Bamboozling Interactions: Interspecific associations within mixed-species bird flocks in bamboo in the Eastern Himalaya

Sidharth Srinivasan[1*], Aman Biswakarma[2], D.K. Pradhan[2], Shambu Rai[2], Umesh Srinivasan[2]

[1]Post-Graduate Programme in Wildlife Biology and Conservation, National Centre for Biological Sciences, Bangalore, India 560 065

[2]Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India 560 012

*Corresponding author
Sidharth Srinivasan - sidharth9611@gmail.com

ABSTRACT

Bamboo is one of the most rarely studied habitats in the world, even though it is widespread and supports significant biodiversity wherever it occurs. Several species across taxonomic groups - including birds - are partial to bamboo habitat, with some species being obligate bamboo specialists. Mixed-species bird flocks (hereafter, flocks) are an important and regular feature of tropical and temperate forest bird communities, and have been very well-studied. However, how and why flocks might differ between bamboo and non-bamboo habitats has never been examined. We studied flocks in rainforest and bamboo stands in winter and summer in the Eastern Himalaya, and used network analysis and null models to quantify and compare the composition of flocks and interspecific associations. We found that bamboo and rainforest flocks differed greatly in their composition and interspecific associations, with bamboo flocks being more cohesive, less modular and their species more connected with each other. Further, bamboo flocks were more consistent in their composition across seasons whereas rainforest flocks were highly diverse and variable. Rainforest flocks partially disintegrated in summer, probably due to an increase in the abundance of arthropods. The loss of arthropods in an entire substrate in bamboo in summer and the increase in arthropod abundance in other substrates was probably not sufficient for flocking to cease in bamboo. We discuss species' roles and the potential costs and benefits for species in flocks in bamboo and rainforest. Our study is one of the few to describe bamboo flocks, and the results highlight the need to conserve bamboo stands to ensure the persistence of these obligate bamboo specialists in the Eastern Himalaya.

Keywords – multi-species groups, network analysis, null model, flock structure, flocking seasonality, resource availability, arthropods, specialist species.

INTRODUCTION

Numerous organisms, including mammals, fish and birds interact to form complex interspecific associations that structure communities and maintain community stability (Paijmans et al., 2019; Sridhar et al., 2009; Stensland et al., 2003; Thébault & Fontaine, 2010). Such associations are well-studied in insectivorous birds, in which an aggregation of two or more species, feeding together and moving in the same direction are known as mixed-species flocks (hereafter, flocks; Kotagama & Goodale, 2004; Sridhar et al., 2009). Many bird species participate in flocks, but some species are more important than others for flock initiation and cohesion; these are called 'nuclear' species. 'Attendant' species follow nuclear species. Associations between species can vary at the individual level and with species and environmental conditions, and tend to be dynamic (Bangal et al., 2021; Goodale et al., 2017; Greenberg, 2000). Two main hypotheses have been proposed to explain interspecific associations within flocks – improved foraging efficiency and lowered predation risk (Morse, 1977). Globally, a large body of literature has been devoted to investigating the structure, composition, and function of flocks (Sridhar et al., 2009, 2012).

Flocks are known to be structured by seasonality and the resulting fluxes in arthropod resources, especially in the Paleotropics and in subtropical and temperate forests. In highly seasonal areas, flocks are also seasonal (McClure, 1967); tropical flocks, on the other hand, are considered to be stable and permanent throughout the year, especially in the Neotropics (Munn, 1985), and in a few Paleotropical systems (Jayarathna et al., 2013). Flock compositions and species' roles in flocks also vary across time and habitats (Jayarathna et al., 2013; Jiang et al., 2020; Morse, 1970), and reduced food availability has been thought to drive mixed-species flocking, especially during periods of resource scarcity (U. Srinivasan & Quader, 2012). Resources in terms of arthropods show distinct seasonal fluctuations, and insectivorous birds are known to alter their ecology in response to these changes (Ghosh et al., 2011). However, almost all our understanding of flocks comes from forests in tropical and subtropical regions, and other habitats like bamboo have been widely neglected.

Bamboo (Poaceae: Bambuseae) is a distinct and diverse group of plants with a uniquely shared ecology. Overlapping with much of the range where avian mixed-species flocks occur, bamboo is found in tropical and subtropical habitats around the world, with Asia harbouring the maximum species richness, followed by South America (with less than half of Asia's species richness; (Bystriakova, 2003; Bystriakova et al., 2004). Unsurprisingly perhaps, over 90 species of primarily insectivorous Neotropical birds across different families have been identified as being partial to bamboo, with at least 20 species being obligate bamboo specialists (Areta et al., 2009; Kratter, 1997; Leite et al., 2013). A recent study suggests the existence of specialist birds in bamboo in the Himalaya well (S. Srinivasan et al., 2023)

Although some of these specialist species are also known to participate in flocks (Parker et al., 1997) and although studies on mixed flocks from the Neotropics are numerous, systematic studies

on flocking assemblages in bamboo are limited not only from this region (Guimarães & Guilherme, 2021), but globally. Therefore, information about the structure and composition of flocks in bamboo is almost non-existent and patterns of interspecific associations between bamboo specialists/other species and the mechanisms that drive flocking in bamboo remain unknown.

We used network analyses to investigate patterns of species associations in flocks in bamboo stands and rainforest in winter and in summer in the Eastern Himalaya. Network theory has been increasingly used to study mixed-species systems as it helps quantify overall community structure and interspecific associations (Bangal et al., 2021; Borah et al., 2018; Montaño-Centellas, 2020; Proulx et al., 2005). Quantifying networks can help uncover network (flock)-level and species-level properties.

We asked the following questions and tested predictions related to flocks and resource availability in bamboo and rainforest in winter and summer in the Eastern Himalaya:

1. How does the structure and composition of flocks differ between bamboo and rainforest, across seasons? Given the presence of bamboo specialist species (S. Srinivasan et al., 2023), we predicted that flock networks and interspecific associations between species in bamboo would be stronger and more cohesive than flocks in the more diverse rainforest. We expected this to be the case based on similarities in behaviour in bamboo specialists that might confer foraging or anti-predator benefits through flocking (Goodale et al., 2020).
2. Do fluxes in resource availability drive the structure and composition of flocks, across both habitats and seasons? Given the inherent differences in arthropod availability in both habitats and seasons (S. Srinivasan et al., 2023), we expected the structure and the composition of flocks to be dissimilar between both habitats and seasons. With increases in arthropod abundance in summer, we expected flocking to reduce (and interspecific associations to weaken) in both habitats.

METHODS

Study area

We carried out this study in the Eaglenest Wildlife Sanctuary, (27.03° to 27.15° N and 92.30° to 92.58° E), situated in the West Kameng district in Arunachal Pradesh, India. Situated within the Himalayan Global Biodiversity Hotspot, this is a region of high bird and bamboo species richness (Bystriakova, 2003; Myers et al., 2000; Orme et al., 2005). Eaglenest Wildlife Sanctuary hosts a great diversity of habitats, from tropical rainforest to high-elevation coniferous and rhododendron forest across its elevational range.

We sampled bamboo and old-growth rainforest at altitudes ranging from 800-1200 m ASL in Eaglenest Wildlife Sanctuary. The vegetation in this area is tropical/sub-tropical wet evergreen forest (Champion & Seth, 1968) interspersed with primary, mature bamboo. In this region, bamboo tends to grow on steep slopes and the dominant bamboo species is *Dendrocalamus longispathus*, with negligible patches of a runny bamboo species which was not identified. *Dendrocalamus longispathus* is a large, clump-forming bamboo with sizable culms (stems) and relatively closed canopies, and forms near-monotypic bamboo-dominated patches. The total area of the bamboo patches in the study area was ~30 ha., with a few very large trees interspersed within these patches. We selected similarly sized undisturbed primary forest patches as the rainforest plots. The study period spanned two seasons, winter from January to mid-March 2022 and summer from mid-March to mid-May 2022.

