



Ecological and behavioural study of mixed species flocks at different altitudes

Roberto Soriente

2024

ABSTRACT

Mixed species flocks are a common phenomenon in the Neotropics across different environments, their presence can vary through changes in altitude, season and vegetation. In the present study it was investigated if the frequency of occurrence, as well as richness and diversity of these flocks change at different altitudes, taking in account other factors like vegetation density, seasonality and time of day as well. It also aimed to analyse the different foraging strategies of the birds present in mixed flocks by species and family to see if any resource partitioning is happening. The results found that even with a discrete altitudinal gradient there is a difference in the occurrence of mixed species flocks and that at least in a two hour frame the flocks are encountered with a similar frequency. It also found that lower vegetation density areas coincide with more observations of these flocks. The study found that birds gathering in mixed species flocks preferred the lower parts of trees to forage, but this is a preference of all the birds and no resource partitioning is present. More importantly, this research helps understanding a behaviour that is not well studied in montane cloud forest as most studies on the subject focus on lowland environments.

1. INTRODUCTION

A mixed flock is a roving group of three or more individuals from at least two species, moving in concert and behaving cohesively while foraging over a non-aggregated food resource (Zhang et al., 2020). Social interactions such as calling, responding to potential threats and coordinated behaviour all provide additional evidence that these birds belong to the same flock (Mangini et al., 2023). The threshold for delimiting a mixed flock, either by the amount of time participants spend together, interindividual distances, or the joint distance covered, will vary from place to place and depend on the kind of mixed flock studied (Mangini et al., 2023).

The behaviour has been observed throughout the Neotropics, down to Patagonia, and up in the Andes, as well as in tropical Africa, Madagascar, Asia and New Guinea (Thiollay, 1999). The phenomenon is widespread, but why does it appear in the first place?

There are two major hypotheses: The first is that birds tend to flock to enhance their foraging success thanks to the information given by other members, therefore the behaviour appears more frequently when resources are scarce. Improved feeding could occur through feeding on insects flushed by other birds (Winterbottom, 1943; Kotagama and Goodale, 2004), avoiding previously exploited areas (Cody, 1971; Beauchamp 2005), copying foraging locations (Krebs, 1973; Waite and Grubb, 1988), and optimal movement patterns (Cody, 1971; Greenberg, 2001). Secondly, flocking decreases predation time while increasing time to feed. In this hypothesis, the behaviour is more present when the predation risk is higher. Reduced predation risk by participation in mixed species flocks can arise through the selfish herd effect (reduced predation risk in relation to the position of other group members; Hamilton, 1971), the dilution effect (reduced probability of being singled out by a predator; Foster and Treherne, 1981), the encounter effect (reduced probability of being encountered by a predator; Inman and Krebs, 1987), the confusion effect (reduced ability of a predator to single out and attack individual prey; Neill and Cullen, 1974), and the 'many-eyes' effect (increased probability of a predator being detected; Pulliam, 1973). Bird species that join mixed flocks more often tend to be smaller, more insectivorous, and more arboreal than intraspecific bird species that join flocks less often (Sridhar et al., 2009). In general, there is a higher participation of insectivorous birds in flocks (Greenberg, 2000). According to Sridhar et al. (2009), diet seems to be the only significant factor influencing joining a flock, suggesting that this

could be the most important determinant of flocking tendencies of species. Mixed-species flocks are also less frequent and have lower numbers of species and individuals during the breeding season than in the non-breeding season, so the two time frames should be separated (Tubelis, 2007).

Rabinovich & Rapoport (1975) observed that the spatial variation of bird richness is explained by climatic and topographic variables. Most mixed-species flocks (MSF) of birds in the Neotropics studies point to climate regimes as the main drivers of latitudinal gradients of bird diversity, which affect various aspects of the ecology of the species directly or indirectly, including diets, use of available microhabitats and behaviour (Ruggiero & Lawton, 1998; Ruggiero, 2001; Salisbury et al., 2012). Altitude is another aspect that seems to vary the ecology of animals, which ecologists have analysed to see differences in the composition and frequency of MSF in a mountainous forest, an environment still lacking in research about this type of flocking (Kajiki et al., 2018). In regards to the time of day birds tend to flock, Davis (1946) reported that the mixed flocks are formed shortly after dawn, coming together, and beginning to call. Once formed, the flock spends the day wandering about a small area.

