

Habitat use by mixed-species bird flocks in tropical forests of the Western Ghats, India

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Research Article

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Abstract

While mixed-species flocks of birds (hereafter ‘flocks’) have been widely studied, few studies have looked at the effect of habitat structure on flock presence and flocking propensity within a site. Here, we employ a use-availability approach in locations with flocks and random locations to ask whether habitat characteristics influence the presence of flocks, and whether structurally similar microhabitats support compositionally similar flocks. We also examine the effect of habitat on flock size and species richness, and the effect of intraspecifically gregarious flock participants on habitat selection. We find that flocks use a narrow subset of available tree density and canopy cover variation and prefer relatively less-dense areas with large trees and a complex foliage structure. Similar microhabitats do not result in compositionally similar flocks, and while foliage complexity was associated with flock size, no habitat characteristics influenced species richness. Flocks led by the intraspecifically gregarious western crowned warbler (*Phylloscopus occipitalis*), a potential nuclear species, showed preference for high foliage complexity and tree density. Thus, habitat preferences of intraspecifically gregarious species, which are followed by other species, could play a strong role in habitat selection in flocks. This suggests that degraded forests that cannot provide a suitable range of tree density, canopy cover, and/or complex vegetation structure may not support some core flock species around which flocks form, which may lead to decreased flocking in those patches.

Introduction

Mixed-species flocks (hereafter ‘flocks’) of birds have been studied in many parts of the world, and have been particularly well-studied in forest habitats. Flocks show wide variation in size, species composition, and duration of association, and participants are believed to derive benefits from one another while moving together through their habitat (Greenberg 2000). These roving groups offer participants protection from predation both in terms of group-size related advantages (confusion, dilution and ‘many-eyes’ effects, see Foster & Treherne 1981, Neill & Cullen 1974, Pulliam 1973) as well as more species-specific benefits (such as the alarm-calling behaviour of sentinel species and reduced vigilance in other species, and the flushing of insect prey by species, see Goodale & Kotagama 2005, Greenberg 2000, Sridhar *et al.* 2013). Intraspecifically gregarious species are often nuclear species in flocks (Greenberg 2000), and larger flocks may only be found when these species are present (Sridhar & Shanker 2014). Nuclear species are present in most flocks (Goodale & Beauchamp 2010), and they are functionally important within mixed-species flock systems (Goodale & Beauchamp 2010, Hutto 1994, Sridhar *et al.* 2009). They have well-developed alarm call systems (Koenig & Dickinson 2004), and when present, are flock leaders, potentially affecting habitat selection for other species (Mammides *et al.* 2015, Williams & Lindell 2019) and playing a role in setting the direction of flock movement (Greenberg 2000).

As a result of flocking, participants may be able to spend less time and energy on vigilance, making available more time for foraging (Sridhar *et al.* 2009). For example, sallying species are more vigilant than species that employ more active foraging methods, and their alarm calls may provide warning of approaching predators (Goodale & Kotagama 2005), thereby allowing other flock members to invest more time in foraging (Radford *et al.* 2011). Additionally, sallying species may benefit from capturing prey that are flushed out by species with more active foraging techniques (Satischandra *et al.* 2007), and there is some evidence that individuals may observe the locations in which other participants forage and revisit/avoid the same (Beauchamp & Benton 2005, Krebs 1973).

Both predator detection and foraging efficiency are influenced by habitat structure. In dense habitats, flocks are well concealed, and a closed canopy and high tree density limit exposure to predators (Thiollay 1999b). However, in such habitats, ambush predators, the primary threat to

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these smaller insectivores, are also better hidden. On the other hand, in open habitats, flock participants can scan their surroundings more effectively for predators (Thiollay 1999b, Zou *et al.* 2018, but see Linley *et al.* 2019). Changes in habitat structure could alter species' propensity to flock (especially in the case of habitat degradation, when core flock species are absent or less abundant in degraded sites and flocks form less frequently) (Mokross *et al.* 2014, Zhang *et al.* 2013, Zou *et al.* 2018), but may also indirectly affect flocks by altering prey dispersion and availability, and predation pressure (Martínez *et al.* 2017, 2018, Ridley *et al.* 2014, Sridhar & Sankar 2008). Past research has shown that insectivorous birds are more likely to forage in mixed-species flocks in areas with less protective vegetation (Radford *et al.* 2011, Tubelis *et al.* 2006), and individuals participate in mixed-species flocks less often in dense forests (Jullien & Thiollay 1998, Thiollay 1999b).