Sampling Design

Flock Sampling

We sampled flocks in line transects established in two habitats – rainforest and bamboo (seven transects in each habitat) and two seasons – summer and winter (see S. Srinivasan et al., 2023 for a map of the transect locations). We also recorded flocks outside transects opportunistically, when walking between transects or on previously established trails in the two habitats. Because of the ruggedness of the terrain, adjacent transects were not likely to be independent of each other in terms of the home ranges of birds, especially in winter. Nevertheless, we treated each flock as an independent sample, because flocks provide a 'snapshot' of the realised interactions within them; members are dynamically participating in and exiting flocks within short time periods (Graves & Gotelli, 1993). We walked transects in the morning and evening but avoided early mornings and late evenings when flocks would be forming or breaking down. We ensured that effort was similar across habitats in each season (47 vs 48.5 km in bamboo and rainforest in winter and 27 vs 24 km in bamboo and rainforest in summer).

We defined a flock as a group of at least two species, moving in the same direction (Kotagama & Goodale, 2004). We followed the 'gambit of the group' method, where individuals that were observed together during a sampling period were considered to be associated (see Farine & Whitehead, 2015; Franks et al., 2010). On encountering a flock, we recorded the species composition of the flock by noting down the time, the identity of the species, and the group size of each species (i.e., the number of individuals). For flocks encountered outside transects, we also recorded the habitat it was observed in. For gregarious species where accurate group size measurements were not always possible, we recorded a range, from the minimum to the maximum number of individuals in the group (Borah et al., 2018; U. Srinivasan et al., 2012). We used the midpoint of this range in subsequent analysis. All the species recorded in a given habitat and season were pooled together to create a flock-by-species matrix.

Arthropod Sampling

To quantify resource availability, we sampled arthropods in both habitats and seasons. We selected 30 points at random in each habitat with a minimum distance of 30m between points. The points were randomly distributed around the transects, in each habitat and were sampled once in each season. We employed two commonly and widely used methods – pitfall traps, for ground-dwelling arthropods and branch beating, for foliage arthropods. The bamboo specialist birds in this region were known to feed from within the bamboo sheaths (S. Srinivasan et al., 2023), and thus, we also sampled arthropods from this substrate (sampled only in winter, as the sheaths fall off the bamboo stems after winter), by adapting the branch beating technique. For further details on arthropod sampling methods, see (S. Srinivasan et al., 2023).

Analyses

Cluster Analysis

We used cluster analysis to categorise flocks into various types. Rainforest flocks from this region are known to be of three types – understorey flocks, led by the Nepal Fulvetta (*Alcippe nipalensis*), midstorey/canopy flocks, led by the Sultan Tit (*Melanochlora sultanea*) or by minivets (*Pericrocotus* sp.) and flocks of large-bodied species led by laughingthrushes (*Garrulax sp.*; Borah et al., 2018; U. Srinivasan et al., 2012). Moreover, it was apparent from fieldwork that there were at least two types of flocks in bamboo, one that was led by the White-hooded Babbler (*Gampsorhynchus rufulus*) and comprised the bamboo specialists, and the other led by the Nepal Fulvetta. Therefore, we used a *k*-means cluster analysis to categorise flock types in each habitat and season and set the number of clusters to three. For further analyses, we then selected the clusters that contained the greatest number of flocks and with the presence of the Nepal Fulvetta for the rainforest flocks and the White-hooded Babbler for the bamboo flocks.

Network Analyses

We used network theory to analyse the flocks and quantify interspecific associations in both habitats and seasons (Borah et al., 2018; Farine & Whitehead, 2015; Proulx et al., 2005). In these networks, nodes represent species and the edges between the nodes represent associations between species. After selecting flocks from the *k*-means cluster analysis, we constructed flock-by-species matrices and used these to construct weighted networks for each habitat and season, where the weights between species in the network represented the frequency of distinct co-occurrences of species. For every network, we calculated network- and node-level metrics.

Network level metrics included network density, modularity, and transitivity. These metrics quantify the overall connectivity (density) and cohesion (modularity and transitivity) of a network (Montaño-Centellas, 2020). Network density is the proportion of all possible connections in a network that are realised (Newman, 2003). Network density, therefore, represents distinct co-

occurrences in a flock and can help understand the overall connectedness of the flock. Transitivity measures the likelihood that two interconnected nodes are part of a larger, more connected group (Wasserman & Faust, 1994). This is also called the clustering coefficient; higher values indicate that the network contains groups of species that are highly interconnected. Modularity calculates the strength of different modules/clusters (closely connected nodes) in a network by estimating how well-separated modules in a network are based on the number of edges within and across modules (Clauset et al., 2004). We calculated modularity using the Louvain method with a community detection algorithm (Bangal et al., 2021). Modularity and transitivity represent measures of the overall cohesion of a network and tend to be inversely correlated (Wasserman & Faust, 1994). Higher transitivity values indicate that all adjacent species in a network are highly connected, therefore implying that there are few or no modules in the network.

We also calculated node-level (species-level) metrics which quantify the importance of a node within a network. We calculated degree, which represents the number of edges connected to a particular node, and weighted degree (association strength), which is the sum of the frequency of distinct co-occurrences for each node. These measures are sensitive to species richness; therefore, we normalised degree by dividing values by the number of possible connections in a flock ($n - 1$, where n is the total number of species recorded participating in the habitat- and season-specific flock) and weighted degree by dividing values by the maximum value of weighted degree in each network. Degree represents the interspecific associations of each species while weighted degree is a measure of centrality, which captures the structural importance of a species in a network. We also visualised the distribution of degrees of the weighted networks, to understand the structure of the networks across habitats and seasons.

Table S1 (Supplementary Material) summarises the network definitions and their biological interpretations.

Random networks

We simulated null networks based on the observed data for each habitat and season to test whether network- and species-level metrics deviated significantly from random expectation. We randomised species' participation within flocks while controlling for flock species richness and the number of flocks that a species participated in each network (i.e., randomising matrix entries while holding row and column totals constant). Thus, the null model preserves differences in species richness among habitats and seasons but assumes that differences in flock participation within each habitat and season are proportional to observed species occurrences. We simulated 10,000 null flocks and compared the distribution of the null metrics with the metrics calculated from the observed networks to infer if the observed values lie within null expectation. This iterative permutation procedure allows us to test if interspecific associations are potentially caused by underlying social interactions between individuals or by some other factors, such as congregations between individuals due to their specificity for habitat or resource (Montaño-Centellas, 2020).

Arthropod abundances

We analysed per-point arthropod abundance in both habitats and seasons. The order Hymenoptera (mostly ants) was removed before analysis, as it increased considerably in the summer, making it harder to compare abundances. We encountered a single point in bamboo pitfall traps in the summer that contained a hyper-abundance of Isoptera (875 individuals). This was clearly an outlier and therefore, we removed Isoptera as well.

We carried out all analyses in program R (R Core Team, 2022). We created random networks using the package *EcoSimR* (Gotelli et al., 2015) and network analyses using the package *igraph* (Csardi & Nepusz, 2006).

RESULTS

We observed 2,004 individuals represented by 96 species in 304 flocks across both habitats and seasons. We filtered these to remove rare species (occurring in less than 1% of all flocks) and categorised them by habitat and season.

