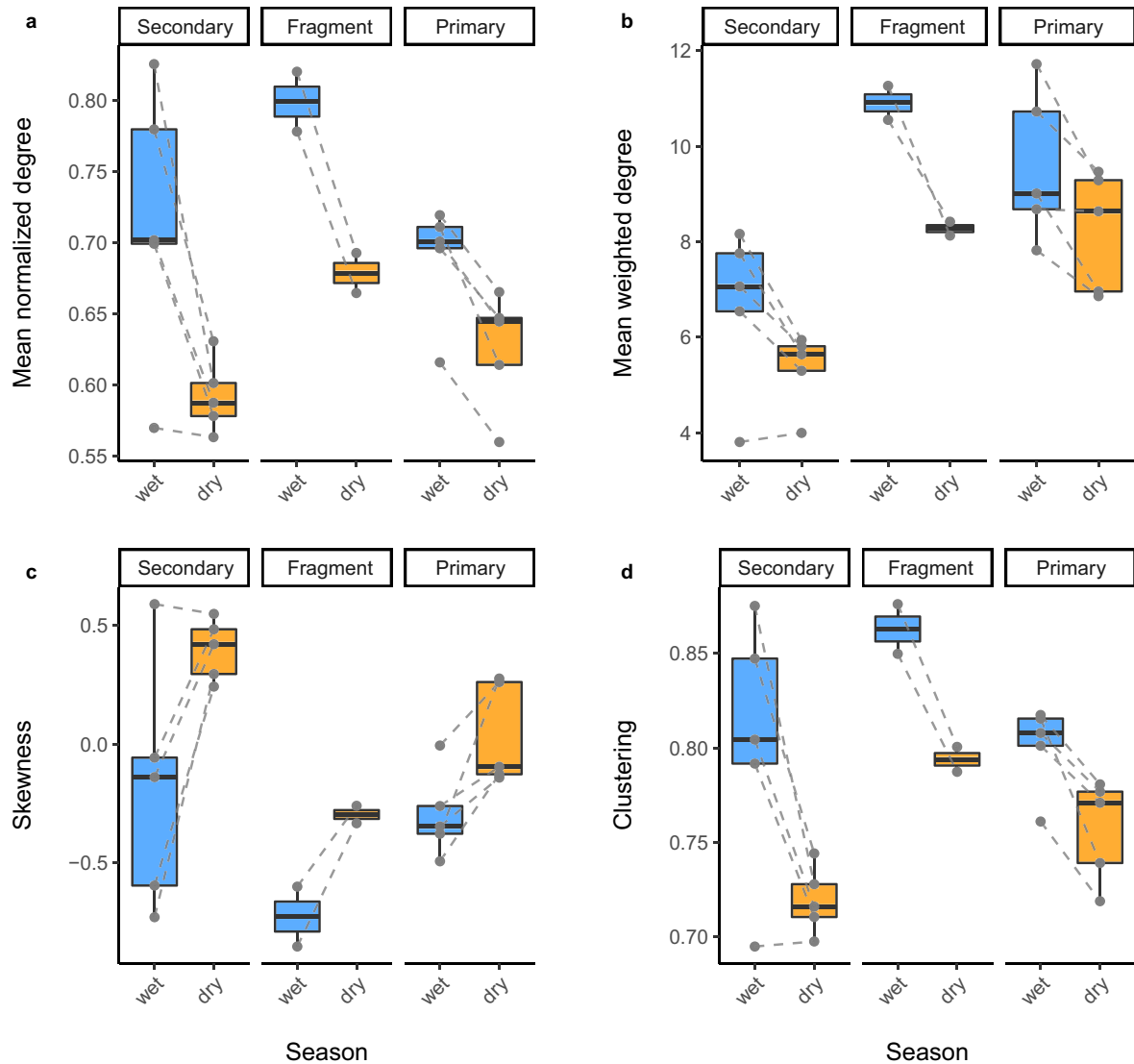


FIG. 5. Across all treatments, box plots reveal substantial seasonal variation for flocks in both interspecific interactions (a, b) and network structure (c, d). The four ecological network metrics are (a) mean normalized degree, (b) mean weighted degree, (c) skewness, and (d) clustering. Flock means are displayed for each of these metrics, which are derived from 1,000 bootstrapped networks in each season. Boxes range from the first to the third quartile, and the central line represents the median. Dashed lines connect values from the same flock across seasons. Wet season values are indicated in blue and dry season values in orange.

interspecific associations and are shifted to include more species with relatively few connections, consistent with differences between disturbed and intact habitats (Mokross et al. 2014). Moreover, all of these seasonal changes were most pronounced in small forest fragments and regenerating secondary forest, habitats that are less buffered from seasonality (see also Appendix S1: Fig. S4). Because of this larger seasonal shift in disturbed habitats, correctly interpreting differences among habitats requires considering the sampling period. Finally, because we are looking at within-flock changes for a large community of resident birds (excluding rare migrants), we can focus on the changing propensity of

species and individuals to join flocks by eliminating differences in bird density as a causal factor, which might otherwise confound inferences across disparate habitats.

