The effect of disturbance-induced changes in vegetation structure and arthropod abundance on mixed-species bird flocks in the oak forests of the Western Himalaya

by

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Under the supervision of

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Dr. Priti Bangal
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भारतीय वन्यजीव संस्थान
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AcSIR

DECLARATION

I hereby declare that the work conducted under the thesis entitled **"The effect of disturbance-induced changes in vegetation structure and arthropod abundance on mixed-species bird flocks in the oak forests of the Western Himalaya",** is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. Navendu Page** of the **Wildlife Institute of India**, **Dr. Priti Bangal** of the **Nature Conservation Foundation** and **Dr. Ghazala Shahabuddin** of **Ashoka University**. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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CERTIFICATE

This is to certify that the thesis by **Aditya Satish** entitled "**The effect of disturbance-induced changes in vegetation structure and arthropod abundance on mixed-species bird flocks in the oak forests of the Western Himalaya"** is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Aditya Satish has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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1. Executive Summary

1. Mixed-species flocks are an interactive group of insectivorous birds that forage together and move in the same direction. Flocks provide foraging and anti-predatory benefits to participants. Habitat disturbance may affect flocks by – a) altering presence or abundance of participating birds in the community or b) altering flocking propensities of species.

2. I investigated the effects of habitat disturbance on flocks in the Western Himalaya of Uttarakhand, India. Disturbance was mediated through two mechanisms – changes in vegetation structure and arthropod abundance (food availability). I examined how these environmental variations impacted flocks at a community level through changes in flock richness, flock size, number of flocks encountered and flock composition. I also explored how flocking propensity (a species-specific tendency to join flocks) is impacted by these variables.

3. Flocks are a subset of the insectivorous bird community. I found that insectivore richness and abundance decreased with reduced structural complexity of vegetation caused by disturbance. Reduced structural complexity also led to a corresponding decline in flock richness, size and number of flocks encountered in disturbed sites. With regards to variation of flock composition with disturbance, I found no clear species-composition-based clustering in transects with similar disturbance levels.

4. There seems to be an interactive link between arthropods, insectivorous birds and disturbance. Disturbance was correlated with strong declines in foliage arthropod abundance, which in turn contributes to lower insectivore richness and abundance. Flying arthropod abundance largely remained constant with disturbance, so I would like to draw

attention to the effect of foliage arthropod abundance on flock variables in the following sections.

5. The number of flocks encountered increased with foliage arthropod abundance. Since insectivores in undisturbed sites are supported by a larger prey base, the higher frequency of flocking may be correlated to the larger pool of insectivores that are available to flock at a given time. I did not find significant effects of foliage arthropod abundance on flock richness and flock size.

6. I found that flocking propensity of the three most common species (Gray-hooded Warbler, Black-throated Tit and Green-backed Tit) in flocks showed a declining trend with higher disturbance. I also observed that the propensity of these species showed an increasing trend with higher foliage arthropod abundance. However, none of these relationships were statistically significant. More detailed research is recommended to investigate these preliminary patterns further, to better understand the complex interactions between propensity, disturbance and food availability.

7. To conclude, disturbance was found to have a negative impact on mixed-species flocks, primarily by altering the presence and abundance of insectivorous birds. From a habitat perspective, insectivores suffered declines due to the simplification of vegetation structure. Insectivores also face food scarcity as foliage arthropod abundance decreases. The combined effect of habitat loss and reduced food availability in disturbed sites leads to lower insectivore richness and abundance, which is in turn reflected in fewer, smaller and more species-poor flocks.

2. Introduction

What are mixed-species flocks and why do they form?

Mixed-species bird flocks (hereafter flocks) consist of a group of insectivorous forest birds that move and forage together (Morse, 1970). Flocking is a common, widespread and well-studied phenomenon across tropical and temperate forests worldwide.

Flocking differs markedly from ostensibly similar feeding aggregations that involve multiple species gathering at a food resource. These aggregations are events that occur because many species congregate at the site of a clumped resource, such as frugivores drawn to a fruiting tree (Diamond & Terborgh, 1967). However, flocks are not necessarily dependent on proximity to a food resource. Rather, they arise due to repeated and consistent patterns of associations between participants that are moving as a group (G. V. N. Powell, 1985).

Flocks are thought to form for two reasons – they may be used to increase foraging efficiency or to gain better protection from predators (Sridhar et al., 2009). These factors may not be mutually exclusive – birds may join flocks to avail increased fitness from both or either of these benefits on offer.

Flock participants may increase their foraging efficiency by profiting on the behavioural traits and activity of other members. Gleaning individuals that flush arthropods from substrates, due to their high speed and intensity of movement, may facilitate prey capture for other participants (Winterbottom, 1943). Individuals may learn to forage at sites where prey may be abundant, or avoid previously exploited sites to save energy, through social copying (Waite and Grubb, 1988).

Participating individuals also rely directly on vigilance benefits derived from flocking behaviour. Through the ‘many eyes effect’, a participant’s fitness might be boosted because more flock members can lead to faster detection of predators (Pulliam, 1973). By associating with a flock, a participant may also reduce its own chances of being predated through simple dilution effect (Foster & Treherne, 1981). A participating individual may lower predation risk by occupying a position in the flock that is less susceptible to a predatory attempt (selfish herd hypothesis) (Hamilton, 1971) or reduce the predator's capability to target a particular individual, following the 'confusion effect' (Neill & Cullen, 1974). Furthermore, participants may make use of the strength in numbers and/or exploit the aggressive behaviour of certain species to mob potential predators in the vicinity.

These benefits may also work in tandem to cause feedback effects. For example, participants may also be able to exploit the vigilance of others, to spend less time scanning for predators and thereby increase time spent foraging (Greenberg, 2001).

However, participants in a flock may incur costs from interspecific aggression, competition for food and kleptoparasitism (Morse, 1977). Therefore, birds join flocks based on an energetic trade-off principle – the benefits of joining a flock must outweigh the potential costs that individuals may suffer whilst participating in one.

In the literature, flock participants have been broadly divided into two groups – 'leaders' (those species that are joined by other individuals) and 'followers' (those that follow other species) (Moynihan, 1962). Leadership is solely based on the position of a particular species in a flock. Leadership can be quantified observationally by enumerating the number of times a species is seen at the forefront of a flock, especially when crossing a clearing or trail (Kotagama & Goodale, 2004). Leaders tend to be intraspecifically gregarious or sallying species (Sridhar et al., 2009); these behavioural traits are hypothesised to provide foraging and/or antipredator benefits to other participants.

Flock literature has also made use of the term 'nuclear species' to describe those that are crucial for flock formation, maintenance and cohesion (Moynihan, 1962). Nuclear species are thought to have certain characteristics, such as presence in a high proportion of flocks, high propensity to flock, gregarious nature, prominent vocal activity etc. A species may qualify as nuclear if it satisfies one or more of these conditions.

The distinction between nuclearity and leadership is now more well-defined. However, previous studies have used the terms interchangeably and in different contexts because there is some overlap in the definitions of leaders and nuclear species (Bangal & Sridhar, 2023).

Flocks as models to study ecological communities

A flock is a subset of the bird community in space and time. They consist of small to medium-sized bird species largely operating in the insectivorous foraging guild. The behaviour of insectivory among birds in flocks means that participant species share a common (dietary) trait, which is a feature of a horizontal community. Therefore, patterns of species diversity in flocks are easier to establish and compare among the same guild of birds, especially across an ecological gradient. Since insectivorous birds comprise a large portion of flocking species, trends in patterns of flock variables (flock richness, flock size etc.) can also serve as a surrogate for the entire insectivore community.

Current knowledge of flock responses to disturbance

Interactions in flocks are complex ecological phenomena which are likely to vary based on how anthropogenic disturbances alter the species composition, behaviour of species and other underlying factors such as changes in vegetation complexity and arthropod abundance, that govern flock formation. Flock responses to disturbance, in terms of community parameters like flock richness, flock size and turnover in composition, has been extensively studied across the globe. Studies on flock responses to disturbance have primarily focused on fragmentation and land-use intensity (Goodale et al., 2015; Zou et al., 2018). The general consensus is that flock variables such as richness, flock size and encounter rate decline as the intensity of degradation increases (Colorado Zuluaga & Rodewald, 2015; Jones & Robinson, 2020; Maldonado-Coelho & Marini, 2004; Zhang et al., 2013).

Disturbance has been found to affect flocks primarily through a simplification of the vegetation structure (Zou et al., 2018). This reduction in complexity can lead to the decline of flocks in two ways –

a) By altering species composition: The loss of forest insectivores and/or nuclear species may alter the species pool of birds available to flock. This may have cascading effects by resulting in reduced flocking in disturbed areas, thereby leading to a decline in flock richness and flock size (Maldonado-Coelho & Marini, 2004; Sridhar & Sankar, 2008).

b) By affecting the drivers of flocking, i.e., resource availability and perception of predation risk: For example, insectivorous birds in forest habitats may be unable to detect ambush predators concealed in dense foliage. Opening of the habitat caused by disturbance may alter perceived predation risk for flocking birds (Thiollay & Jullien, 2008). Furthermore, arthropod abundance is known to diminish with a reduction in canopy cover and higher day temperatures, making them more prone to desiccation (Barlow & Peres, 2004; Richards & Windsor, 2007; Silveira et al., 2010).These disturbance-induced phenomena can lead to a variation in the tendency of species to flock, also known as flocking propensity. Propensity is defined as the proportion of a species' abundance within flocks relative to total abundance (both inside and outside flocks).

However, there have been some studies which report no significant differences in flock richness and size with disturbance. Some reasons behind this could be that the presence and abundance of nuclear species is maintained even in disturbed areas (Jernakoff et al., 2023) or that landscape-level heterogeneity masks the effect of local-scale habitat degradation (Vásquez-Ávila et al., 2021).

The response of flock variables to changes in arthropod abundance (food availability) has not been well-studied in the literature. Develey and Peres (2000) have explored how seasonal fluctuations in arthropod availability have impacted the structure of flocks. Gentry et al. (2019) have attempted to investigate how fat scores and foraging time budgets of flocking individuals mediate propensity across a disturbance gradient, which is perhaps more relevant for this study. They found that flock participants experienced energetic deficits and spent more time foraging in disturbed areas.

Research on flock responses to disturbance in India has shown mixed results. Sridhar and Sankar (2008) found similar richness and composition along a fragmentation gradient in the Western Ghats, but a distinct decline in flock size. Another study in the same area by Sidhu et al., 2010 reported richness to be similar between forest and plantations of coffee and cardamom. However, the study also found a total absence of flocks in plantations of teak and tea. Apart from measuring standard community responses to disturbance, work in the Eastern Himalayas by Borah et al. (2018) has investigated flock responses to degradation at a finer scale through changes in network associations. Understory flocks were shown to display a reduced proportion of interspecific associations with increasing logging intensity (Borah et al., 2018).

Knowledge gaps

Previous work on flocks in India has largely been focussed in the Western Ghats and the Eastern Himalaya. There is a paucity of descriptive and ecological information on flocks in the temperate oak-pine forest system of the Western Himalaya. Oak forests are known to harbour high bird species richness, but are subject to extractive activities that can reduce biodiversity

(Menon et al., 2019; Shahabuddin et al., 2021; Shahabuddin & Thadani, 2018). There have been a few studies that provide baseline information on flock composition in this region (Chauhan and Jolli, 2022; Macdonald & Henderson, 1977). However, none of these studies assess flock responses to disturbance. This gap of knowledge is especially important to address, given that oak is being replaced by pine due to a combination of intense extraction, reduced soil moisture and increased recruitment of pine in the understory of oak forests (Das et al., 2021).

In this study, I quantified flock responses to disturbance at a community level, using variables such as flock richness, flock size and composition. I also examined species-specific responses to disturbance through variations in flocking propensities. To the best of my knowledge, species-specific propensities from data collected on birds inside and outside flocks have hitherto not been directly compared across a gradient of disturbance in India.

Although improving foraging efficiency is thought to be one of the main drivers behind flocking (Sridhar et al., 2009), we know little about the relationships of flock variables with food availability. Previous studies have examined the impact of disturbance on food availability through surrogates such as fat scores and time spent foraging (Gentry et al., 2019), but not directly by quantifying arthropod abundance.

I examined the effect of disturbance on flocks through the combined effects of changes in vegetation structure and arthropod abundance. Therefore, this study aims to fill these lacunae in information for flocks in the Western Himalaya, thereby contributing to the ever-growing body of literature on mixed-species flocks.

Objectives

To study the effect of disturbance (measured through vegetation attributes) on flock variables and investigate the associated mechanisms.

Flock variables (response variables) that were of interest to this study were –

- Flock richness (mean no. of species per flock) and flock size (mean no. of individuals per flock)
- Number of flocks encountered
- Flock composition
- Flocking propensity (species-specific index of the tendency to flock)

  Propensity is mathematically represented as a ratio between:

  $$\text{Propensity} = \frac{\text{No. of individuals inside flocks}}{\text{Total abundance}}$$

  I examined propensities of the three most common species in flocks, namely the Gray-hooded Warbler, Black-throated Tit and Green-backed Tit.

Research questions:

I aimed to investigate the effect of disturbance on flock variables through two dimensions –

1. Vegetation structure (habitat)

Question 1: What is the effect of disturbance-induced changes in vegetation structure on

a) flock richness, flock size, number of flocks encountered and flock composition?

b) flocking propensity of select species?