Cluster Analysis

The *k*-means cluster analysis categorised the flocks in each habitat in each season into three types. We selected the category with the most number of flocks and with the presence of the Nepal Fulvetta in rainforest flocks and the White-hooded Babbler in the bamboo flocks. (Table 1) contains the details of the number of flocks selected for each habitat and season based on the cluster analysis.

Structure and composition of flocks

Flocks were composed of species that were distinct in each habitat and season and few species were common across all habitats and seasons. Rainforest flocks were mostly composed of the Nepal Fulvetta, Lesser Racket-tailed Drongo (*Dicrurus remifer*), Chestnut-crowned Warbler (*Phylloscopus castaniceps*), and the Grey-headed Canary Flycatcher (*Culicicapa ceylonensis*) in winter, while in the summer, the Blyth's Leaf Warbler (*Phylloscopus reguloides*) and Whistler's Warbler (*Phylloscopus whistleri*) replaced the latter two winter species as the most common species. In bamboo, the most common species were the Lesser Racket-tailed Drongo, White-hooded Babbler, Nepal Fulvetta, Grey-cheeked Warbler (*Phylloscopus poliogenys*), and the Pale-billed Parrotbill (*Chleuasicus atrosuperciliaris*), in winter; in summer, the White-hooded Babbler, Pale-billed Parrotbill and the Nepal Fulvetta were encountered the most. The composition of flocks in bamboo differed from that of the rainforest mainly due to the presence of bamboo specialist species such as the Pale-headed Woodpecker (*Gecinulus grantia*), Red-billed Scimitar Babbler (*Pomatorhinus ochraceiceps*), White-breasted Parrotbill (*Psittiparus ruficeps*), Yellow-bellied

Warbler (*Abroscopus superciliaris*), White-hooded Babbler and Pale-billed Parrotbill, which were entirely absent from rainforest flocks. Likewise, the rainforest flocks harboured a few species that were never encountered in the bamboo flocks; for instance, the Green-backed Tit (*Parus monticolus*), Pin-striped Tit-Babbler (*Mixornis gularis)* and the Indian White-Eye (*Zosterops palpebrosus*). Seasonally, flocks differed due to the absence of the winter migrants in the summer, as migrants moved to breed at higher elevations.

Network Analyses

Table 1 - Characteristics of flocks used in the analyses. Number of flocks represents the total number of flocks selected in each habitat and season based on the k-means cluster analysis. For definitions and biological interpretations of the metrics, please refer to Table S1 in Supplementary Material.

Flock Characteristic	Rainforest, Winter	Bamboo, Winter	Rainforest, Summer	Bamboo, Summer
Number of flocks	52	31	13	21
Network Metrics				
Density	0.32	0.45	0.30	0.47
Modularity	0.04	0.04	0.10	0.00
Transitivity	0.74	0.92	0.70	0.92
Species Metrics (averaged across species)				
Normalised Degree	0.65	0.91	0.61	0.93
Normalised Weighted Degree	0.30	0.46	0.34	0.54

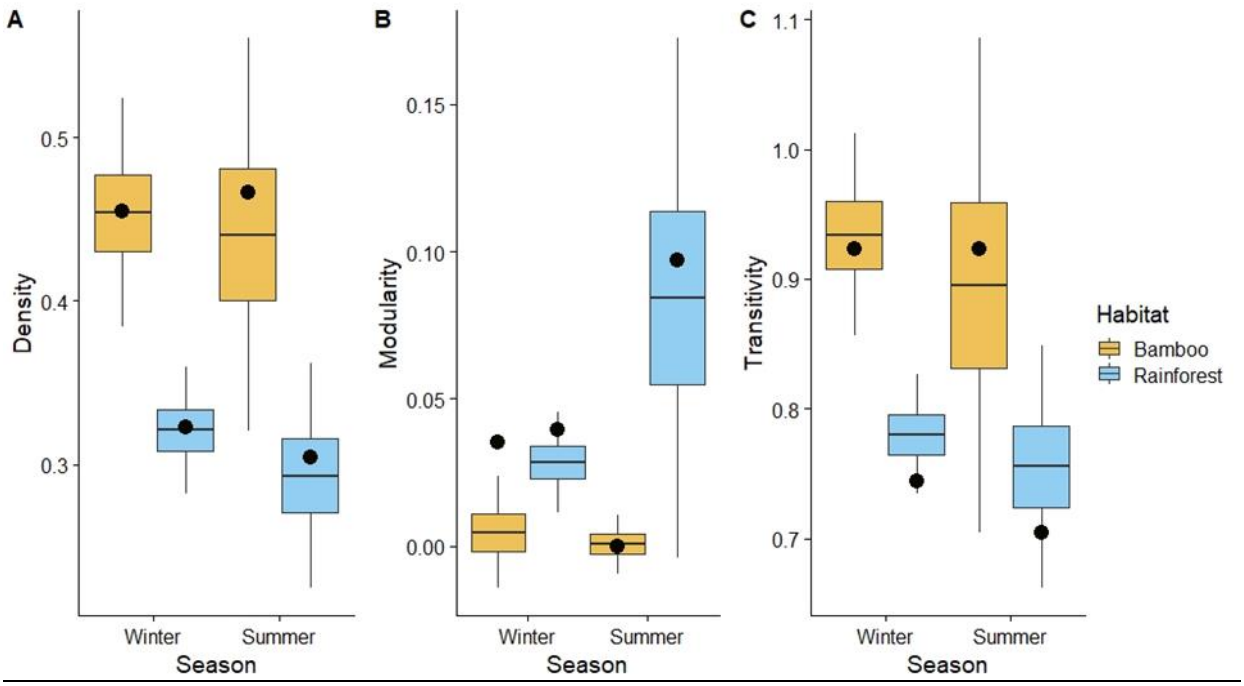

Figure 1 - Network-level metrics for flocks in both habitats and seasons. Network-level metrics represent density (**A**), modularity (**B**) and transitivity (**C**). Dots represent values of each metric from the observed flocks while the box plots depict the mean and the standard deviation of the metrics from the null models and the whiskers represent the minimum and maximum.

Network structure was distinct between habitats and within a season but was similar between seasons and within a habitat both at the network-level and at the species-level (Fig 1, Fig 2). Network-level metrics from the observed networks indicated that bamboo flocks were more connected, less modular, and had stronger interspecific associations, irrespective of the season. Bamboo flocks were denser, implying that there were more realised interspecific connections in the flock out of all possible connections. Across seasons, bamboo flocks were less modular and more transitive, suggesting a more cohesive flock that had fewer divisions and more connections among adjacent species than in rainforest (Fig 1, Table 1). Normalised degree, a species-level metric, also indicated more connected bamboo flocks across seasons. The normalised weighted degree distribution or the association strength was higher in bamboo flocks and increased as the season progressed from winter to summer in both habitats (Fig 2, Table 1). Moreover, the network-level metrics indicated a more consistent flock even across seasons in bamboo, with the values for cohesion and connectivity remaining higher than rainforest and being less variable within bamboo between seasons.

Rainforest flocks were less connected and less cohesive than bamboo flocks. Across seasons, flocks were less consistent with values for density, transitivity and normalised degree decreasing from winter to summer (Fig 1, Fig 2). This indicates that the rainforest flocks in summer were more sparsely connected and more clustered, further validated by their lower transitivity values.

Surprisingly, the normalised species' association strength increased from winter to summer, but only marginally (Fig 2).

