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Article

The effect of forest gap dynamics on tropical rainforest birds

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Abstract
Forest gap dynamics are a key driver of bird community structure. Understanding the effect of forest gaps on abundance and communities is critical in an era of increasing anthropogenic disturbance in tropical forests. In this study, we investigated the impact of natural rainforest gaps on bird communities and abundance in a highly diverse lower montane rainforest in Thailand. We employed mist-netting in a 5-year study (2015-2019) to assess bird assemblages and abundance across paired sites in forest gaps and under closed canopy, resulting in 1,148 captures of 81 species. Total abundance did not differ between forest gaps and under the closed canopy. The long-term study design captured seasonality in bird composition, highlighting dynamic assemblages driven by seasonal migration. We observed a strong effect of forest gaps on bird assemblages. Interestingly, we found Hill Blue Flycatcher (*Cyornis whitei*) species with a strong preference for forest gaps increased in abundance with total gap size. Most species showed no relationship with forest gap sizes in this area. Our findings support previous research showing that gap sizes of 130–1,020 m^2 in the lower montane forest are not highly detrimental, yet still reduce bird abundance. This highlights that even moderate habitat disturbances can negatively affect sensitive bird species. Nonetheless, forest gaps may also play a key role in promoting tropical biodiversity by facilitating niche differentiation and specialization among understory birds.

Key words Forest gap, Mist-net, Pattern, Banding, Tropical bird.

Introduction

In all forests, the tree canopy is changing continuously, through growth, death, and succession. The fall of one or multiple large trees generally creates a hole in the canopy or a “canopy gap”, this is the initial step of the succession process in forest ecosystems worldwide (Burslem, 2004). Natural disturbances, such as treefalls, can affect the dynamics of both the plant assemblage and the resident faunal (Panayotov *et al*. 2011; Crausbay & Martin, 2016). Moreover, the effects of natural disturbance provide a suitable niche and create the highest levels of biodiversity in terms of the intermediate disturbance hypothesis (IDH) (Connell, 1978; Viljur *et al*., 2022). Thus, natural forest gaps play a key role in the dynamics of forest ecology and are important to maintaining diversity of ecosystem structure, species and functions, adaptive and evolutionary potential (Muscolo *et al*., 2014; Hunter *et al*., 2015; Kuuluvainen *et al*., 2021). In addition, the falling of a tree caused by natural disturbances (old age, windstorms, lightning strikes and parasitic plant) introduces environmental heterogeneity and to the mature forest through changes in light intensity, temperature, litter depth, and tree regeneration (Whitmore, 1989; Gharehaghaji *et al*., 2012). Heterogeneity is important for maintaining the complexity of structure and composition in the dynamics of forest gaps and the whole ecosystem (Denslow, 1980).

Forest gaps are crucial for bird assemblages due to their spatial and temporal variability in resource availability, which creates unique microhabitats that promote the distribution and utilization of bird communities. (Gharehaghaji *et al*., 2012; Moorman *et al*., 2012; Perkins & Wood, 2014; Siri *et al*., 2019; Lima & Guilherme, 2021). Much research has demonstrated the importance of forest gap for diversity of avian communities and populations abundance (Schemske & Brokaw, 1981; Leaver *et al*., 2020; Lewandowski *et al*., 2021). In a tropical forest, forest gaps influence the bird community via their influence on microhabitat variation and resources; for example, they can be keystone places for frugivorous and nectarivorous birds (Banks-Leite & Cintra, 2008). Moreover, the presence of nectarivores was significantly higher in the gaps compared to the forest areas. (Wunderle *et al*., 2006; Siri *et al*., 2019; Lima & Guilherme, 2021). Furthermore, the heterogeneity in microclimates and resources provided by gaps can increase the overall stability of populations and assemblages within forests (Ponpituk *et al*., 2022).

Global studies indicate that the abundance and composition of fauna often fluctuate alongside reductions in forest structural complexity due to logging (Barlow & Peres, 2004; LaManna & Martin, 2016). Many countries are experiencing increased timber demand driven by the growing needs of the construction sector and industrial applications. Logging alters forest structure and tree species composition, leading to changes in faunal composition (Jati *et al*., 2018; Soares *et al*., 2021). In South Africa, informal selective timber harvesting has led to a 30% increase in the number of canopy gaps. The habitat gradient from intact forests to canopy gap conditions negatively impacts insectivorous birds, cavity-nesting birds, ground-nesting birds, and species that engage in hawking and arboreal probing (Leaver *et al*., 2020). Furthermore, selective logging in tropical regions and clearcut logging in temperate areas have resulted in species loss across all forest strata, contributing to declines in species richness of up to 27% (LaManna & Martin, 2016). In addition, assemblage changes were predicted by vertical stratification of forest use, particularly affecting avian species in the understorey and mid–upper levels; in disturbed areas, birds may adapt their foraging strategies by foraging at lower heights, switching food sources, or spending more time foraging, especially those relying on canopy insects or fruits that face resource shortages (Harris *et al*., 2023). In subtropical, post-logging effects alter avian predator density, with generalist predators negatively impacted by canopy openness (Tallei *et al*., 2022). Insectivorous and frugivorous birds exhibited significantly lower abundances in the logged areas, while the species found in these areas tend to be more resilient to human disturbance (Felton *et al*., 2008). Moreover, tropical understorey birds (frugivore and omnivore) exhibit reduced body size in selectively logged forests, as their sensitivity to changes in forest structure may result from physiological intolerance, limited food availability, increased predation risk, and avoidance of gaps (Thiollay, 1997; Messina *et al*., 2021).

In the context of climate changes in forest dynamics during the Anthropocene, understanding the impact of forest gaps on the forest bird community is increasingly important (Pfeifer *et al*., 2018; Pollock *et al*., 2020). The relationships between climate change and birds are becoming more obvious. Warming temperatures caused by climate change are changing bird habitats, seasons, and the timing of bird migration patterns (Carey, 2009). However, the impact of forest gap dynamics in terms of gap sizes on the forest birds of tropical rainforests has not been assessed clearly. The insight into the forest gap is necessary to apply landscape management for bird conservation.

In this study, we surveyed understory birds at 12 paired sites in forest gaps and under closed canopy every month for five years. In previous studies, it has been found that forest gaps influence bird foraging behavior and leg morphology (Siri *et at*., 2019; Siri *et al*., 2020). We focus on understory birds because these species are sensitive to habitat disturbance (Loaiza *et al*., 2020; Fontúrbel *et al*., 2021). Long-term studies cover 5 years which to help understand how the different patterns of birds in the heterogeneity interact. We address three questions: First, how do bird assemblages differ between habitat conditions (forest gap and under closed canopy); Second, do the patterns vary between seasons and, finally, is there a difference in the abundance of birds across gap sizes?

Materials and Methods

Study site. The study was conducted in the lower montane forest at Huai Kogma sub-watershed (18° 54' N–98° 54' E), an area of a 16-ha permanent plot on Long Term Ecological Research Sites (LTER) in Doi Suthep-Pui National Park, Chiang Mai Province, northern Thailand. The nearest road was located approximately 1 kilometer from the permanent plot in a straight-line distance. The elevation ranges from approximately 1,250 to 1,540 meters above mean sea level (Siri *et al*., 2019). This area has two seasons: a dry season from November to April, and a wet season from May to October (Nutiprapun *et al*., 2022). The average annual precipitation is 1,350–2,500 mm/year, with an average minimum temperature of 20.8°C and a maximum temperature of 32.2°C. The natural vegetation in this permanent plot is a mature evergreen forest. Marod *et al*. (2022) found 220 species of trees, the dominant species is *Castanopsis acuminatissima*, *Schima wallichii*, *Castanopsis armata* and *Styrax benzoides*.