2. Arthropod abundance (food availability)

Question 2: What is the effect of disturbance-induced changes in arthropod abundance on

a) flock richness, flock size and number of flocks encountered?

b) flocking propensity of select species?

3. Methods

3.1 Study area

Physical geography

The study was carried out in Mukteshwar, Nainital district in the state of Uttarakhand in north-west India. The study area is bounded by the latitudes 29° 31.919'N to 29° 31.463'N and the longitudes 79° 29.244'E to 79° 42.505'E. The study area is located in the mid-elevation zone of the Western Himalayas, comprising an altitudinal range of 1700-2200 m. The forest type is classified as Himalayan moist temperate forest (Champion and Seth, 1968), with the flora composed primarily of *Quercus leucotrichophora* (Banj oak), *Quercus floribunda* (Moru), *Pinus roxburghii* (Chir pine), *Rhododendron arboreum* (Burans), *Myrica esculenta* (Kaafal), *Aesculus indica*, *Cupressus torulosa*, *Acer* spp. etc. *Quercus leucotrichophora* forms monodominant stands in this elevational belt (Singh and Singh, 1986). The study area experiences a monsoonal climate, with an annual rainfall of 1200 mm falling largely from July to September. Mid-elevation Himalayan oak forests host high bird diversity due to their complex vegetation structure, evergreen phenology, dense leaf litter and moist micro-climate (Shahabuddin et al., 2021).

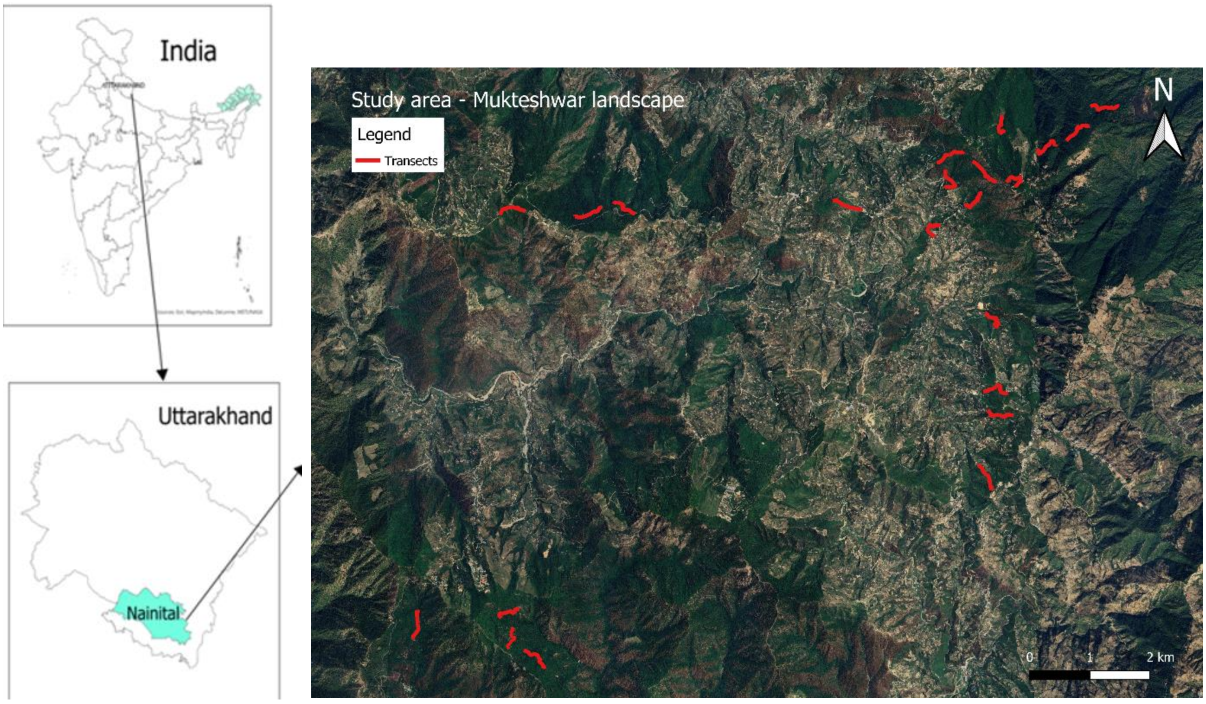


Figure 1: Map of study area in Nainital district of Uttarakhand state, India. The red lines depict the 22 transects walked during the study.

Socio-economic setting

Van Panchayats: The study area comprises of Van Panchayats (also known as village forests) that are owned by the state government, but are managed by the local community (Agrawal, 2005). They are subjected to varying degrees of extraction depending on the intensity of use by members of the local community.

Mahesh Khan RF and IVRI ('Natural' forests): These are forest tracts under 'conventional' government jurisdiction. They are suitable as controls, since they are relatively free of disturbance (Menon et al., 2019).

Both sites are dominated by Banj oak forests. Banj oak is subjected to extractive activities in Van Panchayats. Lopping of branches for livestock fodder and fuelwood is prevalent. There is occasional livestock grazing and grass cutting that impacts the grass community in the understory of oak forests. Leaf litter is also extensively collected in the winter season for composting and livestock bedding (Shahabuddin & Thadani, 2018).

3.2 Field Methods

Bird sampling

I set up 22 transects each of length 500 m. Transects were chosen based on prior local knowledge of the study area to adequately capture a gradient of disturbance. I walked each transect 9-14 times from late December to late March. Transects were walked at a slow pace throughout the day from 0800 hours to 1730 hours. All birds seen or heard within a strip width of 25 m on either side of the transect were recorded. I did not sample birds on overcast, rainy or snowy days. While walking transects, I recorded two kinds of data –

a) Flock data: If a flock was encountered on the transect, I recorded the species composition of the flock and the abundances of each species in the flock. I also sampled flocks that were observed while returning on the transect, as well those that I saw opportunistically on the transect. Flocks were defined as the spatial association of at least two birds who were at most 10 m from the next closest bird and travelling in the same direction. I considered flocks seen on the same occasion as independent samples if the distance between them was greater than 250 m.

b) Data for birds outside flocks: In addition, I also recorded the identity and abundance of all bird species observed outside flocks while walking the transect in the first instance. I did not collect data on abundances of birds outside flocks while returning on the transect.

Method (a) was used to collect data on flock richness, flock size, number of flocks encountered and flock composition.

Method (b) was used to collect data on the overall bird community found on the transects.

A combination of data from (a) and (b) was used to calculate flocking propensity for certain species of interest. I did not use the data from return/opportunistic samples of flocks for calculating propensities.

Arthropod sampling

The aim of arthropod abundance sampling was to understand how resource (prey) availability changes across the gradient for insectivorous birds, and as a result, flocks. I sampled two kinds of arthropods – foliage and flying arthropods to capture the prey of both, birds that glean insects off the foliage and those that sally to capture insects mid-air.

Foliage arthropods: I used the branch bagging technique to capture foliage arthropods, performed at regular intervals on the same transects that were used for bird sampling (Ghosh-Harihar, 2012). Branches were randomly selected at the designated intervals using a randomizer mobile app. Foliage arthropods were sampled in January and February parallelly with bird sampling. Identically-sized polythene bags were placed gently to enclose the entire branch. The branch was then clipped to capture arthropods perched on the leaves and bark surface. The captured arthropods were euthanized by dropping a cotton ball soaked with a few drops of chloroform in the bag. This technique is useful for calculating the resource availability for gleaning bird species that occupy the understory and midstory. Foliage arthropods were sampled by enclosing 15 branches per transect, over five temporal replicates.

Flying arthropods: I suspended yellow sticky traps (20L x 15W x 7.5H cm) on each transect at regular intervals to catch flying arthropods (Aggarwal et al., 2023). Branches on which traps were deployed were randomly selected at the designated intervals using a randomizer mobile app. Each trap was suspended on the transect for 140-170 hours. Flying arthropods were sampled in February and March parallelly with bird sampling. Flying arthropods were sampled by putting up 8 traps per transect, over two temporal replicates.

The foliage and flying arthropods captured through the bagging and sticky trap methods respectively were taken back to base camp, where they were counted and identified to the Order level.

Vegetation sampling

Vegetation sampling was carried out on all 22 transects. We used two kinds of vegetation plots (namely L = Large plot and R = Regeneration plot) to measure vegetation structure variables of interest. Each transect had four 10 m radius circular plots (L plots) and four 5 m radius circular plots (R plots) that were distributed at regular intervals on either side of the transect, in an alternating fashion. The 5 m circular plots were nested within the 10 m circular plots.

Table 1. Vegetation variables collected during field sampling

Sno	Plot type	Variable	Field sampling
1	L	Stem density	Individuals >= 20 cm in girth were counted and identified
2	R	Stem density	Individuals < 20 cm in girth and > 50 cm in height were counted and identified
3	L	GBH	The circumference of each individual >= 20 cm in girth was measured at 1.33 m from the ground
4	L	Tree height	The height of each individual >= 20 cm in girth was visually estimated
5	L	Foliage height (height at which the foliage starts)	The foliage height of each individual >= 20 cm in girth was visually estimated
6	L	Lopping score	To measure lopping intensity, each individual was scored as 1 (no lopping), 2 (moderate lopping) and 3 (extreme lopping)
7	L	Understory cover (<50 cm height)	Understory cover of shrubs < 50 cm in height was visually estimated
8	L	Leaf litter cover	Leaf litter cover was visually estimated. Each L plot was given a score that ranged from 0-3 (0 = bare ground with absence of leaf litter, 1 = little leaf litter, 2 = presence of a thin layer of dry leaves indicating one year's litter, 3 = presence of dry leaves along with a well-developed and deep humus layer
9	L	Grass cover	Grass cover was visually estimated
10	L	Number of coppices	Visually counted

11	L	Number of stumps/cut stem	Visually counted
12	L	Canopy density	Using a densiometer, 16 readings per L plot were obtained and their mean was calculated. Canopy density (%) was obtained using the following formula – Canopy density = 100 – (Mean*1.04)

3.3 Analytical methods

3.3.1 General summaries of bird data

Bar plots were used to compare guild richness of the bird species that participated in flocks. Frequency histograms were employed to quantify species participation in flocks.

Non-metric multidimensional scaling (NMDS) was used to compare dissimilarity of flock composition based on body size using ‘vegan’ package in R (R Core Team, 2021). The data matrix for this analysis was one where rows represented species and the columns represented unique flock IDs.

3.3.2 Quantifying the disturbance gradient

Since we had recorded 12 different vegetation variables (Table 1) as a measure of disturbance, I used Principal Component Analysis (PCA) to reduce the dimensionality of the vegetation predictor variables and condense them to a few composite axes of disturbance (Raman et al., 1998; Sridhar & Sankar, 2008). The site scores on the chosen axis were then used as a measure of disturbance for that site. I specified the PCA to categorise the transects into five clusters based on the intensity of disturbance. This procedure was carried out using the ‘stats’ package in R.

3.3.3 Relationships of bird and flock variables with disturbance

Linear models were used to build regressions between the response variables and PC1 scores (as a composite measure of disturbance determined from the PCA - predictor variable). I compared PC1 scores against insectivore richness, insectivore abundance, flock richness, flock size and flocking propensity. In the case of the flock variables, we used log-transformed values of the observed data to ensure that the assumptions of normality were not violated.

3.3.4 Variation of flock composition with disturbance

Flock participants of each transect were arranged in a species-site matrix format based on presence-absence data. The transects were then grouped into five clusters based on the intensity of disturbance, from the categorisation obtained by the PCA. A dissimilarity matrix of the species-site matrix was created using Jaccard’s index. NMDS ordination was then used to visualise how flock composition varied with disturbance.

3.3.5 Relationships of arthropod abundance with disturbance

Linear models were used to build regressions between the foliage arthropod abundance and flying arthropod abundance versus PC1 scores (predictor variable) separately.

3.3.6 Relationships of bird and flock variables with foliage arthropod abundance

Linear models were used to build regressions between the response variables and foliage arthropod abundance (predictor variable). We compared foliage arthropod abundance against insectivore richness, insectivore abundance, flock richness, flock size and flocking propensity. In the case of the flock variables, we used log-transformed values of the observed (count) data to ensure that the assumptions of normality were not violated.

4. Results

4.1 Flock descriptions

A total of 120 flocks were seen throughout the study period (late December 2023-late March 2024). 84 species were detected in the study, out of which 55 species (65%) were observed to participate in flocks to varying degrees. Most species in flocks were insectivores (45 species). Within the insectivore dietary guild, 24 species were foliage gleaners, 8 species each were bark-gleaners and salliers and 5 species were ground-feeders (Figures 2a and 2b).

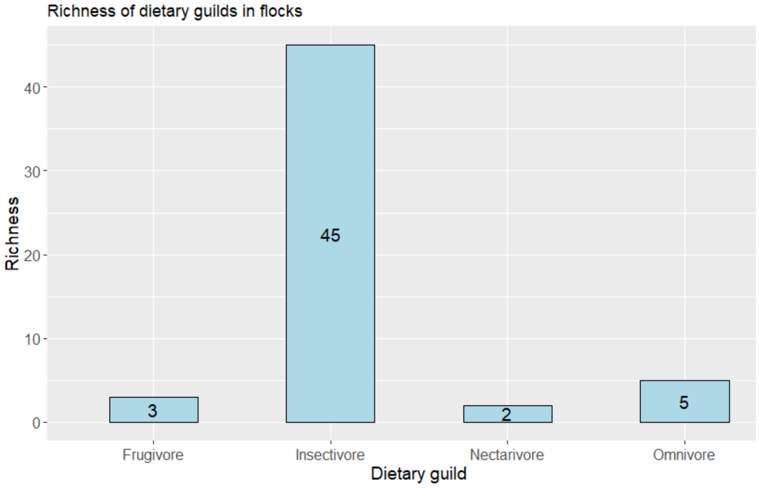


Figure 2a: Bar plot depicting the species richness of each dietary guild (Frugivore, Insectivore, Nectarivore and Omnivore) in flocks.

