Species interactions within mixed-species bird flocks along an elevational gradient in the Western Himalaya

Thesis submitted for the award of the degree of

Master's in Wildlife Science

by

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to

Saurashtra University

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July, 2021

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DECLARATION

I, **Pranav Gokhale**, hereby declare that the research work entitled **"Species interactions within mixed-species bird flocks along an elevational gradient in the Western Himalaya"**, carried out in partial fulfilment of the M.Sc. (Wildlife Science) degree of the Saurashtra University, Rajkot is an original piece of dissertation research. This research work was carried out under the supervision of Dr. R. Suresh Kumar and Dr. Dhananjai Mohan of the Wildlife Institute of India, Dehradun and Dr. Umesh Srinivasan of the Indian Institute of Science, Bangalore from January 2021 to June 2021. I hereby declare that this work has not been submitted for any other degree of any University.

Mr. Pranav Gokhale

(XVII M.Sc. Course)

Date: July, 2021

Place: Dehra Dun

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CERTIFICATE

This is to certify that **Mr. Pranav Gokhale** has carried out an original piece of research in partial fulfilment of the Master's Degree in Wildlife Science of the Saurashtra University, Rajkot. The topic of his dissertation is **"Species interactions within mixed-species bird flocks along an elevational gradient in the Western Himalaya"**. The study was carried out under our supervision from January 2021 to June 2021. We hereby certify that this work has not been submitted for any degree of any University.

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TABLE OF CONTENTS

LIST OF FIGURES

SUMMARY

Mixed-species bird flocks (hereafter, “flocks”) are an interactive community of largely insectivorous birds, which move and forage together to gain enhanced access to resources and protection from predation. In this study, I aimed to investigate a question: do interspecific interactions within mixed-species flocks change along an elevational gradient? To test this, I carried out this study in the Garhwal region of the Western Himalaya in Dehradun District, Uttarakhand from January to April 2021 (spanned across two seasons). The study areas comprised of three field sites along an elevation gradient from western part of the Rajaji Tiger Reserve (300 m ASL) to Mussoorie (2200 m ASL).

I sampled flocks and relative abundances of birds on the two pre-existing trails in each of the three field sites. I walked each trail 10 to 13 times. I recorded species identity, group/cluster size of all birds seen inside as well as outside flocks on the trail and within 10 m on either side of the trail. I assessed arthropod prey availability in winter for the flocking species by using branch bagging technique on the same trails. In total, I clipped 150 branches for the three elevations.

I calculated species-specific flocking propensity for each elevation from the information on birds seen within and outside flocks. I used network density (potentially realised associations) and weighted degree (associated strength) to quantify the interspecific interactions (associations) within flocks. To control for the influence of species availability on flock network properties, I generated null flocks using an abundance-based null model.

I recorded 80 flocking species in 412 flocks, of which, 179 flocks were observed at the High elevation, 156 at the Mid elevation and 77 at the Low elevation. Majority of species in the Western Himalayan flocks were insectivorous gleaner. I found insect prey availability (resource) to decrease with increasing elevation in winter. As expected, flocking propensity, network density and weighted degree increased with elevation in both seasons indicating greater potentially realised associations and high strength of associations between species. Interestingly, the Low elevation flocks disintegrated completely at the onset of summer possibly due to the greater availability of resources, or an upward migration of species for breeding. I did not analyse the Low elevation flocks in summer due to small sample size (n=5). Flocking propensity and network density decreased from winter to summer at Mid and High elevation while, weighted degrees decreased only for the Mid elevation. This is likely that true summer may not have started at the High elevation during the course of my fieldwork.

To conclude, with increasing elevation in both seasons, species not just flocked more, but associated with many species and these associations became stronger, potentially due to the scarcity of resources. It is possible that species may not be able to access resources efficiently when foraging on their own at the High elevation, compelling them to participate in flocks to avail complementary benefits from many other species.

1. INTRODUCTION

What comes to one's mind when thinking about a group of social animals? A pack of wolves, a pod of whales, an ant colony, fish schools or flocks of starlings and pigeons are a few of the most fascinating social animal groups. These groups are composed of a single species, and have been extensively studied. However, some very common groups in nature contain more than one species. These mixed-species groups are found in various taxa, including birds, mammals and fishes (Morse, 1977). Of these mixed-species groups, mixed-species bird flocks (Figure 1) have been comparatively well studied throughout the world for more than 150 years, and insights from such studies are central to our understanding of various foundational ecological concepts (Bates, 1863; Cody & Diamond, 1976; Goodale et al., 2010; Graves & Gotelli, 1993; Morse, 1970, 1977; Sridhar et al., 2009).

Mixed-species groups of birds occur throughout the world in all terrestrial habitats. Such bird groups could either be feeding aggregations, or more cohesive mixed-species bird flocks. Feeding aggregations are incidental groups (Powell, 1985) that are generally formed due to the localised nature of certain resources such as fruit (Diamond & Terborgh, 1967; Leck, 1971), or the enhancement of resources through phenomena such as fires (Winterbottom, 1949) or ant swarms that enhance the availability of resources such as arthropods (Willis, 1967; Willis & Oniki, 1978). On the other hand, mixed-species flocks arise from cohesive and consistent associations between participant species (Powell, 1985). In such groups, therefore, participant species forage together whether or not they are situated at a source of resource (Morse, 1970).

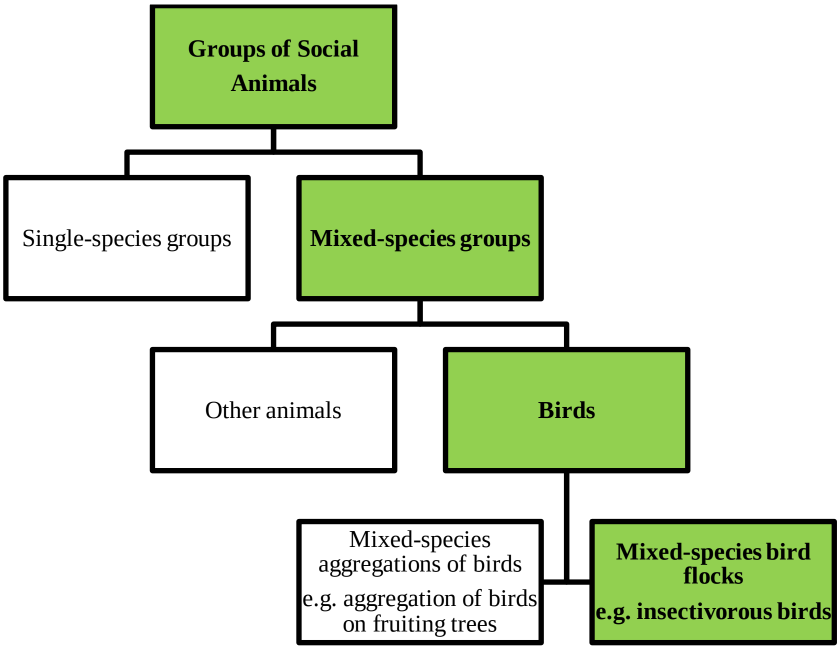

Figure 1. Hierarchy in the classification of the Groups of Social Animals. Depicting how Mixed-species bird flocks are different?

What are mixed-species bird flocks?

Mixed-species bird flocks (hereafter, “flocks”) are a common phenomenon throughout the world in terrestrial habitats. Flocks are an interactive community of largely insectivorous birds, which move and forage together to gain enhanced access to resources and protection from predation (Sridhar et al., 2009, 2012). While gaining resource and predation benefits, flock participants might simultaneously incur costs such as competition between species and kleptoparasitism (Morse, 1977);

however, given that niche overlaps between different flocking species are expected to be much lower than within groups formed by conspecifics, benefits are expected to outweigh competition costs (Powell, 1989). Indeed, species would be expected to participate in flocks only if the benefits of joining a flock are greater than the associated costs, as well as greater than the costs of participating in a conspecific group.

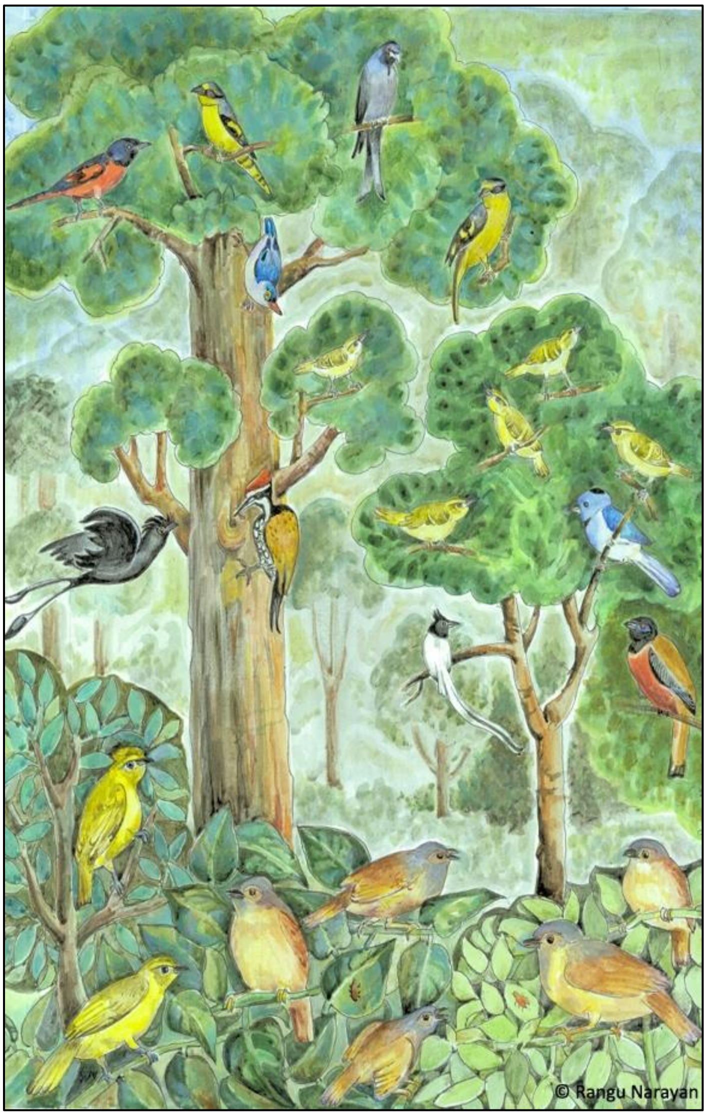

Figure 2. Depiction of different insectivorous birds associating to form a mixed-species flock in the Western Ghats. (Credit: Rangu Narayan)

Flocks are led by one or more nuclear species, which are important for the initiation and the maintenance of flock cohesion. Nuclear species are joined by attendant species (Goodale et al., 2020); however, species roles in flocks are context-specific, and vary in a more complex manner than just this simple dichotomy (Srinivasan et al., 2010). For instance, in the absence of a highly nuclear species, another less nuclear species may initiate, maintain and lead flocks. Nuclear species are often intraspecifically gregarious or feed by sallying (also called flycatching). Both these types of species give contact and alarm calls, and known to play important roles in flock formation and cohesion by attracting other participant species (Sridhar & Shanker, 2014).

Flock participants exploit the vigilance of other flock members, which in turn reduces their own time spent in vigilance, allowing them to increase foraging activity (Greenberg, 2000). Unlike in single-species foraging groups, species in mixed-species flocks can exchange complementary anti-predator and resource-access benefits with heterospecifics; these benefits arise from specialised behaviours that can differ markedly between member species (Diamond, 1981; Powell, 1985). Therefore, flocking species might be expected to show stronger associations with each other when resources are scarce and/or predation risk is high (Berner & Grubb, 1985; Develey & Peres, 2000; Jiang et al., 2020). The importance of positive interactions in structuring ecological communities in stressful conditions has long been recognised – this has often been termed the Stress Gradient Hypothesis, which posits that interactions between species switch from being competitive under conditions of high resource availability to being facilitative under conditions of resource stress (He et al., 2013; Stachowicz, 2001).

Why are flocks useful model systems for studying communities?

Flocks are subsets of the bird community in time and space and present an ideal system to investigate pattern and process in ecological communities. A majority of bird species participating in flocks are small- to medium-sized insectivorous, and are therefore relatively homogenous in terms of diet (Sridhar et al., 2009). Further, arthropod resources that form the diet of such species are often distributed more uniformly in the environment than resources such as fruit or nectar. Flocks are composed of species embedded in complex webs of multiple interactions, and investigating how these interactions lead to flock composition (or community structure) offers insights into species coexistence. Because of such complexity, understanding community organization cannot be drawn only from the identity of species and the composition of groups, but requires a representation of the network of interspecific interactions within them (Ings et al., 2009). Interspecific interactions link species and structure communities, which can then be represented as a network of ecological interactions, with species as “nodes” and the interactions between them as “edges” (Bascompte, 2007; Gravel et al., 2019).

So far, most studies on ecological networks have focused on trophic-interactions such as food webs and plant-animal mutualisms (Ings et al., 2009; Pascual & Dunne, 2006). However, little is known about non-trophic interactions such as those within mixed-species flocks (Valiente-Banuet et al., 2015), despite the fact that non-trophic interactions are recognised to play a crucial role in the dynamics, stability and structuring of a community (Kéfi et al., 2015).