The high species richness of flocks in mature forests is associated with a complex habitat structure, and even small changes in the structural complexity of secondary and early successional forests could have a positive effect on the species richness and abundance of flocks (Zuluaga & Rodewald 2015). In degraded habitats, habitat structure may also affect flock composition and size, wherein the overall flocking propensity of insectivorous birds decreases when the canopy is more open as a result of logging gaps and tracks (Thiollay 1999b). Species that participate in flocks have varying morphologies and preferences in foraging strategies and strata in their habitat (Kotagama & Goodale 2004, Morse 1970, Robin & Davidar 2002), and the lack of a complex forest structure could mean that flocks do not contain certain species, even if they remain present in the habitat (Zou *et al.* 2018). For example, understory flock participants could have specialised strategies to forage in dim-light conditions of the forest interior, and these strategies may not be suitable in disturbed or open forest patches (Thiollay 1992). Reduced prey availability can have an effect on flocks (Thiollay 1999a, 1992), and vegetation structure could influence flock participation by affecting prey availability (Develey & Peres 2000).

Despite the fact that a majority of the insectivorous species found in tropical forests participate in flocks (King & Rappole 2001, Sridhar & Sankar 2008, Zou *et al.* 2018), there has been little research on the influence of habitat structure on flock presence and flocking propensity of species within sites. Flock size has been shown to be strongly associated with habitat structure and area of fragmented forest (Sridhar & Sankar 2008). Logging can result in species joining flocks less frequently (Thiollay 1999b), and affect interspecific associations in flocks by altering predation pressure and resource availability (Borah *et al.* 2018). Some species become locally extinct in small fragments (Stratford & Stouffer 1999), and if these are nuclear species, flock composition may be indirectly affected by changes in other species' propensity to flock (Cordeiro *et al.* 2015, Mammides *et al.* 2015).

Habitat heterogeneity is an important factor in maintaining flock richness, and a simplified habitat structure brought about by anthropogenic disturbance could cause a decline in flocking (Lee *et al.* 2005, Zhang *et al.* 2013, Zhou *et al.* 2019). While there have been studies on the effects of habitat degradation and fragmentation at the landscape level (Borah *et al.* 2018, Sridhar & Sankar 2008), little is known about how flock characteristics are affected by habitat structure within the relative homogeneity of a single forest site. Hence, we examined within-site variation in habitat structure to explore changes in flock composition and structure. We also examined whether flock habitat use might reflect habitat choice of the most commonly occurring

intraspecifically gregarious species – brown-cheeked fulvetta (*Alcippe poiocephala*), orange minivet (*Pericrocotus flammeus*), and western crowned warbler (*Phylloscopus occipitalis*) – one or more of which are usually found leading flocks in the Western Ghats (Sridhar *et al.* 2013).

First, we used a habitat use-availability approach in locations where flocks were encountered and random locations to test whether specific habitat characteristics influence the presence of flocks. We then asked whether structurally similar microhabitats support flocks with similar species composition and tested whether these habitat characteristics might have an effect on flock size and richness. Finally, we examined the effect of the presence of intraspecifically gregarious species on habitat selection.

Methods

Flock sampling

Fieldwork was carried out in the Anshi Range of Kali Tiger Reserve (formerly Anshi-Dandeli Tiger Reserve, 15°00'97.8"N, 74°38'72.2"E) in the Western Ghats (Figure 1), a 1500 km mountain range that runs north to south along the western coast of peninsular India. Data were collected from the evergreen forest site from December 2017 to March 2018, which corresponds to the non-breeding season for the bird species studied. Ten trails (Figure 1), ranging from 1.8 – to 5 km in length, were walked 3 to 9 times to observe mixed-species flocks, within a limit of 30 m on either side of a trail. All trails used for sampling were around Anshi village (14°59'33.0713"N, 74°22'3.2358"E) and Anshi nature camp (15°0'34.0693"N, 74°23'4.551"E).

Data were collected from 8h to 14h by PH. A group of birds was considered to be a flock if it comprised two or more species that stayed together for at least five minutes and moved in the same direction (Sridhar *et al.* 2013). Each species observed also had to be within 10 m of at least one other individual belonging to a different species to qualify as a flock participant. The five-minute cut-off ensured that random associations of birds were not considered mixed-species flocks. Each flock was observed only until all species were identified, to obtain a 'snapshot' of the flock and to reduce the possibility of species turnover. Prior to the start of the study, PH, PB, and HS had observed flocks in this area and determined that it would take around 15 minutes to identify the majority of participating species in flocks. Frugivorous species of birds were not considered to constitute a mixed-species flock, as they are likely to have been feeding aggregations (Greenberg 2000). Hence, observations were restricted to insectivorous species only. It is possible that some individuals were observed in multiple flocks, but since they were part of flocks with different compositions, such repetitions were considered valid for the purpose of the study.