These findings illustrate that, even in lowland rain forest, seasonal effects should not be ignored and need to be explicitly controlled for or considered alongside habitat effects. Seasonal effects, particularly in disturbed habitats, can exceed habitat effects, thus leading to improper conclusions if seasonality is ignored. For example, species richness is clearly highest for flocks in primary forest, intermediate in fragments, and lowest in secondary forest (Fig. 4). This conclusion is apparent whether we consider habitats separately across seasons

(i.e., dry vs. dry or wet vs. wet) or together, throughout the full annual cycle. However, if we had sampled these habitats in successive seasons, beginning with secondary forest during the wet season, the results would be different. In this scenario, we would have instead described fragment flocks (50.2 species during the dry season) as having the same number of species as flocks in primary forest (49.8 species during the wet season). Because these seasonal trends are consistent across habitats, we would have similarly uncovered quantitatively different results elsewhere (e.g., fragment flocks switching from having the highest mean normalized degree to the lowest; Fig. 5a). Therefore, in the absence of sampling data across a full annual cycle, we recommend standardizing effort by season (e.g., Wolfe et al. 2015b, Pollock et al. 2017, Rutt et al. 2020; Stouffer et al. 2020).

Some tropical birds have been shown to respond predictably to seasonality in lowland rain forests, although more subtly than in drier, more seasonal habitats (Woodworth et al. 2018). Much like their temperate counterparts, some tropical birds show strong breeding seasonality, increasing and decreasing the size of their gonads and nesting at predictable times of the year (Snow and Snow 1964, Fogden 1972, Gradwohl and Greenberg 1982, Wikelski et al. 2000, Wikelski et al. 2003). However, in the central Amazon, this pattern is obscured by different seasonal preferences and prolonged breeding seasons, resulting in only a modest seasonal peak in breeding activity across the entire community (Stouffer et al. 2013). Likewise, the schedule of molting in this community generally lags 1–2 months behind that of breeding, but high variability and protracted molts again results in no major seasonal peak (Johnson et al. 2012). Although most species are sedentary and seasonal migration is rare, a few species of Amazonian frugivores have been documented performing seasonal movements, primarily departing during the dry season, likely due to the scarcity of canopy fruits (Stouffer and Bierregaard 1993, Naka 2004). More subtle movements include seasonal shifts in habitat selection along local moisture and vegetation gradients (Karr and Freemark 1983). Yet, in spite of the evidence that seasonality structures the life cycles of some rain forest birds, few studies have examined the seasonal dynamics of interspecific interactions in these relatively stable environments.

Seasonality in mixed-species flocks has drawn attention for some time (Davis 1946), but few studies have examined this rigorously in the tropics, where flocking is a year-round phenomenon, and none have quantified seasonal changes using network theory. Furthermore, failing to analyze home range size in concert with species richness and flock size limit previous inferences about seasonality. In Neotropical lowlands, the majority of previous work on seasonality in mixed-species flocks stems from the Brazilian Atlantic Forest (Davis 1946, Develey and Peres 2000, Maldonado-Coelho and Marini 2000, 2004), where understory flocks form around the cardinalid *Habia rubica*. These flocks contain relatively

few species and individuals (averaging 6–7 species and 9–11 individuals), similar in size to temperate flocks (Develey and Peres 2000, Maldonado-Coelho and Marini 2004). For comparison, our primary forest flocks averaged 32 species and 43 individuals per 3-h flock-following bout. Nonetheless, Atlantic Forest flocks showed a slight increase in species richness and flock size during the dry season, which coincided with reduced arthropod abundance and the non-breeding season of this more synchronous breeding community (Davis 1945, Develey and Peres 2000, Maldonado-Coelho and Marini 2004). Similarly, Fogden (1972) and Croxall (1976) found that the size of Bornean mixed-species flocks peaks at the end of the dry season, when insects are least abundant and before forest birds begin breeding. Elsewhere, groups of two antwren species on Barro Colorado Island (Panama), perhaps an incipient mixed-species flock, moved more quickly across and expanded the size of their co-defended home range during the dry season, prior to an increase in their arthropod prey and the start of breeding activity (Gradwohl and Greenberg 1982, Greenberg and Gradwohl 1985). This leads us to evaluate the two primary, but non-mutually exclusive, hypotheses for seasonality during the annual cycle of mixed-species flocks: the breeding season and changing food availability. The results of our study, with more complex and speciose flocks, allow us to assess these hypotheses with more nuance and detail in a system in which the breeding season and peak arthropod abundance do not coincide.