1.1 Altitude

Species diversity and community composition are known to change with elevation in a somewhat predictable fashion: overall species diversity decreases with elevation, not necessarily following a linear pattern (McCain, 2009; McCain & Grytnes, 2010). Elevational gradients result in significant changes in several environmental conditions (e.g., temperature, precipitation, oxygen levels), with lower temperatures and more seasonal climatic regimes characterizing higher elevations (McCain & Grytnes, 2010). The gradients in these abiotic factors strongly influence the distribution of floral and faunal species, and therefore the changes in dominant communities and habitat that we notice as we climb in elevation (McCain & Grytnes, 2010). On the effect that this parameter has on species richness, contrasting results are present in literature. For example, species richness doesn't decrease with increased altitude (Givnish, 1999). For birds, Montaña-Centellas (2015) presented an example of flock variation along a well-preserved elevational gradient in Bolivia. This study used network theory to test for the effect of elevation on the structure of social networks in mixed species flocks of birds, along a continuous transect (2000–3550 m.a.s.l.) that largely lacks human presence and

dissects a protected area. The research found that species composition, species richness in flocks, as well as network-level metrics vary with elevation. Taking into account trends of birds all over the world, studies on avian mountain endemics demonstrated their greatest diversity at intermediate elevations between 1500 and 3000 m, although somewhat lower on shorter mountains (Grytnes and McCain, 2007). Kajiki et al. (2018) demonstrated that mixed-species flocks of birds differed along a discrete environmental gradient in *terra firme* forest, a plain tropical rainforest that is not flooded periodically, both in richness and species position within the network. Examining the effect of environmental variables (elevation and normalized difference vegetation index) in species richness and structure of mixed species flocks in a *terra firme* forest in the Brazilian Amazon, where elevation varied by less than 130 m between highest and lowest point.

These results suggest that birds are responding to small-scale environmental heterogeneity (Cintra & Naka, 2012) and that even small differences in elevation can result in different network properties. On the number of birds present in mixed flocks, high abundances of montane passerines might compensate for the small areas available at high elevations, and as a result they can maintain population sizes comparable to those of their lowland-forest counterparts (Ferenc et al., 2016).

But can altitude have any effect on the food birds are eating? The abundance and species richness of insect assemblages had no relationship with elevation in the Andes, even though insect communities from lower elevations (2200–2700 masl) were more abundant and diverse than communities from higher elevations (2800–2900 masl) (Cuartas-Hernández & Gómez-Murillo, 2015).

1.2 Vegetation

Vegetation type and vegetation structure can have a great impact on the detectability of mixed flocks; factors like density of trees can significantly reduce the detectability of mixed flocks. Zuluaga and Rodewald (2015) found that contrasting effects come from the vegetation structure, with significant increases in the richness and size of flocks in forest with greater foliage height diversity. Previous studies on avian communities of the forest understorey (Stouffer and Bierregaard, 1995; Dale et al., 2000; Maldonado-Coelho and Marini, 2004; Lee et al., 2005) showed that species assemblage varies from forest interior to edge (or pristine to

disturbed areas), either through changes in the general frequency or in the flocking propensity of the species. Péron and Crochet (2009) found strong evidence that intrinsic preference for edge or interior habitat drove the composition of the flocks. A series of studies revealed a lower participation of forest birds in mixed species flocks in denser, more protective vegetation (Ulfstrand, 1975; Thiollay & Jullien, 1998; Thiollay, 1999). Moreover, foraging at greater distances from forests means longer time of exposure in less protective vegetation and more time required to escape to cover (gallery forest). All these studies suggest more frequent mixed flocks in open vegetation areas and forest edges.

1.3 Foraging Behaviour

Foraging behaviour includes all the methods by which an organism acquires and utilizes sources of energy and nutrients. It is a complex behavior that ranges from detecting and searching for food, capturing prey, and determining if it should be swallowed or rejected (Khursigara et al., 2023). Various studies have indicated that birds alter their foraging behaviour when participating in MSFs compared to when foraging with conspecifics or alone (Latta and Wunderle, 1996; Hino, 2000; Jullien and Clobert, 2000; Chen and Hsieh, 2002; Thiollay, 2003; Satischandra et al., 2007; Zou et al., 2011; Hsieh and Chen, 2011). Changes in attack manoeuvres and foraging locations, particularly height and substrates, were among the recorded modifications in mixed species flocking birds (Latta and Wunderle, 1996; Zou et al., 2011). Flocking may also allow certain bird species to forage in more exposed locations, likely the result of the protection offered by the flock members through mutual vigilance (Latta and Wunderle, 1996; Thiollay, 2003). Modifications in foraging habits in mixed-species flock context can be explained by decreased predation risk and increased foraging efficiency (Sridhar et al., 2009; Zou et al., 2011). Foraging in MSFs allows birds to forage in risky microhabitats, access foraging resources made available by the foraging of other birds and copy foraging behaviour of other birds. These phenomena might coincide with the foraging location of the nuclear species, where follower species may receive benefits (Satischandra et al., 2007; Farine and Milburn, 2013) and feed on arthropods flushed by other flock members (Srinivasan and Quader, 2012).