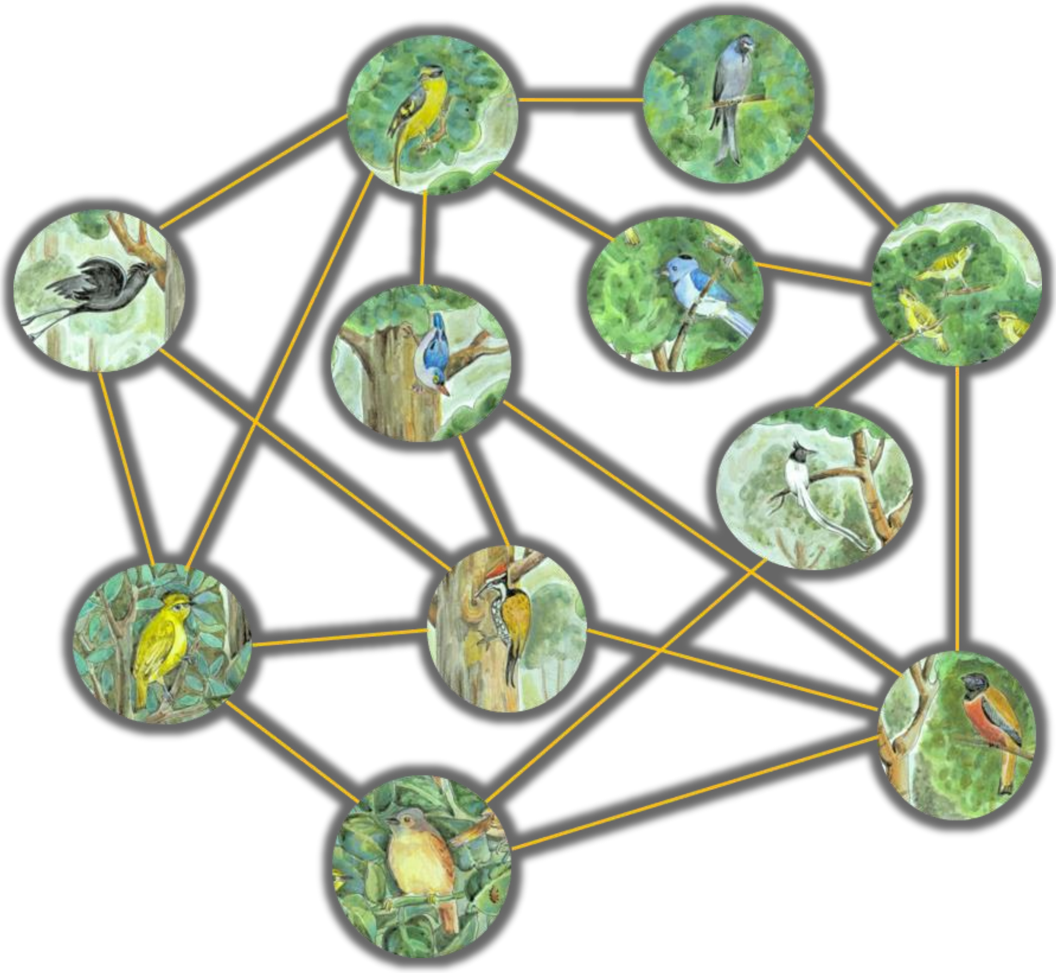

Figure 3. Network of ecological interactions of Mixed-species bird flocks, with species as "nodes" and the interactions between them as "edges". (Credit: Priti Bangal & Rangu Narayan)

One of the most fundamental questions in ecology investigates how species interactions within communities respond to the environment. Such responses can be investigated along different gradients, both natural and anthropogenic. Variation in interactions within an interspecific network along a gradient may be driven by (a) turnover in species composition, (b) variation in species abundances, and (c) changes in the strength of associations between species, all of which are influenced by the abiotic and biotic environment (Pellissier et al., 2018). While changes in species richness and community composition along different environmental gradients has been studied widely (e.g., with latitude or elevation), how interspecific interactions might change along either natural or anthropogenic gradients is relatively poorly known (Borah et al., 2018; Goodale et al., 2015, 2020; Montaño-Centellas, 2020; Zhou et al., 2019).

Elevational gradients and flocks

Elevation is one of the starkest natural gradients, and has important effects on the species richness and composition of ecological communities, especially in biodiversity-rich tropical mountains, where the bulk of terrestrial biodiversity is concentrated. Elevational gradients provide a test of the role of interspecific interactions in structuring flock "mini-communities" because: (a) abiotic characteristics such as temperature and seasonality change over short distances, leading to (b) changes in the biotic environment (e.g., vegetation, resource availability – i.e., arthropod diversity and abundance; Danks, 1992). Both these in turn, should influence (a) the community of flocking bird species, and (b) interactions between species with elevation. Therefore, flock networks might be expected to change strongly along elevational gradients because of changes in the potential for, and realisation of, the frequency and nature of interactions (Hoiss et al., 2015; Montaño-Centellas, 2020)

1.1. Literature review

“.....one may pass several days without seeing many birds; but now and then the surrounding bushes and trees appear suddenly to swarm with them. There are scores, probably hundreds of birds, all moving about with the greatest activity.....The bustling crowd loses no time, and although moving in concert, each bird is occupied, on its own account, in searching bark or leaf or twig..... In a few minutes the host is gone, and the forest path remains deserted and silent as before...” – Bates, 1863

One of the earliest descriptions of flocks date back to the mid-19th century from the forests of the Amazon (Bates, 1863). Since then, flocks have been of interest to many naturalists and ecologists.

What we know globally?

Flocks occur in many different ecosystems including pelagic, wetland, grassland and forests ecosystems (Harrison & Whitehouse, 2011), but are particularly common in forests of all kinds. Flocking is prevalent year-round in the Neotropics, where multi-species flock territories are jointly defended by all participant species (Martínez & Gomez, 2013); elsewhere, however, birds predominantly flock during the non-breeding winter (or dry) season when resources are scarce (Grubb T. C., 1987; Hogstad, 1987; Klein, 1988; Zhang et al., 2016). Most of the research on flocks has been focused on those in tropical and temperate forests (Sridhar et al., 2009), with an emphasis on understanding patterns in flock composition and the roles of participant species (Bates, 1863; Diamond, 1981; Goodale et al., 2010; Graves & Gotelli, 1993; Srinivasan et al., 2012). A large-scale metanalysis of global data showed that flocks are composed of "leader/ nuclear" and "follower" species, where followers tend to be smaller-bodied, and leaders tend to be cooperative breeders (Sridhar et al., 2009). Species that associate with each other in flocks also tend to be more similar in body size and feeding behaviour and more phylogenetically related than expected at random (Sridhar et al., 2012). Interestingly, many participant flock species, both in the Neotropics and in the Old World, share common colour patterns, in which birds appear to have converged on one or more common colours (Diamond, 1987; Moynihan, 1968). Flocks show immense variations in size, ranging from two to more than a hundred individuals of similar or different phenotypes (Diamond, 1987; Goodale et al., 2020; Sridhar et al., 2009). For instance, a recent study by Bangal et al. (2021) showed that smaller flocks (i.e., with fewer species) are more phenotypically clumped with respect to body size whereas larger flocks incorporate more random body size variation.

Over the past two decades, there has been a renewed interest in flocks, especially along different environmental and human-induced gradients (Borah et al., 2018; Colorado & Rodewald, 2015; Goodale et al., 2015; Kajiki et al., 2005; Mammides et al., 2015; Mokross et al., 2014; Montaño-Centellas, 2020; Zhou et al., 2019). Recent studies have found that species interaction networks change along different gradients (Borah et al., 2018; Goodale et al., 2015; Mammides et al., 2018; Mammides et al., 2015; Montaño-Centellas, 2020; Rutt & Stouffer, 2020; Zhou et al., 2019).

Behavioural interactions within, and the structure of, flock networks appear to be highly sensitive to environmental change (Mokross et al., 2014). Anthropogenic gradients such as habitat fragmentation and land-use intensity have been well studied in the Neotropics and South-east Asia -- generally, flock properties such as species richness, size, encounter rates and network complexity decreases as fragmentation or intensity of land-use increases (Goodale et al., 2015; Kajiki et al., 2018).

Flock responses to natural environmental gradients such as temperature (i.e., seasonality) and elevation, however, have been poorly studied. Flocking is a seasonal phenomenon (except in the Neotropics), most prevalent during cold temperatures in winter or during dry season. Flocks often have lower size (number of individuals) and richness (number of species), and their participant species lower propensity and association strength in the summer than in winter, potentially to minimise competition between similar species (Jones et al., 2021). In Amazonia, Rutt et al. (2021) studied flocks across seasons and found that flock species richness and home range sizes increased in the dry season, and flock attendance and network strength declined in the wet season, possibly because of the onset of the nesting season and potentially increased arthropod availability. To my knowledge, there are only two studies (from the tropical Andes and southwest China) examining the effect of elevation on interaction networks within flocks. The connectivity and cohesion of Andean flock networks increased with elevation (Montaño-Centellas, 2020), while southwest Chinese flocks did not show any significant change with elevation, potentially because land-use type was a confounding variable that affected propensity and encounter rate (Zhou et al., 2019).

Flock research in India

In concordance with global patterns, solitary sallying and intraspecifically gregarious species are of significantly higher importance in flock initiation and cohesion in India. Flocks in India are usually led by fulvettas, tits, minivets, and drongos (Sridhar et al., 2013; Srinivasan et al., 2010). Flocks in the Western Ghats and northeast India have been relatively well studied from the perspective of their composition and interspecific interactions (Borah et al., 2018; Goodale et al., 2014; Mammides et al., 2015; Sridhar & Sankar, 2008; Srinivasan, 2013). The responses of flock networks to habitat change has not been explored in India, apart from a single study from northeast India, which found that the proportion of realized associations and association strength changed with selective logging, and that understory and midstory flocks responded differently to logging (Borah et al., 2018), potentially because selective logging alters vegetation structure, which in turn can affect resource availability and predation pressure. Despite being home to the world's highest mountain range, flocks have not been studied along elevation gradients in India.

1.2. Conceptual framework for this study

This study aims to understand how species interaction networks of flocks change along an elevation gradient in the Western Himalaya. I expect that the key variable affecting flock networks along the elevational gradient would be resource availability and distribution (i.e., arthropod density and diversity). However, an additional source of variability in flock networks might arise from differences in the “availability” of species to participate in flocks with elevation, because of species turnover or changes in the abundances of species with elevation. Here, I therefore use null models to control for the influence of species availability on flock network properties (see Methods).

I predicted that, all else being equal (in terms of the “availability” of species to participate in flocks), resource availability, which is negatively correlated with temperature, would be the most crucial factor influencing the structure of flock networks. I investigated how flock network properties changed in space (across the elevational gradient) and time (winter and summer at different elevations). I hypothesised that: (a) in general, the decline in temperature with increasing elevation would result in a decrease in arthropod availability, causing bird species to flock more strongly and cohesively with each other as elevation increases, and (b) as temperatures rise with onset of spring, arthropod availability should increase at all elevations, but more so at lower than at higher elevations, because of the relatively delayed onset of summer at higher elevations. Therefore, I predicted that flock cohesiveness should reduce in summer, and more strongly at low elevations than at high elevations.

1.3. Research Question/ Objective/ Hypothesis/ Prediction

Research Question 1: **Are interaction networks of mixed-species bird flocks influenced by elevation in the Western Himalaya?**

Objective 1: ***To study the composition of mixed-species flocks along an elevational gradient.***

Hypothesis: Altitudinal migration would result in lower flock species richness with increasing elevation, because most bird species occupy lower elevations in winter.

Prediction: Flock species richness would be higher at lower elevations than at higher elevations

Objective 2: ***To study the flocking propensities and interspecific interactions between flocking species along an elevational gradient.***

Hypothesis: Decreasing temperature with increasing elevation should result in decline in arthropod availability at progressively higher elevations, compelling birds to increase participation in flocks to avail of foraging benefits.

Prediction 1: Flocking propensities of species will be higher at higher elevations than at lower elevations.

Prediction 2: Network density (i.e., the proportion of potential associations that are actually realised) would increase with increasing elevation.

Prediction 3: The strength of interspecific associations (i.e., weighted degree) will be higher at higher elevations than at lower elevations.

Research Question 2: Are interactions within mixed-species bird flocks influenced by seasonal changes along an elevation gradient in the Western Himalaya?

Objective: To study the flocking propensities and interspecific interactions between flocking species across seasons along an elevational gradient.

Hypothesis: As temperatures and therefore arthropod availability rises with the onset of spring/summer, foraging benefits associated with flocking should decline. The propensity of species to join flocks and the cohesion of flocks should reduce with change in season from winter to spring.

Prediction 1: Species' flocking propensities will be lower in summer than winter.

Prediction 2: The proportion of potential interspecific associations that are actually realised (i.e. network density) will decrease in summer.

Prediction 3: Association strengths (i.e. weighted degrees) of species will be higher in winter than in summer.

2. STUDY AREA

I carried out this study in the lower Garhwal region of the Western Himalaya in Dehradun District, Uttarakhand from early January to late April 2021. Biogeographically, the study area lies to the north of Gangetic Plains and South of Greater Himalaya. For sampling, I selected three field sites separated by ~800 m altitude located on south facing slopes of the Lesser and Outer Himalaya (Shivaliks) along an elevation gradient; from the western part of the Rajaji Tiger Reserve (300 m ASL) to Mussoorie (2200 m ASL) (Figure 4). At each of these study sites (Low = 300 – 500m, Mid = 1100 – 1300m and High = 1700 – 2200m), I selected two pre-existing trails in relatively undisturbed habitat (to minimise any human influence on flocks) for sampling. Each trail was 2.6 to 3.3 km in length, and traversed the same habitat and vegetation structure of the given elevation. The elevational gradient covers an aerial distance of 40 km between the lowest and highest elevations.

The Low elevation site lies in the Shivalik foothills in the western part of the Rajaji Tiger Reserve (300 – 500 m ASL). I sampled flocks on trails located in the Dhoulkhand and Chillawali range. This area characterized by undulating hills with very prominent ravines becoming broad pebble/boulder filled streams in the plains. Based on the physiognomy, the forest type of the landscape can be classified as Northern Mixed Deciduous Forest (Champion & Seth, 1968). The mixed forest comprised of *Shorea robusta, Mallotus philippensis, Bombax ceiba, Anogeissus latifolia, Acacia catechu, Albizaa procera, Terminalia tomentosa, Mitragyna parviflora, Bridelia retusa, Gmelina arborea, Litsea glutinosa, Trewia nudiflora,* *Cassia fistula, Sterculia villosa, Butea monosperma, Ziziphus xylopyra, Ziziphus mauritiana, Erythrina suberosa, Emblica officinalis* and *Tectona grandis*. The average temperature is 20-25 °C in winter but the rises rapidly to 40-45 °C in summer; annual rainfall ranges between 1200-1500 mm (en.climate-data.org).