Gap survey in the field. This study particularly focuses on forest gaps that have been created by natural single-tree falls (small-scale) (Sapkota & Oden, 2009). Twelve gaps were selected based on vegetative maps. The geographic position of all forest gaps was determined Global Position System (GPS). All trees with a diameter at breast height (DBH) ≥ 2 cm in the permanent plot were measured, tagged, and identified species, (Marod *et al*., 2022). The forest gaps which had been created by natural large tree falls (Fig. 1), DBH between 43.2–124.2 cm. The large single tree species that cause forest gap comprise *Persea gamblei* (DBH 43.2 cm), *Markhamia stipulata* (DBH 51 cm), *Elaeocarpus floribundus* (DBH 55.7 cm), *Catanopsis acuminatissima* (DBH 58.3–82.2 cm), and *Choerospondias axillaris* (DBH 124.2 cm).

Figure 1. The examples of the forest gaps created by natural tree falling due to wind, lighting and tree death because of longevity in 16-ha permanent plot.

Forest gap size was measured in the field according to procedures laid out by Runkle (1992). The sampling protocol was constructed by locating and measuring two perpendicular lines in each gap: the length (L) is the longest distance within the gap and the width (W) is the greatest distance perpendicular to the length. In this study, forest gaps size ranged from 130 m^2 to 1,020 m^2 (Fig. 2).

Figure 2. Canopy gaps from smallest to largest (see left to right: size 130 m^2, 154 m^2, 209 m^2, 240 m^2, 380 m^2, 392 m^2, 442 m^2, 450 m^2, 494 m^2, 532 m^2, 589 m^2, 1,020 m^2) in the study area.

Mist-net survey. Mist-netting was used to capture understory birds in forest gaps (FG) and under closed canopy (UCC). Mist-nets were used at each forest site in two different microhabitat types (12 sites in FG, 12 sites in UCC), and the distance between the forest gap and under closed canopy was about 10 m. Nets at each site were opened before sunrise from 06:00 am to 16:00 pm, and the open mist-nets were inspected every 30–60 min (Bibby *et al*., 1998; Wunderle *et al*., 2006). Data were collected for twelve sites, with three sites sampled per day over four consecutive days of bird sampling each month. All individual birds were banded. We captured 1,148 individual birds of 81 species (Appendix 1). We detected 628 individuals of 61 species in the forest gap, and 520 individuals of 67 species in under canopy. All birds were identified by species, sex, and age (juvenile or adult). Bird banding followed the protocols of the Department of National Park, Wildlife and Plant Conservation of Thailand (granted permission issued no. DNP 0907.4/9819). Bird sampling was carried out from January 2015 through October 2019.

Statistical analyses.

Microhabitat assemblage structure: We conducted all analyses with R version 4.2.1 (R Core Team, 2022). Principal Component Analysis (PCA) was used to examine the assemblage structure based on species and number of individuals and test the relationships between environmental variables and bird assemblage structure at each site. The PCA was done using the factoextra package (Kassambara & Mundt, 2020). Additionally, we examined the relationships between the assemblage structure as represented by the PCA score of each dimension using Pearson correlations.

Patterns of bird abundance: We examined the patterns of abundance in individual bird species for the species with sufficient data to enable higher resolution analysis (10 species). (Supplementary B) including: the Hill Blue Flycatcher (*Cyornis whitei*) (N=161, Recapture=71), Yunnan Fulvetta (*Alcippe fratercula*) (N=136, Recapture=181), Grey-throated Babbler (*Stachyris nigriceps*) (N=78, Recapture=100), Puff-throated Bulbul (*Alophoixus pallidus*) (N=61, Recapture=36), Bianchi's Warbler (*Phylloscopus valentini*) (N=56, Recapture=28), Blyth's Leaf Warbler (*Phylloscopus reguloides*) (N=53, Recapture=7), Orange-headed Thrush (*Geokichla citrina*) (N=44, Recapture=4), Martens's Warbler (*Phylloscopus omeiensis*) (N=42, Recapture=18), Mountain Bulbul (*Ixos mcclellandii*) (N=41, Recapture=9), and Silver-breasted Broadbill (*Serilophus lunatus*) (N=37, Recapture=3). We analyzed individual bird data, excluding recapture data from the analysis. Differences in the average number of individual birds between forest gap and under closed canopy in the dry season and wet season were assessed using Pairwise Wilcoxon Rank Sum Test. To statistically test whether the number of individual birds (dependent variable) differed by habitat type (forest gap and under closed canopy) and across months (January–December), we fitted a generalized linear mixed-effects model (GLMM) using the package lme4, function "glmer", family "Poisson" (Bates *et al.*, 2015).

Relationship between birds and forest gap size: The relationship between the forest gap size and the number of individual birds or each species was examined using Generalized Additive Models (GAM) package gamair (Wood, 2006; 2017). Prior to conducting the comparison of means, we tested the normality of the data using Shapiro–Wilk's test and assessed the homogeneity of variances among groups using Bartlett's test. Differences in the number of individual birds and forest gap size (130 m^2–1,020 m^2) were evaluated with One-Way ANOVA and using Tukey's post-hoc tests to analyze differences in the number of individuals between gaps with different sizes.

Results

Bird assemblage structure

Over five years of field study, bird assemblages varied depending on specific habitat conditions. We found microhabitats strongly shaped the bird assemblage in our study systems. There was a significant difference between the bird assemblages in forest gaps and under the canopy (Fig. 3A). In the principal component analysis, the first two axes (Dim 1 and Dim 2) of the site assemblage structure explained 11.7% and 10.8% of the variation in assemblage structure. The bird assemblage under the forest canopy was less variable across sites than within the gaps. The standard deviation (S.D.) and variance of the first axis were significantly higher in the forest gap S.D. =2.41 than in under closed canopy S.D. =1.67. Demonstrating that the bird assemblage in the gaps was more variable and the pattern suggested that this variation is related to gap size. However, although there was a positive relationship between the PCA axis and gap size it was not statistically significant (Fig. 4).

Table 1. Average no. of individual birds in forest gap (FG) and under closed canopy (UCC) based on season, and Wilcoxon Rank Sum Test between FG and UCC in the dry season and wet season in a 16-ha permanent plot from 2015-2019.

Common name	Dry season			Wet season		
	FG	UCC	p-value	FG	UCC	p-value
Puff-throated Bulbul	6.20±0.86	3.60±0.67	0.07	2.80±0.73	6.00±1.89	0.39
Mountain Bulbul	1.80±0.80	2.20±0.80	0.74	3.00±1.09	2.08±0.66	1.00
Hill Blue Flycatcher	5.60±0.92	7.00±1.92	0.75	10.60±2.44	18.80±4.66	0.24
Grey-cheeked Fulvetta	16.80±4.61	13.60±3.41	0.46	13.80±1.77	10.00±2.88	0.52
Grey-throated Babbler	3.80±0.73	10.80±1.31	0.01*	6.20±2.24	9.20±1.90	0.29
Silver-breasted Broadbill	2.00±0.50	2.40±0.06	0.58	1.00±0.44	2.40±0.92	0.27
Orange-headed Thrush	0.20±0.20	0.40±0.24	0.60	2.80±0.58	5.80±1.15	0.04*
Blyth's Leaf Warbler	6.40±1.46	2.40±0.67	0.09	1.80±0.80	1.00±0.54	0.58
Bianchi's Warbler	4.20±1.39	6.40±1.72	0.40	1.80±0.71	2.20±0.71	0.74
Martens's Warbler	3.20±1.68	4.40±1.02	0.52	1.60±0.92	2.00±1.30	1.00

* Statistically significantly different mean values ($p<0.05$).