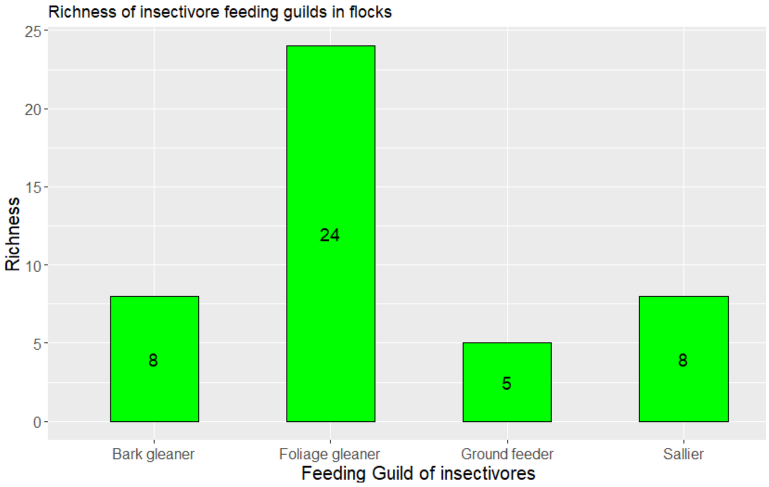


Figure 2b: Bar plot depicting species richness of each feeding guild within the insectivore dietary guild.

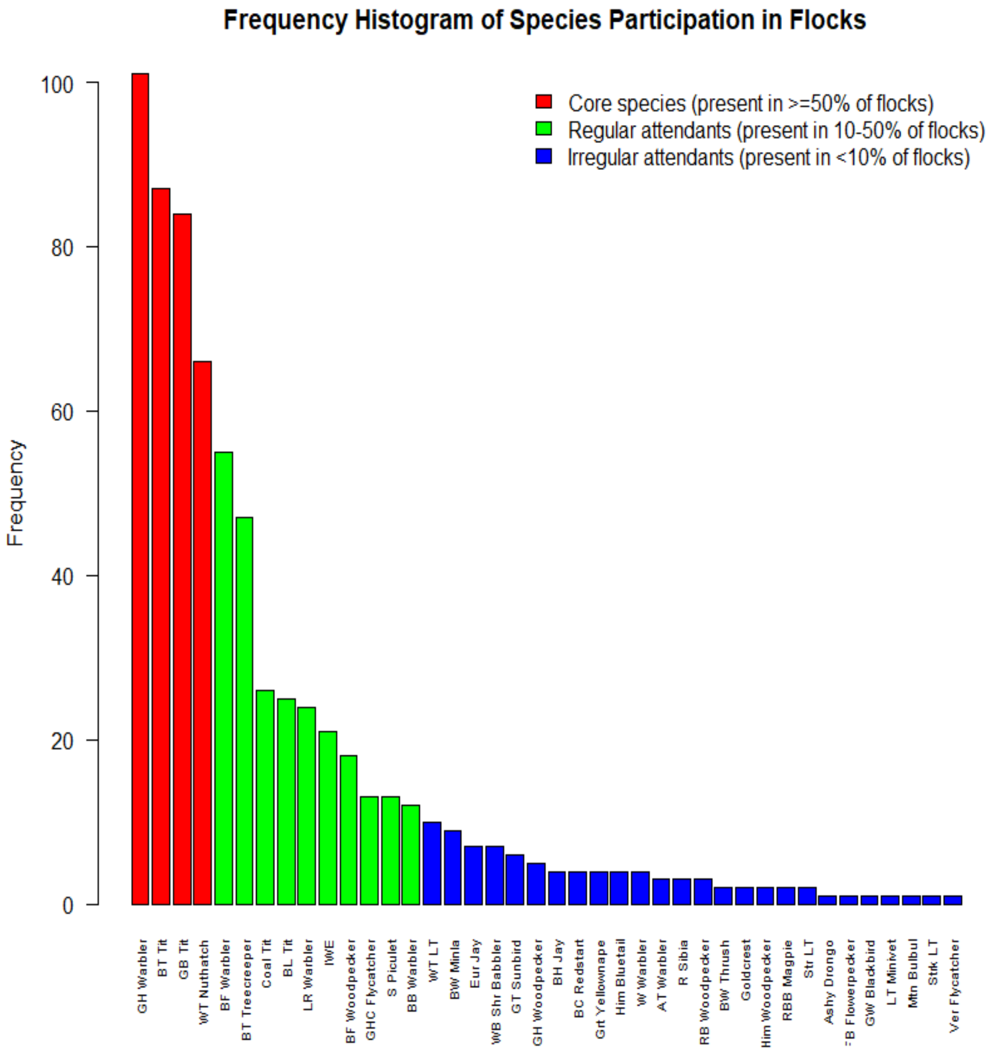


Figure 3: Frequency histogram quantifying species participation in flocks. Species in red represent core species, species in green represent regular attendants and species in blue represent irregular attendants.

I classified flocking species into three categories, i.e., core species, regular attendants and irregular attendants. These categorisations were based on the degree to which each species participated in flocks.

Core species: Species in red represent ‘core species’ that were seen to participate in >50% of flocks observed. In this study, the core species were the Gray-hooded Warbler, Black-throated Tit, Green-backed Tit and White-tailed Nuthatch.

Regular attendants: Species in green represent ‘regular attendants’ that participated in 10-50% of the flocks observed. Examples of regular attendants include the Black-faced Warbler and Bar-tailed Treecreeper.

Irregular attendants: Species in blue represent ‘irregular attendants’ that participated in <10% of the flocks observed. Examples of irregular attendants include the Blue-winged Minla and White-browed Shrike-Babbler.

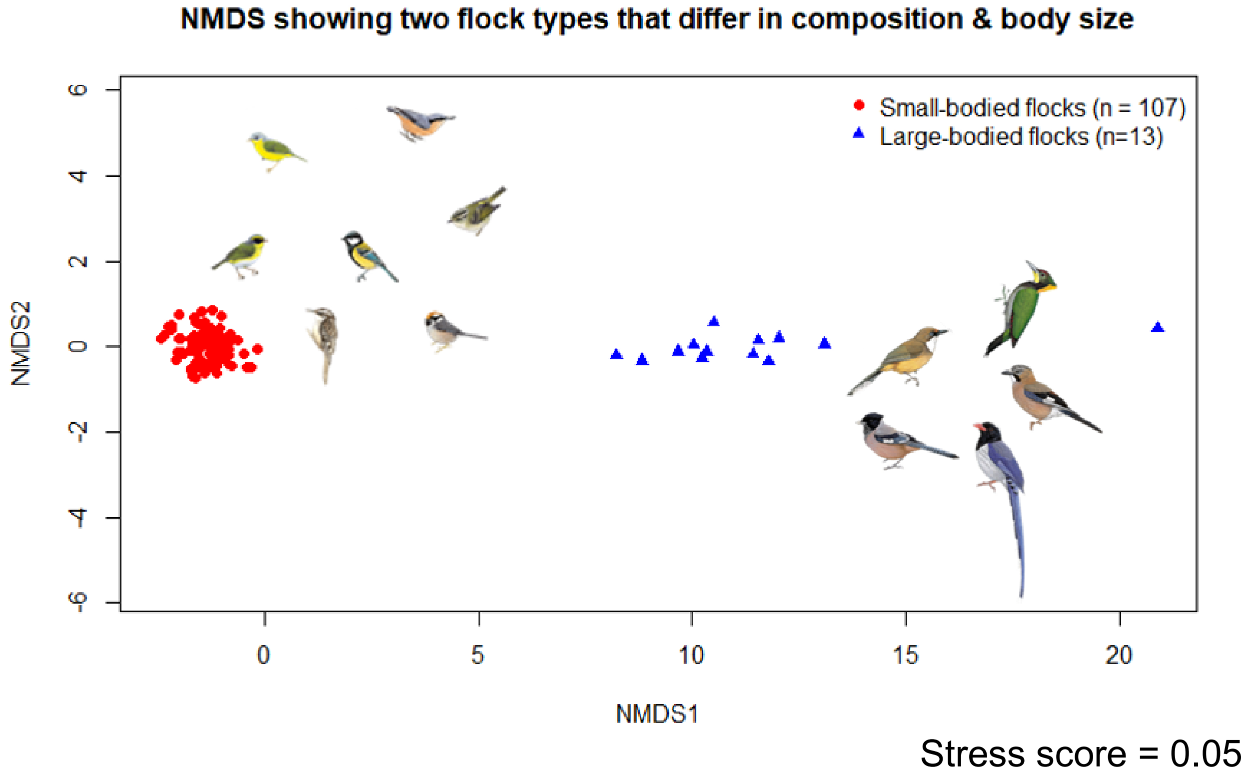


Figure 4: NMDS plot displaying the two different flock types in the study area based on differences in species composition and body size of participating species.

Flock types: There were two starkly different flock types in the study area, based on composition and body size of participants – Small-bodied flocks and Large-bodied flocks.

If the majority (>80%) of species in a particular flock were <=40 g, then the flock was classified as a ‘small-bodied flock’. In contrast, if 80% of species in a flock were >40g, then the flock was classified as a ‘large-bodied flock’.

4.2 Quantifying the disturbance gradient

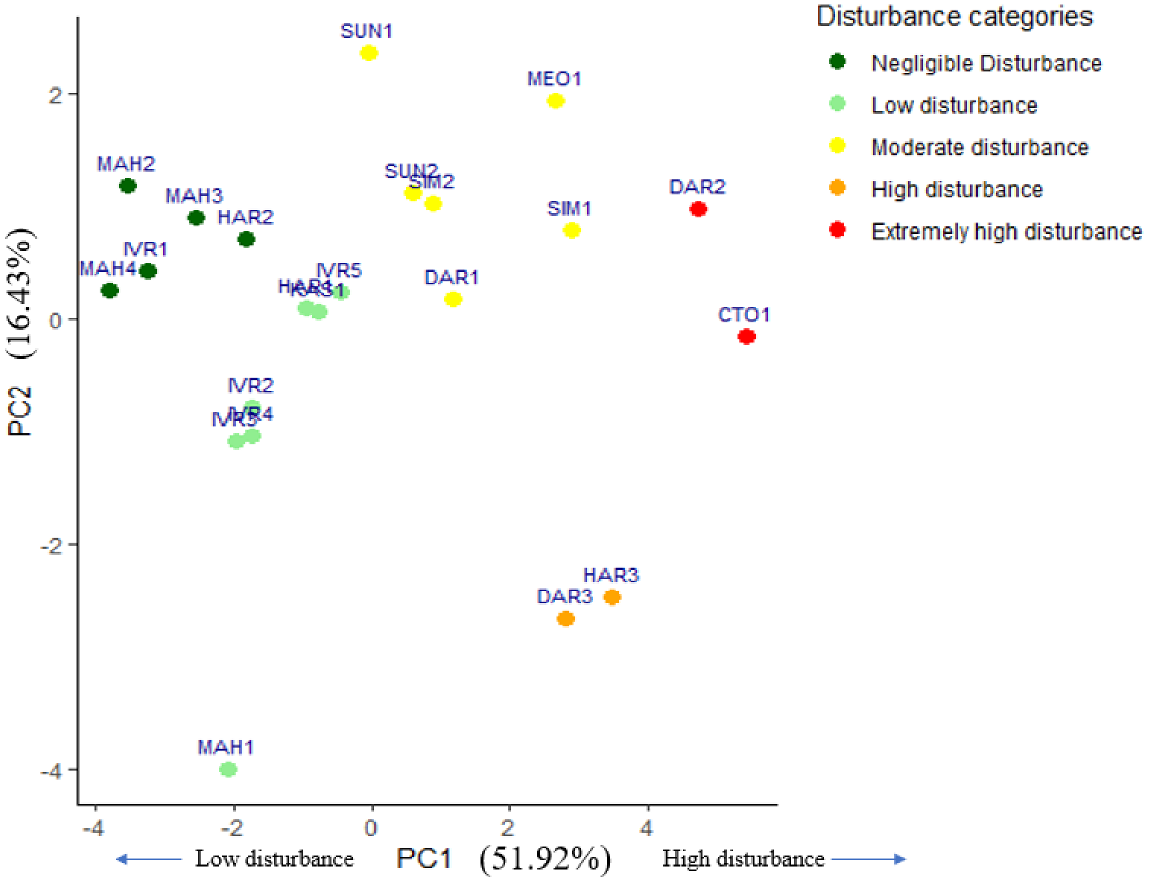


Figure 5: Principal Component Analysis (PCA) depicting clustering of sites based on similarity in intensity of disturbance. The PCA resulted in five categories of disturbance, arranged in increasing intensity of disturbance: Negligible disturbance (dark green), Low disturbance (light green), Moderate disturbance (yellow), High disturbance (orange), Extremely high disturbance (red).