Along the northern boundary of Dehradun Valley, the Mid elevation site is located at the base of Lesser Himalaya (1100 – 1300 m ASL). The trails were located at the Shikhar Falls, Rajpur and in Maldevta near Maldevata-Dhanoulti road. Terrain of the area is rugged and mountainous characterised by steep slopes running into the valleys. According to the Champion & Seth (1968), the forest type of the area is predominately Northern Dry Mixed Deciduous Forests and Dry Deciduous Scrub on the steep slopes. The forest and scrub comprised of *Falconeria insignis, Bahunia retusa, Mallotus philippensis, Lannea coromandelica, Erythrina suberosa, Ougeinia oojeinense, Nyctanthes arbor-tristis, Toona ciliate, Acacia catechu, Boehmeria rugulosa, Haldina cordifolia, Casseria tomentosa, Bridelia verrucosa, Cassia fistula, Murraya koenigii, Lantana camara, Colebrookea oppositifolia* and *Woodfordia fruticosa.* The average temperature in winter 10- 25 °C and rises to 23-34°C in summer; the average precipitation is ~1400mm (en.climate-data.org).

The High elevation site is located on the southern aspect of Mussoorie ridge (1700 - 2200 m ASL). I sampled flocks on two trails in Mussoorie Wildlife Sanctuary (Binog), Mussoorie and Woodstock School Campus, Landour. Steep forested slopes, hilly terrain and limestone outcrops are characteristic features of the area. The forest type is Himalayan Moist Temperate Forest and Himalayan Sub-tropical Pine Forests

(Champion & Seth, 1968). Banj Oak (*Quercus leucotrichophora*) occupies over 70% of the total forested area where the *Rhododendron arboretum* and *Lyonia ovalifolia* are its main associates (Champion & Seth, 1968). The common shrubs in the understory are *Berberis* spp., *Vibrunum* spp., *Coriaria nepalensis* and *Rosa moschata*. In damp areas, other species such as *Machilus* spp. *Phoebea lanceolata, Acer* spp. *Toona serrate, Populus ciliate* and *Alnus nepalensis* are present. *Pinus roxburghii, Pinus wallichiana* and *Cedrus deodara* also occur in small interspersed patches, but such habitats are generally devoid of understory. Temperature varies from 0-5°C in winter and rises to 20-30 °C in summer; the annual rainfall is 1800-3000 mm (Verma & Jha, 2010).

The Western Himalayan landscape provides a great opportunity to test the effect of elevation on flock interactions, and to examine and compare flock responses to harsh climatic conditions at the higher elevations with the lower Bhabar-Shivalik landscape.

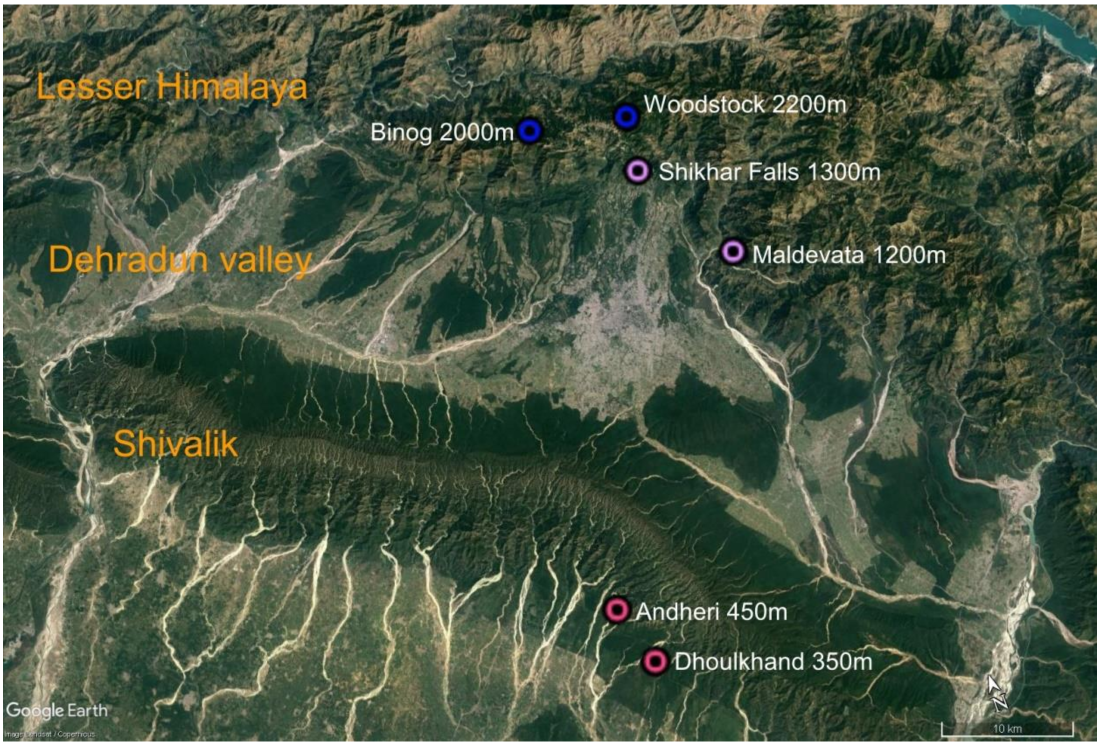

Figure 4. The map showing entire study area from Dhoulkhand in the western part of the Rajaji Tiger Reserve (300 m ASL) to Woodstock in Mussoorie (2200 m ASL). The three study sites (Low, Mid and High) marked in different colours from the bottom to top.

3. METHODS

3.1. Sampling methods

3.1.1. Bird sampling for relative abundances:

I sampled the relative abundances of birds on the six pre-existing trails, two in each of the three elevations (sites, see section on Study Area). I walked these trails slowly at the same pace during each survey in the morning from 0800 to 1100 hours, when flock activity was the highest. I recorded all birds seen inside as well as outside flocks on the trail and within 10 m on either side of the trail. The fundamental assumption of this method is that detection is always perfect within the 10m strip on either side of the trail (here, 20m; 10m on both sides of the trail). I used visual as well as aural detections to maximise detection probability and excluded all birds beyond 10m perpendicular distance from the trail. After detecting birds during each walk, I recorded species identity, group/cluster size and if detected within a flock, and marked the set of flocking species separately in the form of a flock with a unique identity. I recorded the date, time and weather conditions at the start and end of the trail; I walked each trail on at least 10 occasions during the entire field data collection period.

The birds on this gradient move dynamically, such that species migrate from high to low elevations in winter and move back at the onset of summer; Therefore, I pseudoreplicated trail walks multiple times to enable a more accurate estimate of species' relative abundances, especially across seasons. I used a pair of Nikon

Aculon (8*42) binocular to observe birds, and occasionally a Canon EOS 600D + Sigma 150-500 mm (DSLR) camera for identification.

3.1.2. Mixed-species flock sampling:

I sampled flocks on the same trails during sampling for the relative abundances of species between 0800 to 1100 hours. In order to minimise sampling biases, I avoided sampling early in the morning when flocks would be forming (Srinivasan et al., 2012). I walked trails when the weather was good enough to observe flocks and did not sample during cloudy and snowy days.

I considered flocks as a group of two or more species foraging and moving together in the same direction (Morse, 1970). After detecting a flock from the trail, I observed and followed it for five minutes to characterise species composition and the cluster sizes of each species. This approach allows the exclusion of species that could appear to be present in the flock just by a chance or aggregated around a localised resource such as fruit; such species do not typically move with a flock. Because individuals within flocks can leave and join at over short timeframes, I considered flocks sampled on the same trail but on different occasions as independent from each other (Graves & Gotelli, 1993). I also sampled flocks opportunistically after finishing a trail walk while walking back and later in the evening between 1500 to 1700 hours.

3.1.3. Arthropod sampling:

To quantify resource availability across the elevational gradient in winter season, I used the branch bagging method for arthropod sampling (Ghosh-Harihar, 2012). I used identically sized polythene bags for bagging at every 100m on the trail on alternate sides, 5m away from the trail. I placed a branch carefully inside a bag without disturbing arthropods, to minimise the risk of arthropods from escaping by flight. Before closing the mouth of the bag, I placed a cotton plug soaked in chloroform within the bag to dislodge arthropods. I then clipped the branch from the parent tree after closing the mouth of the bag. In total, I clipped 50 such branches (25 bags per trail) for each elevation, thereby totalling 150 bags for the three elevations. I brought back the bags to the laboratory for arthropods identification and counting. I used a simple dissection microscope to identify arthropods into different insect orders and spiders (Araneae; Lloyd et al., 1978).

Flocks are mainly composed of foliage-gleaning and sallying birds; both depend on arthropods hiding in the foliage. Salliers mainly feed on insects flushed by gleaners from the foliage. Therefore, bagging of branches is an effective method to sample the arthropods of our interest.

3.2. Analytical methods

3.2.1. Flock types:

I used a hierarchical agglomerative clustering with Jaccard’s Similarity Index (UPGMA) to find flock clusters based on their species composition separately for each elevation (Maechler et al., 2021; R Core Team, 2021). Based on the results from the cluster analysis, I separated flocks into different types.

3.2.2. The use of flocking propensities of the species to distinguish winter and summer:

Because flock sampling spanned four months and included the seasonal change from winter to summer, flocks were likely to change in response to changing abiotic and biotic conditions (Jones et al., 2021; Rutt & Stouffer, 2021). Therefore, I split flock data between seasons and analysed flocks from each season separately.

I calculated species-specific flocking propensity from the information on birds seen within and outside flocks. I defined flocking propensity as the proportion of a species’ incidence within flocks relative to total incidence (both within and outside flocks). Because many species joined flocks in conspecific groups (clusters), I used the relative abundance of groups to calculate propensities. I used the average propensity of all species at each elevation across sampling period to detect seasonal change. After separating flock data into two time periods, I followed the same analytical framework to analyse flocks separately in each season (see below).

3.2.3. Flocking propensities of species:

Flocking propensity is an innate behaviour of a species that determines its strength of association with other species; however, propensity is dependent on resource availability and predation pressure. Resource (arthropod) availability is sensitive to temperature because of the small body and ectothermy of arthropods (Danks, 1992), and is therefore, expected to change along an elevation gradient. I studied the effect of elevation on flocking by calculating propensity values separately for the same species at each elevation at which it occurred. Finally, I used a Two-Sample Weighted *T*-Test "Welch; Paired" (Pasek, 2021; R Core Team, 2021) to quantify the effect of elevation on species-specific flocking propensities, where I weighed propensity values by relative abundances of species. I used this approach to correct for the variability in the relative abundance of a species in adjacent elevations (higher relative abundances are associated with more precise propensities).

3.2.4. Network construction, null model and randomisation:

I constructed weighted networks where the edges (associations between species) were weighted by the frequency of each interspecific association, representing the strength of association between two species (Csardi & Nepusz, 2006; R Core Team, 2021). Weighted networks are best suited to characterise flocks because species do not interact randomly and evenly with other species; instead patterns in association are likely to reflect the costs and benefits involved in co-occurring.

I created an observed flock-by-species matrix containing presence-absence information for each elevation separately and I used the package *igraph* in R to calculate the observed value of various network metrics (Csardi & Nepusz, 2006; R Core Team, 2021). If only species observed co-occurrence data is used to draw inferences on interactions (associations), results could be misleading because elevation can not only affect resource availability, but also community composition or abundances of species (Hart et al., 2011; Supriya et al., 2019), and therefore the “availability” of different species to join flocks (Srinivasan et al., 2012). For instance variation in resources can change associations, but so can the relative abundances of species. Elevation can therefore potentially affect species associations via two main mechanisms: (a) from changes in resource availability, which determines species’ flocking propensities and interspecific associations, and (b) from changes in the availability of flocking species (i.e., abundances of flocking species). It is important to control for the “availability” of species to join the flocks with the help of an abundance-based null model to study the effect of resource availability across elevations. This potentially provides with a clearer understanding of whether species participate in mixed flocks simply in proportion to their abundances, or whether changes in species networks are largely driven by other factors (i.e. changes in the availability of resources along the elevational gradient).

For each elevation in each season separately, I used an abundance-based null model to generate null flock-by-species matrices, where a species was represented in flocks in proportion to its relative abundance at that elevation (Srinivasan et al., 2010). The species richnesses for the null flocks were set as the same as those actually observed flocks. Because species joined flocks in conspecific groups (clusters), I used the relative abundance of species groups (or clusters) to simulate null flocks. As many null flocks were simulated as the observed number flocks for each elevation. Simulated null flocks were assumed to be truly abundance-based, such that species' occurrence in flocks was in direct proportion to their availability or abundance (i.e., more abundant species would have a greater representation in null flocks than rare species).

Network density (flock-level):

Network density is the realised proportion of all potential associations in a network (Wasserman & Faust, 1994). A "potential association" is an association that could occur between two species regardless of whether or not it actually does. For instance, two species can co-exist in an area but they may or may not associate within flocks. The maximum possible associations in an undirected network is determined by the species richness of the network -- thus $s(s-1)/2$ is the maximum number of possible associations that can be present in a network, where s = species richness. Density (D) is the ratio of number of associations that are actually present i.e. realised (L), to the maximum possible number of associations. Therefore, network density (D) = $L/s(s-1)/2$.

Weighted Degree (species-level):

For any species (or node) in a network, its degree is the number of associations with other species, whereas the weighted degree is sum of the frequency of interspecific associations (i.e., association strength). I normalised weighted degrees by dividing the calculated values by the number of all possible interspecific associations (n-1, where n = species richness), because degree is sensitive to species richness.