2. METHODS

2.1 Study Site

Cloudbridge Nature Reserve (N9.472299046356728, W 83.57709672709753), is located on the Pacific slope of the Talamanca mountain range, adjacent to mount Chirripó (Figure 1). Cloudbridge uses replanting and natural regeneration as their methods for reforestation. The park has an area of 2.83 km² mostly occupied by tropical cloud forest, a type of mountainous rainforest that gets typically cloudy for the majority of the year. Tropical cloud forests account for no more than 2.5% of the world's tropical forests (Bubb et al., 2004). This makes them a rare and fragile, but valuable ecosystem, because they are characterized by high biodiversity and are home to many endemic species. Cloud forests occur within a wide range of annual and seasonal rainfall patterns, from 500–6000 mm/year (Bubb et al., 2004). They are found wherever clouds and mist are frequently in contact with a mountain slope. They typically form a belt of vegetation over an elevational range of about 500 m, but there is considerable variation in the altitude at which they are found (Bubb et al., 2004). On large inland mountain systems cloud forests may typically occur between 2000 and 3500 m, whereas in coastal and insular mountains this zone may descend to 1000 m (Bubb et al., 2004). The area presents mostly a reforested environment with different types of vegetation (old growth, young growth, planted, primary forest). It possesses a rich environment with a variety of animals, including numerous birds. Because the area spans different altitudes (Figure 2) some of the species present change. For this study three of the trails were chosen to take data, two of them (Montaña and Jilguero) with a major span in altitude between 1600 and 2100 masl and one (Rio) with less difference in altitude (in total) but more variations, i.e. instead of going straight upwards, it presents more up and downs. The areas used for data collection presents different types of vegetation, spanning from planted to mature forest; these types of vegetation present different complexity, medium tree heights (van der Laan, 2019) and different quantities of open spaces which can contribute to differences in mixed species flocks across altitudes.