The PC1 axis explained 51% of the variance in the data, while the PC2 axis explained 16% of the variance in the data. PC1 was positively correlated to mean lopping score, number of coppices, number of stumps, and negatively correlated to canopy density, tree height and foliage height. PC2 was negatively correlated with cumulative basal area and tree density.

I assume that change in vegetation structure is an outcome of the anthropogenic disturbance in the study area, since most human activity leading to disturbance are likely to affect vegetation structure. We therefore used PC1 scores (composite of vegetation variables/disturbance) as a measure of disturbance. This was supported by the observation that the variables that loaded on PC1 axis were those that manifest as a consequence of disturbance, such as reduced canopy density and tree height, and higher lopping scores and number of coppices. Transects with negative scores on PC1 were adjudged to be relatively undisturbed, while transects with more positive scores on PC1 were relatively disturbed. This translated into obtaining a disturbance gradient, which also corroborated with observations from the field.

4.3 The effect of disturbance on flocks and insectivores by altering vegetation structure

4.3.1 Insectivores decline with increasing disturbance

I found a weak negative relationship between insectivorous bird richness and disturbance intensity at the study site (Figure 6a). On the other hand, I found a stronger negative relationship between insectivorous bird abundance and disturbance (R-squared = 0.33) (Figure 6b).

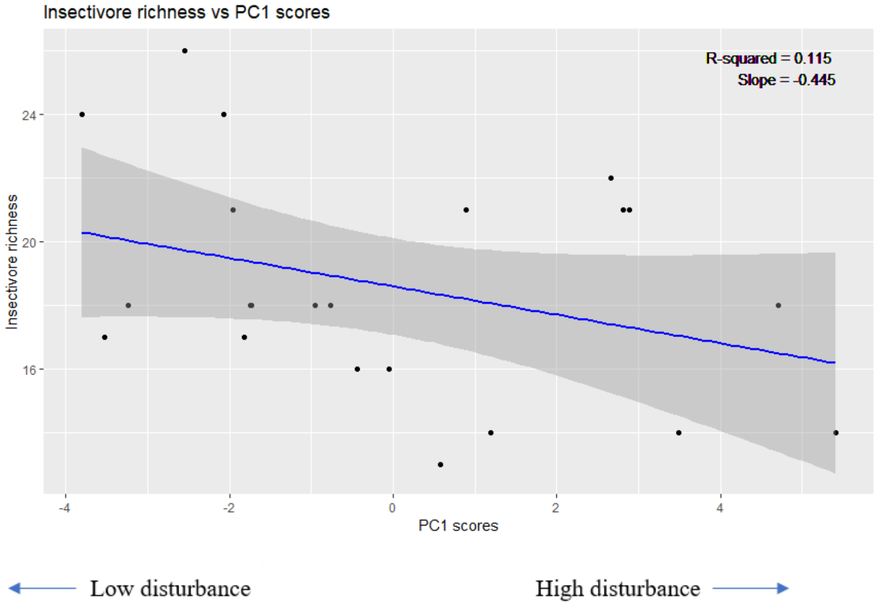


Figure 6a: Linear regression depicting the relationship between insectivore richness and PC1 scores.

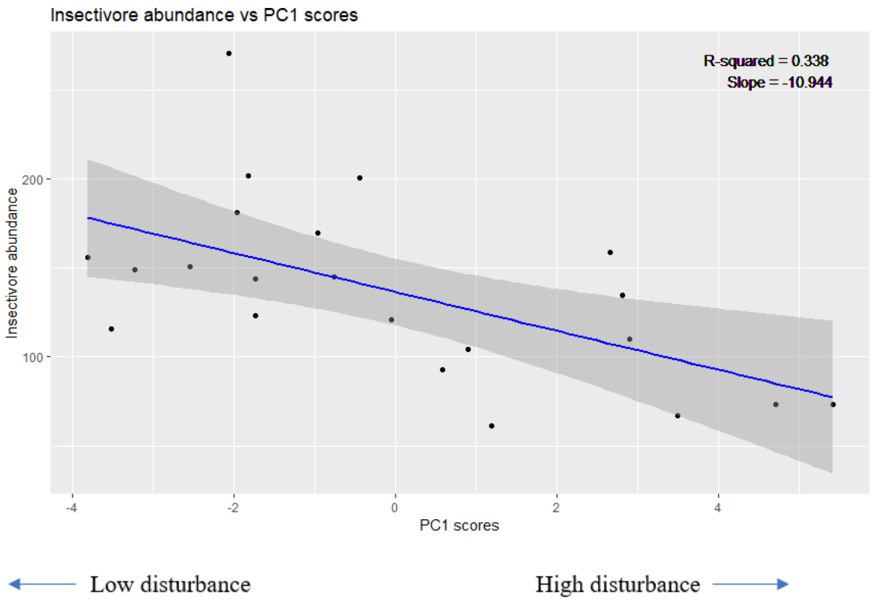


Figure 6b: Linear regression depicting the relationship between insectivore abundance and PC1 scores.

4.3.2 Flock variables decline with increasing disturbance

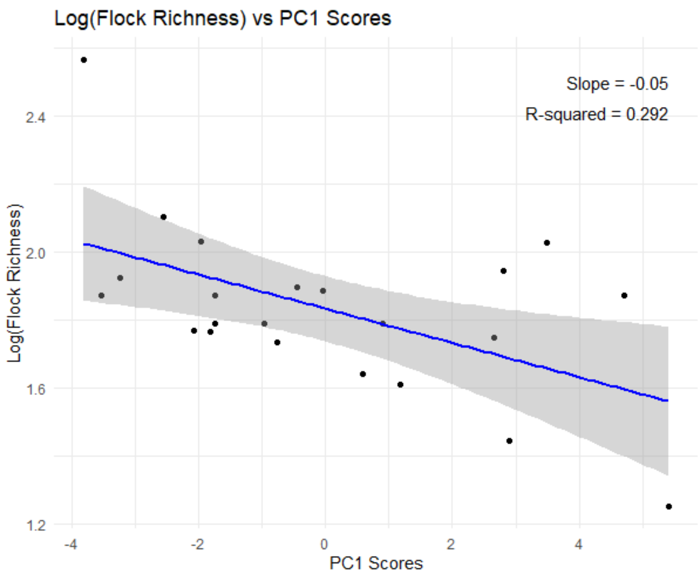
The relationship between PC1 scores and log of Flock richness, log of Flock size and log of No. of flocks encountered was each plotted separately using a linear model (Table 2). PC1 scores had a significant effect on Flock richness, Flock size and No. of flocks encountered ($p < 0.05$).

All three flock variables showed a negative trend with increasing disturbance (i.e. increase in PC1 scores).

Table 2: Linear models of log(Flock richness), log(Flock size) and log(No. of flocks encountered) analysed separately against PC1 scores

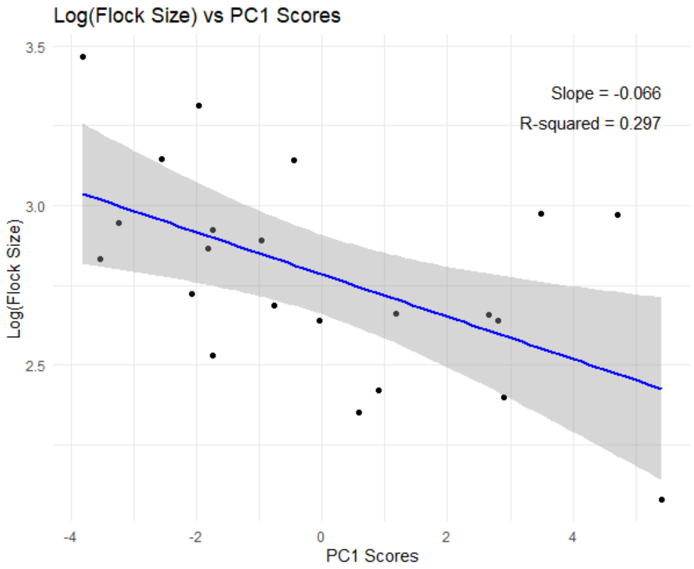
lm(formula = log(Flock.richness) ~ PC1.scores)				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	1.83401	0.0461	< 2e-16	0.2924
PC1.scores	-0.05031	0.0175	0.00937	
lm(formula = log(Flock.size) ~ PC1.scores)				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	2.78454	0.06006	< 2e-16	0.2966
PC1.scores	-0.06622	0.0228	0.00877	
lm(formula = log(No.of.flocks.9.reps) ~ PC1.scores)				

	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	1.34513	0.12630	1.09e-09	0.2188
PC1.scores	-0.11347	0.04795	0.0282	



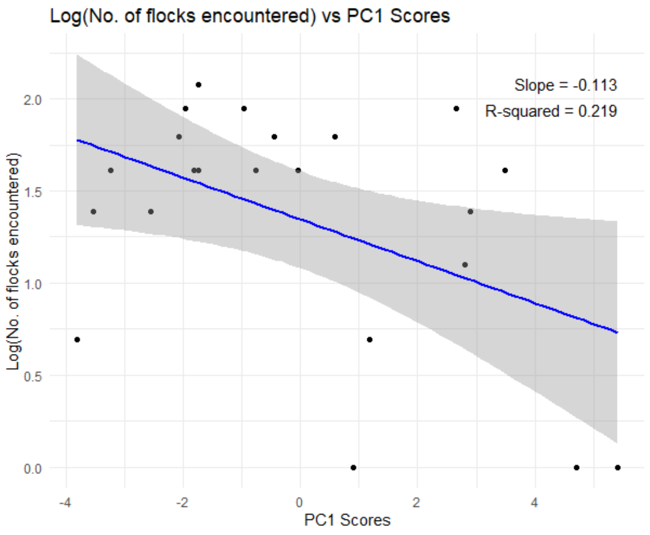
Low disturbance High disturbance

Figure 7a) Linear regression depicting the relationship between log(Flock richness) and PC1 scores.



Low disturbance High disturbance

Figure 7b) Linear regression depicting the relationship between log(Flock size) and PC1 scores.



← Low disturbance High disturbance →

Figure 7c) Linear regression depicting the relationship between log of No. of flocks encountered and PC1 scores.

4.3.3 Lower flocking propensities for select species with increasing disturbance

The log of Propensity of Gray-hooded Warbler, Black-throated Tit and Green-backed Tit was each plotted separately against PC1 scores using a linear model (Table 2). PC1 scores did not have a significant effect on the flocking propensity of any of these species ($p > 0.05$).

The propensity of all three species showed a negative trend with increasing disturbance (i.e. increase in PC1 scores), with the relationship strongest for the Black-throated Tit.

I focussed on these three species since they were the most common species in flocks. They were also were present in sufficient numbers across all transects to enable a comparison of propensity across the disturbance gradient.

Table 3: Linear models of log(Propensity of Gray-hooded Warbler), log(Propensity of Black-throated Tit) and log(Propensity of Green-backed Tit) analyses separately against PC1 scores

lm(formula = log(Propensity.GHW) ~ PC1.scores)				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	-1.33257	0.17040	1.65e-07	0.03326
PC1.scores	-0.05366	0.06469	0.417	
lm(formula = log(Propensity.BTT) ~ PC1.scores				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	-1.01667	0.15460	2.09e-06	0.1188
PC1.scores	-0.09639	0.05869	0.116	
lm(formula = log(Propensity.GB.tit) ~ PC1.scores				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	-1.26074	0.13357	8.28e-09	0.05917
PC1.scores	-0.05687	0.05071	0.275	

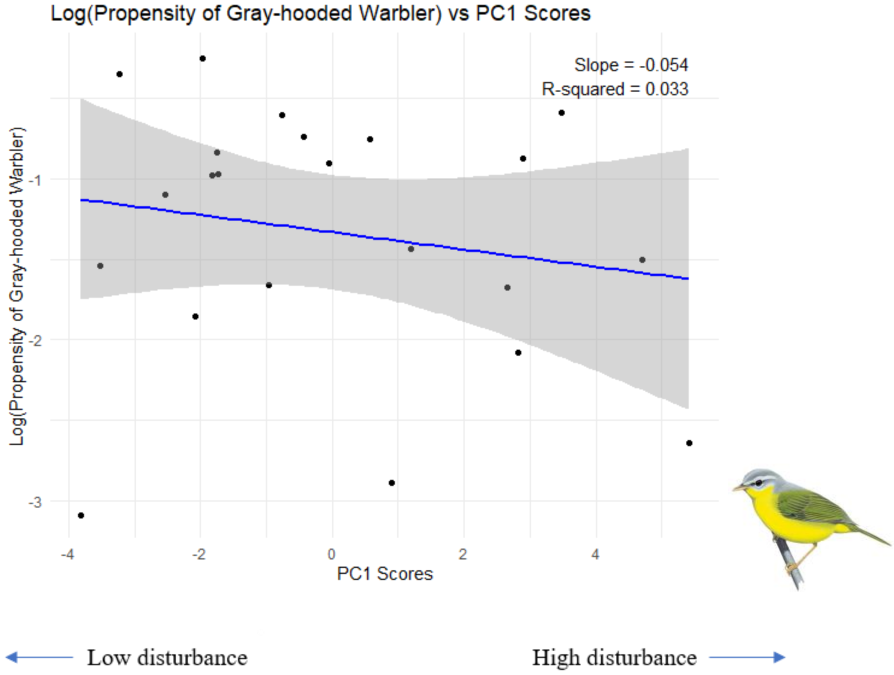


Figure 8a): Linear regression depicting the relationship between log(Propensity of Gray-hooded Warbler) and PC1 scores.