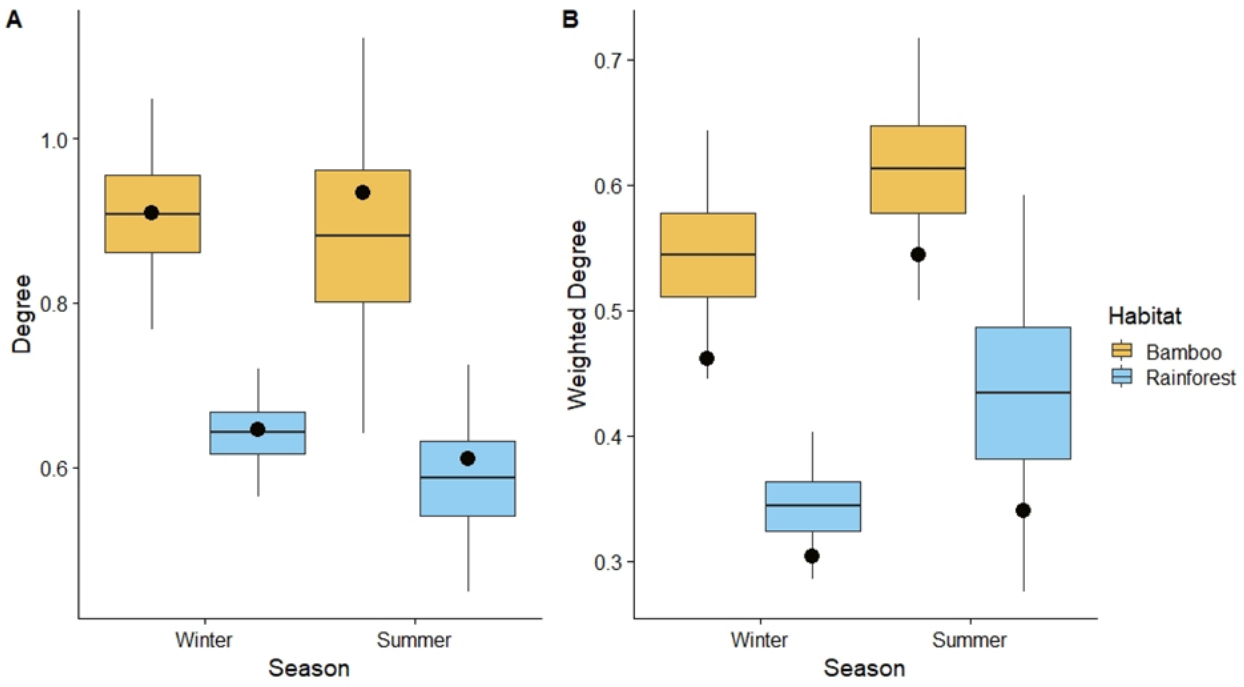

Figure 2 - Species-level metrics for flocks in both habitats and seasons. Species-level metrics represent degree (**A**) and weighted degree (**B**). Dots represent values of the metrics from observed flocks while the box plots depict the mean and the standard deviation of the metrics from the null models and the whiskers represent the minimum and maximum.

The metrics for observed flocks did not differ significantly from the results of the randomised networks (Fig 1, Fig 2). The only exception was the value for modularity from flocks in bamboo in winter, which was higher than the null expectation.

The normalised frequency distribution of interspecific interactions (association strength) for each habitat and season indicated that rainforest had very few species that were highly connected with each other, with most species only sparsely associated with rainforest flocks (Fig 3). This was especially true in winter, where few species had very high weighted degree values but most species had much lower values, indicating a skewed network with very sparse connections. In summer, the steepness of the curve seemed greater, with even fewer species being very highly associated with others and most species having few connections with other species. Thus, relative to the total number of species, more species seemed to have higher weighted degree values in bamboo than in rainforest, indicating stronger associations in bamboo.

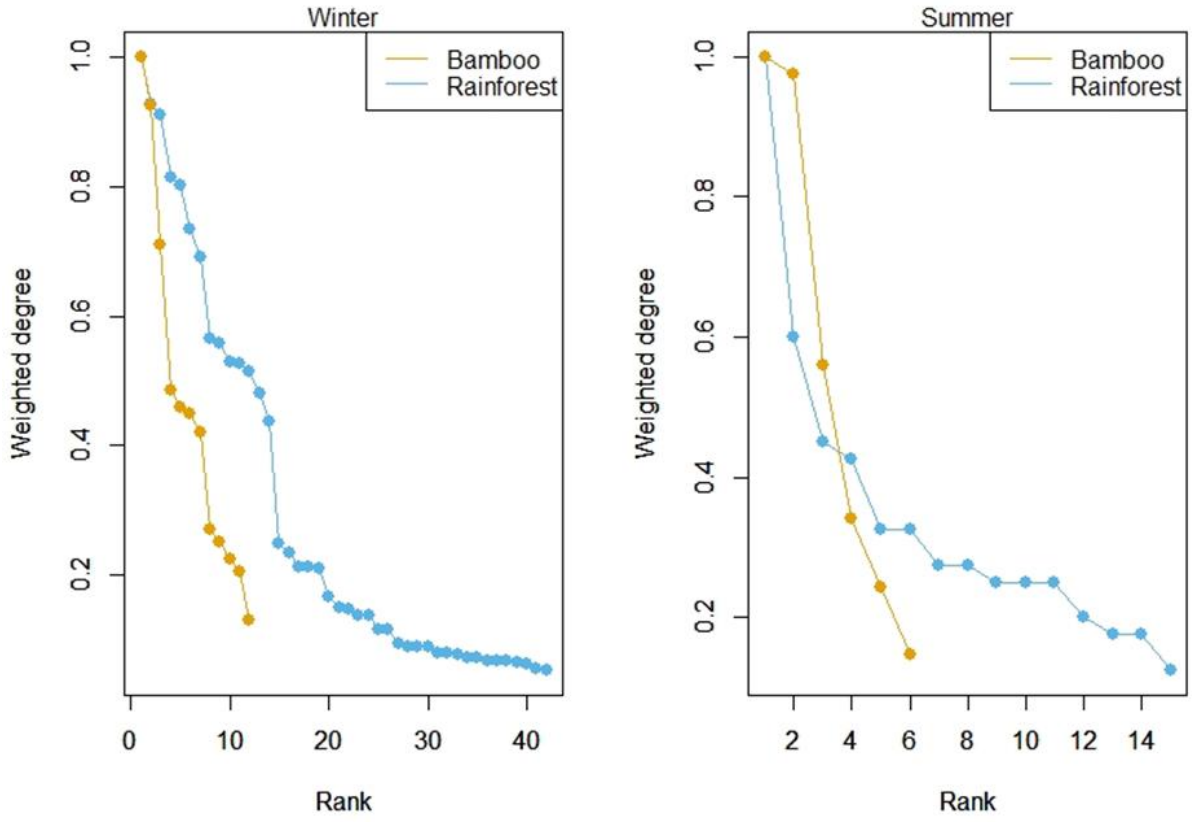

Figure 3 - Normalised weighted degree distribution of flocks across seasons. The left panel represents flocks in winter and the right panel represents flocks in summer.

Arthropod abundances

Sampling across habitats and seasons yielded 7,354 individuals representing 21 orders. The major orders were – Araneae, Hymenoptera (> 90% were ants), Acarina, Diptera, Blattodea, Hemiptera, Orthoptera, Psocoptera, Coleoptera and Collembola. Arthropod abundances increased greatly in the summer across substrates, irrespective of the habitat. The abundances in both habitats seemed to be comparable in winter (notches overlapped considerably; Fig 4) but the abundance of arthropods in rainforest was distinctly higher than that of bamboo in the summer. This was apparent in both the ground and the foliage-dwelling arthropods. The abundance of arthropods in sheaths in bamboo was not considerably different from the abundances in other substrates within bamboo or rainforest, in winter. In summer, however, the sheaths fall off the bamboo stems and the arthropods are unavailable.