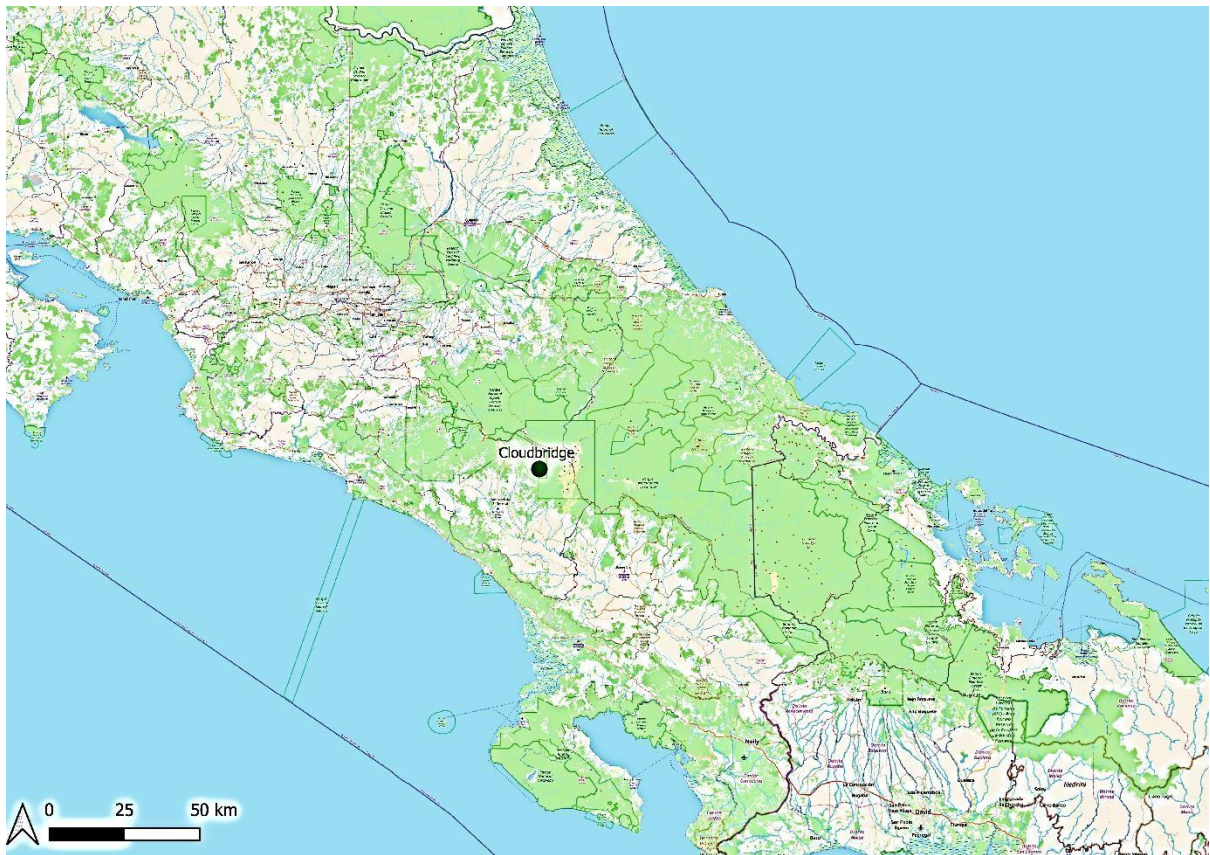


Figure 1: Map of Costa Rica with Cloudbridge site pointed out, made with QGIS

2.2 Data Collection

The data has been collected using transects with a set bout of time (2 hours total) in which a trail will be walked. The transect where data is collected are part of the Jilguero trail (from the Jilguero loop until the crossing with Gavilan trail), Montaña (until a 2030 masl point) and Rio (all of it excluding the maintenance trail) (Figure 2). Every encounter of mixed-species flocks was recorded, together with the altitude (Garmin® GPS), time of the day, number of birds present, and when the flocks were encountered the behaviour of the individuals was analysed together with the composition of the flock. The bouts of observations of the birds' behaviour lasted the time needed to understand if the members of the flock were moving together and went until dispersion made it no longer possible to observe them. The observed flocks were localised either by hearing or visually. A visual assertion of the species was performed either by binoculars (fully coated, 10x42) or by the naked eye when near enough. An initial vocalisation identification could be done by hearing songs or with the app Merlin Bird ID, but

sight was always required for sureness, as well as numbering the birds and taking the behavioural data. When a flock was encountered during the set period the observation could proceed after the end of the transect time and until the end of that observation. The foraging behaviour was also observed during the same time. The behavioural observations noted were about foraging substrate, foraging height, and foraging manoeuvre (Robinson and Holmes, 1982; Remsen and Robinson, 1990). The manoeuvre types were classified as either gleans (stationary prey on any substrate) or hawks (flying prey taken from mid-air). For stationary prey, the substrates were categorised as either foliage (generally green substrate, but also including petioles and flowers) or woody (brown substrate such as twig or branch). For foliage gleans, it was noted whether a bird used an aerial manoeuvre to attack prey (non aerial vs. sally-glean). All foraging manoeuvres were placed in one of four categories: hawk, foliage-glean, woody-glean, or sally-glean (George, 2009). An approximation of the height at which the birds are foraging on the tree was recorded dividing the tree height in 4 meters sections. Movements of the birds along the height of the tree was also recorded to examine possible effects of foraging height on foraging behaviour, considering it a new foraging observation when a bird moves to another substrate or changes foraging height >2 m (Newell et al., 2014); foraging height categorised as <4 m, 4–8 m, or 8-12 m, >12 m (following the mean dimensions of the trees present in the reserve).