For every elevation and season separately, I calculated both these metrics for observed flocks and for simulated flocks. I iterated the process of simulation 10,000 times and calculated network density and weighted degree for each such iteration. This procedure produced a distribution of 10,000 null network density values and a species-specific distribution of 10,000 null weighted degree values. I obtained the non-parametric 95% confidence interval (0.025 and 0.975 quantiles) of the null distributions (simulated values) and compared this distribution with an observed network metric value (Figure 5).

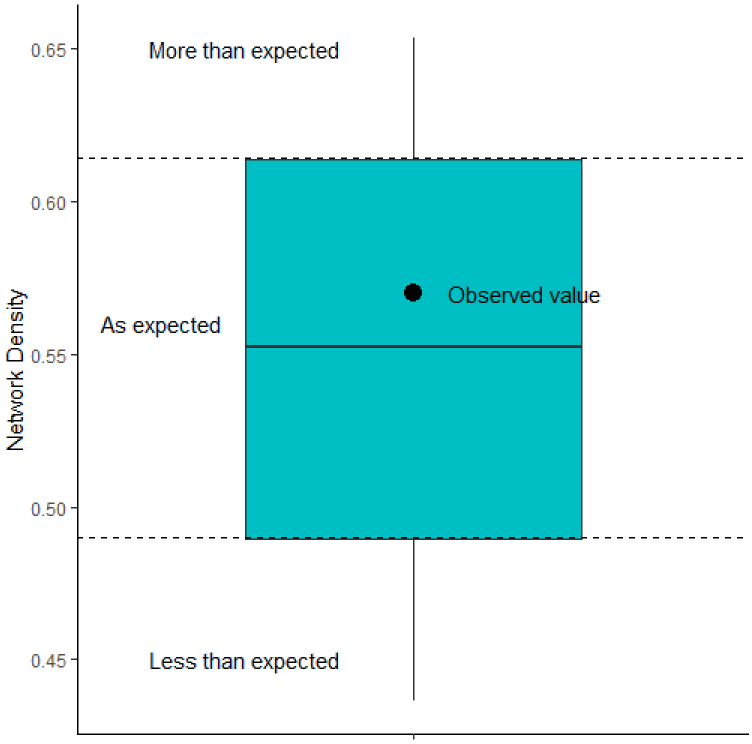

Figure 5. The boxplot represents mean and lower and upper non-parametric 95% confidence interval of the simulated network density; the whiskers extend to the minimum and maximum. The black point shows an observed value of the network density calculated from the observed flocks.

I calculated a z-score for each metric by subtracting the mean of simulated values from the observed value and dividing this by the standard deviation of the distribution of simulated metric. The z-score represents how far the observed value is from the null expectation.

$$Z\text{-score} = \frac{\text{Observed value - Mean of simulated values}}{\text{SD of simulated values}}$$

I compared network density by using calculated z-scores, and visually with the help of a boxplot representing 95 % C.I. of simulated network densities (simulated values) and the whiskers extending to the minimum and maximum and a point showing the observed network density (Figure 5). I compared weighted degrees with the help of species-specific z-scores in a pair-wise fashion between the shared species at adjacent elevations. To understand the effect of seasonality, I compared network density and weighted degrees across two seasons in the same abovementioned framework. I used a paired T-test to check for a potential effect of elevation well as season on the weighted degree.

3.2.5. Arthropod availability:

I classified arthropod data were into different insect orders and Araneae (spiders). I plotted the numbers of arthropods (Insects + Araneae) and insects per bag separately against elevation in the form of a boxplot to visually examine the effect of elevation on arthropod availability. I also calculated order-level Shannon Diversity Index (H’) for each elevation separately.

4. RESULTS

I walked each trail 10 to 13 times during the entire sampling period. The total effort of 71 trail walks equalled approximately 210 km. In total, I observed 408 flocks, of which, 179 flocks were observed at the High elevation, 152 at the Mid elevation and 77 at the Low elevation.

4.1. Delineation of flock data into two seasons based on the flocking propensities of species

Average flocking propensities of all species showed a decline in the period from 1st to 20th March (Figure 6). This decline occurred later at higher elevations. I used 15th March as the boundary to separate the flock data into two seasons for each elevation. Therefore, I categorised period from 1st January to 15th March as winter and the period from 16th March to 30th April as summer.

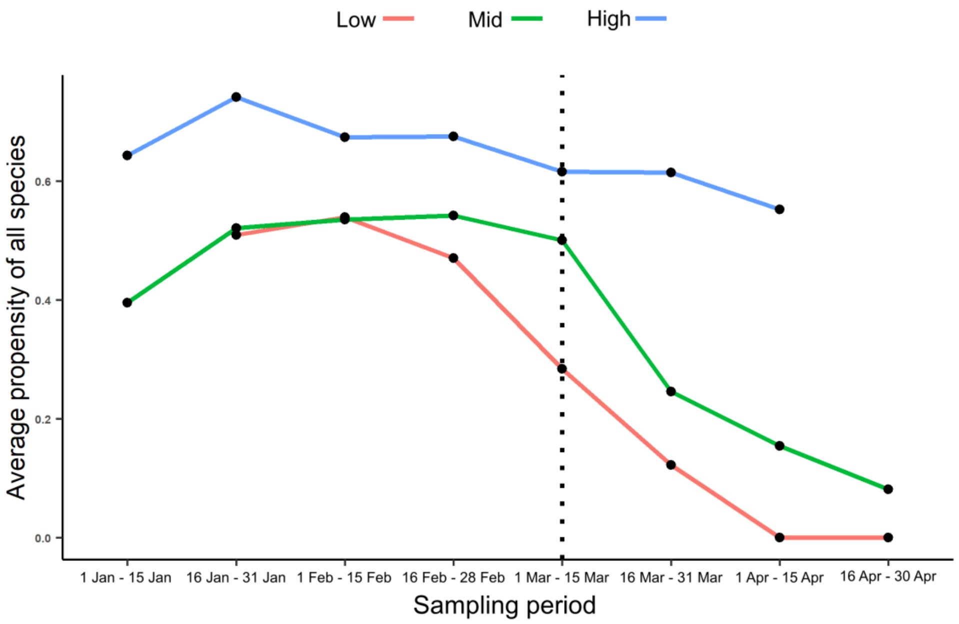

Figure 6. The average propensity of all species at each elevation is plotted against the sampling period. The dotted black line is used to demarcate the seasonal boundary.

4.2. Flock composition

4.2.1. Flock types:

A hierarchical agglomerative clustering by Jaccard's Similarity Index with UPGMA (average) linkage resulted in the following flock types at different elevations in two seasons; unlike at the High elevation, I did not observe two distinct flock types at the Low and Mid elevations.

I) High elevation:

I detected 121 flocks in winter in which 36 species participated at least once, while 33 species participated at least once in 58 summer flocks. It was evident during sampling that two different flock types that differ in species composition were present in both seasons (Figure 7).

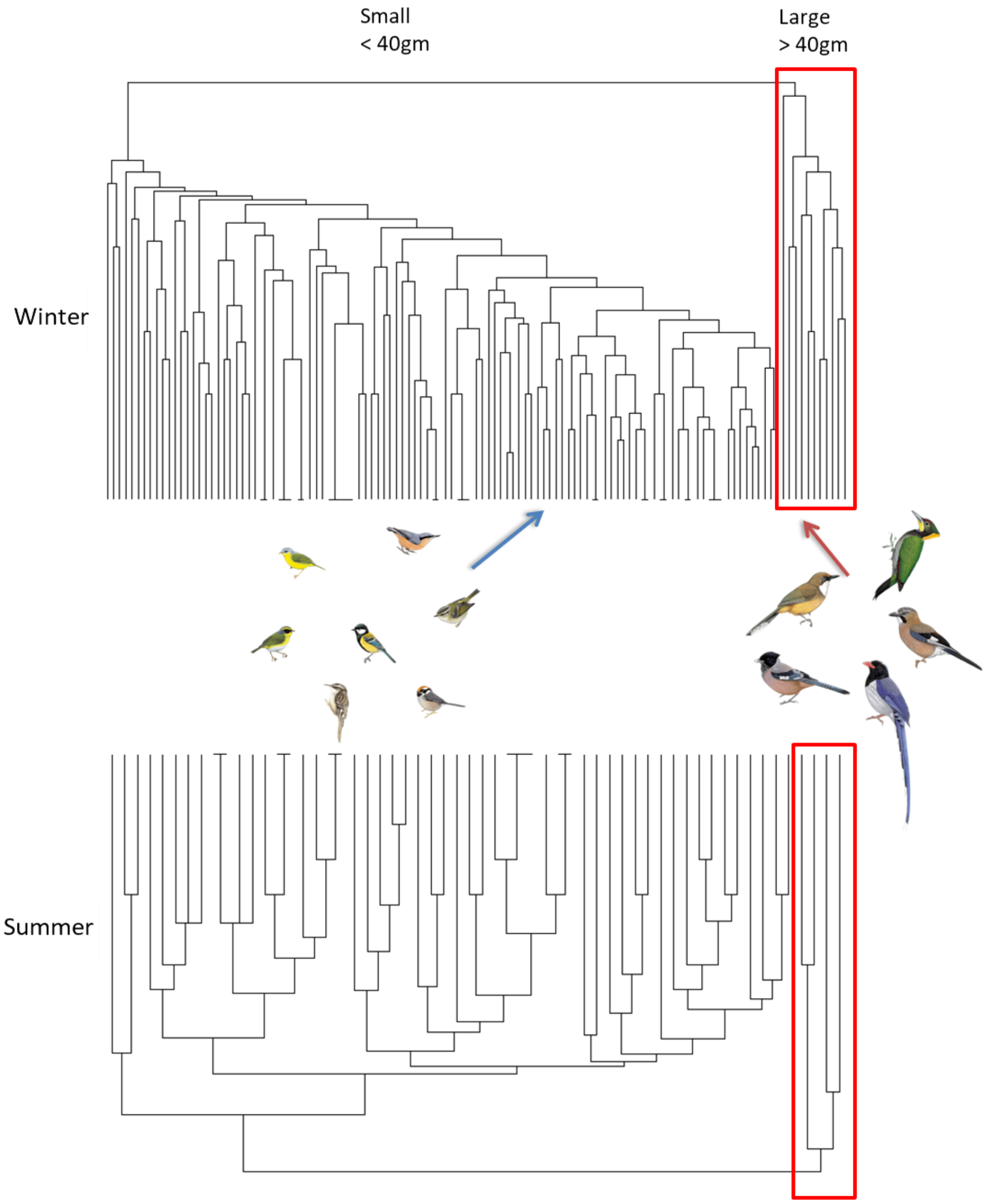

Figure 7. Dendrograms showing two distinct flock types at high elevation that differed in species composition in both seasons. Each branch of a dendrogram is a flock. A set of flocks marked in red are composed of species with significantly larger body weights (>40gm)

(a) Small-bodied bird flocks (winter = 110 flocks, summer = 54 flocks):

In winter, the average number of species per flock (flock richness) was 5 ± 2.20 SD (ranging from 2 to 13 species), and in summer, reduced to 4.09 ± 1.79 SD (ranging from 2 to 8 species). The most common species in winter flocks were Green-backed Tit, Black-throated Tit, Gray-hooded Warbler, Lemon-rumped Warbler, Ashy-throated Warbler, Bar-tailed Treecreeper, Bar-throated Siva, Black-faced Warbler and Brown-fronted Woodpecker; and the summer flocks were composed of species such as Green-backed Tit, Black-lored Tit, Black-throated Tit, Gray-headed Canary-flycatcher, Gray-hooded Warbler, Lemon-rumped Warbler and Western-crowned Warbler.

(b) Large-bodied bird flocks (winter = 11 flocks, summer = 4 flocks):

Flock richness was 4.83 ± 2.09 SD in winter (ranging from 2 to 6 species) and reduced in summer to 3.84 ± 1.66 SD (ranging from 2 to 6 species). These flocks were composed of species such as Greater Yellownape, Gray-headed Woodpecker, Red-billed Blue Magpie, Black-headed Jay, Eurasian Jay, White-throated Laughingthrush, Blue Whistling Thrush and Rusty-cheeked Scimitar Babbler; summer flocks were composed of Black-headed Jay, Eurasian Jay and Maroon Oriole, which were seen associating with a few small-bodied birds such as the Black-winged Cuckooshrike, Long-tailed Minivet and Ashy Drongo. Due to the low sample size, these flocks were not considered for further analyses.

II) Mid elevation:

I detected 110 flocks in winter in which 47 species participated at least once, while 23 species participated at least once in 42 summer flocks.

Small-bodied bird flocks (winter= 110 flocks, summer= 42 flocks):

Flock richness was 5.52 ± 3.24 SD (ranging from 2 to 17 species) in winter and reduced in summer to 3.26 ± 1.86 SD (ranging from 2 to 10 species). The participant species did not change appreciably across seasons. The most common participant species in these flocks are Himalayan Black-lored tit, Black-throated Tit, Oriental White-eye, Gray-headed Canary-flycatcher, White-throated Fantail, Velvet-fronted Nuthatch, Chestnut-bellied Nuthatch, Gray-hooded Warbler, Lemon-rumped Warbler, Speckled Piculet, Green-tailed Sunbird and Black-chinned Babbler. A few large-bodied birds such as the Lesser Yellownape, Gray-headed Woodpecker, Rufous-bellied Woodpecker, Rusty-cheeked Scimitar Babbler and Maroon Oriole also flocked a few times with small-bodied bird species.

III) Low elevation:

I detected 72 flocks in winter in which 35 species participated at least once, while 10 species participated at least once in 5 summer flocks.

Small-bodied bird flocks (winter = 72 flocks, summer = 5 flocks):

In winter, flock richness was 6.72 ± 3.49 SD (ranging from 2 to 15 species) but reduced in summer to 2.8 ± 0.83 SD (ranging from 2 to 4 species). Winter flocks were largely composed of species such as Cinereous Tit, Gray-headed Canary-flycatcher, White-throated Fantail, White-bellied Drongo, Oriental White-eye, Common Iora, Common Woodshrike, Velvet-fronted Nuthatch, Chestnut-bellied Nuthatch, Small Minivet, Long-tailed Minivet, Gray-breasted Prinia and Gray-capped Pygmy Woodpecker. In summer, species such as Oriental-white eye, Velvet-fronted Nuthatch and Gray-breasted Prinia participated in flocks. Due to a low sample size, summer flocks were not analysed further.