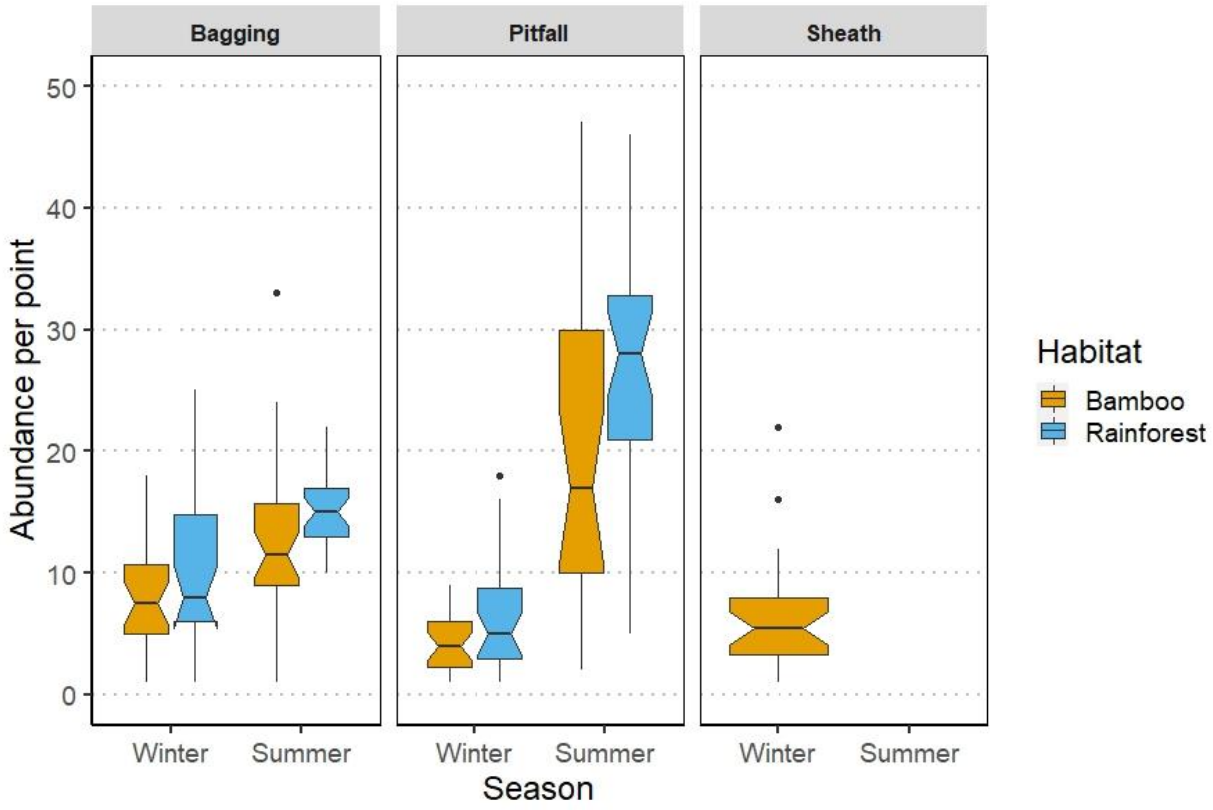

Figure 4 - Notched box plot depicting per point arthropod abundances by method of sampling, in each season and habitat.

DISCUSSION

We provide one of the first quantitative assessments of mixed-species bird flocks in bamboo from anywhere in the world. We found that in the Eastern Himalaya, the structure and composition of bamboo flocks are distinct from those in rainforest, across seasons. Bamboo flocks mainly consisted of bamboo specialist species, and while these species readily associated with each other, they rarely associated with species that were not bamboo specialists. The results of the cluster analysis separated this flock from the other flocks in bamboo, corroborating observations from the field.

Species' roles in flocks

The bamboo flock in the Eastern Himalaya is unique and is mostly composed of species that are bamboo specialists (S. Srinivasan et al., 2023). The White-hooded Babbler is possibly acting as the 'leader' or the 'nuclear' species in these flocks. Nuclear species are those responsible for the initiation and/or maintenance of flocks while 'attendant' species tend to join flocks and follow

these leaders. Corroborating field observations, the White-hooded Babbler has the highest association strength (1.00) across both seasons and is very vocal and interspecifically gregarious, making it an ideal nuclear species (Goodale et al., 2015; Goodale & Beauchamp, 2010; U. Srinivasan et al., 2010). Frequent non-bamboo specialist species that were found in bamboo flocks in winter include the drongos (*Dicrurus sp.),* and these species are known to be excellent 'sentinels' (Goodale & Kotagama, 2005; Sridhar & Shanker, 2014). Sentinel species such as drongos are salliers that forage in flocks to feed on prey that is usually flushed out by gleaners (U. Srinivasan & Quader, 2012). These species are also very vocally active, providing reliable social signals to other species in the flock in the form of anti-predator alarm calls (Goodale & Kotagama, 2005). Hence, drongos in the Eastern Himalayan bamboo might be acting as sentinel species, salling and foraging on the prey flushed out by the bamboo specialists. Attendant species found in bamboo flocks in winter such as the Common Green Magpie (*Cissa chinensis*; 0.22) and the Black-winged Cuckooshrike (*Lalage melaschistos*; 0.25) were probably opportunistic flocking species in bamboo. In summer, the bamboo flock was composed entirely of the bamboo specialists, barring the Lesser Racket tailed Drongo.

In rainforest, the Nepal Fulvetta had one of the highest association strengths across both seasons (0.92 in winter, 1.00 in summer). Like other species of the genus *Alcippe*, it is a known nuclear species in rainforests in this region (U. Srinivasan et al., 2012; Zhou et al., 2019). Other species that had high association strengths include the Chestnut-crowned Warbler (1.00 in winter), Grey-headed Canary Flycatcher (0.81 in winter) and the Golden Babbler (*Cyanoderma chrysaeum*; 0.56 in winter, 0.6 in summer). These are common small-bodied understorey species, known to flock together in forests in this region (U. Srinivasan et al., 2012). The Lesser Racket-tailed Drongo, probably acting as the sentinel species, also had relatively high association strengths across both seasons (0.91 in winter, 0.45 in summer). Attendant species included various other understory small-bodied species such as warblers and did not seem to be very different from the flocks commonly encountered in forests from other studies in this region (U. Srinivasan et al., 2012).

Flock structure and composition

Network and species-level metrics showed considerable differences across habitats. Bamboo flocks were more cohesive than rainforest flocks (Fig 1, Table 1). Bamboo flocks had more (and stronger) interspecific connections. They were therefore less modular (and consequently also more transitive) than rainforest flocks, implying the lack of distinct clusters within them. On the other hand, rainforest flocks had subsets of species associating more strongly amongst themselves and loosely with species in other clusters, and were more clustered overall than bamboo flocks. Across seasons, bamboo flocks in summer harboured slightly denser associations, had fewer clusters and equally strong connections within them than in winter. Rainforest flocks became more loosely associated, had fewer connections and were highly modular, signalling the (at least partial) breakdown of flocks in summer. Species-level metrics indicated a similar pattern (Fig 2, Table 1). Species in bamboo flocks had high overall mean normalised weighted degree values, indicating

the strength of the interspecific associations in bamboo flocks. While the number of associations remained similar across seasons, the associations became stronger in summer in both habitats, with bamboo flocks being consistently stronger and more cohesive than rainforest flocks.