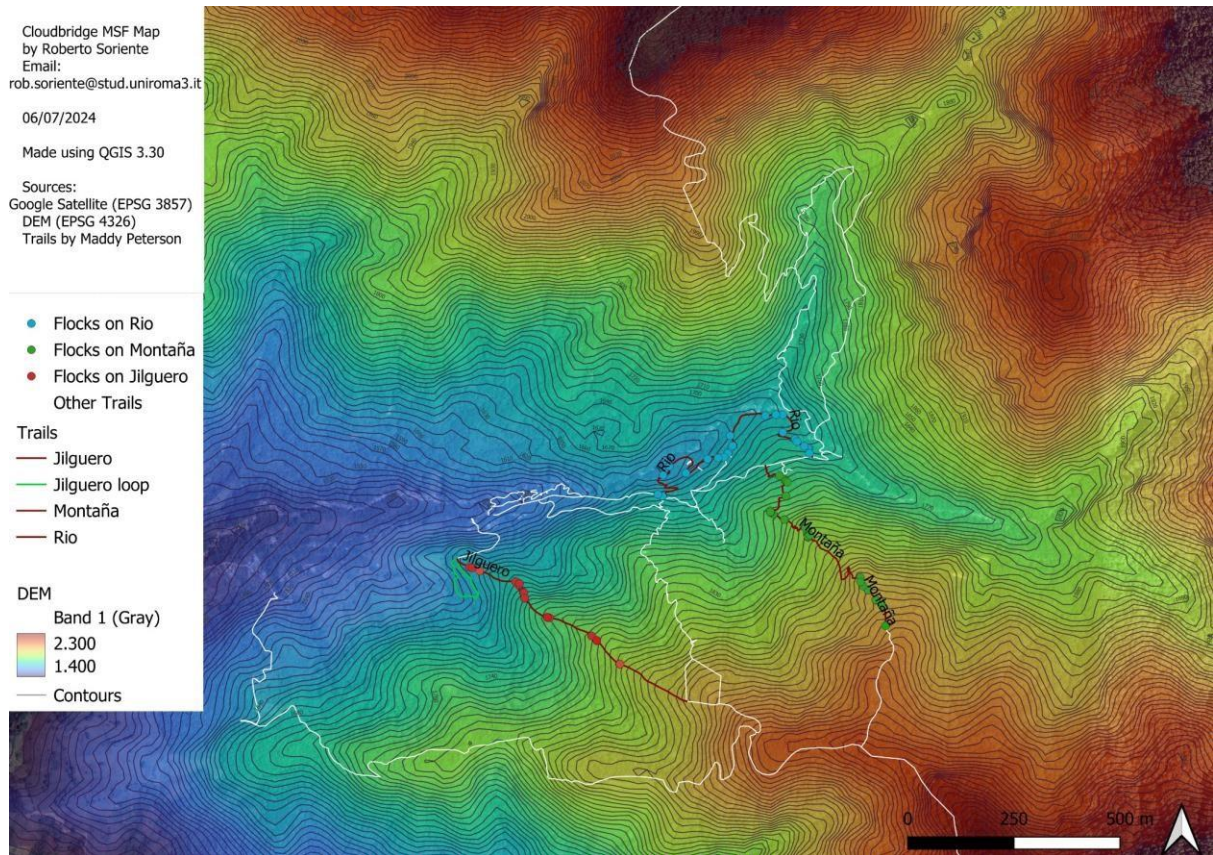


Figure 2: Map of Cloudbridge with the different trails and altitudes, highlighted are the transects used: Green = Jilguero; Red = Montaña; Blue = Rio. The points are the MSF observed during the surveys.

2.3 Data Analysis

2.3.1 Occurrence of Mixed Species Flocks

Frequency of occurrence of mixed flock was analysed by a Logistic Regression Analysis in order to understand how changes in altitude are associated with changes in the occurrence of MSF, in this analysis different weights were given to the lower and higher altitudes (respectively 1630-1640 masl and 1960-2030 masl) as they were misrepresented in the surveys (once weekly versus twice weekly). A Logistic Regression Analysis was also performed to see if the difference was instead correlated to the time of day analysing for the occurrence of MSF with time of day, converting time to a numerical format which is the hours and minutes after midnight.

2.3.2 Variations in the MSFs

How the MSFs change with altitudes was assessed by comparing the number of individuals and species within flocks between altitudes; generalized linear mixed-effects models was used with “trail” as a random effect to account for repeated observations of the same individuals at a site (Zuur et al., 2009).

2.3.3 Behavioural Analyses

Foraging height (the height of the tree where the birds were eating) was compared using a oneway ANOVA test, the test was used to compare the families most present in MSF, followed by paired T-tests to see what foraging heights were differing. The same analysis was done within family members with the three most represented warblers: Slate-throated Redstart (*Myioborus miniatus*), Golden-crowned Warbler (*Basileuterus culicivorus*) and Costa Rican Warbler (*Basileuterus melanotis*) and the two major Thraupidae species: Silver-throated Tanager (*Tangara icterocephala*) and Speckled Tanager (*Ixothraupis guttata*); to try to find differences within families for the foraging height.

The six focal species belonging to the same families (5 above) plus Common Chlorospingus (*Chlorospingus flavopectus*), chosen because it's the most commonly observed bird on the reserve, were also analysed by foraging behaviours, manoeuvre types and substrate types using chi-square tests followed by Bonferroni adjusted 2 tests. The first behavioural trait was also analysed between families using the same approach.