The bird assemblage during the wet season represented a resident assemblage that was a subset of the larger, more variable assemblage present in the dry season (Fig. 3B). The more complex and variable dry season bird assemblage is influenced by the complex pattern of migratory arrival and departure of the 27% of the overall assemblage that is seasonally migratory. The first ordination axis comparing assemblage structure at each site in the dry versus wet season (Dim 1: explained 9.7%), and the second axis (Dim 2 explained 8.8% of seasonal assemblage structure (Fig. 3B). A major difference between the two season was the high variability in assemblage structure during the dry season. A value of S.D. and variance of dry season 3.51 (S.D.), 12.30 (variance) significantly higher than the under closed canopy 0.88 (S.D.), 0.78 (variance).

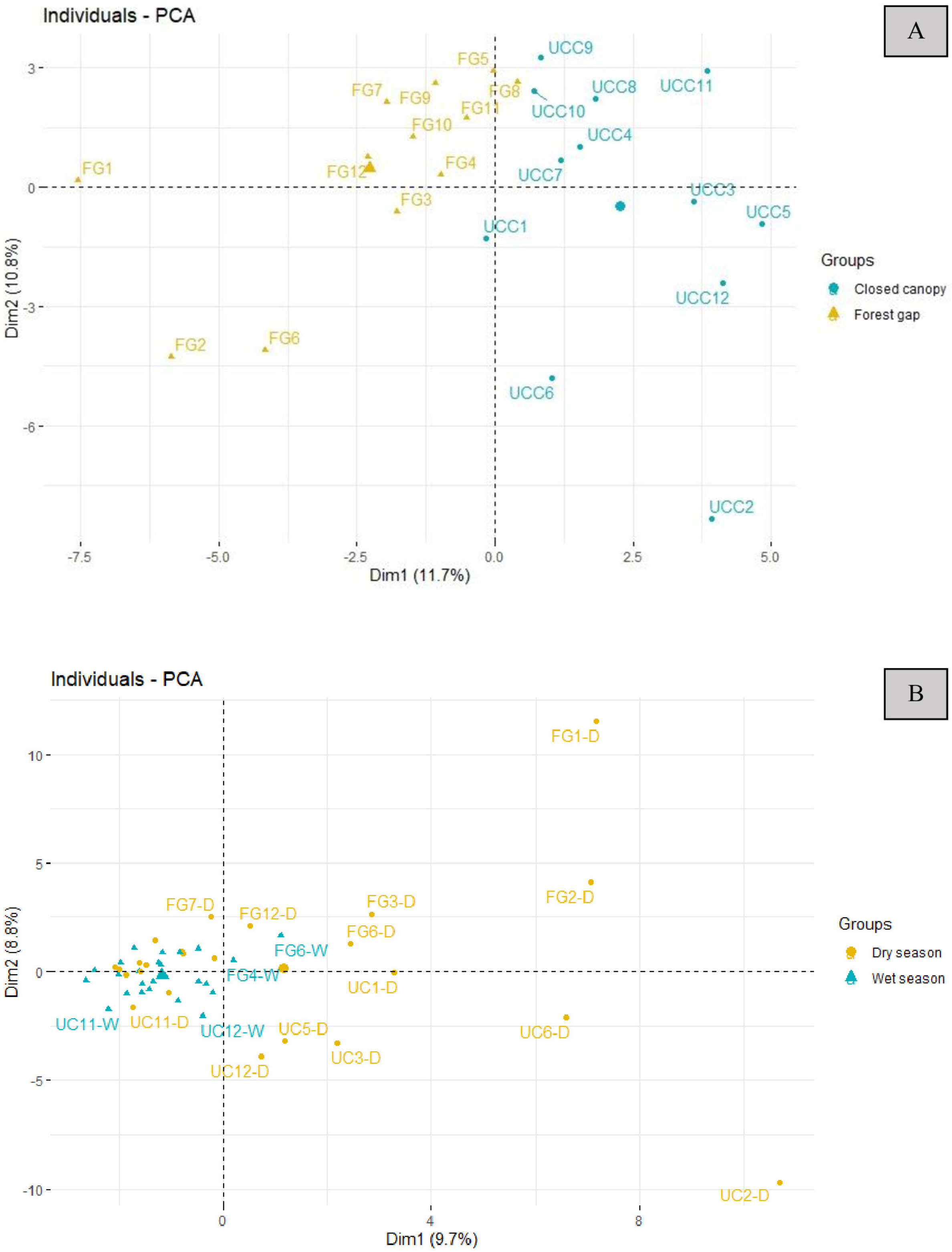

Figure 3. Principal component analysis (PCA) showing (A) the distribution of 24 local microhabitat site in the 12 sites of under closed canopy and 12 site in the forest gap and (B) microhabitat site based on season (wet and dry).

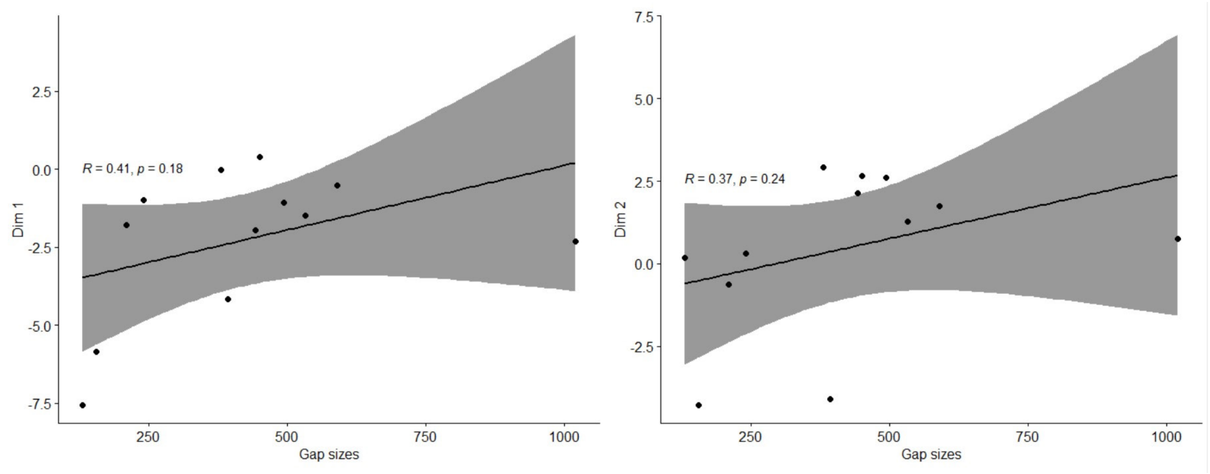

Figure 4. Scatter plot show Pearson's correlation coefficients between PCA score of site assemblage and size of forest gap (130 m^2–1,020 m^2) from 2015-2019 in a 16-ha permanent plot.