4.2.2. Flock structure:

I recorded 80 species representing 28 families from 2 orders as participating in flocks across the entire elevational gradient (Appendix 1). Of these, 85% were Passeriformes and 15% were Piciformes. The most abundant families were Picidae (14%) followed by Phylloscopidae (11%), Muscicapidae (8%), Campephagidae (6%) and Paridae (6%) (Figure 8).

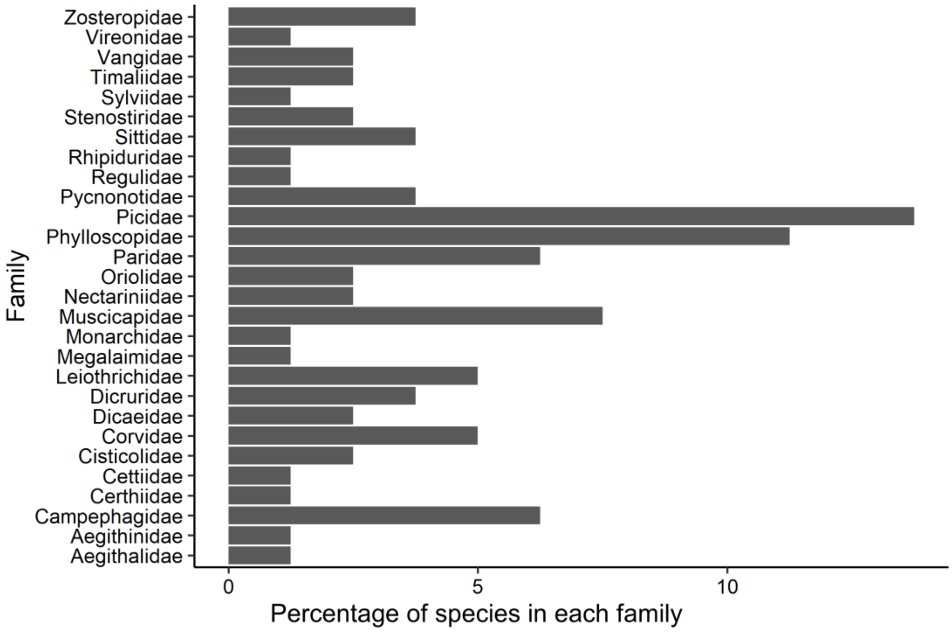

Figure 8. Percentage of species across different families in the mixed-species bird flocks in the Western Himalaya.

The majority of species in Western Himalayan flocks were insectivorous (72%) followed by omnivorous (21%), frugivorous (4%) and nectarivorous (3%) (Figure 9). Species varied in foraging styles. Overall, 61% were foliage gleaners, 18% bark gleaners, 11% salliers, 9% sally-gleaners and 1% hoverers (Figure 9). Of all species, 80% were small-bodied (body mass < 40g) and 20% were large-bodied (body mass > 40g). I collected information on species-specific traits from Billerman et al. (2020).

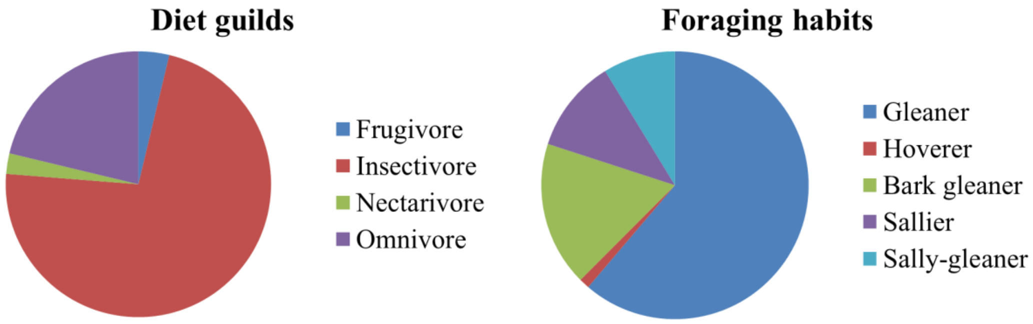

Figure 9. Diet Guilds and Foraging Habits of species in the Mixed-species bird flocks.

4.3. Species richness

In winter, the highest flocking species richness (total species recorded in flocks) was recorded at the Mid elevation followed by the High and Low elevations (Figure 10). In summer, however, the highest flocking species richness was recorded at the High elevation followed by the Mid and Low elevation.

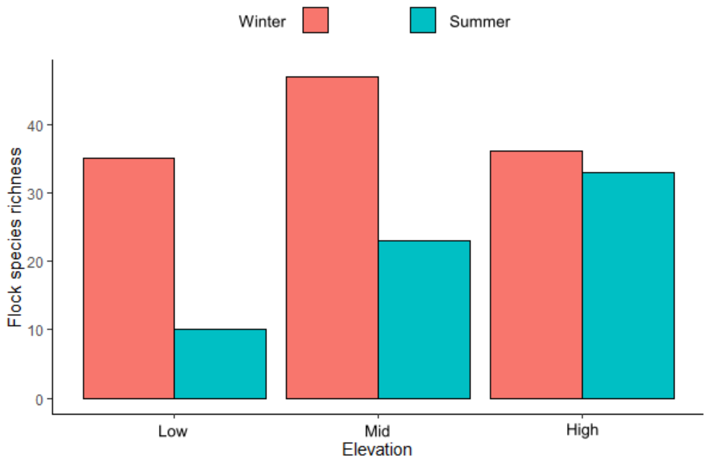

Figure 10. Flock species richness along an elevation gradient in the Western Himalaya.

The flock richness (average number of species per flock) decreased with elevation in winter; this pattern was reversed in summer (Figure 11). However, the pattern is statistically not significant due to the overlapping error bars (SD).

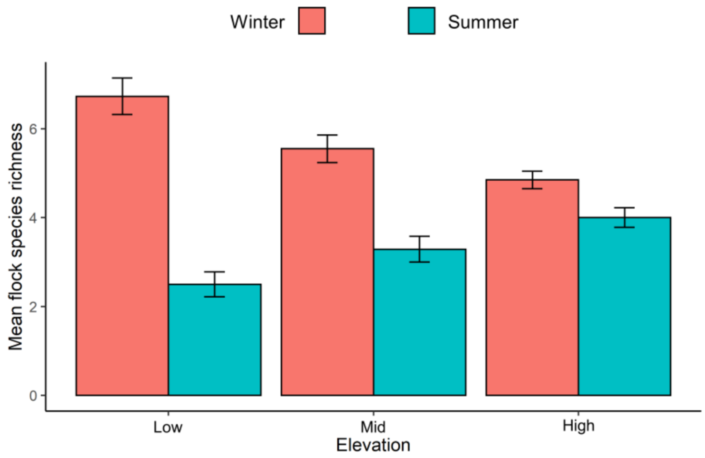

Figure 11. Mean flock species richness along an elevation gradient in the Western Himalaya. Here, the error bars (SEM) showing variability around the mean.

4.4. Relationships between arthropod availability and mixed-species flocking

Arthropod data from 150 bags (50 per elevation) yielded 1,012 arthropods belonging to 13 insect orders and Araneae in winter. The arthropods were classified into following categories (arranged according to their relative abundances): Araneae, Coleoptera, Hemiptera, Hymenoptera (71% ants), Psocoptera, Lepidoptera, Diptera, Orthoptera, Phasmatodea, Thysanoptera, Mantodea, Dermaptera, Mecoptera and Trichoptera.

The mean number of insects per bag for low elevation was 5.68 ± 4.78 SD, mid elevation 3.88 ± 3.73S SD and high elevation 3.12 ± 4.33 SD (Figure 12). On the contrary, when insects and Araneae were analysed jointly, the mean number of arthropods at High elevation was the highest 7.3 ± 5.51 SD followed by Low elevation 7.12 ± 5.09 SD and Mid elevation 5.82 ± 4.90 SD; the boxplots did not indicate any significant difference in arthropod availability (Figure 12).

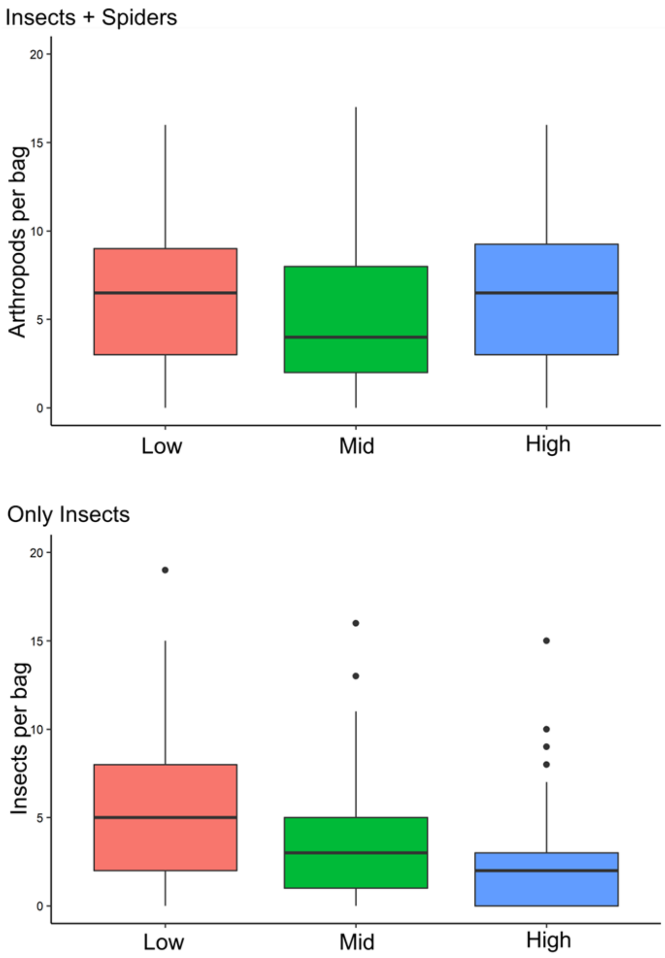

Figure 12. Number of insects per bag decreasing with increasing elevation; however, number of arthropods (Insects + Araneae) per bag does not indicate any differences visually; although, the means are different.

Therefore, in winter, while insect abundance decreases along the elevational gradient, total arthropods (insects + Araneae) behave differently. The arthropod availability seemed to be similar along elevational gradient due to the high relative abundance of Araneae (57%) at High elevation. The order-level Shannon Diversity Index (H') for the arthropods was 1.89, 1.85 and 1.38 for the Low, Mid and High elevation, respectively. Arthropod availability was not assessed for the summer season.

4.4.1. Flocking propensities of species:

For species common to two adjacent elevations, pairwise weighted analysis of propensities between adjacent elevations showed that species-specific flocking propensities significantly increased from Mid to High elevations in winter (t= 5.12; df= 17; $p < 0.05$) but did not significantly change between Low and Mid elevation (t=0.20; df=18; p= 0.8) (Figure 13a).

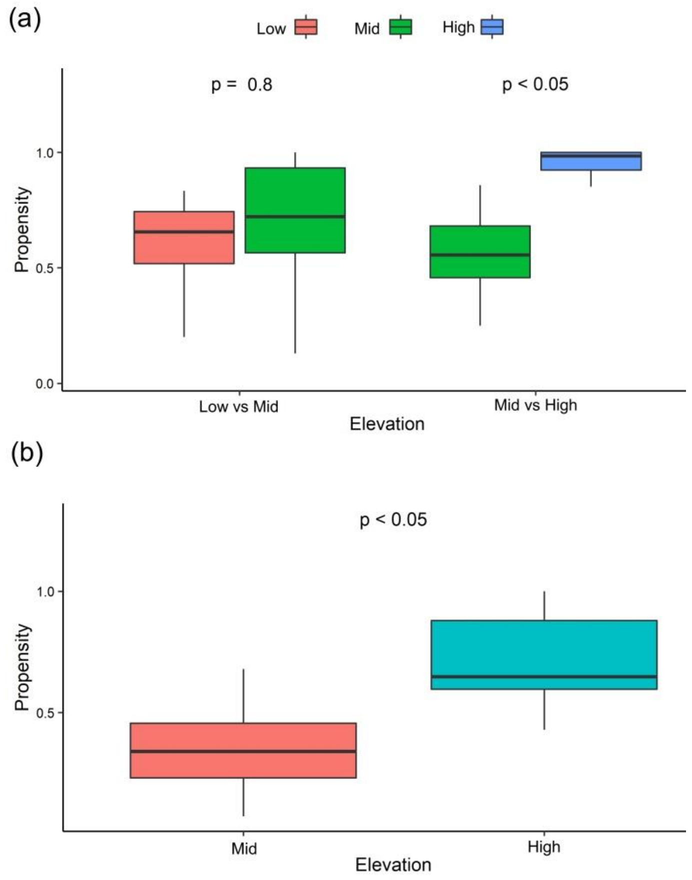

Figure 13: (a) Winter (b) Summer: The propensities of the common species between two adjacent elevations have been calculated and compared with the help of a Weighted Paired-T Test.

In summer, the pairwise weighted analysis of propensities shows that the propensities increased from the Mid to High elevation (t=3.56; df=9; $p < 0.05$) (Figure 13b). Also, when compared across seasons, propensities decreased from winter to summer for the Mid and High elevation (Mid t=4.84; df=17; $p < 0.05$, High t=5.28; df= 17; $p < 0.05$) (Figure 14).