A total of 72 flocks were recorded over the study period, with species composition and abundance being noted in each case. When it was not possible to identify the exact number of individuals of a species, an appropriate size class of abundances (1–5, 5–10, 10–15, 15–20, 20–25) was assigned. Birds were identified using calls as well as sightings.

Habitat structure sampling

Since flocks were observed only long enough to get a snapshot of the participating species, it was possible to assign a central location for each flock. This was considered the 'flock location' and was roughly the centre of where most participants were foraging. In

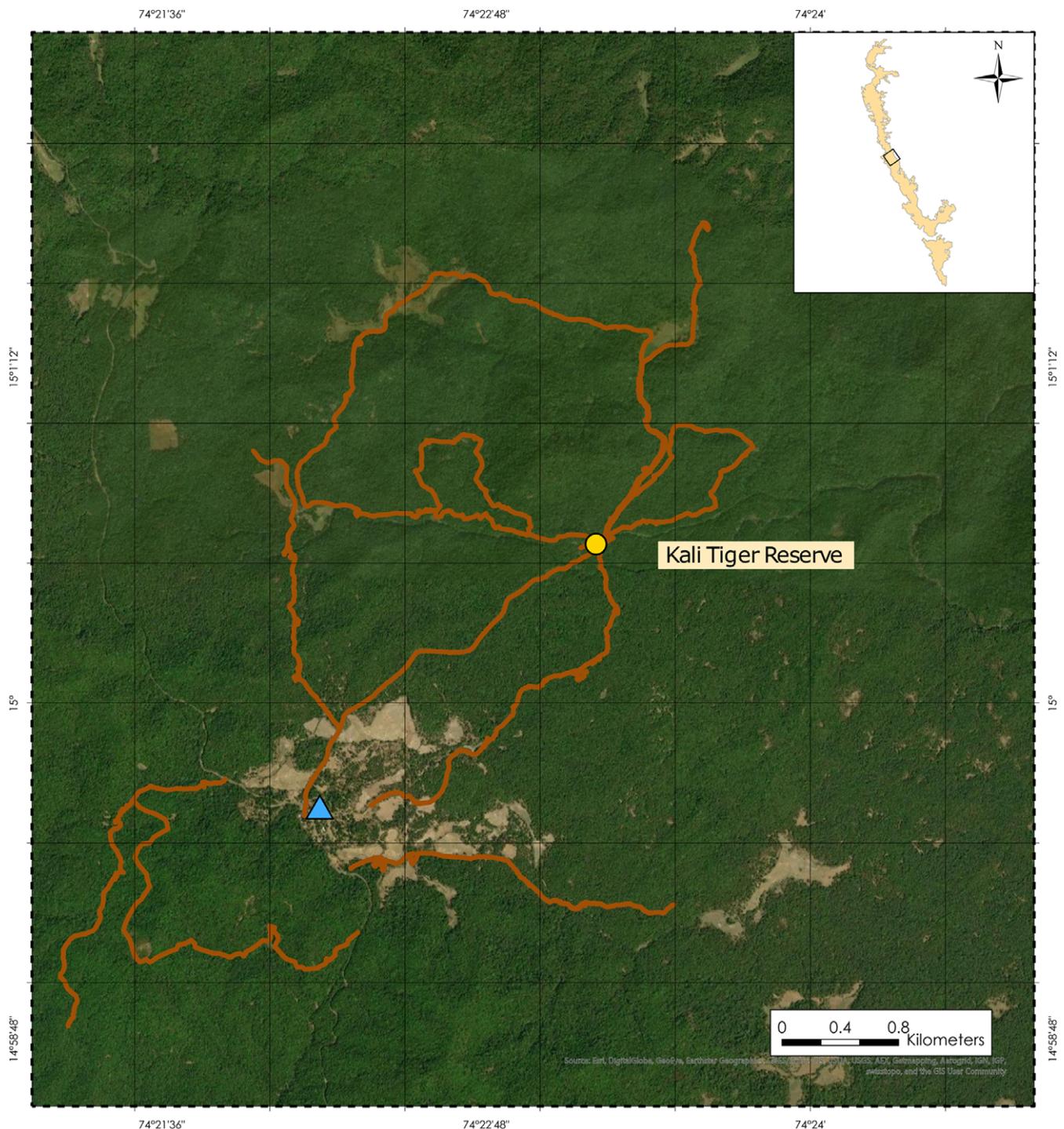


Figure 1. Location of Kali Tiger Reserve in the Western Ghats (inset) and trails (brown lines) around Anshi village (blue triangle) and Anshi nature camp (yellow circle).