The breeding season may physically and temporally constrain species from participating in Amazonian mixed-species flocks. In the Guiana Shield, flock obligates predominantly breed during the mid- to late dry season (August–November; C. L. Rutt, *unpublished data*; Jullien and Thiollay 1998, Stouffer et al. 2013). However, even when they have active nests, members of these flock obligates often continue to accompany flocks (C. L. Rutt, *unpublished data*; Munn and Terborgh 1979), and fledged young are rapidly incorporated into the parent flock (Munn and Terborgh 1979, Jullien and Thiollay 1998). In the central Amazon, the nuclear species, *Thamnomanes caesius*, is critical for flock cohesion and exerts a disproportionate influence on flock space use and time budgets. Although tropical flocks may respond idiosyncratically to the breeding season of their nuclear species (Jayarathna et al. 2013, Jiang et al. 2020), we repeatedly watched as *T. caesius* led the entire flock to its nest, which it proceeded to build for upwards of 44 minutes, while the remainder of the flock stalled out and waited silently nearby (see a similar account in Develey and Peres [2000] for flocks led by *Habia rubica*). Therefore, we would predict that constraints of nesting for both *T. caesius* and the various constituent species would shrink home range sizes, decrease attendance rates and species richness, and weaken flock networks. This could explain the slightly diminished attendance rates (Fig. 3) and reduced network structures (Fig. 5) that we found

during the breeding (dry) season. However, it is more challenging to interpret the ~20% increase in space use, as well as the growing number of species that availed themselves to flocks (+11–21%, depending upon habitat), that occurred simultaneously.

Seasonal changes in food availability may also influence flock dynamics and could be the ultimate factor that dictates when flocking species breed. Theory predicts that flock foraging benefits increase with reduced food availability (Morse 1970, Clark and Mangel 1984), and the literature consistently shows that arthropod biomass and abundance in lowland tropical rain forests is lowest during the dry season, both generally (Fogden 1972, Gradwohl and Greenberg 1982) and across discrete microhabitats: forest floor (Pearson and Derr 1986, Mestre et al. 2010, Levings and Windsor 1982), understory (Develey and Peres 2000, Richards and Windsor 2007), and suspended dead leaves (Gradwohl and Greenberg 1982), although there are exceptions (Wolda 1978, Boiniski and Fowler 1989). This would lead us to predict that, during the dry season, flocks should expand their home ranges, include more species, increase species attendance, and strengthen their networks. We again find partial support for these predictions, as home ranges generally expanded and more species utilized flocks, but flock attendance and especially network metrics were depressed during the dry season. If larger core areas and home ranges indicate resource scarcity and lower quality habitat (Litvaitis et al. 1986, Powell et al. 2016, Mokross et al. 2018), then the dry season increase in area requirements for fragment flocks is particularly compelling. Although these isolated flocks lack neighbors and were almost completely confined by fragment borders, they ranged over a relatively small fraction of available habitat during the wet season (Fig. 2, Table 1). However, both core areas (+74%) and home ranges (+57%) increased dramatically during the dry season, suggesting that habitat that was previously sufficient needed to be expanded.

In the face of mixed evidence for breeding season constraints and changing food availability, perhaps the most parsimonious explanation invokes balancing both hypotheses. Coupled with the individual constraints of nesting in the dry season, flocks that range over a wider area (during a time of diminished arthropod abundance) would maximize opportunities for more species to temporarily join flocks. Simultaneously, however, these two competing pressures would also decrease the ability of those species and individuals to linger with flocks, thereby scaling up to diminish the structure of flock networks. However, for individual flock members, we suspect that regularly separating from flocks while breeding would primarily serve to increase commuting time, without a loss of foraging information, unlike birds that rely on social cues to commute to localized and ephemeral resources.

This study also suggests that the perceived conservation value of human-modified habitats may depend upon both when a study takes place (an artifact; see

Gove et al. 2005) and on the biologically important seasonal requirements of a species or system. Distinguishing between these two interpretations has received little attention. Our results from lowland rain forest demonstrate that the seasonal contrast for flocks was most pronounced in disturbed habitats, suggesting that primary forest is relatively buffered from the effects of seasonality. Interacting with deforestation and fragmentation, the dry season may extend the penetration of edge effects (Kapos 1989), increase solar radiation (Chazdon and Fetcher 1984), alter local and regional rainfall regimes (Lawrence and Vandecar 2015), and lengthen the period of food scarcity (Fogden 1972). Moreover, evidence is mounting that seasonality itself is increasing in central Amazonia (Feng et al. 2013, Almeida et al. 2017). As temperatures continue to climb in the Amazon, long-term trends indicate that the difference in seasonal rainfall has also increased (generally, a wetter wet season and a drier dry season; Almeida et al. 2017). Furthermore, the frequency of extreme large-scale climatic cycles (the El Niño-Southern Oscillation) is increasing and will intensify typical climatic swings by promoting periods of severe heat and drought (Cai et al. 2014, Jiménez-Muñoz et al. 2016). For tropical birds, these El Niño events have been shown to affect population dynamics (Wolfe et al. 2015a) and can shift the timing of events in the avian life cycle, such as breeding (Styrsky and Brawn 2011). Thus, although we do not know how seasonality in mixed-species flocks may affect the fitness of its members, increasing climate seasonality is likely to exacerbate seasonal changes and further delay recovery in human-modified habitats. How these tropical animals, which have evolved in relatively stable rain forest, will cope with an increasingly unstable climate will be an important question for future research.

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2235/full>

## DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.15dv41nvv>.