The observed values of network and species-level metrics did not differ significantly from null expectation, except that winter bamboo flocks were significantly more modular than expected. A possible reason for this is that the composition of null flocks might not be creating a truly 'null' flock. This is because of the high degree of consistency in species participation in bamboo flocks. Bamboo flocks were only composed of species that are always associated with each other, and therefore shuffling species participation in flock-by-species matrices might not actually lead to observable differences from empirical flocks. The non-significant departure from null expectation also characterised network- and species-level metrics in rainforest flocks, but this could be due to the higher variation in flock composition in this habitat.

Seasonal arthropod availability drives flocking

The Eastern Himalaya is a monsoonal system with summer and winter representing distinct wet and dry periods respectively but seems to host both seasonal and permanent flocks. Rainforest flocking decreased drastically with the onset of summer (Fig S1, Supplementary Material). Bamboo flocks also showed declines in summer, though the magnitude of decrease was far lower. With resident birds occupied with breeding activities in the summer, this decrease in flocking in both rainforest and bamboo was not unexpected. However, for the bamboo flock system that consisted only of bamboo specialists, species associated with each other consistently in the summer as well. This was contrary to our expectation – bamboo flocks did not break down in summer even though arthropod availability in the habitat increased (Fig S1, Supplementary Material). However, in summer, this increase was much greater in rainforest, and abundances across substrates were significantly higher when compared to bamboo (Fig 4). This might have been sufficient to contribute to the partial breakdown of flocking in rainforest, as evidenced by the network-level metrics (Fig 1). In contrast, similar increases in arthropod abundances in other strata of bamboo were probably not sufficient to compensate for the loss of sheath arthropods. This might explain why bamboo flocks do not disintegrate during the summer and rainforest flocks do (at least partially), as arthropod resources in bamboo are not as abundant as they are in rainforest (Fig 4). Bamboo flocks, composed of specialist species, thus seem to be obligate in bamboo, with resource availability being a key factor in driving flocking throughout the year.

Benefits and costs associated with flocking in bamboo

Individuals join flocks based on the risks and benefits associated with flocking. The benefits and costs accrued by individuals in flocks will depend on joining a flock as a unit and not associating only with a particular individual or species within a flock (Sridhar et al., 2009; Sridhar & Shanker, 2014). Associating in flocks can help individuals spend more time foraging and less time being vigilant (Sridhar et al., 2009). The benefits gained by participating in flocks enhance the fitness of

flocking individuals (Dolby & Grubb jr, 1998; U. Srinivasan, 2019). Species can provide complementary (benefits provided by a flocking individual that are lacking in its associate) or supplementary benefits (benefits provided by a flocking member that are similar to its associate) in flocks with respect to anti-predator and foraging benefits (Goodale et al., 2020).

In the Eastern Himalayan bamboo flock, supplementary benefits could be provided by the bamboo specialist species. Because they employ the same foraging strategy, social copying - where one individual observes and copies the foraging location or some other information related to foraging - is possible (Krebs, 1973). Birds are known to visit locations where their associates have had success in foraging (Waite & Grubb Jr, 1988). Members of the flock might also have information on previous foraging sites and might help participants avoid sites that have already been exploited (foraging efficiency theory, Diamond, 1981). In addition, complementary benefits can also be gained in tandem. The bamboo specialists might have traded off their vigilance for their specialised feeding behaviour, peering into the sheaths, internodes, and holes in bamboo, thereby temporarily occluding their vision (Jones et al., 2020). Hence, these species might require others to alert them about the presence of a nearby predator. This role is usually carried out by the sentinel species but can also be taken up by the nuclear species – drongos and the White-hooded Babbler respectively in this case. The White-hooded Babbler is known to forage in family groups, with juveniles and adults participating in flocks. Hence, kin selection would predict that the White-hooded Babbler would warn their kin in the presence of a predator (Hamilton, 1964), and it would not be surprising to learn that other bamboo specialist species could have evolved to eavesdrop on these calls. Similarity in traits such as diet, body size and foraging behaviour might be key to acquiring these benefits (Goodale et al., 2020; Sridhar et al., 2009, 2012) and this could explain the stronger interspecific associations, more cohesive and consistent flocks in bamboo across seasons than in rainforest (Fig 1, Fig 2).

There are some costs associated with flocking together as well - the more similar the niches of species in a flock, the more they might compete for the same resources. This presents a potential trade-off to bamboo specialists in flocks; however, such competition might still be lower than if they were in purely intraspecific flocks. Studies suggest that by not having to ‘match their activity’ (i.e., change behaviour to associate together in flocks), they might incur lower costs and find flocking more beneficial than intraspecific flocking (Sridhar & Guttal, 2018). This could also explain the strong and consistent interspecific associations within the bamboo flocks recorded in our study. These species are possibly obligate flock participants and might depend on flocks to obtain food and anti-predatory benefits. Obligate flocking species have been known to have higher survival rates than facultative and non-flocking species (Jullien & Clobert, 2000), but future research estimating demographic vital rates might be necessary to test this hypothesis.

Role of the habitat

Vegetation is known to structure flocks around the world (Jones & Robinson, 2021; Martínez et al., 2018; Montaño-Centellas & Jones, 2021; Sridhar & Sankar, 2008). Studies have theorised that the structure of bamboo plays an important role in the specialisation of several species in the Neotropics (Kratter, 1997; Lebbin, 2007; Socolar et al., 2013). Moreover, bamboo is also hypothesised to provide anti-predatory refugia to birds (Reid et al., 2004). This raises interesting questions with respect to bamboo flocks in the Eastern Himalaya – is vegetation structure also playing a role in structuring flocks in this region? If the habitat is already providing anti-predatory benefits, does associating in flocks provide yet more anti-predatory benefits, or are species associating in flocks for a different reason? Moreover, because bamboo specialists and bamboo flocks are known to have very small home ranges (Guimarães & Guilherme, 2021; Lebbin, 2013) and because bamboo reduces the need for individuals to travel widely to obtain food (more foraging substrate; Lebbin, 2007; Reid et al., 2004), do the individuals of the bamboo specialist species exhibit flock fidelity? Bamboo flocks from this region present several interesting questions that remain unanswered.

Bamboo is often characterised as a successional, ephemeral habitat that is also important to resident human communities as a resource (Bystriakova, 2003). Thus, bamboo specialist species are forced to cope with an inherently fluctuating habitat that is being made more variable due to anthropogenic use. This could potentially threaten specialist species that seem to be highly interdependent and reliant on flocking in bamboo and are exclusive to this habitat. The loss of a nuclear species in flocks reduces the fitness of other participant species (Dolby & Grubb jr, 1998) and more studies in this habitat are needed to know the extent to which the fitness of these species is affected by their interdependency. Nevertheless, this study emphasises the need to conserve large, contiguous bamboo stands at the landscape level in the Eastern Himalaya, which might be key to the survival of this unique specialist flock.

CONCLUSIONS

This is one of the first studies that describes mixed-species bird flocks in bamboo globally. Flocks in bamboo and rainforest in the Eastern Himalaya showed considerable differences in their structure and composition across two seasons. Bamboo flocks were more highly connected, had stronger interspecific connections and were less modular than the rainforest flocks in both winter and summer. Bamboo flocks were mainly composed of only bamboo specialists and were also more consistent across seasons, while the flocks in rainforest were more diverse and highly variable. Flocking seemed to be largely driven by seasonal availability of arthropod resources in both habitats. The unique foraging behaviour of bamboo specialists, and the relative costs and benefits of associating in flocks can also help discern the patterns of grouping that are seen in the

Eastern Himalayan bamboo flocks. Conservation of bamboo stands in the Eastern Himalaya might thus be essential for the persistence of these obligate bamboo specialist flocks.