Abundance patterns of individual bird species

The abundance of individual bird species during the dry and wet seasons in the forest gap and under the closed canopy habitats were clearly shift defined by seasons. The abundance of individual bird species exhibited four general patterns: First, birds were more abundant in forest gaps (FG) and under closed canopy (UCC) during the dry season (D > W), including the Silver-breasted Broadbill, Blyth's Leaf Warbler, Bianchi's Warbler, and Martens's Warbler. Second, bird abundance was higher during the wet season (W > D), including the Hill Blue Flycatcher and Orange-headed Thrush. Third, bird abundance did not differ between seasons (D = W), as observed in species like the Mountain Bulbul, Grey-cheeked Fulvetta, and Grey-throated Babbler. Finally, no specific pattern was found for the Puff-throated Bulbul (Fig. 5).

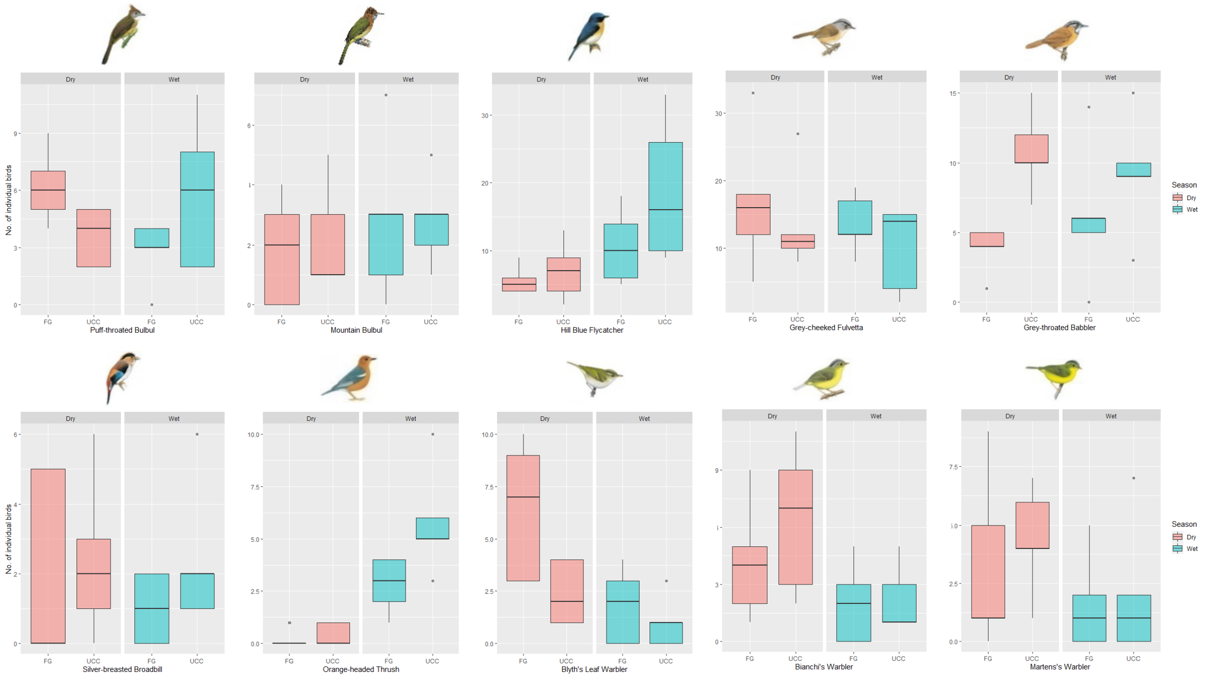

Figure 5. Boxplot of 10 dominant understory bird species in forest gap and under closed canopy between dry season and wet season in a 16-ha permanent plot.

Moreover, bird abundance differed significantly between habitats in specific seasons. The abundance of Grey-throated Babbler was more abundant under closed canopy than in forest gap in the dry season (p=0.01), and the Orange-headed Thrush were abundance in the under closed canopy than in forest gap in the wet season (p=0.04). We found the abundance of birds influenced significantly related with the habitat localities and across months. The forest gap and months were significant predictors of the Hill Blue Flycatcher's abundance, the forest gap (β=0.35, z=2.57, p=0.01) and month (β=0.05, z=2.97, p=0.00). There is also evidence that variation across months can influence the abundance of migratory birds such as the Blyth's Leaf Warbler, the Bianchi's Warbler, and the Martens's Warbler (Table 2). However, the dimension of such effects is still more related to depend on species' unique traits such as resource requirements, breeding season, and migration period.

Table 2. Fixed effect from generalized linear mixed-effects models estimating variation in the abundance of 10 species of understory bird from 2015-2019 in a 16-ha permanent plot.

Fixed effects	Estimated coefficient	S.E.	z-value	p-value
Puff-throated Bulbul				
(Intercept)	-2.071	0.313	-6.612	0.000
Month	0.008	0.030	0.284	0.776
Site_Gap	0.176	0.204	0.862	0.388
Mountain Bulbul				
(Intercept)	-2.940	0.379	-7.758	0.000
Month	0.065	0.044	1.488	0.137
Site_Gap	0.165	0.289	0.570	0.569
Hill Blue Flycatcher				
(Intercept)	-1.099	0.172	-6.390	0.000
Month	0.058	0.020	2.927	0.003*
Site_Gap	-0.352	0.136	-2.572	0.010*
Grey-cheeked Fulvetta				
(Intercept)	-0.897	0.186	-4.812	0.000
Month	-0.012	0.017	-0.686	0.493
Site_Gap	0.479	0.117	4.107	0.000*
Grey-throated Babbler				
(Intercept)	-0.995	0.219	-4.533	0.000
Month	-0.005	0.023	-0.249	0.803
Site_Gap	-0.664	0.166	-3.993	0.000*
Silver-breasted Broadbill				
(Intercept)	-1.079	0.342	-3.147	0.000
Month	-0.283	0.058	-4.819	0.000*
Site_Gap	-0.471	0.329	-1.429	0.153
Orange-headed Thrush				
(Intercept)	-2.334	0.378	-6.176	0.000
Month	0.009	0.042	0.233	0.815
Site_Gap	-0.735	0.308	-2.389	0.017*
Blyth's Leaf Warbler				
(Intercept)	-2.271	0.336	-6.767	0.000
Month	-0.087	0.039	-2.196	0.028*
Site_Gap	1.009	0.282	3.578	0.000*
Bianchi's Warbler				
(Intercept)	-3.065	0.343	-8.913	0.000
Month	0.153	0.037	4.095	0.000*
Site_Gap	-0.103	0.234	0.439	0.660
Martens's Warbler				
(Intercept)	-2.732	0.351	-7.777	0.000
Month	0.078	0.039	1.968	0.049*
Site_Gap	-0.079	0.263	-0.300	0.764

Relationship between birds and forest gap size

Differences in bird abundance among gap size (ANOVA): Overall, gap size influenced bird abundance at the community level in the forest gap (p<0.05), but only a few species showed significant differences in abundance across gap sizes. Notably, the highest abundance was observed in gaps of approximately 209 m², which had 116 more individuals than other gap sizes. At the species level, One-way ANOVA revealed significant differences in abundance across gap sizes for Puff-throated Bulbul (F = 4.23, df = 11, $p < 0.05$) and Grey-cheeked Fulvetta (F = 2.61, df = 11, $p < 0.05$) (see Table 4).