2.3.4 Seasonality and Vegetation

A comparison of the number of individuals and species within flocks between seasons was performed using generalized linear mixed-effects models with trail as a random effect (Zuur et al., 2009). The date to separate the two seasons was decided as the 18th of April following the data from the Ministerio de Ambiente y Energía, Instituto Metereológico Nacional which set the

start of the rainy season between the 16th and the 19th of April for the year 2024 in the Pacifico Sur region of Costa Rica (SIG y Unidad de Climatología, Departamento de Desarrollo, Instituto Metereológico Nacional San José, Costa Rica, 2023).

The vegetation density was analysed using QGIS and graphically compared to a concentration map of the MSF to highlight for any pattern in the concentration due to vegetation (Figure 14).

3. RESULTS

A total of 51 surveys were performed between the beginning of March and the beginning of July. The total number of MSF was 55, 14 observed in Jilguero, 20 in Montaña and 21 in Rio (Figure 2), with an equal number of surveys (17) for each transect. The mean number of MSF per survey was 1,08, in which there was an average 6,57 birds belonging to an average of 3,34 species; the families these species belonged to are reported in Figure 3. The species present in the MSF observed were 60% insectivorous and 40% omnivorous.

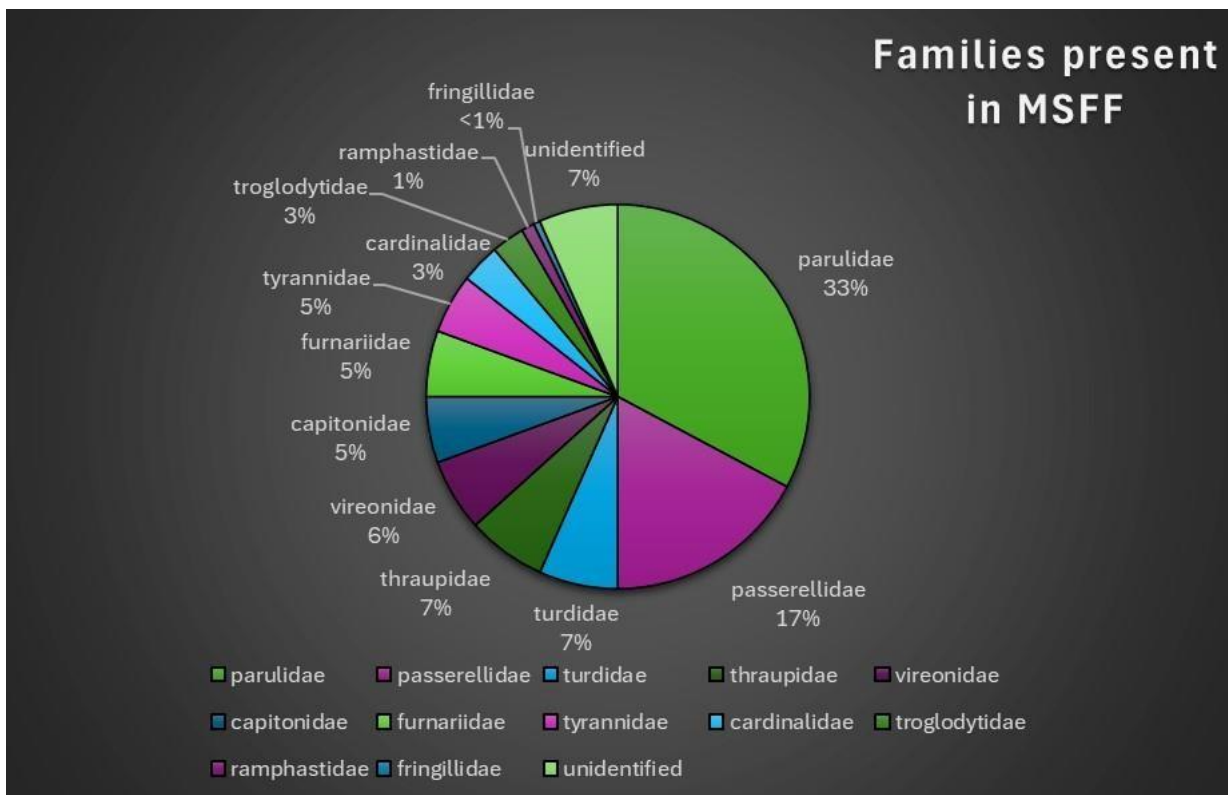


Figure 3: Percentages of each family presents in the observed MSF

3.1 Occurrence of mixed species flocks

The logistic regression analysis found a significant difference in the mixed species flocks by altitude, with a p-value of 0,00153 and a negative relation as shown by Figure 4.