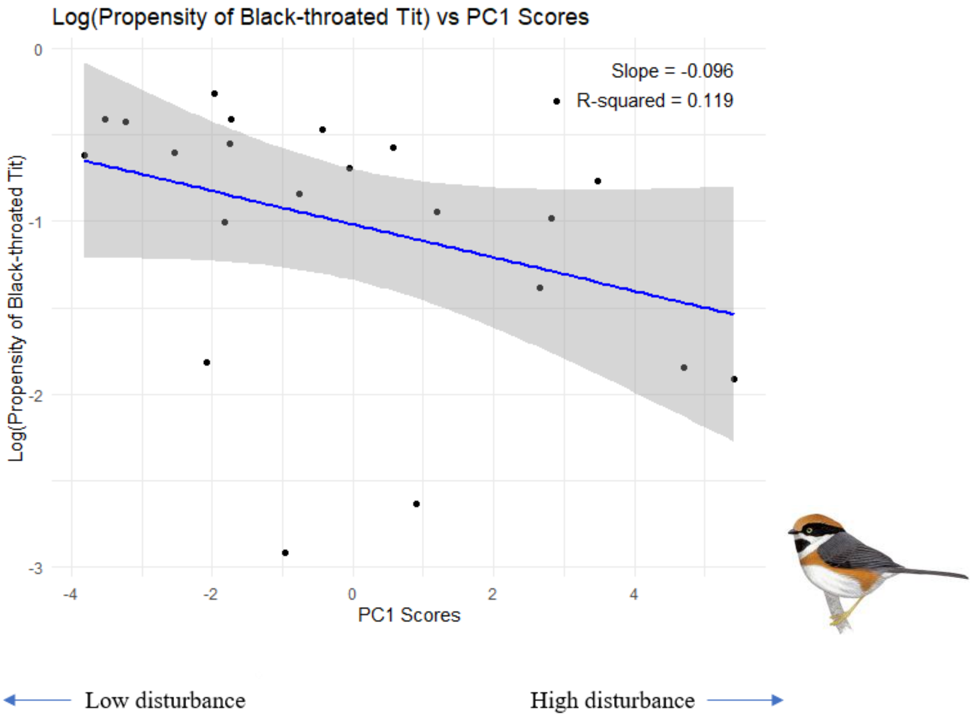


Figure 8b): Linear regression depicting the relationship between log(Propensity of Black-throated Tit) and PC1 scores.

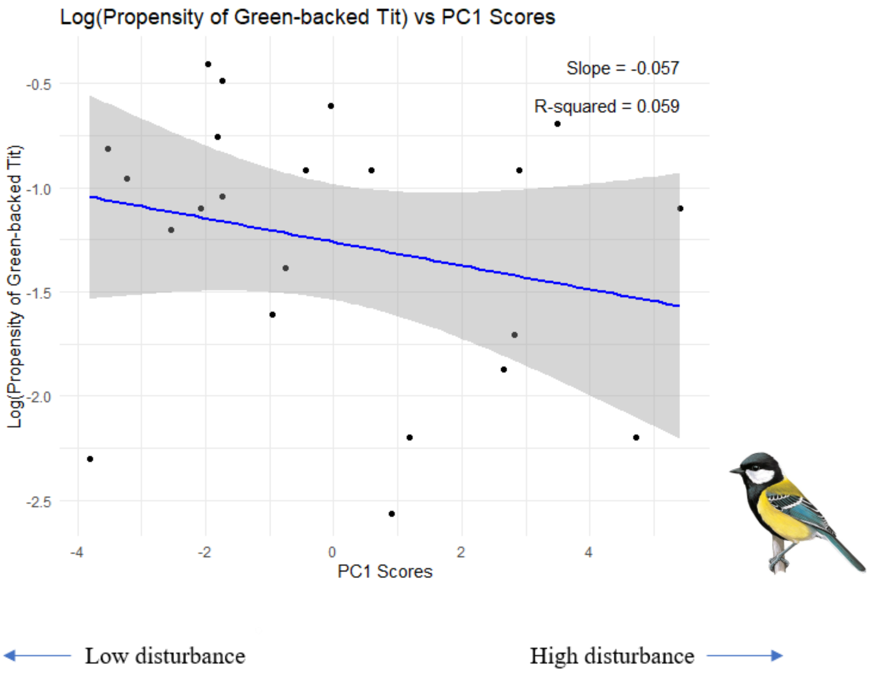


Figure 8c) Linear regression depicting the relationship between log(Propensity of Green-backed Tit) and PC1 scores.

4.3.4 Variation of flock composition with disturbance

Negligible Disturbance and Low Disturbance transects cluster together in terms of composition of flock participants. However, overall there doesn't seem to be clear species composition-based clustering of transects with similar disturbance. This suggests that transects that are similar in intensity of disturbance may not necessarily possess similar flock composition.

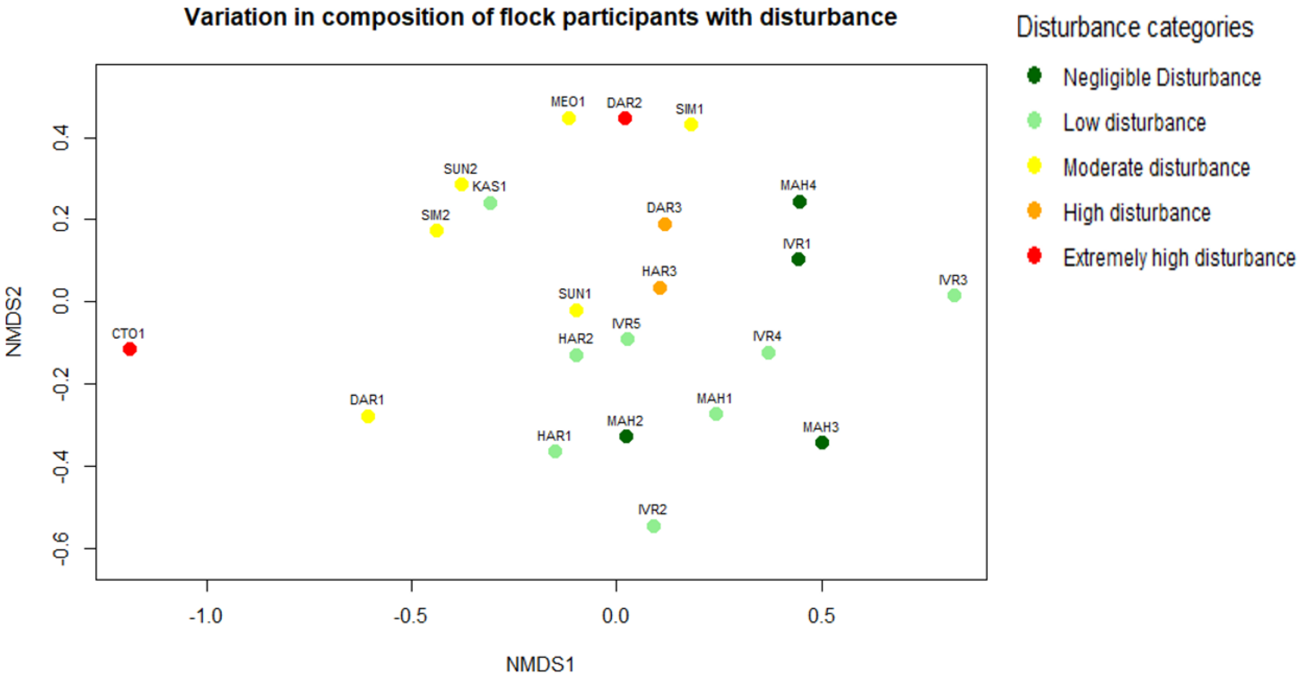


Figure 9: NMDS ordination showing flock composition in different disturbance categories. Each circle represents a transect assigned to one of five disturbance categories, as mentioned in the legend.

4.4 The effect of disturbance on flocks and insectivores through changes in arthropod abundance

4.4.1 Foliage arthropods respond negatively to disturbance, while flying arthropod abundance largely remains constant with disturbance

Foliage arthropod abundance showed a strong negative trend with increasing disturbance (R-squared = 0.40) (Figure 10a). Flying arthropod abundance showed little change with increasing disturbance (R-squared = 0.001) (Figure 10b).

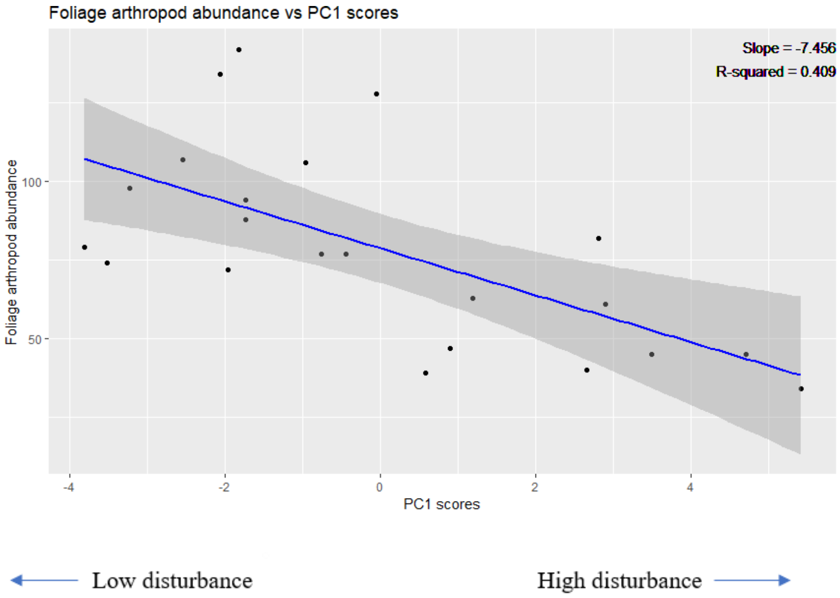


Figure 10a: Linear regression depicting the relationship between foliage arthropod abundance and PC1 scores.

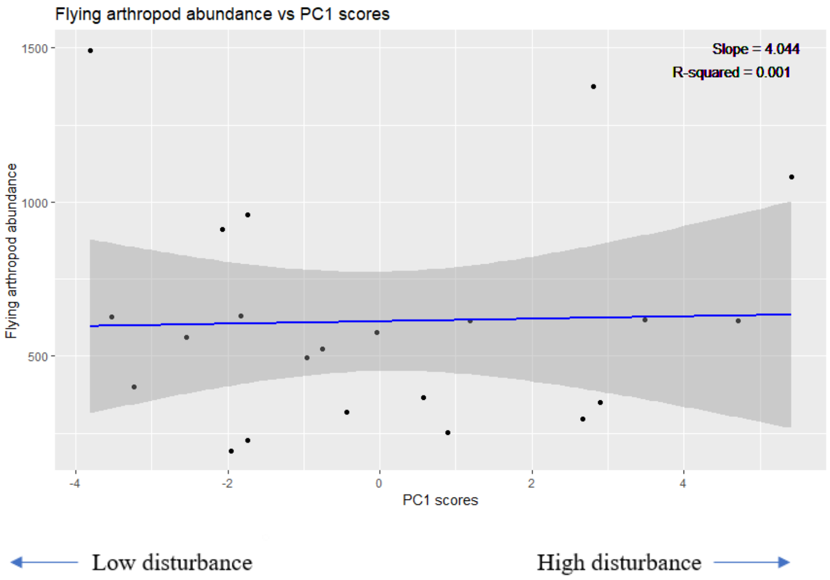


Figure 10b: Linear regression depicting the relationship between flying arthropod abundance and PC1 scores.

4.4.2 Insectivores show an increase in richness and abundance with an increase in foliage arthropods

Both insectivore richness and abundance show a positive relationship with increase in foliage arthropod abundance. The strength of the relationship is quite strong for the latter (R-squared = 0.46)

The corollary of this result is that insectivore richness and abundance would decline with reduction in foliage arthropod abundance. It is worth keeping this in mind for the discussion section below.

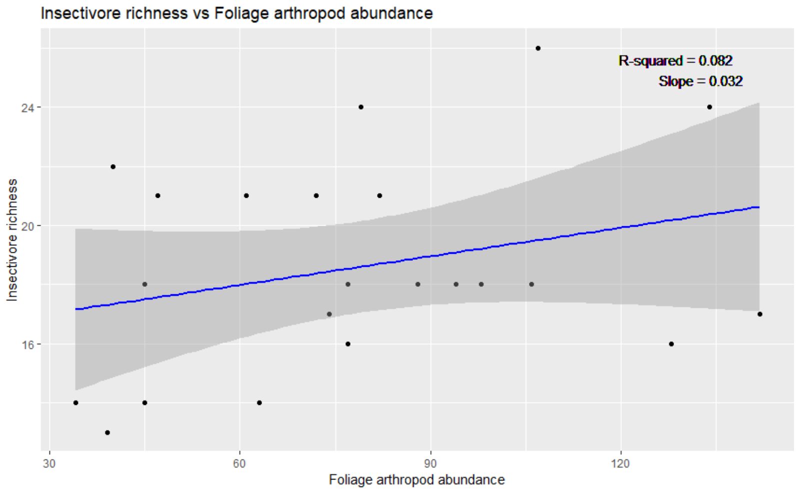


Figure 11a: Linear regression depicting the relationship between insectivore richness and foliage arthropod abundance.