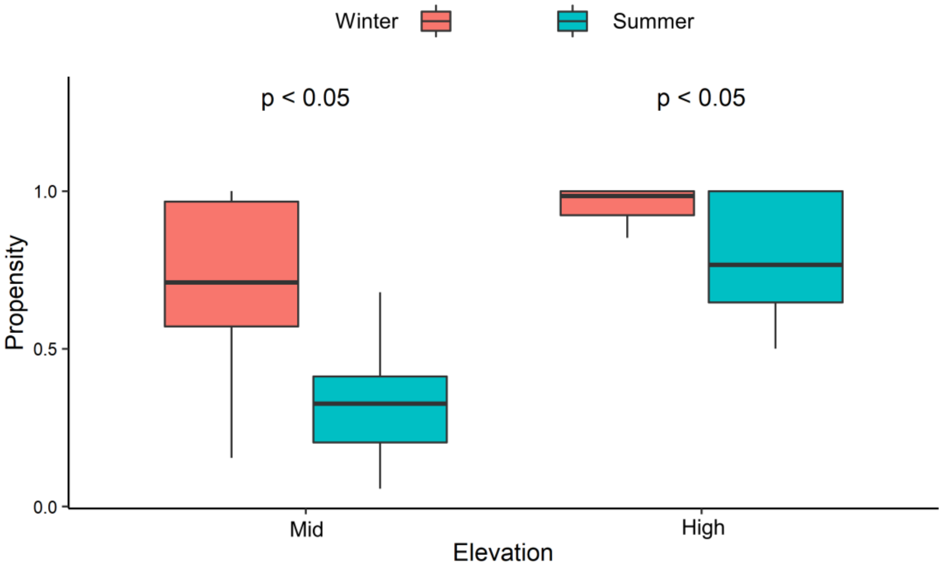

Figure 14: The propensities of the common species for an elevation in the two seasons have been calculated and compared with the help of a Weighted Paired-T Test.

Due to low sample size (n=5) in summer at the Low elevation, I did not compare propensities between Low and Mid elevation in summer and across seasons for the low elevation.

4.4.2. Network Density (potential realised interspecific associations):

In winter, observed network densities calculated were 0.61, 0.44 and 0.57 for the Low, Mid and High elevation, respectively (Figure 15a & 16). The observed network density was less than expected for Low and Mid elevations but as expected for the High elevation if species co-occurred in flocks solely based on their relative abundances. Network density *z*-scores increased from -7.6 (Low) to -3.8 (Mid) to 0.5 (High) elevations, suggesting that the network densities reaching closer to the null expectation with increasing elevation (Figure 15b). Therefore, species at the high elevation are associating more than those in Mid and Low elevation flocks.

In summer, observed network densities were 0.4 and 0.48 for the Mid and High elevation, respectively (Figure 15a & 16). The observed network density was less than expected for the Mid elevation but as expected for the High elevation if species co-occurred solely based on their relative abundances. The *z*-scores increased from -5.1 for the Mid to -0.7 for the High elevation (Figure 15b). Also, across seasons, the proportion of realised associations decreased for the High elevation (*z*-scores, 0.5 to -0.7) and Mid elevation (*z*-scores, -3.8 to -5.1) (Figure 15b & 16). I did not analyse network density for the Low elevation because of the disintegration of flocks in late March, therefore and small sample size (n = 5).

Overall, the potentially realised interspecific associations increased (closer to null expectations) with increasing elevation in both winter and summer but decreased from winter to summer at any given elevation.

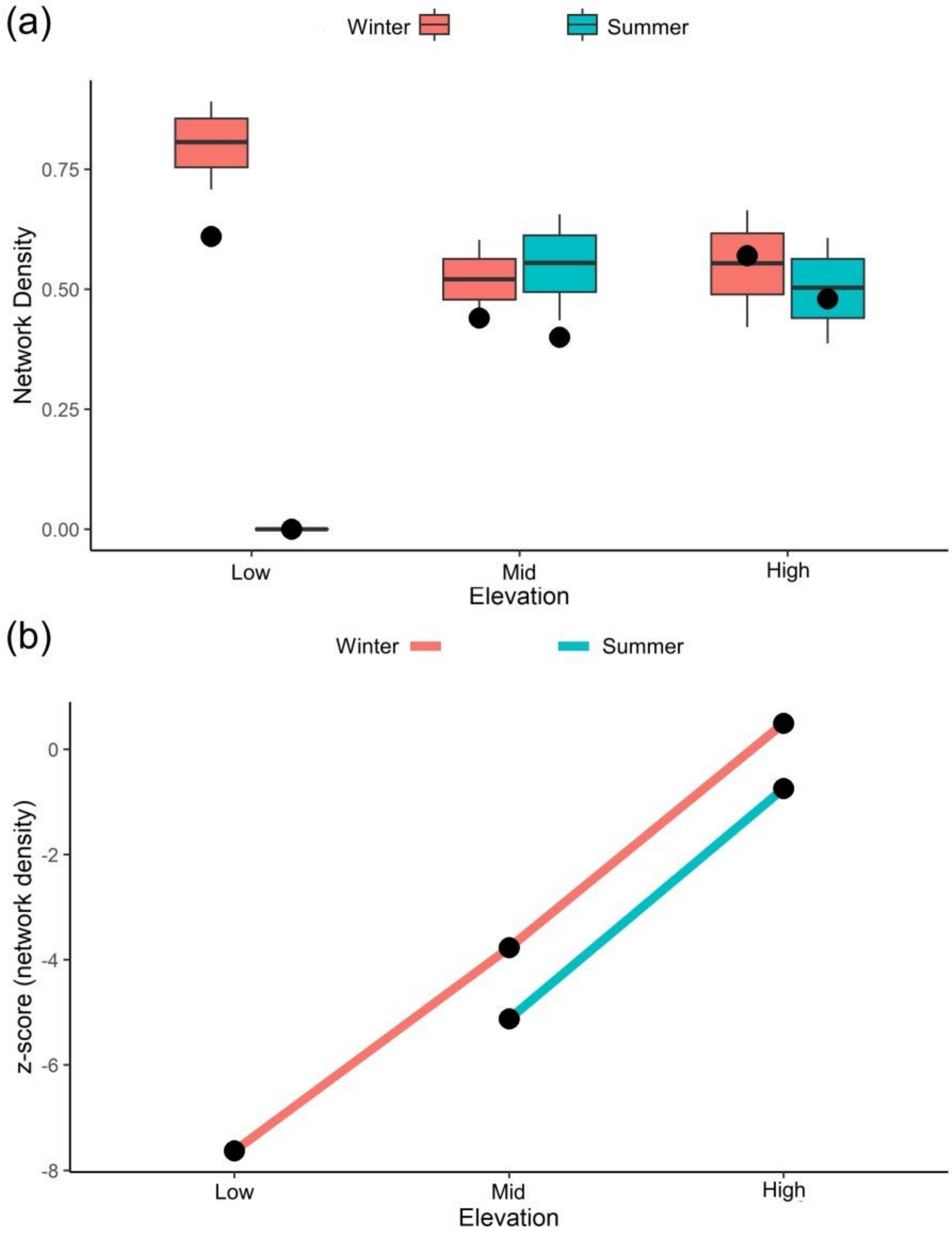

Figure 15. (a) The boxplot represents mean and lower and upper non-parametric 95% confidence interval of the simulated network density; the whiskers extend to the minimum and maximum. The black point shows an observed value of the network density calculated from the observed flocks. (b) The z-scores have been calculated by subtracting the mean of simulated densities from the observed density and divided by the SD of simulated densities.

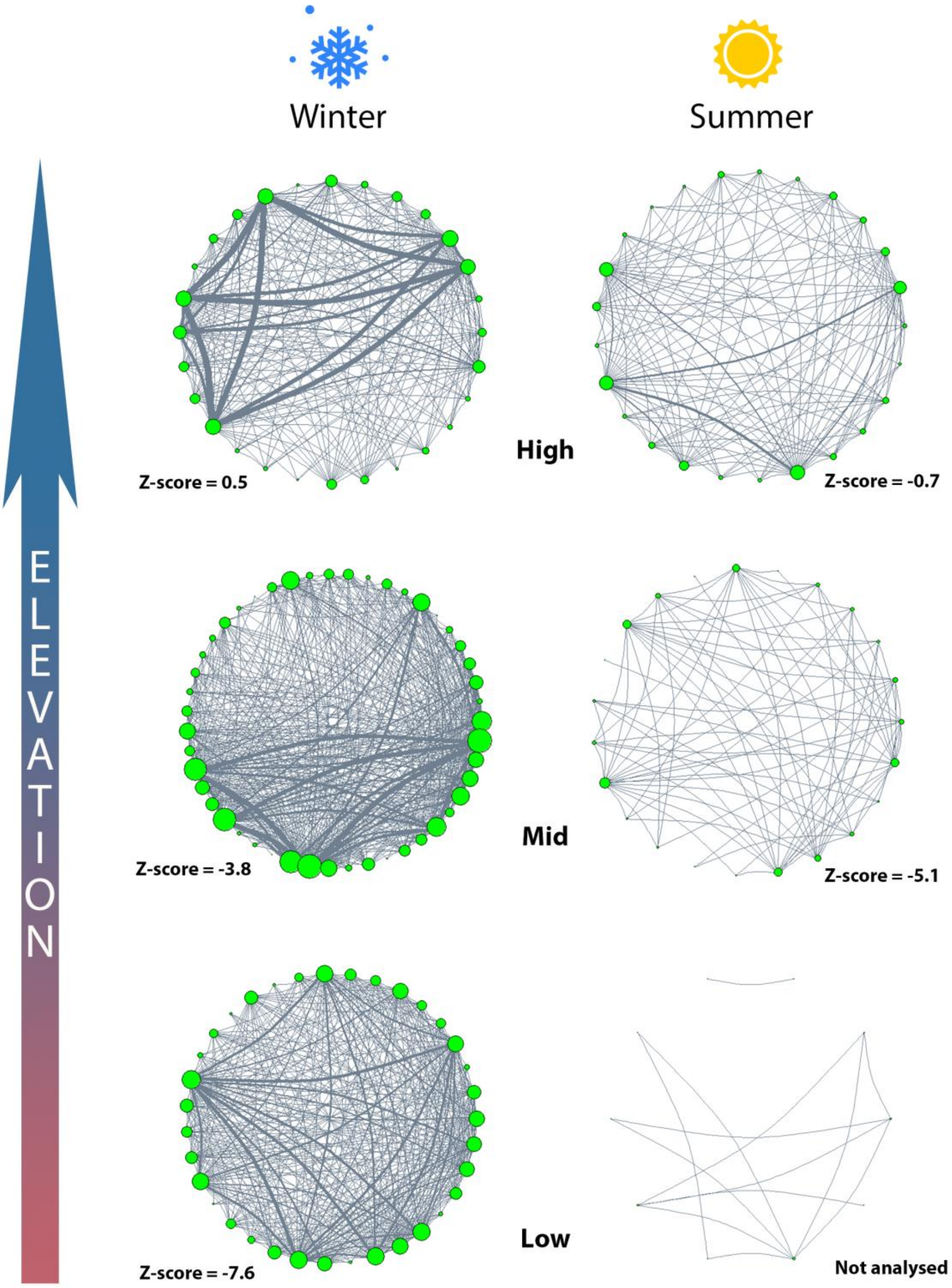

Figure 16. Networks representing nodes (circles) as "species" and edges (connections) as "associations" where the size/thickness of nodes and edges are proportional to the strength of association between species.

4.4.3. Weighted degree (pair-wise, between two elevations):

In winter, weighted degree increased with elevation. Pairwise species comparison of *z*-scores between adjacent elevations yielded significant results of increasing weighted degrees from Low to Mid (t=4.51; df=18; $p < 0.05$) and from Mid to High elevation (t=3.87; df=17; $p < 0.05$) (Figure 17a); the same set of species at lower elevations had weaker association strengths compared with association strengths at the adjacent higher elevation.

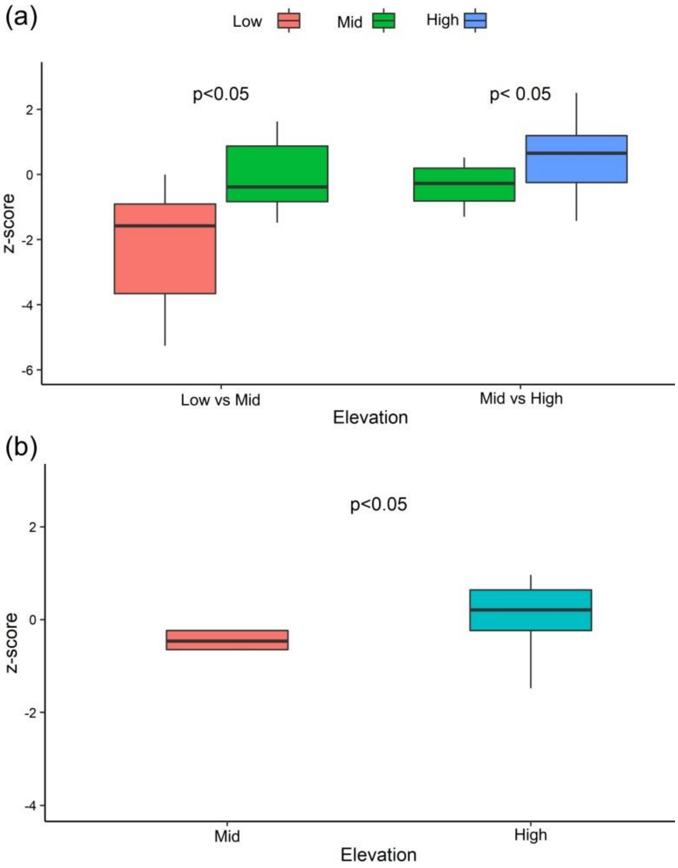

Figure 17. (a) Winter: The z-scores of the common species between two adjacent elevations have been calculated and compared with the help of a Paired-T Test. (b) Summer: The z-scores of shared species between the High and Mid elevations have been calculated and compared with the help of a Paired-T Test.