In addition to flock data, the following habitat variables were measured in each of the flock locations: density and basal area of trees (with girth at breast height (gbh) more than 30 cm), density of plants above 2 m in height but less than 30 cm gbh (hereafter, plants), percentage cover of plants under 1 m in height (hereafter, saplings), canopy cover, and foliage complexity.

Density and basal area of trees was calculated by using the point-centered quarter (PCQ) method (Hill *et al.* 2005), wherein gbh (in cm) and distances (in m) of the four closest trees from a central point were noted. Plants were counted in a 5 × 5 m plot.

Sapling cover was estimated in a 1 × 1 m plot. Foliage complexity was estimated by imagining a cylinder of radius 0.5 m around the observer in the centre of the PCQ plot and noting the presence or absence of foliage in the following size classes (in m, aboveground): 0-1, 1-2, 2-4, 4-8, 8-16, 16-32, >32 (Sridhar & Sankar 2008). A rangefinder was used to ensure that the height of foliage was measured accurately. Following Daniels *et al.* (1992), canopy cover was assigned one of four ranks: 1 (no canopy overhead), 2 (canopies barely touch), 3 (there is overlap of canopies, but the sky is still visible) or 4 (complete overlap, no sky visible).

Each trail where sampling for flocks was carried out was mapped on QGIS. The fixed distance buffer tool was used to draw a polygon around these trails, with a 30 m belt on each side of the trails. Random points were generated inside these polygons to represent available habitat. A total of 149 random points (approximately twice the number of use locations observed) was generated on ten trails, with 10 to 16 points occurring on each trail. Nineteen of these points occurred in fields, villages or water bodies and were not considered to be representative of available habitat for flocks. The remaining 130 random locations were visited (with an accuracy of 2 m), and measurements of all the habitat variables detailed above were taken.

Statistical analysis

Analysis was primarily carried out in R (R Core Team 2018). Density of trees was calculated using the formula $\text{density} = 1/D_m^2$ where ' D_m ' is the mean of distances from a central point to each tree (Hill *et al.* 2005). Plant and sapling cover were assigned to size classes. Basal area was calculated using $\pi(d/2)^2$ where ' d ' is the diameter of trees at breast height. To obtain a measure of basal area with respect to the PCQ data, the average basal area at each flock location/random location was multiplied by the density of trees (JoVE Science Education Database 2018). Each flock location and random point was assigned a score for foliage complexity by summing up the number of classes in which foliage was present. We used a combination of multivariate and univariate statistics to test our three objectives, as appropriate.

For the first objective, we carried out 10,000 iterations of 72 randomly selected points out of 130 random availability points and calculating the means and standard deviations of each of the six habitat variables. Habitat variables were not highly correlated (Spearman's correlation $\leq \pm 0.5$). The distributions of the bootstrapped standard deviations and means were compared to those of the use sites, one variable at a time. Following this, a binomial generalized linear model (GLM) was run to determine whether use sites (the response variable) were characterised by a combination of the predictor variables (Beyer *et al.* 2010, Edwards *et al.* 1994, Keating and Cherry 2004).

For the second objective, namely to examine similarities between habitat variables of the use sites and flock composition, we used the Bray–Curtis dissimilarity index from the 'vegan' package in R. Based on this, the data were transformed into distance matrices, and a Mantel test was carried out with 999 permutations, to understand whether similarities in flock composition corresponded to similarities in habitat structure of the use sites, and assess the statistical significance of the regression coefficients. We also carried out a Poisson GLM with habitat structure variables as predictors, and flock size and species richness as response variables.

For the final objective, the habitat structure of flocks with and without particular intraspecifically gregarious species was compared with a Mann-Whitney U test, one variable at a time. This was done to see if flocks differed in habitat use based on the presence or absence of a particular gregarious species.

Results

Forty-four species were observed across 72 flocks, with an average of 5.43 (± 2.41 SD) species and 17.6 (± 8.77 SD) individuals in each. Seventy-two flock locations constituted 'use' points. The 130 randomly generated points were considered 'availability' points.