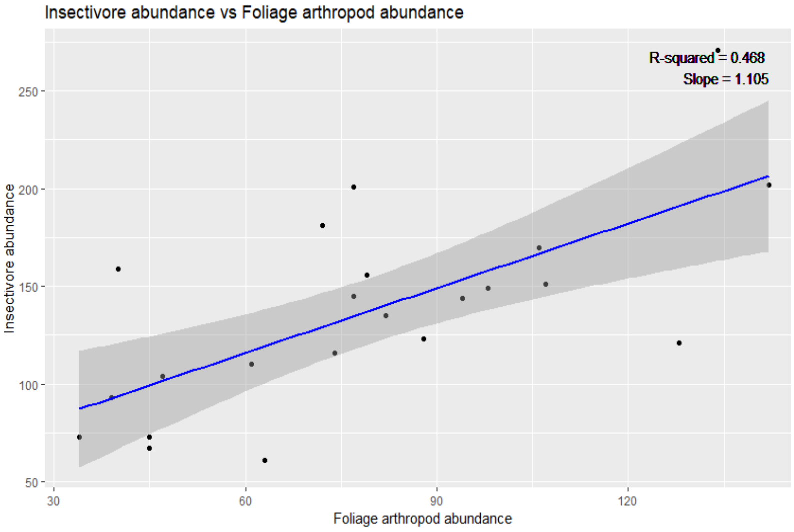


Figure 11b: Linear regression depicting the relationship between insectivore abundance and foliage arthropod abundance.

4.4.3 Flock variables show weak positive relationships with increase in foliage arthropod abundance

Foliage arthropod abundance did not have a significant effect on either of flock richness, flock size or no. of flocks encountered ($p > 0.05$) (Table 4).

All the flock variables showed weak positive correlations with foliage arthropod abundance (Figures 12a, 12b and 12c).

Table 4: Linear models of log(Flock richness), log(Flock size) and log(No. of flocks encountered) analysed separately against Foliage arthropod abundance (Represented in the model as 'No..of.bagged.arthropods')

<table>
<tr><td colspan="5">lm(formula = log(Flock.richness) ~ No..of.bagged.arthropods)</td></tr>
<tr><td></td><td>Estimate</td><td>Std. Error</td><td>Pr(>|t|)</td><td>R-squared</td></tr>
<tr><td>(Intercept)</td><td>1.669611</td><td>0.145626</td><td>3.03e-10</td><td rowspan="2">0.06839</td></tr>
<tr><td>No..of.bagged.arthropods</td><td>0.002088</td><td>0.001723</td><td>0.24</td></tr>
<tr><td colspan="5">lm(formula = log(Flock.size) ~ No..of.bagged.arthropods)</td></tr>
<tr><td></td><td>Estimate</td><td>Std. Error</td><td>Pr(>|t|)</td><td>R-squared</td></tr>
<tr><td>(Intercept)</td><td>2.528547</td><td>0.187341</td><td>1.66e-11</td><td rowspan="2">0.09711</td></tr>
<tr><td>No..of.bagged.arthropods</td><td>0.003252</td><td>0.002217</td><td>0.158</td></tr>
<tr><td colspan="5">lm(formula = log(No.of.flocks.9.reps) ~ No..of.bagged.arthropods)</td></tr>
<tr><td></td><td>Estimate</td><td>Std. Error</td><td>Pr(>|t|)</td><td>R-squared</td></tr>
<tr><td>(Intercept)</td><td>0.615450</td><td>0.352241</td><td>0.0959</td><td rowspan="2">0.1982</td></tr>
<tr><td>No..of.bagged.arthropods</td><td>0.009268</td><td>0.004169</td><td>0.0379</td></tr>
</table>

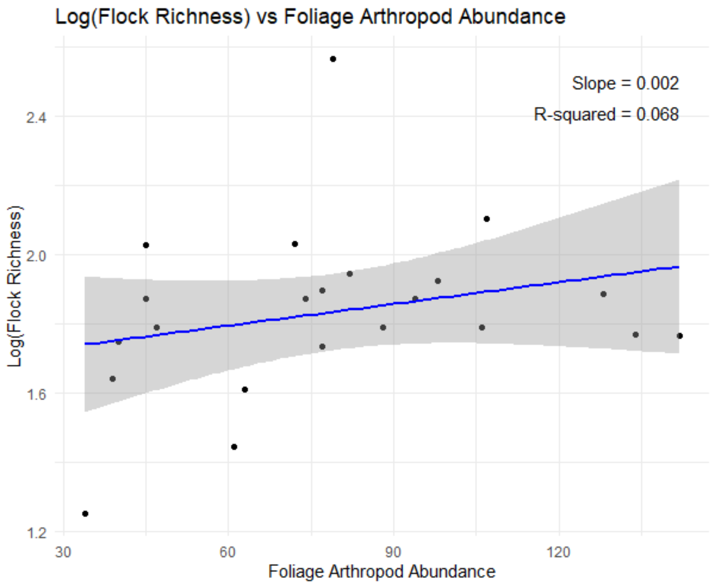


Figure 12a: Linear regression depicting the relationship between log of flock richness and foliage arthropod abundance.

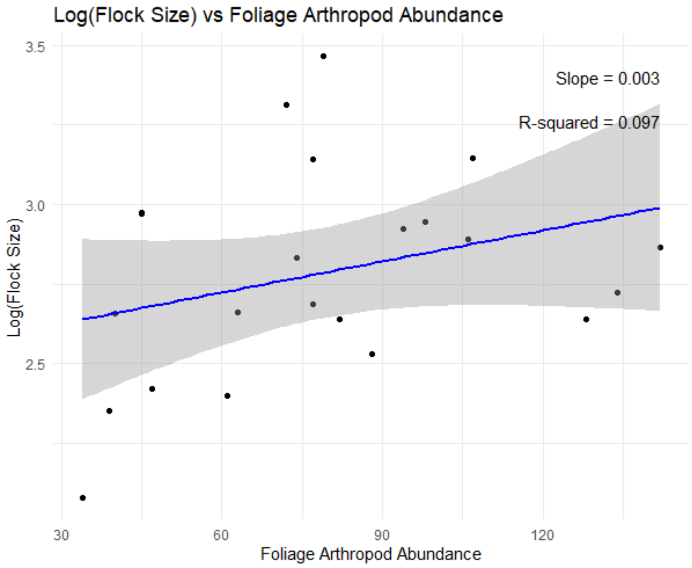


Figure 12b: Linear regression depicting the relationship between log of flock size and foliage arthropod abundance.

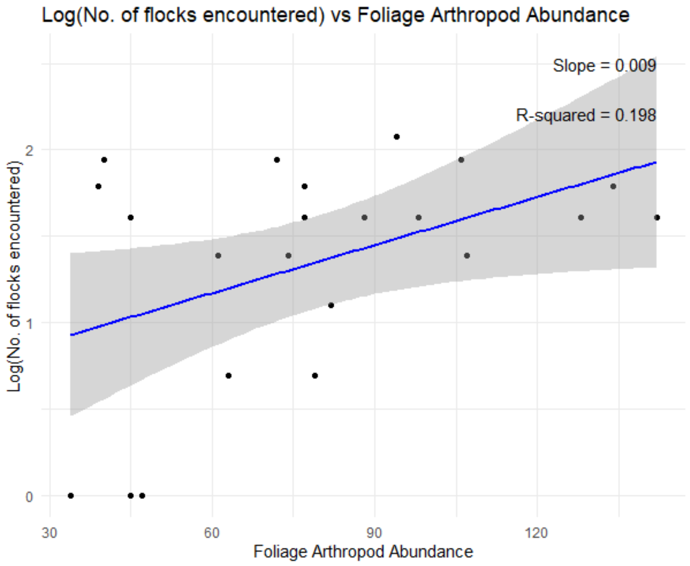


Figure 12c: Linear regression depicting the relationship between log of no. of flocks encountered and foliage arthropod abundance.

4..4.2 Propensity of select species show weak positive relationships with increase in foliage arthropod abundance

Foliage arthropod abundance did not have a significant effect on flocking propensity of any of the three species ($p > 0.05$) (Table 5).

The propensity of all three species showed weak positive correlations with an increase in foliage arthropod abundance.

Table 5: Linear models of log(Propensity of Gray-hooded Warbler), log(Propensity of Black-throated Tit) and log(Propensity of Green-backed Tit) analysed separately against Foliage arthropod abundance (Represented in the model as 'No..of.bagged.arthropods')

lm(formula = log(Propensity.GHW) ~ No..of.bagged.arthropods)				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	-1.721506	0.467898	0.00149	0.03828
No..of.bagged.arthropods	0.004940	0.005537	0.38290	
lm(formula = log(Propensity.BTT) ~ No..of.bagged.arthropods)				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	-1.175509	0.451803	0.0171	0.007069
No..of.bagged.arthropods	0.002018	0.005347	0.7099	
lm(formula = log(Propensity.GB.Tit) ~ No..of.bagged.arthropods)				
	Estimate	Std. Error	Pr(>|t|)	R-squared
(Intercept)	-1.781063	0.357944	7.27e-05	0.1085
No..of.bagged.arthropods	0.006609	0.004236	0.134	

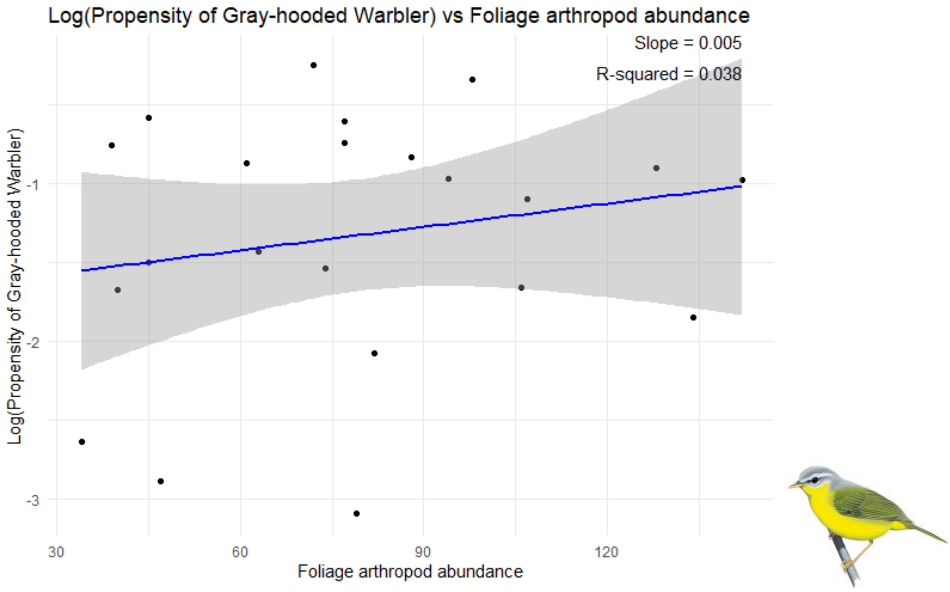


Figure 13a) Linear regression depicting the relationship between log of propensity of Gray-hooded Warbler and foliage arthropod abundance.

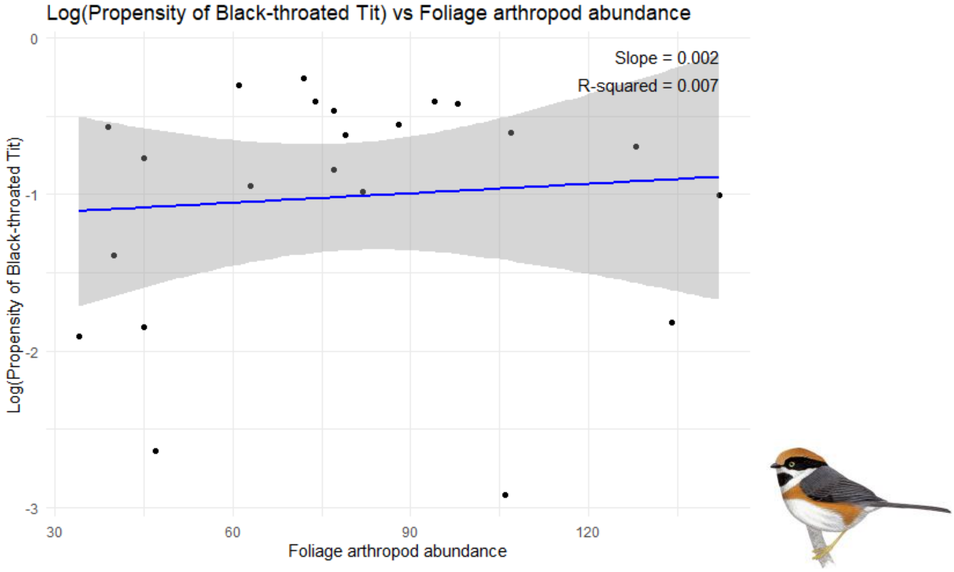


Figure 13b) Linear regression depicting the relationship between log of propensity of Black-throated Tit and foliage arthropod abundance.