In summer, weighted degrees increased from the Mid to High elevation (t=3.55; df=9; p<0.05) (Figure 17b) but did not change significantly across seasons for the High elevation (t=1.1; df=17; p=0.1) (Figure 18), unlike the observed significant decreases for the Mid elevation (t=2.46; df=17; p < 0.05)

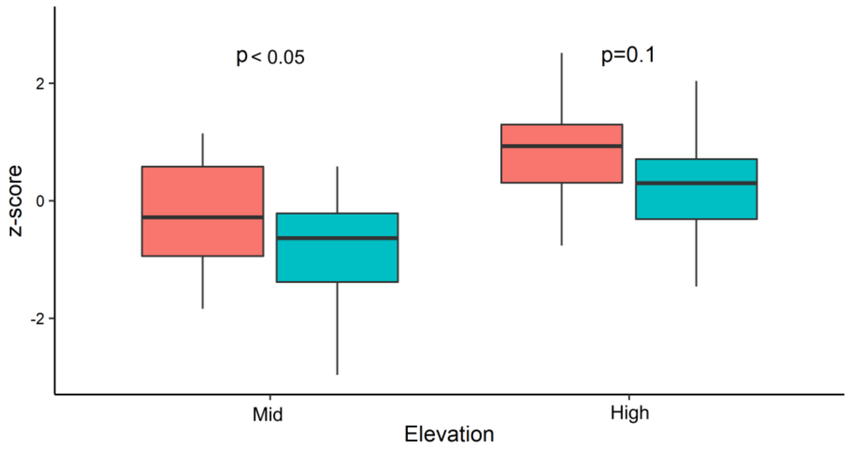

Figure 18. The z-scores of the common species for an elevation in the two seasons have been calculated and compared with the help of a Paired-T Test.

5. DISCUSSION

5.1. Flock composition

In concordance with global patterns (Sridhar et al., 2009), a large proportion of species in the flocks of the Western Himalaya were primarily insectivorous (72%). Amongst other species that are not obligate insectivorous, the omnivorous tits (*Parus* spp.) and nuthatches (*Sitta* spp.), frugivorous flowerpeckers (*Dicaeum* spp.) and nectarivorous sunbirds (*Aethopyga* spp.) do consume significant amount of insects in their diet (Billerman et al., 2020). I also found that flocks were dominated by passerines, particularly those that fed by gleaning and sallying. The mutualistic association between these two kinds of species is well known in the flocks from across the world (Morse, 1970).

A notable variation in body masses of flocking species was observed across the three elevations. Overall, 80% of flocking species were small-bodied (weighing less than 40g), while larger species that formed a separate and distinct flock type. These larger-bodied flocks were only observed only at the High elevation field site. The co-existence of multiple flock types has been reported elsewhere from the lowland dipterocarp forests of North-east India and Myanmar (King & Rappole, 2001; Srinivasan et al., 2012).

The question still remains: why would birds of different body sizes flock separately? Small-bodied flocks move much faster than large-bodied flocks, and it may not be possible for the large-bodied birds to follow hyperactive smaller species. Further, species of different sizes might have different foraging styles and might not be able to facilitate the foraging of one other, and hence there might not be any benefit of flocking together. Apart from these potential mechanisms, predation pressure might also structure flocks because the anti-predatory benefits of joining a flock are likely to differ between similarly and differently sized species; for instance, large-bodied birds in the small-bodied flocks are likely to be more conspicuous (oddity effect) and small-bodied birds when in large-bodied bird flocks may not provide any benefit to the large-bodied birds.

Small-bodied birds, however, are believed to be more vulnerable to predation (Buskirk 1976; Thiollay & Jullien 1998). Therefore, flock participation can provide additional anti-predatory benefits through behaviours such as predator mobbing (Goodale et al., 2019; Jiang et al., 2020). During my data collection, I observed (a) a flock composed of tits, warblers and yuhinas mobbing an Asian Barred Owlet (*Glaucidium cuculoides*), a potential predator of such small birds, (b) a Eurasian Sparrowhawk (*Accipiter nisus*) depredating on a Himalayan Flameback (*Dinopium shorii*) when it was outside a flock, and (c) a Jungle Owlet (*Glaucidium radiatum*) being mobbed by a Chestnut-bellied Nuthatch in a flock. Further, small-bodied birds may require a constant food supply to maintain basal metabolic rates in cold climates, and flocking by small birds might increase resource access (Moynihan, 1962), allowing species to meet metabolic demands.

5.2. Species richness

Overall flocking species richness varied along the elevation gradient among field sites in both seasons. In winter, the highest flocking species were recorded at Mid elevation (although the High elevation just had one extra species compared with Low elevation). Species richness peaking at the Mid elevation was perhaps due to the downward altitudinal migration of the flocking species, causing them to occupy mid-elevation winter ranges. This pattern was unexpected, since I expected the highest richness to be at the Low elevation. However, the observed pattern might be explained by the fact that many of the flocking species do not cross the Dehradun valley to reach to the Low elevation field site at the base of the Shivaliks. The vegetation, moisture, temperature and 40km wide Dehradun valley may act as barriers for a significant number of Himalayan bird species to reach the Shivaliks. On the contrary, the upward migration of birds at the onset of summer might have resulted in the highest flocking species richness at the High elevation.

Irrespective of flocking species richness, the average number of species per flock (i.e. flock richness) responded differently to the elevation than overall flocking species richness. In winter, flock richness decreased from Low to High elevation and this pattern was reversed in summer. However, simply based on the overall flocking species richness at different elevations in winter, flock richness should have been expected to peak at the Mid elevation. The departure from this randomly-expected pattern strengthens the expectation that flocks are non-random associations formed in response to both positive and negative interspecific interactions (Sridhar et al. 2012).

In summer, overall flocking species richness and flock richness increased with increasing elevation. Such contradictory patterns between the winter and summer may arise due to differences in the resource availability. Interestingly, in summer, flock richness decreased almost by half from winter for the Mid and Low elevation but remained similar for the High elevation until the end of sampling period, indicating that summer truly may not have started at the High elevation, and that arthropod abundance might have not yet increased as much at the high elevations compared with the Low and Mid elevations. In line with my results, a study by Jones et al. (2021) showed that the flock richness was significantly lower in higher temperatures (> 20°C) in Florida, USA.

Interestingly, Low elevation flocks disintegrated completely at the onset of summer towards the end of March, possibly due to the greater availability of resources, or an upward migration of the flocking species for breeding; however, even resident species that continued to flock did so only in conspecific groups. On the contrary, in Amazonia, Rutt & Stouffer (2021) found higher flock richness in the breeding season (dry season) perhaps due to the scarcity of resources, and they speculated that the flocks might be constrained by these two competing pressures.

5.3. Relationships between arthropod availability and mixed-species flocking:

Our results showed that insect availability (w/o Araneae) decreases with increasing elevation in winter, most likely because of decreasing temperature. Arthropods are known to be sensitive to climate (temperature) because of their small body size and ectothermy (Danks, 1992); however, I found higher arthropod availability in the coldest High elevation site because of the high relative abundance of Araneae (57%). Further, the Shannon Diversity Index for arthropods was found to decrease with increasing elevation. Considering the varied foraging styles and the wide dietary spectrum of insectivorous birds, the diversity of arthropods at any given elevation could be as important as just the number of arthropods in supporting insectivorous birds. However, a study carried out in West Bengal, India by Supriya et al. (2019) found that the majority of the diet of insectivorous Passerines is composed of insects from the orders Lepidoptera, Coleoptera and Hemiptera.

5.3.1. Flocking propensities along an elevation gradient:

Flocking propensity is an innate behaviour of a species that determines its strength of association with other species, but it is dependent on the resource availability (Jones et al., 2021). Resource availability is sensitive to temperature and expected to change along an elevation gradient. As predicted, the flocking propensities of species changed with increasing elevation. This is likely to be because of decreasing insect prey availability and arthropod prey diversity (resources) with elevation. Due to the greater availability and diversity of resources at Low elevation, species propensities might also be low; as resource scarcity increases with elevation, flocking propensities might increase significantly to allow enhanced access to resources via flocking. The flocking propensities of species were not significantly different between the Low and Mid elevations, perhaps due to the similar availability of resources. Species may tend to have low propensities when the benefits of joining flocks are less than the associated costs. At the Low elevation, along with the greater availability of insects, overall arthropods are more evenly abundant across orders (highest Shannon Diversity Index), and therefore have the high diversity. In such situations, species may be able to exploit resources easily on their own or in conspecific groups instead of via participation in flocks.

On the other hand, during resource scarcity, it might be difficult for species to forage on their own because of the inaccessibility of insects. In such situations, therefore, participation in flocks can be beneficial because the flock participants exploit the vigilance of other flock members, which in turn reduces their own time spent in vigilance, allowing them to increase foraging activity (Greenberg, 2000). Such a mechanism can explain why the propensities of species were significantly higher at High elevations compared with Mid and Low elevation.

Similarly, during summer, I found that the flocking propensities of species decreased compared with winter propensities at all elevations, possibly because of the greater availability of resources with seasonal change. Apart from this, the activity of these resources can be higher in summer which may also influence flocking propensities to decrease perhaps due to the higher relative foraging efficiency of birds to capture insects (Jones et al., 2021). The flocking propensities of High elevation species were still higher than those of the Mid elevation species in summer; true summer may not have started at the High elevation during the course of my fieldwork.

5.3.2. Effect of elevation on the interspecific association networks of the mixed-species bird flocks:

Elevation is important in structuring entire ecological communities including flocks (Montaño-Centellas & Jones, 2021; Montaño-Centellas, 2020). Interspecific interactions within flocks can change along an elevational gradient because environmental characteristics such as vegetation and temperature change over short distances; this then has further consequences on resource availability for flocking bird species. Therefore, flock networks might change because of changes in the frequency and structure of associations (Hoiss et al., 2015; Montaño-Centellas, 2020).

If only "observed" species co-occurrences (Figure 15) are used to draw inferences on interactions (associations), results could be misleading because elevation can not only affect resource availability, but also community composition and the abundances and presence of species participating in flocks (Hart et al., 2011; Supriya et al., 2019), and therefore their "availability" to join flocks (Srinivasan et al., 2012). By using an abundance-based null model and randomisation, I quantified network density and the weighted degrees of species if they just participated based solely on their relative abundances. I then compared these simulated metrics that are devoid of any interspecific associations with the observed metrics that are a result of interspecific associations in response to variability in resource availability.

As predicted, I found network density and species’ weighted degrees change with elevation during winter, presumably as a result of changes in resource availability. As resources decrease with increasing elevation, network density and species’ weighted degrees increased. During the period of resource scarcity (winter), the realised interspecific associations (network density) were higher than when resources are abundant. Although, the “observed” network density was highest at the Low elevation, it is far less than expected (null) if species participated just based on their relative abundances (Figure 14); suggesting a sort of avoidance in flocking by species at the Low elevation perhaps due to greater availability of resources.

On the other hand, at the High elevation, species are associated as expected from the null model making the association network highly connected. It is possible that species may not be able to access resources efficiently when foraging on their own at the High elevation, compelling them to participate in flocks to avail complementary benefits from many other species. Interestingly, Andean flocks also responded similarly, resulting in high network density with increasing elevation (Montaño-Centellas, 2020).

In addition, the weighted degrees (association strength) of species also increased with the scarcity of resources, suggesting that the species are not just associating with more species but also that the strength of these associations with the same set of species is higher. For instance, if there are 10 species in an area then in order to avail the flocking benefit, a species will try to associate with as many species as possible, and it will do this more frequently making the associations extremely strong. On the contrary, in the Andes, elevation had a positive effect only on the number of associations per species (degree) but not association strength (Montaño-Centellas, 2020).

Species will only associate strongly with other species if the benefits are higher than the costs; these benefits arise from the exchange of complementary anti-predator and resource-access specialised behaviours that can differ markedly between the interacting species (Diamond, 1981; Powell, 1985). Interestingly, during field work, I observed a Bronzed Drongo kleptoparasitise a Velvet-fronted Nuthatch in a flock. Although the nuthatch chased the drongo a few times, it did not leave the flock. While there can be a cost associated with these negative associations, the anti-predatory and/or resource-access benefits that the drongo might be providing for the entire flock should is expected to be higher than the cost imposed by it.

In summer, network density for the High elevation was as expected from null randomisations, but was less than in winter. Also, network density was lower than null expectation and decreased significantly for the Mid elevation with the onset of summer. The greater availability of resources in summer irrespective of any elevation would be expected to cause interspecific associations to weaken.

I found no significant change in the weighted degree for the High elevation, but a significant decrease was observed for the Mid elevation from summer to winter. This possibly suggests that the overall realised interspecific associations might be more sensitive than the association strength. Also, because weighted degrees were compared only between shared species, the metric overall may not be sensitive enough to detect this change at the flock level. Like propensities, network density and weighted degrees were significantly higher for the High elevation than Mid elevation indicating a late onset of summer at the High elevation site.

6. CONCLUSION

Mixed-species bird flocks are interacting networks of usually small-medium sized insectivorous birds which move and forage together during resource scarcity. I found flocking propensities and interspecific interactions of species within these flocks to respond to changing abiotic and biotic conditions along an elevational gradient in the Western Himalaya. The key factors responsible for structuring interspecific interactions of mixed-species flocks were likely to be the varying resource availability and the composition of the flocking community. Intriguingly, for the exchange of complementary resource-access benefits with heterospecifics, species increased their propensities, realised interspecific interactions and association strength to increase foraging activity during resource scarcity. Flocks disintegrated completely during high resource availability because the costs associated with joining a flock can be higher than the benefits. The associations between species switched from being non-facilitative under conditions of high resource availability to being facilitative under conditions of resource stress. Changes in abiotic and biotic conditions due to climate change can have cascading effects on the interaction networks of mixed-species flocks and entire bird communities.

7. LIMITATIONS OF THE STUDY AND WAY FORWARD

- This study did not cover an entire Western Himalayan elevation gradient but attempts have been made at least to cover the Shivalik (350 m) and Lesser Himalaya (2200 m). Future studies can include Greater Himalaya, and extend the elevation gradient from the Shivaliks at 350 m to treeline at ~4000 m. Stark resource differences are likely to be expected across this entire gradient potentially affecting the propensities and interspecific associations.