ACKNOWLEDGEMENTS

This study was carried out as a part of SS's Master's dissertation. We thank the National Centre for Biological Sciences-Tata Institute of Fundamental Research (NCBS-TIFR) and the Nature Conservation Foundation for institutional and administrative support. We are also thankful to the Arunachal Pradesh Forest Department for issuing permits to carry out this study (permit no. CWL/GEN/2018-19/Pt.IX/NG/3480-81). SS is grateful to The Habitats Trust for providing him with a grant to carry out this study. Rinchen Angmo and Yeswanth H.M. helped greatly with arthropod identification and Binod Borah provided useful discussions. We also thank Mangal Rai, Nima Tamang, S.K. Pradhan, Bharat Tamang and Binod Munda for their support and help during fieldwork.

AUTHOR CONTRIBUTIONS

SS and US conceived and designed the study. AB, DKS, SR, and SS collected the data. SS analysed the data and was supervised by US. SS wrote the original draft and US and SS contributed in refining subsequent drafts.

CONFLICT OF INTEREST

The authors declare no Conflict of Interest.

REFERENCES

Areta, J. I., Bodrati, A., & Cockle, K. (2009). Specialization on Guadua Bamboo Seeds by Three Bird Species in the Atlantic Forest of Argentina. Biotropica, 41(1), 66–73. https://doi.org/10.1111/j.1744-7429.2008.00458.x

Bangal, P., Sridhar, H., Shizuka, D., Vander Meiden, L. N., & Shanker, K. (2021). Flock-species richness influences node importance and modularity in mixed-species flock networks. Oecologia. https://doi.org/10.1007/s00442-021-05053-z

Borah, B., Quader, S., & Srinivasan, U. (2018). Responses of interspecific associations in mixed-species bird flocks to selective logging. Journal of Applied Ecology, 55(4), 1637–1646. https://doi.org/10.1111/1365-2664.13097

Bystriakova, N. (2003). Bamboo biodiversity: Information for planning conservation and management in the Asia-Pacific region. UNEP World Conservation Monitoring Centre.

Bystriakova, N., Kapos, V., & Lysenko, I. (2004). Bamboo biodiversity: Africa, Madagascar and the Americas (Issue 19). UNEP/Earthprint.

Champion, H. G., & Seth, S. K. (1968). A revised survey of the forest types of India. Manager of Publications, Government of India, New Delhi.

Clauset, A., Newman, M. E., & Moore, C. (2004). Finding community structure in very large networks. Physical Review E, 70(6), 066111.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. InterJournal, Complex Systems, 1695(5), 1–9.

Diamond, J. M. (1981). Mixed-species foraging groups. Nature, 292(5822), 408–409.

Dolby, A. S., & Grubb jr, T. C. (1998). Benefits to satellite members in mixed-species foraging groups: An experimental analysis. Animal Behaviour, 56(2), 501–509. https://doi.org/10.1006/anbe.1998.0808

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. The Journal of Animal Ecology, 84(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Franks, D. W., Ruxton, G. D., & James, R. (2010). Sampling animal association networks with the gambit of the group. Behavioral Ecology and Sociobiology, 64(3), 493–503. https://doi.org/10.1007/s00265-009-0865-8

Ghosh, M., Singh, P., & Mohan, D. (2011). Seasonal variation in foraging ecology of three species of overwintering Leaf Warblers (genus Phylloscopus) in the Himalayan foothills. Journal of Ornithology, 152(4), 869–877. https://doi.org/10.1007/s10336-011-0670-9

Goodale, E., & Beauchamp, G. (2010). The relationship between leadership and gregariousness in mixed-species bird flocks. Journal of Avian Biology. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1600-048X.2009.04828.x

Goodale, E., Beauchamp, G., & Ruxton, G. D. (2017). Mixed-Species Groups of Animals—1st Edition. https://www.elsevier.com/books/mixed-species-groups-of-animals/goodale/978-0-12-805355-3

Goodale, E., Ding, P., Liu, X., Martínez, A., Si, X., Walters, M., & Robinson, S. K. (2015). The structure of mixed-species bird flocks, and their response to anthropogenic disturbance, with special reference to East Asia. Avian Research, 6(1), 1–11.

Goodale, E., & Kotagama, S. W. (2005). Alarm Calling in Sri Lankan Mixed-Species Bird Flocks. The Auk, 122(1), 108–120. https://doi.org/10.1093/auk/122.1.108

Goodale, E., Sridhar, H., Sieving, K. E., Bangal, P., Colorado Z., G. J., Farine, D. R., Heymann, E. W., Jones, H. H., Krams, I., Martínez, A. E., Montaño-Centellas, F., Muñoz, J., Srinivasan, U., Theo, A., & Shanker, K. (2020). Mixed company: A framework for understanding the composition and organization of mixed-species animal groups. Biological Reviews, 95(4), 889–910. https://doi.org/10.1111/brv.12591

Gotelli, N. J., Hart, E. M., & Ellison, A. M. (2015). EcoSimR: Null model analysis for ecological data. R Package Version 0.1. 0.

Graves, G. R., & Gotelli, N. J. (1993). Assembly of avian mixed-species flocks in Amazonia. Proceedings of the National Academy of Sciences, 90(4), 1388–1391.

Greenberg, R. (2000). Birds of many feathers: The formation and structure of mixed-species flocks of forest birds. Á In: Boinski, S. and Garber, PA (eds), On the move: How and why animals travel in groups. Univ. of Chicago Press, pp. 521Á558.

Guimarães, D. P., & Guilherme, E. (2021). Structure and Home Range Size of Mixed-Species Bird Flocks in a Bamboo Forest in Southwestern Amazonia. Acta Ornithologica, 56(1), 95–108. https://doi.org/10.3161/00016454AO2021.56.1.009

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. Journal of Theoretical Biology, 7(1), 17–52.

Jayarathna, A., Kotagama, S., & Goodale, E. (2013). The seasonality of mixed-species bird flocks in a Sri Lankan rainforest in relation to the breeding of the nuclear species, Orange-billed Babbler Turdoides rufescens. Forktail, 29, 138–139.

Jiang, D., Sieving, K. E., Meaux, E., & Goodale, E. (2020). Seasonal changes in mixed-species bird flocks and antipredator information. Ecology and Evolution, 10(12), 5368–5382. https://doi.org/10.1002/ece3.6280

Jones, H. H., & Robinson, S. K. (2021). Vegetation structure drives mixed-species flock interaction strength and nuclear species roles. Behavioral Ecology. https://academic.oup.com/beheco/article/32/1/69/5943631

Jones, H. H., Walters, M. J., & Robinson, S. K. (2020). Do similar foragers flock together? Nonbreeding foraging behavior and its impact on mixed-species flocking associations in a subtropical region. The Auk, 137(2), ukz079. https://doi.org/10.1093/auk/ukz079

Jullien, M., & Clobert, J. (2000). The survival value of flocking in Neotropical birds: Reality or fiction? Ecology, 81(12), 3416–3430.

Kotagama, S. W., & Goodale, E. (2004). The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. Forktail, 20, 63–70.