Table 3. Generalized Additive Models estimating a relationship between the abundance of 10 species of understory bird and forest gap sizes from 2015-2019 in a 16-ha permanent plot.

Common name	Estimate	S.E.	t	p-value
Puff-throated Bulbul				
(Intercept)	0.765	0.269	2.667	0.009
Gap size	0.000	0.000	0.072	0.942
Mountain Bulbul				
(Intercept)	0.535	0.200	2.672	0.009
Gap size	-0.000	0.000	-0.677	0.501
Hill Blue Flycatcher				
(Intercept)	0.621	0.345	1.803	0.076
Gap size	0.002	0.000	2.517	0.014*
Grey-cheeked Fulvetta				
(Intercept)	2.845	0.921	3.087	0.003
Gap size	-0.000	0.001	-0.056	0.955
Grey-throated Babbler				
(Intercept)	0.772	0.353	2.183	0.033
Gap size	0.000	0.000	0.302	0.763
Silver-breasted Broadbill				
(Intercept)	-0.058	0.186	-0.313	0.755
Gap size	0.000	0.000	1.991	0.051
Orange-headed Thrush				
(Intercept)	0.333	0.154	2.165	0.034
Gap size	-0.000	0.000	-0.620	0.537
Blyth's Leaf Warbler				
(Intercept)	0.563	0.279	2.017	0.048
Gap size	0.000	0.000	0.491	0.625
Bianchi's Warbler				
(Intercept)	0.272	0.238	1.144	0.257
Gap size	0.000	0.000	1.247	0.217
Martens's Warbler				
(Intercept)	0.338	0.194	1.737	0.087
Gap size	0.000	0.000	0.461	0.646

Table 4. Results of One-way ANOVA comparing the abundance of birds within forest gap sizes (130 m^2–1,020 m^2).

Common name	ANOVA		
	F	df	p-value
All species (61)	4.53	11	0.00**
Puff-throated Bulbul	4.23	11	0.00**
Mountain Bulbul	1.19	11	0.32
Hill Blue Flycatcher	1.57	11	0.13
Grey-cheeked Fulvetta	2.61	11	0.01*
Grey-throated Babbler	0.88	11	0.56
Silver-breasted Broadbill	0.55	11	0.85
Orange-headed Thrush	1.63	11	0.12
Blyth's Leaf Warbler	1.82	11	0.07
Bianchi's Warbler	1.73	11	0.09
Martens's Warbler	0.77	11	0.66

Relationship between bird abundance and gap size (GAM): For most other species, no significant association was detected (Fig 6), except For the Hill Blue Flycatcher, a statistically significant but very weak positive relationship was observed between abundance and gap size ($\beta = 0.002$, $t = 2.517$, $p = 0.014$), indicating a minimal effect. see in Table 3.

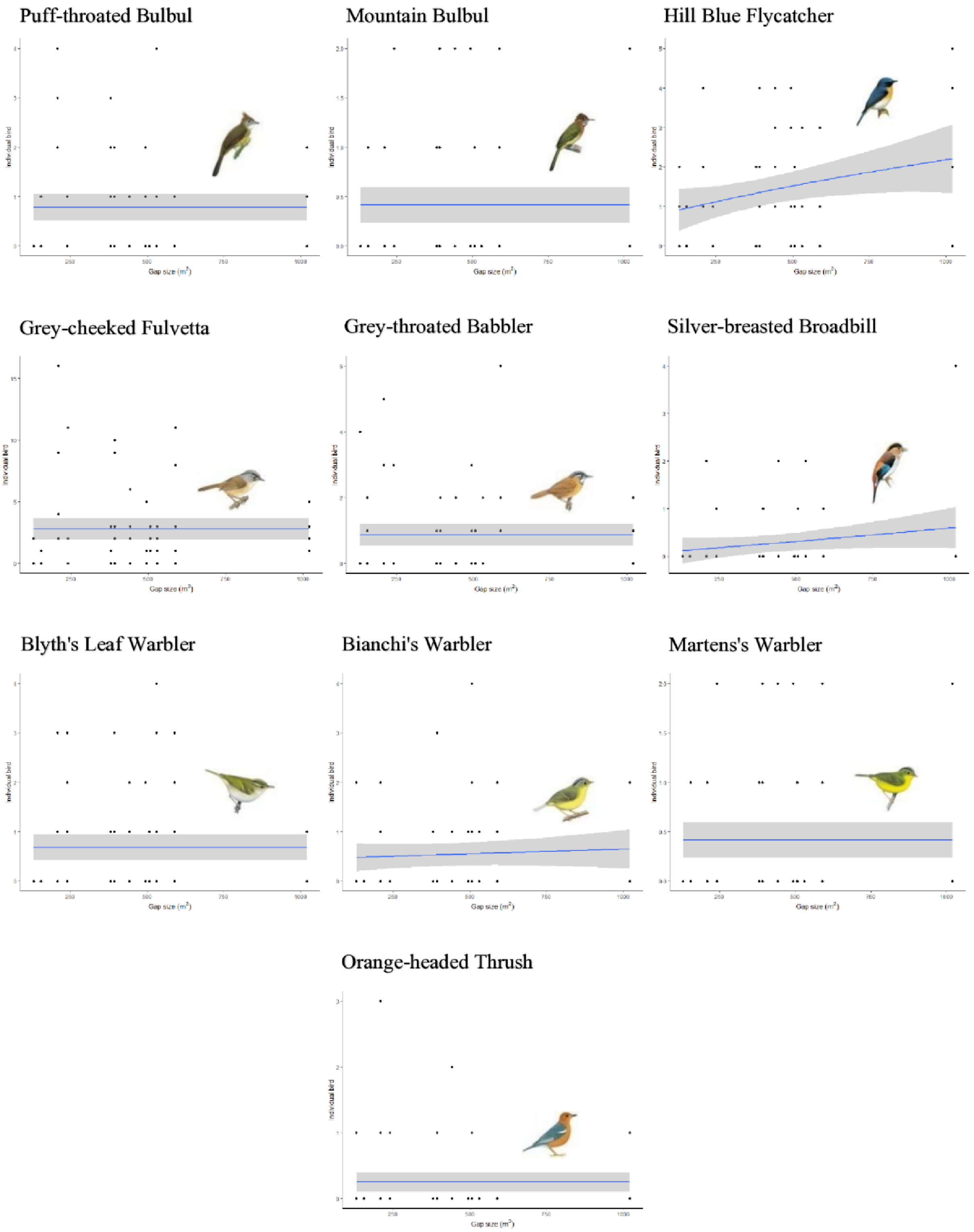

Figure 6. Generalized additive model (GAM) plots showing the size effects of forest gap on the abundance of understory bird in a 16-ha permanent plot at Mae Sa-Kog Ma Biosphere Reserve. The shaded areas indicate the 95% confidence intervals.