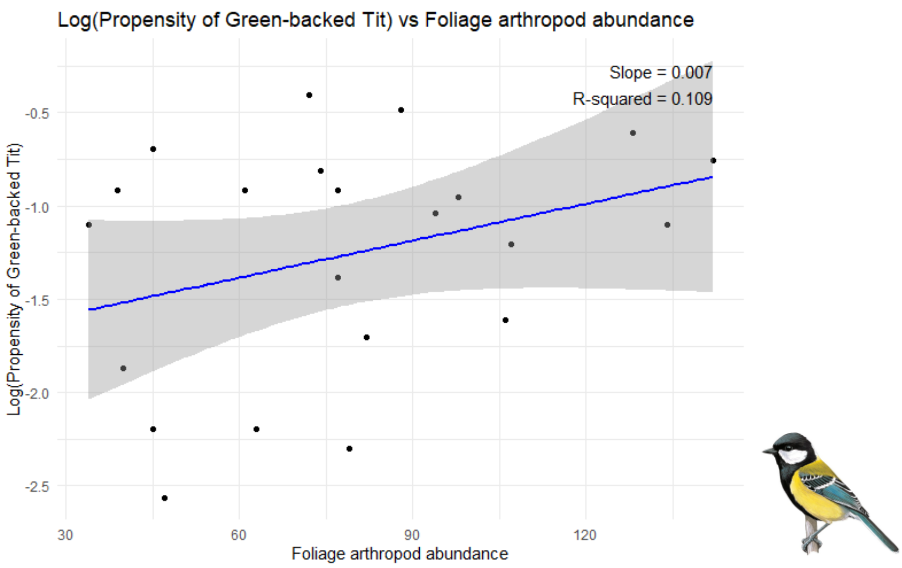


Figure 13c) Linear regression depicting the relationship between log of propensity of Green-backed Tit and foliage arthropod abundance.

5. Discussion

5.1 Flock descriptions

5.1.1 Characteristics of flock participants

I found that a large proportion of the bird community in the Western Himalaya participate in mixed-species flocks in the winter. 84 species were detected in this study, out of which 55 species (65%) were observed to participate in flocks. In concordance with results from a large-scale review on flock literature (Sridhar et al., 2009), most species in flocks in this study were insectivorous passerines (81%). Some omnivores (Corvidae), frugivores (flowerpeckers *Dicaeum* spp.) and nectarivores (sunbirds *Aethopyga* spp.) also occasionally participated in flocks.

Within the insectivore dietary guild, 53% of insectivore species were foliage gleaners (Phylloscopidae), followed by bark gleaners (Sittidae and Certhiidae) and salliers (Muscicapidae) (18% each) and ground-feeding insectivores (Leiothrichidae, Timaliidae) (11%) (Figures 2a and 2b, Appendix).

The core species in flocks (found in >= 50% of flocks) were the Gray-hooded Warbler, Black-throated Tit, Green-backed Tit and White-tailed Nuthatch (Figure 3). Core species in this study seem to have certain characteristics of nuclearity that underlie their importance to the flocks they are part of. For example, these species tend to be found in a high percentage of flocks and/or are gregarious in habit, among other traits (Sridhar et al., 2009). The Black-throated Tit seems to fit these criteria, given that it is a core species whose intraspecific gregarious nature is well-documented (Geldard et al., 2023).

The other three species (Gray-hooded Warbler, Green-backed Tit and White-tailed Nuthatch) were also found to participate in the majority of flocks observed, indicating their importance.

These species are known to occur in small groups/family parties outside the breeding season (Gosler & Clement, 2020; Harrap, 2020; Madge, 2020) being gregarious in habit but to a lesser extent than the Black-throated Tit.

Although we did not test for flock leadership in this work (i.e. species that are at the forefront of flocks while it is travelling), it is worth noting that gregarious species like the Black-throated Tit tend to lead flocks more often (Goodale & Beauchamp, 2010). Flock leaders also tend to be cooperative breeders (Sridhar et al., 2009), which is once again true for the Black-throated Tit (Geldard et al., 2023).

Why do species participate to varied degrees in flocks?

A simple explanation for the differences in the frequency of participation of species in flocks is that they may be a reflection of species' abundances in the community. However, there may be other reasons as to why certain species participate in flocks more than others. Insectivorous species have higher frequency of participation relative to other diet guilds (this work; Greenberg, 2001), which clearly indicates that diet is an important factor in the propensity of a species to join a flock.

The literature suggests that increased foraging efficiency and/or anti-predatory benefits may be the drivers of flocking behaviour (Sridhar et al., 2009). Although I did not test either of these hypotheses with regards to species participating to different degrees in flocks, it is useful to think of reasons as to why this phenomenon occurs. There is relatively little evidence for the foraging efficiency hypothesis (Sridhar & Shanker, 2014). Different species in flocks utilise diverse microhabitats and foraging techniques to find and catch prey. Therefore, the benefits of group foraging are unlikely to provide benefits to all participant species, because they may occupy a vast range of foraging niches that may not be similar to one another. The benefit of increased foraging efficiency seems to apply only to salliers. This is likely due to their ability to fly-catch insects that are flushed by the movement and activity of other birds (Sridhar & Shanker, 2014).

Flocks do not usually possess a high proportion of salliers (in the study areas of this work and Sridhar & Shanker, 2014). Evidence for the anti-predatory hypothesis seems to stem from a corollary of the finding that birds seem to not derive much foraging benefit from participating in flocks. In support of the anti-predation hypothesis, Sridhar et al., 2009 found that species that participate more in flocks tended to smaller, more insectivorous and more arboreal than species that participated less. Species possessing these traits tend to be more vulnerable to predation, which suggests that predation pressure plays a role in shaping a species' flocking propensity (Thiollay & Jullien, 2008). More support for the anti-predation hypothesis comes other studies that suggest flocking is less frequent in the absence of predators (Beauchamp, 2004) and species respond readily respond to alarm calls of other species while in flocks (Goodale & Kotagama, 2005).

Note on non-flocking species: There were 29 species that were not seen to participate in flocks during the study period (however not represented in Figure 3). Most of these species were frugivores (Eg. Great Barbet), omnivores (Eg. Kalij Pheasant) or granivores (Eg. Oriental Turtle-Dove). However, we did observe certain insectivore species that did not participate in flocks during the study period. The Rufous-bellied Niltava is known to be an irregular participant in flocks in other parts of Asia (Chen & Hsieh, 2002), but I did not observe it participating in flocks in my study. Some other insectivores were not detected often on transects because of their rarity (Eg. Rusty-cheeked Scimitar-Babbler) or spring arrival (Eg. Western-crowned Warbler) in the study area, and it is possible that we did not see these species in flocks simply as a matter of chance.

5.1.2 Flock types

There were two distinct flock types in the study area, markedly different in terms of species composition and body size of participants (Figure 4).

Small-bodied flocks: One flock type was composed largely of small-bodied species (body mass <= 40g), largely from the families Phylloscopidae, Aegithalidae, Paridae, Sittidae, Certhiidae and Picidae among others. The most common representatives of these families in small-bodied flocks were the Gray-hooded Warbler, Black-throated Tit, Green-backed Tit, White-tailed Nuthatch, Bar-tailed Treecreeper and Brown-fronted Woodpecker respectively. These flocks would forage largely in the midstory and canopy of the forest, although birds would occasionally descend to the understory while foraging as well.

Large-bodied flocks: The second flock type was composed largely of large-bodied species (>40 g), largely from the families Leiothrichidae, Corvidae, Picidae and Timaliidae among others. Some representative species from each of the families in large-bodied flocks are the White-throated Laughingthrush, Eurasian Jay, Gray-headed Woodpecker and Streak-breasted Scimitar-Babbler. These flocks tended to forage in the understory and on the forest floor.

The presence of different flock types in the same area has been reported elsewhere from North-east India and Myanmar (King & Rappole, 2001; Srinivasan et al., 2012).

Why do bird species of different body sizes not flock together?

A possible explanation could be due to differences in the travelling/activity speed between the two types of flocking birds - Large-bodied species (Eg. Laughingthrushes) may not able to match the speed of small-bodied species (Eg. Warblers) in flocks. One of the benefits that participants are thought to accrue from flocking is to increase foraging efficiency (Morse, 1977). The two flock types in this study were also observed to forage at different vertical strata (see above), suggesting differences in space use. The difference in foraging habits between small and large-bodied species in flocks may not facilitate foraging benefits being gained by either type of participant.

From the perspective of anti-predatory benefits, the predation pressure on small and large-bodied birds may differ. Large-bodied individuals may suffer from higher predation risk due to reduced flight performance and manoeuvrability (Witter et al., 1994). In contrast, other studies suggest that small-bodied species are more vulnerable to predation in flocks (Thiollay & Jullien, 2008). Both studies indicate that size plays a role in shaping degree of predation risk. Therefore, large-bodied and small-bodied species flocking together may not result in anti-predatory benefits accrued by either type of participant.

5.2 Quantifying the disturbance gradient

The PC1 axis explained 51% of the variance in the vegetation variables that were inputted in the Principal Component Analysis. Therefore, PC1 scores were used as a composite measure of disturbance (Raman et al., 1998; Sridhar & Sankar, 2008). Transects with negative values on PC1 were relatively undisturbed, while transects while more positive values were relatively disturbed. The key agent of disturbance that affects vegetation structure in the study area is lopping. Lopping is known to negatively affect canopy density and vertical stratification (Menon et al., 2019). There are also other forms of disturbance such as grass/shrub cutting and collection of leaf litter that impacts the understory stratum.

5.3 Disturbance negatively impacts flock variables by instigating declines of insectivorous birds

5.3.1 Increasing disturbance leads to loss of insectivores

In this study, insectivore richness and abundance were seen to decline with increasing disturbance. These results follow a similar negative relationship between insectivorous birds and disturbance from an earlier study in the same area (Menon et al., 2019). Other studies from the tropics also provide strong evidence that insectivores are threatened by multiple forms of forest degradation due to their ecological specialisation (L. L. Powell et al., 2015; Şekercioğlu et al., 2004; Şekercioğlu et al., 2002). The loss of canopy cover, tree canopy height and vertical stratification due to lopping leads to simplification of forest vegetation structure. This phenomenon alters the habitat for insectivorous birds by reducing the niches available for feeding and nesting.

5.3.2 Flock variables also show declines with increasing disturbance

Flock richness, flock size and number of flocks encountered, all exhibited declines with increasing disturbance (Figures 7a, b and c). PC1 scores were found to have a significant effect on all three of these flock variables, although the effect sizes for some of these were small (Table 2).

Disturbance-induced habitat degradation may affect flocks by altering the presence and abundance of species that may potentially participate in flocks (Sridhar & Shankar, 2008). The previous result of my study established a negative relationship between insectivore richness and abundances with increasing disturbance. Since flocks are a subset of the insectivore bird community, it stands to reason that the decline of insectivores would correspond to fewer, smaller and more species-poor flocks in disturbed transects.

The negative correlations between flock variables and disturbance are comparable with other studies that also show similar trends with increasing disturbance (Lee et al., 2005; Sridhar & Sankar, 2008; Zhang et al., 2013). It is important to note here that previous studies on the effect of disturbance on flocks have not perceived and quantified disturbance in the same way. There has been a wide variety of disturbance regimes investigated, such as the effect of urbanisation and edge effects (Lee et al., 2005), fragmentation (Sridhar and Sankar 2008, (Maldonado-Coelho & Marini, 2000), (Maldonado-Coelho & Marini, 2004), plantations/agroforestry/pasturelands (Colorado Zuluaga & Rodewald, 2015; Sidhu et al., 2010) or a combination of multiple disturbance regimes on flock response variables.

This study defines disturbance differently in the form of local biomass extraction. However, it does have some parallels with past work. Whatever the regime of disturbance, the outcome is largely a less complex vegetation structure in disturbed treatments compared to intact forest controls. The negative relationship between flock variables and disturbance in this work indicates that disturbance acts through simplification of vegetation structure, a result corroborated by a review of the effect of disturbance on flocks (Zou et al., 2018).

5.3.3 Flocking propensities show a weak negative relationship with increasing disturbance

I found that PC1 scores negatively influenced the propensity of certain species, namely the Gray-hooded Warbler, Black-throated Tit and Green-backed Tit (Figures 8a, b, c). Although the effect was not significant, it is useful to discuss possible hypotheses for this trend. The abundances of each species were observed to decline (unpublished result, this work) with increasing disturbance. Lower propensities to flock in disturbed transects may just be a function of lower abundances of these species. An alternate hypothesis suggests a role for the interaction of vegetation structure complexity and predation risk in influencing propensity. Higher predation risk stemming from low detectability of predators in undisturbed, structurally mature forests may lead to species having higher propensity to join flocks (Zhang et al., 2013). In contrast, predators may be more visible to insectivorous birds in disturbed areas. Increased detectability of predators may dissuade potential participants from joining a flock, since participants may also suffer some costs of competition by joining a flock (Sridhar et al., 2009).

5.3.4 Variation of flock composition with disturbance

I found no clear species-composition-based clustering in transects with similar disturbance levels. This could be because other than the body-sized based clustering, mixed-species flocks in our study area may not show distinct species compositions. If the overall community composition of birds reflects in the flock composition, then the latter would also be correlated to the former. This could also be possible if species that participate in flocks are resilient to the changes in disturbance that we were able to capture. However, improved sample sizes of flocks per transect could help ascertain the patterns in species composition similarity (Figure 9).