Kratter, A. W. (1997). Bamboo Specialization by Amazonian Birds. Biotropica, 29(1), 100–110. https://doi.org/10.1111/j.1744-7429.1997.tb00011.x

Krebs, J. R. (1973). Social learning and the significance of mixed-species flocks of chickadees (Parus spp.). Canadian Journal of Zoology, 51(12), 1275–1288. https://doi.org/10.1139/z73-181

Lebbin, D. J. (2007). Habitat specialization among Amazonian birds: Why are there so many Guadua bamboo specialists? [Ph.D. Thesis]. Cornell University New York.

Lebbin, D. J. (2013). Nestedness and Patch Size of Bamboo-Specialist Bird Communities in Southeastern Peru. The Condor, 115(2), 230–236. https://doi.org/10.1525/cond.2013.110092

Leite, G. A., Pinheiro, R. T., Marcelino, D. G., Figueira, J. E. C., & Delabie, J. H. C. (2013). Foraging Behavior of Kaempfer's Woodpecker (Celeus obrieni), a Bamboo Specialist: Comportamiento de Forrajeo de Celeus obrieni, un Especialista de Bambú. The Condor, 115(2), 221–229.

Martínez, A. E., Parra, E., Muellerklein, O., & Vredenburg, V. T. (2018). Fear-based niche shifts in neotropical birds. Ecology, 99(6), 1338–1346. https://doi.org/10.1002/ecy.2217

McClure, H. E. (1967). The composition of mixed species flocks in lowland and sub-montane forests of Malaya. Wilson Bull, 79(2), 131–154.

Montaño-Centellas, F. A. (2020). Interaction networks of avian mixed-species flocks along elevation in the tropical Andes. Ecography. https://onlinelibrary.wiley.com/doi/full/10.1111/ecog.05135

Montaño-Centellas, F. A., & Jones, H. H. (2021). Temperature and vegetation complexity structure mixed-species flocks along a gradient of elevation in the tropical Andes. Ornithology, 138(3), ukab027. https://doi.org/10.1093/ornithology/ukab027

Morse, D. H. (1970). Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs, 40(1), 119–168.

Morse, D. H. (1977). Feeding behavior and predator avoidance in heterospecific groups. BioScience, 27(5), 332–339.

Munn, C. A. (1985). Permanent canopy and understory flocks in Amazonia: Species composition and population density. Ornithological Monographs, 683–712.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853–858. https://doi.org/10.1038/35002501

Newman, M. E. J. (2003). The Function and Structure of Complex Networks. Society for Industrial and Applied Mathematics (SIAM) Review, 35(2), 167–256.

Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., Webster, A. J., Ding, T.-S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Gaston, K. J., & Owens, I. P. F. (2005). Global hotspots of species richness are not congruent with endemism or threat. Nature, 436(7053), 1016–1019. https://doi.org/10.1038/nature03850

Paijmans, K. C., Booth, D. J., & Wong, M. Y. L. (2019). Towards an ultimate explanation for mixed-species shoaling. Fish and Fisheries, 20(5), 921–933. https://doi.org/10.1111/faf.12384

Parker, T. A., Stotz, D. F., & Fitzpatrick, J. W. (1997). Notes on Avian Bamboo Specialists in Southwestern Amazonian Brazil. Ornithological Monographs, 48, 543–547. https://doi.org/10.2307/40157551

Proulx, S. R., Promislow, D. E. L., & Phillips, P. C. (2005). Network thinking in ecology and evolution. Trends in Ecology & Evolution, 20(6), 345–353. https://doi.org/10.1016/j.tree.2005.04.004

R Core Team. (2022). R: A language and environment for statistical computing.

Reid, S., Diaz, I., Willson, M. F., & Armesto, J. J. (2004). Importance of Native Bamboo for Understory Birds in Chilean Temperate Forests. The Auk, 121(2), 515–525. https://doi.org/10.2307/4090415

Socolar, S. J., Robinson, S. K., & Terborgh, J. (2013). Bird Diversity and Occurrence of Bamboo Specialists in Two Bamboo Die-Offs in Southeastern Peru. The Condor, 115(2), 253–262. https://doi.org/10.1525/cond.2013.120061

Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Animal Behaviour. https://doi.org/10.1016/j.anbehav.2009.05.008

Sridhar, H., & Guttal, V. (2018). Friendship across species borders: Factors that facilitate and constrain heterospecific sociality. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1746), 20170014.

Sridhar, H., & Sankar, K. (2008). Effects of habitat degradation on mixed-species bird flocks in Indian rain forests. Journal of Tropical Ecology, 24(2), 135–147.

Sridhar, H., & Shanker, K. (2014). Using intra-flock association patterns to understand why birds participate in mixed-species foraging flocks in terrestrial habitats. Behavioral Ecology and Sociobiology, 68(2), 185–196. https://doi.org/10.1007/s00265-013-1633-3

Sridhar, H., Srinivasan, U., Askins, R. A., Canales-Delgadillo, J. C., Chen, C.-C., Ewert, D. N., Gale, G. A., Goodale, E., Gram, W. K., Hart, P. J., Hobson, K. A., Hutto, R. L., Kotagama, S. W., Knowlton, J. L., Lee, T. M., Munn, C. A., Nimnuan, S., Nizam, B. Z., Péron, G., … Shanker, K. (2012). Positive Relationships between Association Strength and Phenotypic Similarity Characterize the Assembly of Mixed-Species Bird Flocks Worldwide. The American Naturalist, 180(6), 777–790. https://doi.org/10.1086/668012

Srinivasan, S., Pradhan, D. K., Rai, M., Biswakarma, A., & Srinivasan, U. (2023). Poles apart—The structure and composition of the bird community in bamboo in the Eastern Himalaya. bioRxiv, 2023.01.27.525938. https://doi.org/10.1101/2023.01.27.525938

Srinivasan, U. (2019). Morphological and Behavioral Correlates of Long-Term Bird Survival in Selectively Logged Forest. Frontiers in Ecology and Evolution, 7, 17. https://doi.org/10.3389/fevo.2019.00017

Srinivasan, U., & Quader, S. (2012). To Eat and Not Be Eaten: Modelling Resources and Safety in Multi-Species Animal Groups. PLOS ONE, 7(7), e42071. https://doi.org/10.1371/journal.pone.0042071

Srinivasan, U., Raza, R. H., & Quader, S. (2010). The nuclear question: Rethinking species importance in multi-species animal groups. Journal of Animal Ecology. https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2656.2010.01707.x

Srinivasan, U., Raza, R. H., & Quader, S. (2012). Patterns of species participation across multiple mixed-species flock types in a tropical forest in northeastern India. Journal of Natural History, 46(43–44), 2749–2762.

Stensland, E., Angerbjörn, A., & Berggren, P. (2003). Mixed species groups in mammals. Mammal Review, 33(3–4), 205–223. https://doi.org/10.1046/j.1365-2907.2003.00022.x

Thébault, E., & Fontaine, C. (2010). Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. Science, 329(5993), 853–856. https://doi.org/10.1126/science.1188321

Waite, T. A., & Grubb Jr, T. C. (1988). Copying of foraging locations in mixed-species flocks of temperate-deciduous woodland birds: An experimental study. The Condor, 90(1), 132–140.

Wasserman, S., & Faust, K. (1994). Social Network Analysis: Methods and Applications. Cambridge University Press.

Zhou, L., Peabotuwage, I., Gu, H., Jiang, D., Hu, G., Jiang, A., Mammides, C., Zhang, M., Quan, R.-C., & Goodale, E. (2019). The response of mixed-species bird flocks to anthropogenic disturbance and elevational variation in southwest China. The Condor, 121(3), duz028.