Species composition of flocks broadly corresponded with earlier studies (Sridhar *et al.* 2013) in the same site. Core species included the black-naped monarch (*Hypothymis azurea*) which was found in 41 flocks (57%), the brown-cheeked fulvetta (*Alcippe poiocephala*) in 35 (49%), the greater racket-tailed drongo (*Dicrurus paradiseus*) in 36 (50%), the orange minivet (*Pericrocotus flammeus*) in 29 (40%), the western crowned warbler (*Phylloscopus occipitalis*) in 45 (63%) and the yellow-browed bulbul (*Acritillas indica*) in 28 (39%).

Use and availability

In order to compare both the means and standard deviations of use sites and the distributions of bootstrapped availability sites for the first objective, we carried out univariate comparisons for the six predictor variables (Figures 3 and 4). The means of basal area (Figure 2b) and foliage complexity (Figure 2f) were significantly higher in the use sites (bootstrapped CI 95%). Use site mean tree density was lower than that of availability sites (Figure 2a). When the same analysis was carried out for the bootstrapped standard deviations to determine whether use sites formed a narrow subset of availability sites (Figure 3), use site tree density (Figure 3a) had a significantly lower standard deviation than availability sites (bootstrapped CI 95%). Canopy cover (Figure 3e) also differed, with use sites having a lower standard deviation than availability sites.

The GLM ($r^2 = 0.2$) showed that tree density was slightly, but significantly lower ($p = 0.047$) in use sites (mean = 0.08 per m^2 , SE = 0.007) compared to use sites (mean = 0.07 per m^2 , SE = 0.007). While there was some variation in foliage complexity, this was not statistically significant ($p < 0.1$). Other habitat variables did not differ significantly between use and availability sites (Table S1).

Species composition, flock size and species richness

The dissimilarity matrices of habitat structure and flock composition had no zeros, indicating that sites were at least somewhat similar in habitat structure and flock composition, and were not significantly correlated to each other (Mantel's $r = -0.2$, $p = 0.67$). The GLM of habitat structure variables and flock size ($r^2 = 0.2$) showed that foliage complexity was significantly associated with the number of individual birds in flocks ($p < 0.01$), and slightly associated with plant density ($p < 0.1$). The GLM of habitat structure variables and flock species richness ($r^2 = 0.2$) did not reveal any significant patterns (Table S2).

Gregarious species and habitat selection

Three intra-specifically gregarious species were found in at least 40% of flocks that were observed: western crowned warbler (hereafter 'warbler'), brown-cheeked fulvetta (hereafter 'fulvetta') and orange minivet (hereafter 'minivet'). While other gregarious species were present, they were not as frequently encountered as these three and were not considered for further analysis.

Western crowned warbler was found in 63% of all flocks, and was the only gregarious species and leader in 15 flocks. Density of trees (Mann-Whitney $U = 836$, $p < 0.01$) and foliage complexity ($U = 781$, $p = 0.03$) were significantly higher in use sites in which warblers were present compared to use sites in which warblers were absent ($n = 27$) (Table S3). The mean tree density value of flocks with warblers (0.08) was slightly higher than that of use sites (0.07), while flocks without warblers had a lower mean density of 0.05