Discussion

Bird assemblage structure

Our study revealed that differences in habitat sites and seasons had an effect on bird assemblages in lower montane forests. Specifically, the habitat sites included under closed canopy (UCC) and forest gap (FG). Tree falls, resulting in gap formation, are an important natural disturbance in this ecosystem. Furthermore, the results from the Principal Component Analysis (PCA) of site assemblage structure clearly indicated a separation of habitats between FG and UCC. This finding confirmed that small-scale disturbance is a key process linked to the role and function of life in the forest ecosystem (Forsman *et al.*, 2010). Small-scale disturbances, characterized by low severity, exhibit a positive effect on birds in mountain forests (Kebrle *et al.*, 2022). Additionally, during succession, there is an increase in the complexity of environmental conditions in the understorey layer of the forest structure (Matsuo *et al.*, 2021). Micro-environmental conditions, such as light, temperature, crown cover, humidity, and tree density, occurring in the forest gap distinguish the area from undisturbed forest, creating a mechanism that determines species assemblage patterns (Gharehaghaji *et al.*, 2012; He *et al.*, 2019).

The season emerges as a crucial factor in differentiating bird assemblages between the forest gap and under the closed canopy. Seasonal changes exert an influence on microclimates, as well as the dynamics and distributions of forest birds (Frey *et al.*, 2016). Fig. 3B illustrates that during the wet season, the assemblages are relatively similar, as indicated by the tight grouping of sites. However, there is considerable variability in assemblage structure during the dry season. In our study area, migratory birds flock to this region in the late wet season or early dry season, with 23 species recorded between 2015 and 2019; 21 species appeared during the dry season, compared to only nine in the wet season. This pattern suggests greater variability in bird assemblages during the dry season, supported by the wider spread of site groupings in Fig. 3B and the higher number of migratory species observed during this period. Most studies consistently report a higher abundance of bird species in the forest during the dry season compared to the wet season (Mengesha *et al.*, 2011; Muhammad *et al.*, 2018; Santillán *et al.*, 2018; Tessfa *et al.*, 2020; Dinesen *et al.*, 2022). Moreover, Girma *et al.* (2017) affirm that seasonality and habitat types are key factors determining the abundance of both non-migrant and migrant birds, with utilization in the area linked to specific habitat preferences by some species.

Examining the correlations between forest gap size (ranging from 130 m^2 to 1,020 m^2) and PCA scores (Dim 1 and Dim 2) derived from the analysis of site assemblage structure data (refer to Supplementary A), we observed a non-significant positive correlation between gap size and PCA score. The correlation coefficients for gap size with Dim 1 ($R=0.41$, $p > 0.05$) and Dim 2 ($R=0.37$, $p > 0.05$) are presented in Fig. 4. These findings unmistakably show that as the gap size increases, there is a concurrent rise in the PCA scores for both dimensions. Future tree falls resulting in substantial gaps could enhance habitat heterogeneity, potentially leading to more distinct assemblage differences between gap and under-canopy sites.

Abundance patterns of individual bird species

The Generalized Linear Mixed Model (GLMM) results reveal distinct responses among avian species concerning various variables (Table 2). Frugivorous birds, such as the Puff-throated Bulbul and Mountain Bulbul, did not show significant distinctions in response to the considered variables. However, among insectivorous birds, a statistically significant association emerged between the abundance of individuals and either the temporal factor of the month or the spatial factor of distinct sites. The Hill Blue Flycatcher, Grey-throated Babbler, Silver-breasted Broadbill, and Orange-headed Thrush were more frequently observed under closed canopy conditions. These species tended to avoid forest gaps (Table 2). The intricate vertical layers within the forest ecosystem play a pivotal role in sustaining the abundance of insectivorous avian populations, providing essential foraging substrates in mature tropical landscapes (Mansor & Sah, 2012; Castaño-Villa *et al.*, 2019). Notably, the Orange-headed Thrush, characterized as an omnivorous bird with ground foraging habits, capitalizes on aerial leaf litter as an optimal habitat for substantial arthropod populations, constituting a significant foraging resource (Mansor *et al.*, 2019).

In contrast, the Grey-cheeked Fulvetta and Blyth's Leaf Warbler exhibited unfavorable trends under closed canopy conditions (Table 1). These specific species distinctly favor forest gap cover during both the dry and wet seasons, suggesting the potential of forest gaps to consistently support particular understory avian species year-round. As mentioned earlier, the Grey-throated Babbler and Grey-cheeked Fulvetta, both identified as foliage-gleaning insectivores, thrive as abundant residents in our study area. Their strategy of mitigating competition through habitat segregation is evident, with the Grey-cheeked Fulvetta notably preferring forest gaps over closed canopy environments in both seasons, while the Grey-throated Babbler exhibits a consistent preference for dense forest throughout the year. This observed pattern strongly implies a reduction in interspecific competition achieved by utilizing distinct areas characterized by resource partitioning (Traba *et al*., 2015; Naikatini *et al*., 2022).

In a similar vein, research conducted in Iran by Gharehaghaji *et al*. (2012) substantiates the concept of a higher abundance of breeding birds within forest gaps compared to control forest areas. Conversely, the findings by Bowen *et al*. (2007) reveal that during non-breeding periods, numerous bird species exhibit a preference for gap and gap-edge habitats. These studies reinforce the importance of habitat heterogeneity in maintaining diverse avian communities (Chettri *et al*., 2005).

The month variable reveals a significant influence on the abundance of the Hill Blue Flycatcher, particularly under closed canopy conditions (Table 2). After the breeding season of this species, bird abundance, encompassing both adult and juvenile birds, experiences a noticeable increase post-August (Fig. 7). This information is valuable for discerning the specific timeframe when the month positively impacts bird abundance. Understanding bird abundance, population dynamics, habitat utilization, temporal patterns, and spatial distribution offers crucial insights into the mechanisms governing interspecific and intraspecific interactions among birds within a forest ecosystem. This knowledge provides essential data applicable for conservation and management purposes (Magurran & Henderson, 2003; Volkov *et al*., 2003; He, 2005; Callaghan *et al*., 2021). Overall, bird abundance metrics are valuable indicators of habitat quality and ecosystem health on both local and global scales (Hanle *et al*., 2020; Basile *et al*., 2021).

Relationship between birds and forest gap size

Bird Species Responses to Gap Size: The Generalized Additive Model (GAM) indicates a positive correlation between the abundance of the Hill Blue Flycatcher and forest gap sizes (Fig. 6). However, the results from the Analysis of Variance (ANOVA) (Table 4) reveal no significant differences across gap sizes. This suggests that the abundance of the Hill Blue Flycatcher gradually increases with larger gap sizes, despite the lack of statistical significance in ANOVA. Although the species is commonly found under closed canopy conditions throughout the year, its presence in forest gaps highlights its adaptability to a variety of gap sizes within the natural forest. It is well-documented that this species responds sensitivity to environmental changes, notably those related to climate change (Sanz, 2003; Helm *et al*., 2019). Therefore, gap sizes ranging from 130 to 1,020 m², resulting from natural disturbance in this study area, do not appear to negatively affect the abundance of the Hill Blue Flycatcher and may help sustain its population in the lower montane forest.

The Grey-cheeked Fulvetta, a resident foliage-gleaning insectivore, and Blyth's Leaf Warbler, a migratory foliage-gleaner, were primarily observed in forest gaps during all seasons. The Grey-cheeked Fulvetta showed highest abundance in 209 m^2 gaps. During the wet season, these species tended to utilize smaller gaps, while in the dry season, they were present across a broader range of gap sizes. Blyth's Leaf Warbler did not show significant differences in response to gap sizes, suggesting that all gap sizes contribute to its abundance during the dry season.