5.4 Disturbance also negatively impacts flock variables by inducing reductions in foliage arthropod abundances

5.4.1 Foliage arthropods respond negatively to disturbance, while flying arthropod abundance largely remains constant with disturbance

I found a strong negative relationship between foliage arthropods and disturbance. Arthropods, as ectotherms, rely significantly on external temperature and moisture levels to maintain normal physiological functions (Bale et al., 2002; Jaworski & Hilszczański, 2013; Menéndez, 2007). Arthropods generally exhibit limited tolerance ranges for both temperature and moisture and are typically less adept at coping with fluctuations in these environmental factors (Deutsch et al., 2008). Opening of the canopy might result in higher day temperatures and lower moisture levels, which may render arthropods more prone to dessication (Barlow & Peres, 2004; Richards & Windsor, 2007; Silveira et al., 2010).

The abundance of flying arthropods showed a very weak positive correlation with increasing disturbance. Open and sunny patches in disturbed sites may maintain flying arthropod abundance at a level comparable to undisturbed sites (Aggarwal et al., 2023). Since this variable itself did not show a significant relationship with disturbance, and most flocking species in the study area were foliage gleaners, we opted to focus on the effect of foliage arthropods on insectivore and flock variables.

5.4.2 Insectivores show an increase in richness and abundance with an increase in foliage arthropods

Insectivore richness and abundance were shown to rise with increase in foliage arthropod abundance. The relationship for insectivore abundance was far stronger when compared to insectivore richness. I have already established that foliage arthropods decline in abundance with increasing disturbance. If the prey availability for insectivorous birds declines, it is reasonable to expect their abundance to also decline where food becomes scarce. As a corollary of this result, we can say with some certainty that insectivore richness and abundance would decline as disturbance reduces the abundance of foliage arthropods.

Evidence of similar findings that link the loss of insectivores through disturbance-induced changes in arthropod abundance is scant. Lister & Garcia, 2018 show that the decline of insectivores in Puerto Rican rainforest is tied to climate-change driven losses in arthropod biomass. Vergara et al., 2021 found that landscape effects are linked with declines in understory arthropods and corresponding declines in understory insectivore densities.

Very few studies have explored the combined effect of disturbance on insectivores through vegetation structure and arthropod availability. It is plausible that small-scale vegetation biomass extraction may cause loss of insectivores through reductions in arthropod abundance that are mediated by simplification of vegetation structure.

5.4.3 Flock variables show weak positive relationships with increase in foliage arthropod abundance

I found that foliage arthropod abundance had a positive effect on flock richness, flock size and number of flocks encountered, although the effects were only significant for the latter. The number of flocks encountered can be considered a surrogate for the frequency of flocking on a transect. From previous results, we know that undisturbed transects have higher foliage arthropod abundance that also corresponds to higher insectivore richness and abundance. Therefore, the pool of insectivorous birds from which flocks are drawn are larger in undisturbed areas. This indicates a greater degree of flock formation (Zhang et al., 2013) and a higher chance of encountering flocks. On the other hand, in disturbed areas, the impoverished insectivorous bird fauna means that the available birds that co-occur in space and time are lower in number. This may make flock formation a more infrequent event, because the threshold of individuals that are required to form and sustain a flock is lowered.

5.4.4 Propensity of select species show weak positive relationships with increase in foliage arthropod abundance

I found that foliage arthropod abundance had a positive effect on flocking propensity of three species, i.e. the Gray-hooded Warbler, Black-throated Tit and Green-backed Tit. Although the effect was not significant, it is worth discussing possible hypotheses. The result from the previous section indicates that the phenomenon of flocking is more frequent in undisturbed areas with higher arthropod abundance. The greater propensity of species to flock in transects with relatively higher arthropod abundance may be correlated to the presence of a higher number of insectivorous birds that are in turn supported by a higher prey base. On the other hand, flocks are thought to form to increase foraging efficiency of participants (Morse, 1977). An alternative hypothesis suggests that propensity should be higher in disturbed areas due to the scarcity of food availability. Indeed, Gentry et al., 2019 found that core species experienced energetic deficits in disturbed areas in the form of lower fat scores and more time spent foraging. My results are simple correlations between flocking propensity and arthropod abundance. The relationship needs to be explored in more detail to arrive at the exact mechanisms.

6. Conclusion

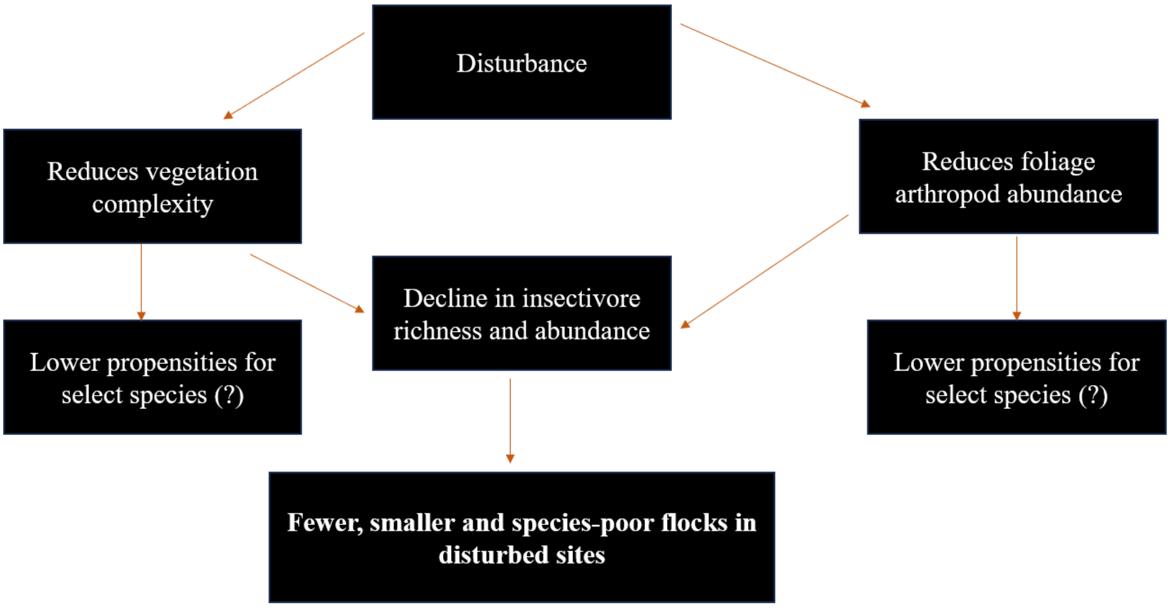


Figure 14: Flow diagram depicting a mechanism for the effect of disturbance on flock variables

The effect of disturbance is mediated through two dimensions – a) Vegetation structure and b) Foliage arthropod abundance. Disturbance causes simplification of vegetation structure that reduces the quality and complexity of habitat, ultimately leading to a decrease in the richness and abundance of insectivorous birds. Disturbance also leads to a reduction in foliage arthropod abundance, which decreases the food availability for insectivores. The combined loss of habitat quality and prey availability results in an impoverished insectivorous bird community in disturbed sites. As a result of a depauperate species pool, fewer flocks are formed that also tend to be smaller and more species-poor. I found a negative correlation between flocking propensity and disturbance, and a positive correlation between propensity and foliage arthropod abundance for the Gray-hooded Warbler, Black-throated Tit and Green-backed Tit. However, these relationships were not statistically significant. More detailed research is recommended to better understand the complex interactions between propensity, disturbance and food availability.

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Appendix

List of species observed during the study, both inside and outside flocks. Information on diet guild and foraging method is a result of information from Birds of the World and personal observations in the field.

Sno	Species name	Flock participation	Diet guild	Foraging method
1	Ashy Drongo	✓	Insectivore	Sallier
2	Ashy-throated Warbler	✓	Insectivore	Foliage gleaner
3	Bar-tailed Treecreeper	✓	Insectivore	Bark gleaner
4	Black Bulbul	×	Frugivore	N/A
5	Black-chinned Babbler	×	Insectivore	Foliage gleaner
6	Black-faced Warbler	✓	Insectivore	Foliage gleaner
7	Black-headed Jay	✓	Omnivore	N/A
8	Black-throated Tit	✓	Insectivore	Foliage gleaner
9	Black-winged Cuckooshrike	×	Insectivore	Foliage gleaner
10	Blue Whistling-Thrush	✓	Insectivore	Ground feeder
11	Blue-capped Redstart	✓	Insectivore	Sallier
12	Blue-throated Barbet	✓	Frugivore	N/A
13	Blue-winged Minla	✓	Insectivore	Foliage gleaner
14	Blyth's Leaf Warbler	×	Insectivore	Foliage gleaner
15	Brown-fronted Woodpecker	✓	Insectivore	Bark gleaner
16	Buff-barred Warbler	✓	Insectivore	Foliage gleaner
17	Chestnut-bellied Nuthatch	×	Insectivore	Bark gleaner
18	Chestnut-crowned Warbler	✓	Insectivore	Foliage gleaner
19	Coal Tit	✓	Insectivore	Foliage gleaner
20	Collared Owlet	×	Carnivore	N/A
21	Dark-sided Flycatcher	×	Insectivore	Sallier
22	Eurasian Jay	✓	Omnivore	N/A
23	Fire-breasted Flowerpecker	✓	Frugivore	N/A
24	Fire-tailed Sunbird	✓	Nectarivore	N/A
25	Goldcrest	✓	Insectivore	Foliage gleaner
26	Gray Treepie	✓	Omnivore	N/A
27	Gray-headed Canary-Flycatcher	✓	Insectivore	Sallier
28	Gray-headed Woodpecker	✓	Insectivore	Bark gleaner
29	Gray-hooded Warbler	✓	Insectivore	Foliage gleaner
30	Gray-winged Blackbird	✓	Insectivore	Ground feeder
31	Great Barbet	×	Frugivore	N/A
32	Greater Yellownape	✓	Insectivore	Bark gleaner
33	Green Shrike-Babbler	✓	Insectivore	Foliage gleaner
34	Green-backed Tit	✓	Insectivore	Foliage gleaner
35	Green-tailed Sunbird	✓	Nectarivore	N/A
36	Hair-crested Drongo	×	Insectivore	Sallier
37	Hill Partridge	×	Omnivore	N/A
38	Himalayan Black-lored Tit	✓	Insectivore	Foliage gleaner
39	Himalayan Bluetail	✓	Insectivore	Sallier
40	Himalayan Bulbul	×	Frugivore	N/A

41	Himalayan Cuckoo	✗	Insectivore	Foliage gleaner
42	Himalayan Prinia	✓	Insectivore	Foliage gleaner
43	Himalayan Woodpecker	✓	Insectivore	Bark gleaner
44	Hume's Warbler	✗	Insectivore	Foliage gleaner
45	Indian White-eye	✓	Insectivore	Foliage gleaner
46	Kalij Pheasant	✗	Omnivore	N/A
47	Large-tailed Nightjar	✗	Insectivore	Sallier
48	Lemon-rumped Warbler	✓	Insectivore	Foliage gleaner
49	Lesser Racket-tailed Drongo	✓	Insectivore	Sallier
50	Lesser Yellownape	✓	Insectivore	Bark gleaner
51	Long-tailed Minivet	✓	Insectivore	Foliage gleaner
52	Maroon Oriole	✗	Insectivore	Foliage gleaner
53	Mistle Thrush	✗	Insectivore	Ground feeder
54	Mountain Bulbul	✓	Frugivore	N/A
55	Olive-backed Pipit	✗	Insectivore	Ground feeder
56	Oriental Turtle-Dove	✗	Granivore	N/A
57	Red-billed Blue-Magpie	✓	Omnivore	N/A
58	Rufous Sibia	✓	Omnivore	N/A
59	Rufous-bellied Niltava	✗	Insectivore	Sallier
60	Rufous-bellied Woodpecker	✓	Insectivore	Bark gleaner
61	Rufous-gorgeted Flycatcher	✓	Insectivore	Sallier
62	Russet Sparrow	✗	Granivore	N/A
63	Rusty-cheeked Scimitar-Babbler	✗	Insectivore	Ground feeder
64	Scaly-bellied Woodpecker	✗	Insectivore	Bark gleaner
65	Scarlet Minivet	✓	Insectivore	Foliage gleaner
66	Slaty-headed Parakeet	✗	Frugivore	N/A
67	Small Niltava	✗	Insectivore	Sallier
68	Speckled Piculet	✓	Insectivore	Bark gleaner
69	Spotted Forktail	✗	Insectivore	Ground feeder
70	Streak-breasted Scimitar-Babbler	✓	Insectivore	Ground feeder
71	Streaked Laughingthrush	✓	Insectivore	Foliage gleaner
72	Striated Laughingthrush	✓	Insectivore	Foliage gleaner
73	Tickell's Thrush	✗	Insectivore	Ground feeder
74	Tytler's Leaf Warbler	✓	Insectivore	Foliage gleaner
75	Ultramarine Flycatcher	✗	Insectivore	Sallier
76	Verditer Flycatcher	✓	Insectivore	Sallier
77	Western-crowned Warbler	✗	Insectivore	Foliage gleaner
78	Whistler's Warbler	✓	Insectivore	Foliage gleaner
79	White-browed Scimitar-Babbler	✓	Insectivore	Ground feeder
80	White-browed Shrike-Babbler	✓	Insectivore	Foliage gleaner
81	White-tailed Nuthatch	✓	Insectivore	Bark gleaner
82	White-throated Fantail	✓	Insectivore	Sallier
83	White-throated Laughingthrush	✓	Insectivore	Ground feeder
84	Yellow-browed Tit	✓	Insectivore	Foliage gleaner