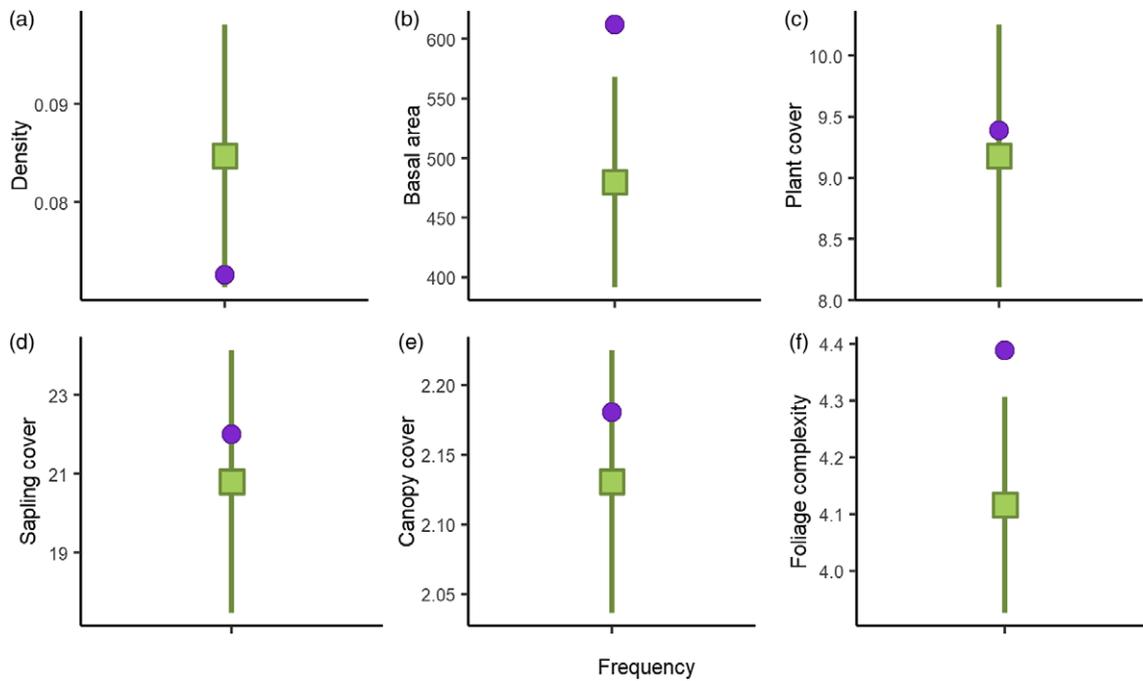


Figure 2. Distribution of bootstrapped means of availability (green) and use (purple) for (a) density of trees (per m²), (b) basal area (cm² per sq. m), (c) plant cover (count), (d) sapling cover (percentage cover), (e) canopy cover (score) and (f) foliage complexity (score).

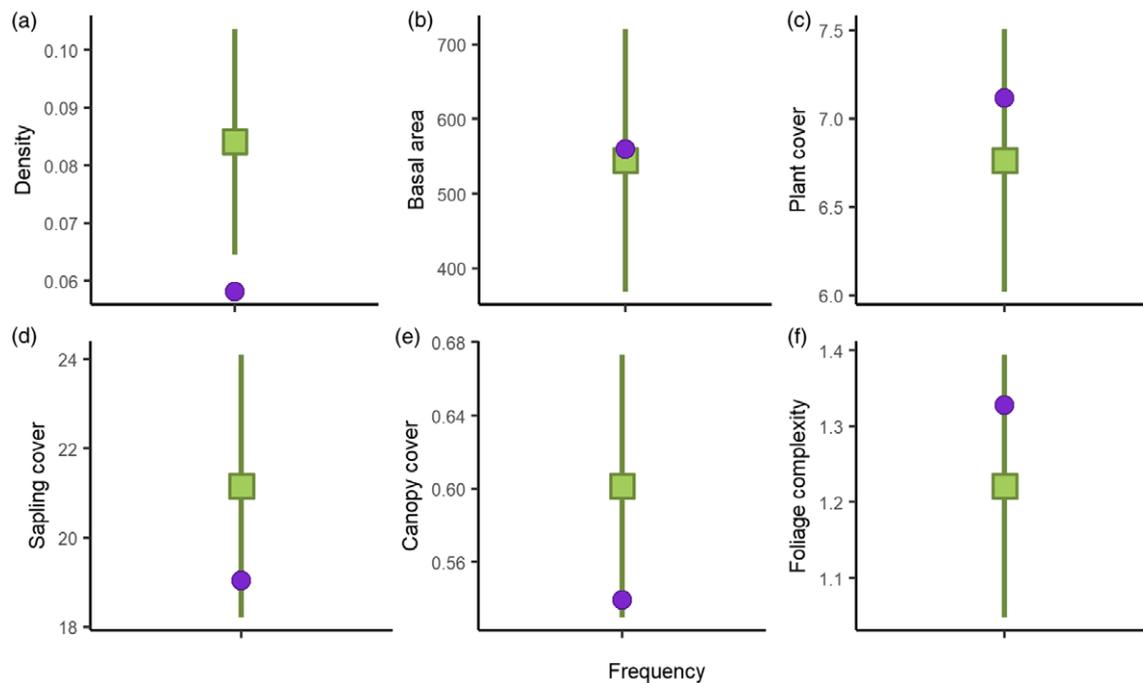


Figure 3. Distribution of bootstrapped standard deviations of availability (green) and use (purple) for (a) density of trees (per m²), (b) basal area (cm² per sq. m), (c) plant cover (count), (d) sapling cover (percentage cover), (e) canopy cover (score) and (f) foliage complexity (score).

(Figure 4a). The mean use site foliage complexity was between that of flocks with and without warblers (Figure 4b).