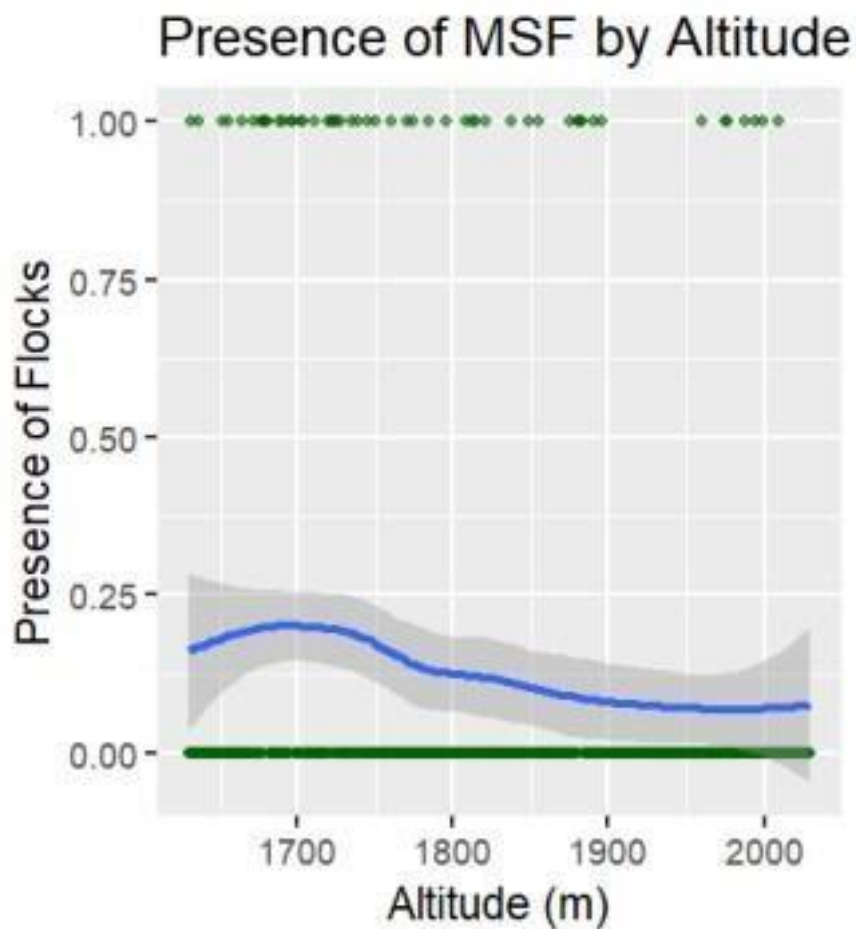


Figure 4: Logistic Regression Analysis of the MSF presence by altitude with the predicted values, with 1 signifying flocks present, and 0 meaning no flocks present.

The time when the observation of mixed species flocks was observed was analysed with the same method as the altitude to see if the time of day had an impact on the MSF presence. The p-value for this analysis was 0,492. The regression graphs (Figure 5) here also report a negative relation with time, but not significant.