The Puff-throated Bulbul, a frugivorous bird, exhibits high abundance in forest gaps during the dry season, with peak numbers in 209 m^2 gap. However, it was found across the full range of gap sizes (130 –1,020 m^2), indicating that a variety of gap sizes supports its presence.

Ecological Mechanisms: Gap formation alters forest microclimates, particularly in terms of light intensity. While no significant difference was found in average temperature between forest gaps (19.75±0.25 °C) and under closed canopy (19.67±0.24°C), light intensity was significantly higher in forest gaps (6,423.22±452.98 lux) compared to under closed canopy conditions (5,716.37±1,380.96 lux). Increased light influences the spatial distribution of (de Cauwer *et al*., 2006), which in turn affects the abundance of insectivorous birds. A decline in flying insect abundance has been associated with reductions in insectivorous bird populations (Nebel *et al*., 2010).

In addition, gaps promote fruiting in fleshy-fruited trees due to increased solar irradiance, as documented by Takahashi *et al*. (2015) & Chapman *et al*. (2018). This benefits frugivorous birds such as Puff-throated Bulbul, which also play a key role in seed dispersal in montane forests (Rueangket *et* *al*., 2019). In disturbed or open habitats adjacent to lower montane forests, this species may help restore vegetation by dispersing seed into large canopy gaps.

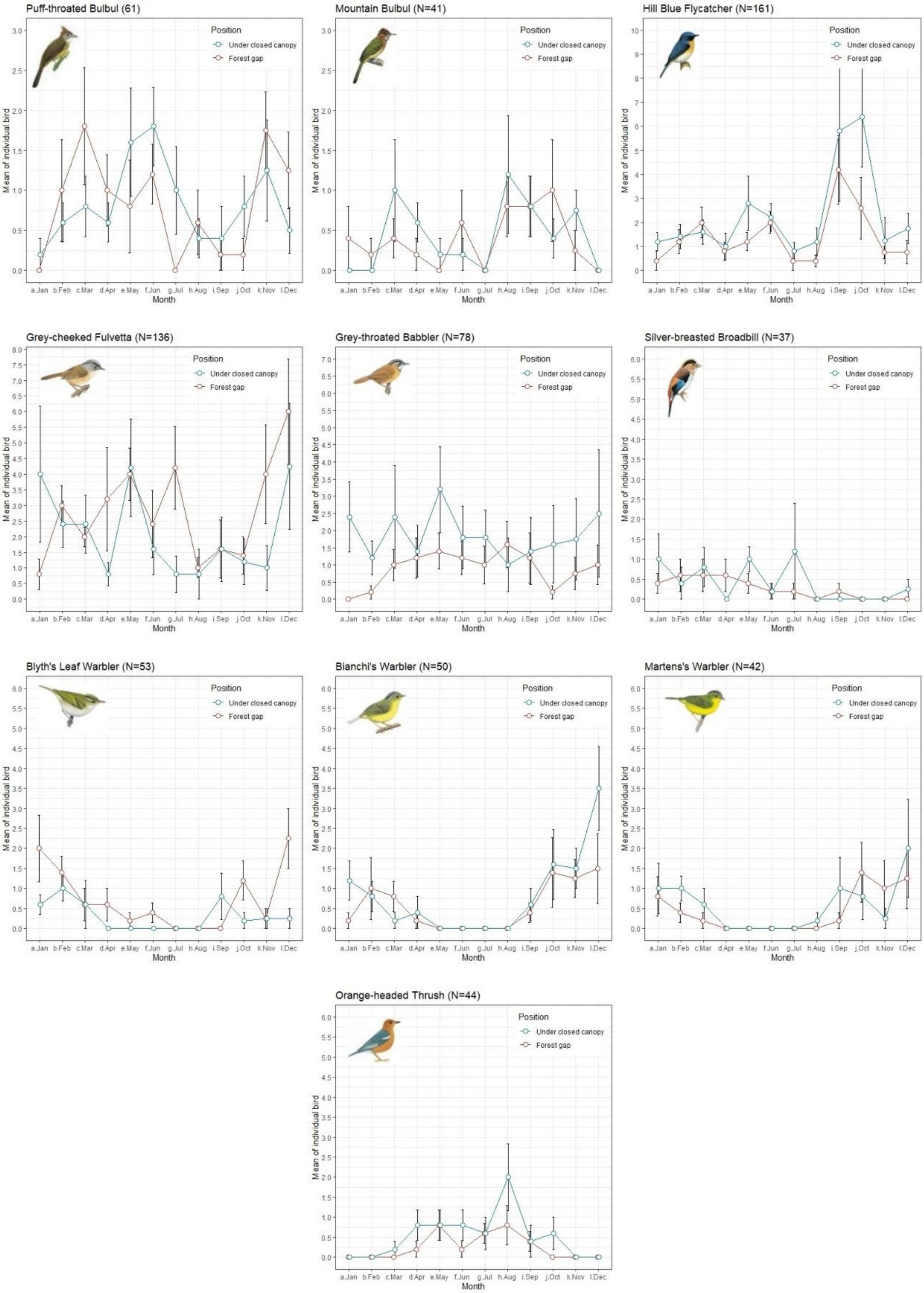

Figure 7. Mean of individual birds in January through December between forest gap and under closed canopy in a 16-ha permanent plot.

Forest Structure and Disturbance: Gap size is determined by tree basal area and the number of tree falls (Van Der Meer & Bongers, 1996). Gaps can range from 10 to 5,000 m² (Schliemann & Bockheim, 2011), In northern Thailand, Wannaprasert (1985) reported gap sizes up to 1,236 m^2 in a hill evergreen forest. These structural features reflect the scale of forest disturbance and are key drivers of microclimate variation and habitat complexity (Jiao-jun *et al*., 2007).

Gap size has been shown to influence bird abundance and richness, especially insectivores (Banks-Leite & Cintra, 2008). For example, the Cerulean Warbler in North America selects canopy gaps ranging from 50–3,163 m², depending on forest structure. The Cerulean Warbler prefers to inhabit oak stands that include gaps in the forest canopy. They select gaps based on forest structure, with male Cerulean Warblers establishing territories in gaps ranging from small sizes (50-100 m^2) to the largest sizes (300-3,163 m^2). Conservation efforts recommend creating gaps of 50–100 m² to support their populations (Perkins & Wood, 2014). In our study, a gap size of 209 m^2 was associated with high bird abundance, indicating a potential optimal size for certain species.

Climate Change Impacts: Climate change poses serious threat to the forest ecosystems, ecosystem services, and biodiversity around the world, especially in upland specialist on montane ecosystems (Keenan, 2015; Weiskopf *et al*., 2020; Williams & de la Fuente, 2021). Changing climates are causing significant spatio-temporal shifts in species abundance patterns, assemblage structure, phenology and biotic interaction globally and specifically within tropical forests (Trisurat & Grainger, 2012; IPCC, 2013; de la Fuente *et al*., 2023).

Changing climate is disrupting forest gap dynamics via the premature death of trees due to extreme drought, forest pests, and pathogens, leading to raise damage to trees and increased tree mortality including tree fall (Anderegg *et al*., 2015; Stephenson *et al*., 2019). In addition, climate change has been implicated in accelerating the mortality of canopy trees driving a complex change in habitat structure within forests by increasing gap formation, changing balances between trees and woody lianas, and changes in species composition (Bauman *et al*., 2022). Overall, the relationship between climate change and tree mortality is complex, but it is clear that the changing climate is having a significant impact on the health and survival of trees and forests around the world (Keenan, 2015; Taccoen *et al*., 2022).