The fulvetta was a participant in 49% of all observed flocks, and in seven flocks, this was the only gregarious species. When these sites were compared to 37 use sites in which they were absent, none of the habitat characteristics tested were significantly different (Table S3). Similarly, the minivet, which was found in 40% of

all flocks, was the only gregarious species in six flocks. When these use sites were compared to 43 sites in which minivets were absent, there were no significant differences (Table S3).

Foliage complexity of use sites in which warblers were the only gregarious species ($n = 15$, mean = 5) was somewhat higher than that of use sites with only fulvettas as the gregarious species ($n = 7$, mean = 3.71), but this difference was marginally non-significant

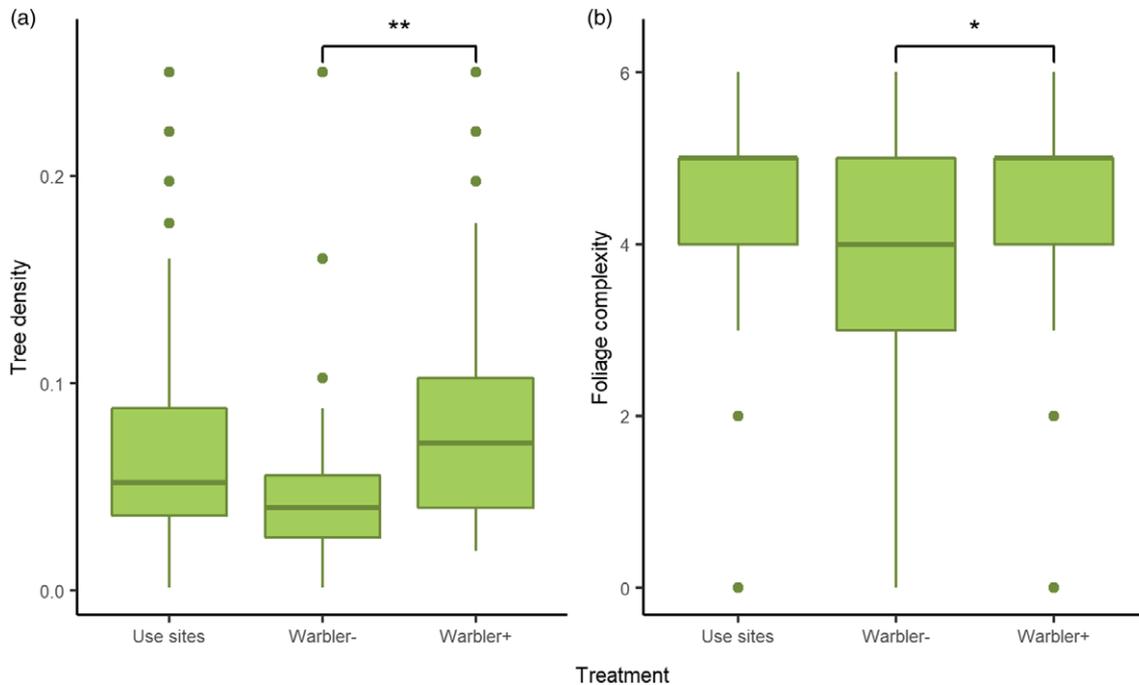


Figure 4. (a) Density of trees and (b) foliage complexity in all use sites, sites with flocks in which warblers were absent, and sites with flocks in which warblers were present. **indicates $p < 0.01$ and *indicates $p < 0.05$.

(Mann-Whitney $U = 78.5$, $p = 0.06$). In comparison, the average foliage complexity of all use sites was $4.39 (\pm 1.32 \text{ SD})$.

Discussion

In this study, we aimed to examine habitat selection of mixed-species flocks within a single site in the Western Ghats of India. We directly compared use and availability sites and also assessed the effect of habitat structure variables on flock composition, size, and richness. Finally, we examined flocks that were led by different gregarious species.

Mixed-species flocks are one among many groups of animals to show habitat selection, with many mammal and bird species across different taxonomic groups preferentially selecting habitat for a variety of reasons (Jain & Balakrishnan 2011, Liu *et al.* 2005, McLoughlin *et al.* 2004, Morales *et al.* 2008). Insects show strong selection for microhabitats within forested habitats (Jain & Balakrishnan 2011) where species may be specialised to forage. Mammal habitat selection can vary seasonally (Liu *et al.* 2005), and their selection may also be limited by the availability of resources such as denning sites (McLoughlin *et al.* 2004). Such habitat selection is not restricted to a single species at a time — in the case of terrestrial mixed-species bird flocks, past work has shown that participating species move through edge-dominated habitats and interior forest habitats at different speeds, with movement slowing in the former, perhaps because food availability is higher in such habitats (Rodewald & Brittingham 2002).