- Discontinuity in this elevation gradient due to the Dehradun valley likely affects the bird community composition and so does the flocks. Although, an abundance-based null modelling approach controls for this gradient discontinuity and resulting beta-diversity; however, studies in future may select a continuous gradient without any barriers for bird migration.

- Vegetation structure and complexity is known to influence the flocks perhaps due to differences in resources and predation pressure. I did not check for the effect of vegetation on flocking which may be explored in future investigations.

- Many flocking species in this study were confined to understorey and midstorey therefore, arthropod sampling was only carried out up to three meter from ground. Since, birds do spread out vertically to forage in the canopy; however, I think this sampling approach is adequate for broad-scale patterns about resource availability. Diet of the flocking species should be studied in detail to know more about their food preferences.

- Behavioural observations of leader/nuclear species in the flocks are another interesting study about how flocks form, move and communicate when foraging. Future studies may focus on functions of nuclear species and how their roles change with elevation.

- Since, predation is known to influence flocking and is an equally important driver as resources; responses of flocks to varying predation pressures can be explored.

- Propensities can be controlled with an incidence-based null model in addition to the species availability to understand effects of propensity and interspecific associations separately.

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Appendix. List of flocking species recorded across elevational gradient during the study (trait information from Billerman et al. 2020). The pink shaded columns refer to presence of species in winter while the green shaded refers to those recorded during summer.

S No	Order	Family	Species	Common Name	body size	Average body mass (g)	Diet guild	Foraging style	High	Mid	Low	High	Mid	Low
1	Passeriformes	Cettiidae	*Abroscopus schisticeps*	Black-faced Warbler	S	6	insectivore	gleaner	1			1		
2	Passeriformes	Leiothrichidae	*Actinodura strigula*	Chestnut-tailed Minla	S	19	insectivore	gleaner	1					
3	Passeriformes	Aegithalidae	*Aegithalos concinnus*	Black-throated Tit	S	6.4	insectivore	gleaner	1	1		1	1	
4	Passeriformes	Aegithinidae	*Aegithina tiphia*	Common Iora	S	15	insectivore	gleaner			1			1
5	Passeriformes	Nectariniidae	*Aethopyga ignicauda*	Fire-tailed Sunbird	S	8.25	nectarivore	gleaner		1				
6	Passeriformes	Nectariniidae	*Aethopyga nipalensis*	Green-tailed Sunbird	S	6.75	nectarivore	gleaner		1				
7	Passeriformes	Certhiidae	*Certhia himalayana*	Bar-tailed Treecreeper	S	9	insectivore	bark gleaner	1	1	1	1		
8	Passeriformes	Stenostiridae	*Chelidorhynx hypoxanthus*	Yellow-bellied Fantail	S	6	insectivore	sallier	1	1		1		
9	Piciformes	Picidae	*Chrysophlegma flavinuchha*	Greater Yellownape	L	175.5	insectivore	bark gleaner	1	1				
10	Passeriformes	Muscicapidae	*Copsychus malabaricus*	White-rumped Shama	S	32	insectivore	gleaner			1			
11	Passeriformes	Campephagidae	*Coracina melaschistos*	Black-winged Cuckooshrike	S	38.5	insectivore	gleaner		1		1		
12	Passeriformes	Stenostiridae	*Culicicapa ceylonensis*	Gray-headed Canary-flycatcher	S	7.5	insectivore	sallier	1	1	1	1	1	
13	Passeriformes	Muscicapidae	*Cyornis tickelliae*	Tickell's Blue Flycatcher	S	15	insectivore	sally-gleaner			1			
14	Passeriformes	Corvidae	*Dendrocitta vagabunda*	Rufous Treepie	L	110	Omnivore	gleaner			1			
15	Piciformes	Picidae	*Dendrocopos canicapillus*	Gray-capped Pygmy Woodepecker	S	23.5	insectivore	bark gleaner		1	1			
16	Piciformes	Picidae	*Dendrocopos hyperythrus*	Rufous-bellied Woodpecker	L	46.5	insectivore	bark gleaner	1			1		
17	Piciformes	Picidae	*Dendrocopos macei*	Fulvous-breasted Woodpecker	S	30.5	insectivore	bark gleaner	1	1	1		1	
18	Piciformes	Picidae	*Dendrocopos nanus*	Brown-capped Pygmy Woodpecker	S	15	insectivore	bark gleaner			1			
19	Passeriformes	Dicaeidae	*Dicaeum agile*	Thick-billed Flowerpecker	S	9.25	frugivore	gleaner		1				1
20	Passeriformes	Dicaeidae	*Dicaeum ignipectus*	Fire-breasted Flowerpecker	S	6	frugivore	gleaner		1				
21	Passeriformes	Dicruridae	*Dicrurus aeneus*	Bronzed Drongo	S	26	insectivore	sallier		1				

S No	Order	Family	Species	Common Name	body size	Average body mass (g)	Diet guild	Foraging style	High	Mid	Low	High	Mid	Low
22	Passeriformes	Dicruridae	*Dicrurus caerulescens*	White-bellied Drongo	S	40	insectivore	sallier			1			
23	Passeriformes	Dicruridae	*Dicrurus leucophaeus*	Ashy Drongo	S	38.5	insectivore	sallier		1		1		
24	Piciformes	Picidae	*Dinopium shorii*	Himalayan Flameback	L	101	insectivore	bark gleaner			1			
25	Passeriformes	Muscicapidae	*Eumyias thalassinus*	Verditer Flycatcher	S	17.5	insectivore	sally-gleaner			1	1	1	
26	Passeriformes	Corvidae	*Garrulus glandarius*	Eurasian Jay	L	163	Omnivore	gleaner	1			1		
27	Passeriformes	Corvidae	*Garrulus lanceolatus*	Black-headed Jay	L	94	Omnivore	gleaner	1			1		
28	Passeriformes	Vangidae	*Hemipus picatus*	Bar-winged Flycatcher-shrike	S	9	insectivore	sally-gleaner		1	1		1	1
29	Passeriformes	Pycnonotidae	*Hemixos flavala*	Ashy Bulbul	S	31	Omnivore	gleaner		1				
30	Passeriformes	Leiothrichidae	*Heterophasia capistrata*	Rufous Sibia	S	37.5	Omnivore	gleaner		1		1		
31	Passeriformes	Pycnonotidae	*Hypsipetes leucocephalus*	Black Bulbul	S		Omnivore	sallier		1		1		
32	Passeriformes	Leiothrichidae	*Lanthocincla albogularis*	White-throated Laughingthrush	L	114	Omnivore	gleaner	1			1		
33	Piciformes	Picidae	*Leiopicus auriceps*	Brown-fronted Woodpecker	L	43.5	insectivore	bark gleaner	1	1		1		
34	Piciformes	Picidae	*Leiopicus mahrattensis*	Yellow-crowned Woodpecker	S	37	insectivore	bark gleaner			1			
35	Passeriformes	Leiothrichidae	*Leiothrix lutea*	Red-billed Leiothrix	S	23	Omnivore	gleaner		1				
36	Piciformes	Megalaimidae	*Megalaima asiatica*	Blue-throated Barbet	L	82	frugivore	gleaner		1				
37	Passeriformes	Muscicapidae	*Myophonus caeruleus*	Blue Whistling Thrush	L	183.5	insectivore	gleaner	1	1				
38	Passeriformes	Muscicapidae	*Niltava sundara*	Rufous-bellied Niltava	S	21.5	insectivore	gleaner		1				
39	Passeriformes	Oriolidae	*Oriolus traillii*	Maroon Oriole	L	74	Omnivore	gleaner		1		1		
40	Passeriformes	Oriolidae	*Oriolus xanthornus*	Black-hooded Oriole	L	62.5	insectivore	gleaner			1			
41	Passeriformes	Cisticolidae	*Orthotomus sutorius*	Common Tailorbird	S	8	insectivore	gleaner			1			
42	Passeriformes	Paridae	*Parus cinereus*	Cenereous Tit	S	17	Omnivore	gleaner		1	1		1	
43	Passeriformes	Paridae	*Parus monticolus*	Green-backed Tit	S	14.5	Omnivore	gleaner	1	1		1		
44	Passeriformes	Paridae	*Parus xanthogenys*	Black-lored Tit	S	16.5	Omnivore	gleaner	1	1		1	1	
45	Passeriformes	Campephagidae	*Pericrocotus cinnamomeus*	Small Minivet	S	9	insectivore	sally-gleaner			1			1
46	Passeriformes	Campephagidae	*Pericrocotus ethologus*	Long-tailed Minivet	S	18	insectivore	sally-gleaner		1	1	1		1

S No	Order	Family	Species	Common Name	body size	Average body mass (g)	Diet guild	Foraging style	High	Mid	Low	High	Mid	Low
47	Passeriformes	Campephagidae	*Pericrocotus roseus*	Rosy Minivet	S	16.5	insectivore	sally-gleaner					1	
48	Passeriformes	Campephagidae	*Pericrocotus speciosus*	Scarlet Minivet	S	21.5	insectivore	sally-gleaner		1	1		1	
49	Passeriformes	Paridae	*Periparus rubidiventris*	Rufous-vented Tit	S	10	insectivore	gleaner	1					
50	Passeriformes	Muscicapidae	*Phoenicurus frontalis*	Blue-fronted Redstart	S	15.5	insectivore	sallier	1					
51	Passeriformes	Phylloscopidae	*Phylloscopus chloronotus*	Lemon-rumped Warbler	S	4.8	insectivore	hoverer	1	1	1	1	1	
52	Passeriformes	Phylloscopidae	*Phylloscopus humei*	Hume's Warbler	S	7	insectivore	gleaner			1	1	1	
53	Passeriformes	Phylloscopidae	*Phylloscopus maculipennis*	Ashy-throated Warbler	S	6	insectivore	gleaner	1	1		1		
54	Passeriformes	Phylloscopidae	*Phylloscopus magnirostris*	Large-billed Leaf Warbler	S	12	insectivore	gleaner			1			
55	Passeriformes	Phylloscopidae	*Phylloscopus occipitalis*	Western Crowned Warbler	S	8.5	insectivore	gleaner		1		1	1	1
56	Passeriformes	Phylloscopidae	*Phylloscopus pulcher*	Buff-barred Warbler	S	6.5	insectivore	gleaner	1			1		
57	Passeriformes	Phylloscopidae	*Phylloscopus trochiloides*	Greenish Warbler	S	8.5	insectivore	gleaner		1	1			
58	Passeriformes	Phylloscopidae	*Phylloscopus whistleri*	Whistler's Warbler	S		insectivore	gleaner	1	1	1	1	1	
59	Passeriformes	Phylloscopidae	*Phylloscopus xanthoschistos*	Gray-hooded Warbler	S	7.5	insectivore	gleaner	1	1	1	1	1	
60	Piciformes	Picidae	*Picumnus innominatus*	Speckled Piculet	S	11.1	insectivore	gleaner		1			1	
61	Piciformes	Picidae	*Picus canus*	Gray-headed Woodpecker	L	145	insectivore	bark gleaner	1				1	
62	Piciformes	Picidae	*Picus chlorolophus*	Lesser Yellownape	L	65.5	insectivore	bark gleaner	1	1		1		
63	Passeriformes	Timaliidae	*Pomatorhinus erythrogenys*	Rusty-cheeked Scimitar Babbler	L	64.5	insectivore	gleaner	1	1		1	1	
64	Passeriformes	Cisticolidae	*Prinia hodgsonii*	Gray-breasted Prinia	S	7.5	insectivore	gleaner		1	1		1	1
65	Passeriformes	Vireonidae	*Pteruthius ripleyi*	Himalayan Shrike Babbler	S	36.5	insectivore	gleaner	1	1		1		
66	Passeriformes	Pycnonotidae	*Pycnonotus leucogenys*	Himalayan Bulbul	S	36	omnivore	gleaner		1	1			
67	Passeriformes	Regulidae	*Regulus regulus*	Goldcrest	S	5.85	insectivore	gleaner	1					
68	Passeriformes	Rhipiduridae	*Rhipidura albicollis*	White-throated Fantail	S	11	insectivore	sallier	1	1	1		1	
69	Passeriformes	Sittidae	*Sitta cinnamoventris*	Chestnut-bellied Nuthatch	S	19	omnivore	bark gleaner		1	1			1
70	Passeriformes	Sittidae	*Sitta frontalis*	Velvet-fronted Nuthatch	S	12.75	insectivore	bark gleaner		1	1		1	1
71	Passeriformes	Sittidae	*Sitta himalayensis*	White-tailed Nuthatch	S	14	omnivore	bark gleaner	1			1		

S No	Order	Family	Species	Common Name	body size	Average body mass (g)	Diet guild	Foraging style	High	Mid	Low	High	Mid	Low
72	Passeriformes	Timaliidae	*Stachyridopsis pyrrhops*	Black-chinned Babbler	S	10	insectivore	gleaner	1	1	1		1	
73	Passeriformes	Sylviidae	*Sylvia curruca*	Lesser Whitethroat	S	13.75	insectivore	gleaner			1			
74	Passeriformes	Paridae	*Sylviparus modestus*	Yellow-browed Tit	S	7	insectivore	gleaner	1					
75	Passeriformes	Vangidae	*Tephrodornis pondicerianus*	Common Woodshrike	S	22.5	insectivore	gleaner			1			
76	Passeriformes	Monarchidae	*Terpsiphone paradisi*	Indian Paradise Flycatcher	S	19	insectivore	sallier					1	
77	Passeriformes	Corvidae	*Urocissa erythrorynha*	Red-billed Blue Magpie	L	168.5	omnivore	gleaner	1			1		
78	Passeriformes	Zosteropidae	*Yuhina flavicollis*	Whiskered Yuhina	S	14.5	insectivore	gleaner	1	1		1		
79	Passeriformes	Zosteropidae	*Yuhina gularis*	Stripe-throated Yuhina	S	19	insectivore	gleaner	1					
80	Passeriformes	Zosteropidae	*Zosterops palpebrosus*	Oriental White-eye	S		omnivore	gleaner	1	1	1	1	1	1