Conclusion

Our findings demonstrate that both habitat characteristics and seasonal variation play a crucial role in shaping bird assemblages in tropical rainforest. Distinct patterns of bird abundance were observed across habitat types between the wet and dry seasons, even among species within the same family, feeding guild, or seasonal status. These patterns underscore the importance of considering species-specific responses to both spatial and temporal habitat conditions. The forest gaps investigated in this study, primarily resulting from natural disturbances such as tree senescence and windthrow, these represent small-scale structural changes that significantly influence avian community composition. Accordingly, a nuanced understanding of how bird species utilize different habitats across seasons is essential for informing effective conservation and management strategies.

Highlighting our findings, we discovered that a gap size of 209 m^2 supports bird abundance in the study area. Gap sizes ranging from 130 to 1,020 m^2 are not severe and do not negatively impact understory birds in the tropical rainforest. Some generalist species occur in forest gaps and cover all sizes of gaps. Based on this study, to maintain a gap size suitable for promoting abundance and diversity in all species, a gap size of at least 200 m^2 should be created in this area. Treefall is a natural phenomenon linked to forest dynamics. Currently, global climate change is impacting tropical Asian forests, leading to changes in forest stand dynamics associated with tree mortality (Anadon *et al*., 2014). Scientists also report significant increases in annual tree mortality due to climate change, particularly in moist tropical forests (Luo & Chen, 2013; Aleixo *et al*., 2019). Considering tree mortality, we can assume an increasing frequency of tree falling, potentially producing large open gaps. This can affect some forest specialist birds that avoid crossing open areas (Bélisle *et al*., 2001). Thus, bird composition will be influenced by tree death, the cause of the forest gap. Hence, long-term monitoring is essential to understanding the pattern, dynamics, and response of bird communities in ecosystems undergoing habitat changes.

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Supplementary Material

Supplementary material A
Principal component analysis (PCA) showing coordinates for the variables explained for the Dim 1 and Dim 2 of the microhabitat site by individual bird data matrix in the forest gap (FG) and under closed canopy (UCC).
Data type: docx file
Link: https://biotaxa.prod.amazon.auckland.ac.nz/em/article/view/87143/82211

Supplementary material B
Number of individual birds in the forest gap, gap sizes range from 130 m^2–1,020 m^2 in a 16-ha permanent plot.
Data type: docx file
Link: https://biotaxa.prod.amazon.auckland.ac.nz/em/article/view/87143/82212

Appendix 1

Number of individual birds in wet and dry season between forest gap (FG) and under closed canopy (UCC) from January 2015 through October 2019 in a 16-ha permanent plot at Huai Kogma sub-watershed.

Common name	**Total**	**Dry season**		**Wet season**	
		FG	**UCC**	**FG**	**UCC**
Hill Blue Flycatcher	161	28	33	48	92
Grey-cheeked Fulvetta	136	75	61	57	48
Grey-throated Babbler	78	13	45	23	34
Puff-throated Bulbul	61	24	16	18	26
Blyth's Leaf Warbler	53	27	12	12	5
Bianchi's Warbler	50	17	26	10	12
Mountain Bulbul	41	7	11	15	13
Martens's Warbler	42	14	19	9	10
Orange-headed Thrush	44	1	5	14	26
Silver-breasted Broadbill	37	10	11	4	11
Buff-breasted Babbler	32	2	14	4	21
Surphur-breasted Warbler	25	15	7	4	0
Speckled Piculet	23	8	3	10	10
White-rumped Shama	23	1	8	7	8
White-bellied Yuhina	22	9	1	9	2
Black-naped Monarch	16	5	5	5	5
White-necked laughigthrush	13	6	3	2	3
Rufous-bellied Niltava	16	4	13	0	0
Streaked spiderhunter	15	3	1	9	3
Black-throated Sunbird	14	9	2	5	1
Little Spiderhunter	12	6	2	4	1
White-tailed Robin	12	2	11	0	0
Clicking Shrike-Babbler	12	3	2	7	4
Puff-throated Babbler	11	0	6	1	6
White-throated Fantail	10	5	2	2	1
Pin-Striped Tit Babbler	10	6	1	5	2
White-browed piculet	9	1	2	2	5
Black-crested Bulbul	8	5	2	0	1
Velvet-fronted Nuthatch	8	2	1	5	0
Eyebrowed Wren Babbler	8	0	4	0	4
Emerald Dove	8	6	1	1	0
Lesser Racket-tailed Drongo	8	2	2	2	2
Davison's Leaf Warbler	7	4	3	2	0
Blue Pitta	7	1	5	2	0
Siberian Blue Robin	7	1	3	1	2
Asian Paradise-Flycatcher	7	2	1	3	1
Chestnut-flanked White-eye	7	7	0	0	0
White-crowned Forktail	6	1	4	1	3
Oriental white-eye	6	4	0	1	1
Blue-throated Barbet	6	2	0	3	1
Asian Stubtail	5	0	4	0	1
Grey-headed Canary-Flycatcher	4	3	1	1	0
Yellow-bellied Warbler	4	1	0	0	0
White-browed Scimitar-Babbler	4	0	1	1	2

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Appendix 1

Black-breasted Thrush	4	0	4	0	0
Ashy Bulbul	4	1	2	1	0
Lesser Necklaced Laughingthrush	2	0	2	0	0
Blue Whistlingthrush	3	0	3	1	0
White-browed Shrike-Babbler	3	1	2	0	0
Snowy-browed Flycatcher	3	0	3	0	0
Common Green Magpie	2	0	1	1	1
Black-naped Woodpecker	2	2	0	0	0
Pale-legged Leaf Warbler	2	0	2	0	0
Orange-bellied Leafbird	2	2	0	0	0
Scaly Thrush	2	1	1	0	0
Eyebrowed Thrush	2	0	2	0	0
Bronzed Drongo	2	1	1	0	0
Black-throated Laughingthrush	2	0	0	1	1
Fire-breasted Flowerpecker	2	0	0	2	0
Vivid Niltava	2	0	2	0	0
Pin-tailed Parrotfinch	1	1	0	0	0
Ferruginous Flycatcher	1	0	0	1	0
Yellow-streaked Warbler	1	0	1	0	0
Chestnut-bellied Rock-Thrush	1	0	1	0	0
Yellow-browed Leaf Warbler	1	1	0	0	0
Chinese Leaf Warbler	1	1	0	0	0
Collared Owlet	1	0	0	0	1
Dark-sided Thrush	1	0	1	0	0
Lesser Cuckoo	1	0	0	0	1
Banded Bay Cuckoo	1	0	0	0	1
Chestnut-winged Cuckoo	1	0	1	0	0
Blue throated Flycatcher	1	0	1	0	0
Scaly-breasted Partridge	1	0	0	0	1
Greater Necklaced Laughingthrush	1	0	1	0	0
Grey-backed Shrike	1	0	0	1	0
Greater Racket-tailed Drongo	1	0	0	1	0
Ruby-cheeked Sunbird	1	1	0	0	0
Verditer Flycatcher	1	0	1	0	0
Flavescent Bulbul	1	0	0	1	0
Green Cochoa	1	0	1	0	0
Striated Yuhina	1	0	0	1	0