In our study site, 'use' sites showed relatively lower variability in tree density and canopy cover, suggesting that flocks form in a narrow subset of available tree density and canopy cover variation. Flock presence was associated with relatively less dense microhabitats, indicated by low mean tree density of use sites, and with a complex, heterogeneous foliage structure with large trees, indicated by the high mean basal area of use sites. This is consistent with

other findings in which mixed-species flocks have been found to prefer structurally complex forests (Lee *et al.* 2005, Zhang *et al.* 2013), and insectivorous species were less likely to participate in flocks in densely forested areas (Jullien & Thiollay 1998, Thiollay 1999b, Tubelis *et al.* 2006). Degraded forests are often characterised by an open canopy and reduced density of mature trees, and our study suggests that such homogenous reduction in these habitat variables do not provide a suitable habitat for mixed-species flocks. Considering that many nuclear species participating in flocks are forest-specialists particularly sensitive to disturbance, it is unlikely that flocks led by these species will be found in significantly human-modified landscapes.

Overall habitat use by flocks could be strongly influenced by gregarious species' preferences. Williams and Lindell (2019), for example, found that greater racket-tailed drongos might lead flocks to forage in relatively less densely vegetated areas. In our study, we encountered flocks led by western crowned warblers in particularly complex microhabitats with a high average tree density. When this gregarious species was not present and other species such as the brown-cheeked fulveta and the orange minivet led flocks, flocks foraged in less dense habitats. If gregarious species do have strong habitat preferences, given their role as nuclear species, it is likely that flock habitat choice might reflect gregarious species habitat choice and influence where other species forage. Just as there are costs of activity matching in mixed-species bird flocks (Hutto 1988), there may also be costs associated with such microhabitat matching, which merits further investigation.

Species that are important in mixed-species flocks, such as gregarious nuclear species, create opportunities in terms of new ecological niches for other birds which flock with them (Harrison & Whitehouse 2011). If such species had specific preferences within forests, then the loss of these conditions could lead to a reduction in the number of nuclear species, which could lead to compromised foraging niches that the flock creates. This may in turn lead to

reduced flock participation of other species in the area. Since participating in flocks is known to have an effect on fecundity and survival (Goodale *et al.* 2015, Jullien & Clobert 2010), reduced flocking could adversely affect obligate flock participants that rely on flocks to forage. Degraded forests, with their simplified vegetation structure, may be particularly vulnerable to the loss of mixed-species flocks, and studying the response of these complex social organisation structures to any subsequent restoration or succession in such habitats would provide us with a better understanding of tropical bird communities (Kotagama & Goodale 2004). Several species that participate in mixed-species flocks in the Western Ghats are long-distance migrants (such as the greenish warbler and western crowned warbler) or endemic species (such as the white-bellied blue flycatcher), and studying their response to habitat change in the context of the larger bird community in this biodiverse region would be particularly valuable (Zhang *et al.* 2013).

One of the caveats of our study is that the relatively small sample size of 72 flocks could have prevented the detection of significant differences in habitat variables between use and availability sites. Our availability sites were also not 'absence' sites, and it is possible that flocks could have used these sites during the field season. The small sample size could have also resulted in limited variation in terms of the species composition and richness, which could explain why we were unable to detect any effect of habitat variables on these flock characteristics. While we did find that foliage complexity played a significant role in the size of flocks, we interpret these results cautiously as the 72 flocks we observed consisted of an average of 18 individuals, and 36 flocks (50%) had 10–20 individuals. Moreover, other characteristics that were not measured as part of this study could have also played a role in birds selecting some microhabitats over others. For example, prey abundance and distances from edges of various kinds (clearings, streams, trails, roads, fields and villages) may influence habitat selection (Cuttriss *et al.* 2015). The measurement of these variables was beyond the scope of this study. In the future, it would also be interesting to see how flock characteristics, especially species richness and composition, vary with changes in microhabitat structure, perhaps in a site with greater heterogeneity.

In conclusion, we find that flocks in the Western Ghats may be selectively foraging in the habitat available to them, even within a single seemingly homogenous site. Understanding the habitat preferences of mixed-species flocks is crucial to identifying conditions that are important for the survival of several tropical bird species, many of which are obligate flock participants. Furthermore, intraspecifically gregarious species may have a particularly important role to play in the selection of habitat within sites, and studying their specific habitat requirements may help identify broader patterns of habitat use in flocks as well.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S026646742200030X>

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Conflict of interest. None.

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