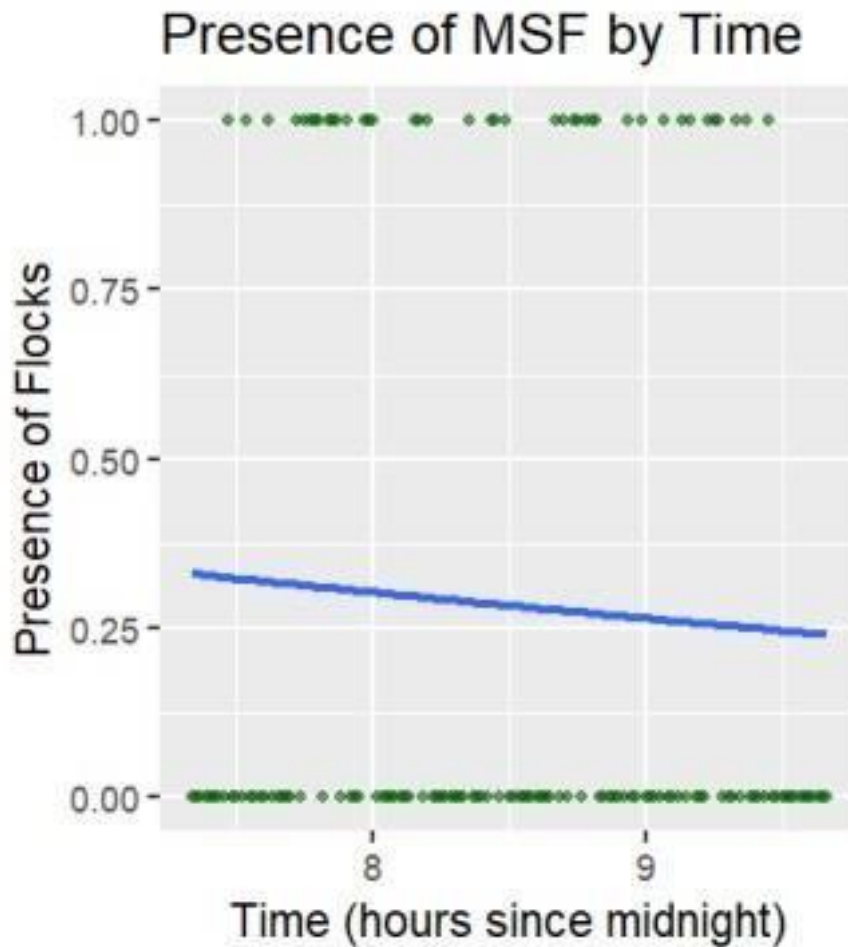


Figure 5: Logistic Regression Analysis of the MSF presence by time of day with the predicted values, where 1 means flocks present, and 0 means no flocks present.

3.2 Variations in the MSFs by altitude

The analysis of the number of individuals by altitude with mixed effect models didn't give any significant result, with a p-value of 0,4765. Similar results were obtained from the same analysis but with the number of species analysed by altitude, with a p-value of 0,2485. Figure 6 also shows the actual numbers and number of species by altitude, where it is visible that the numbers don't differ greatly. All the altitudinal ranges also show similar numbers in diets (Figure 7).

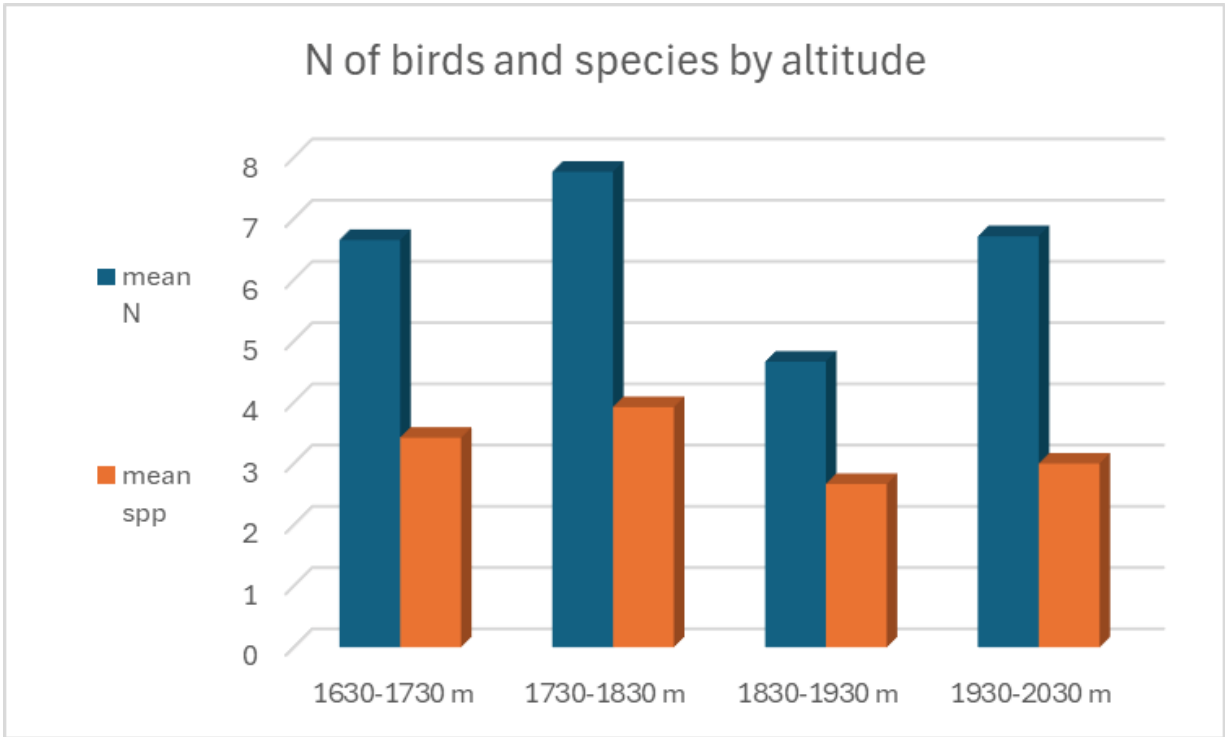


Figure 6: Bar chart of the number of birds and number of species of MSFs by altitude.

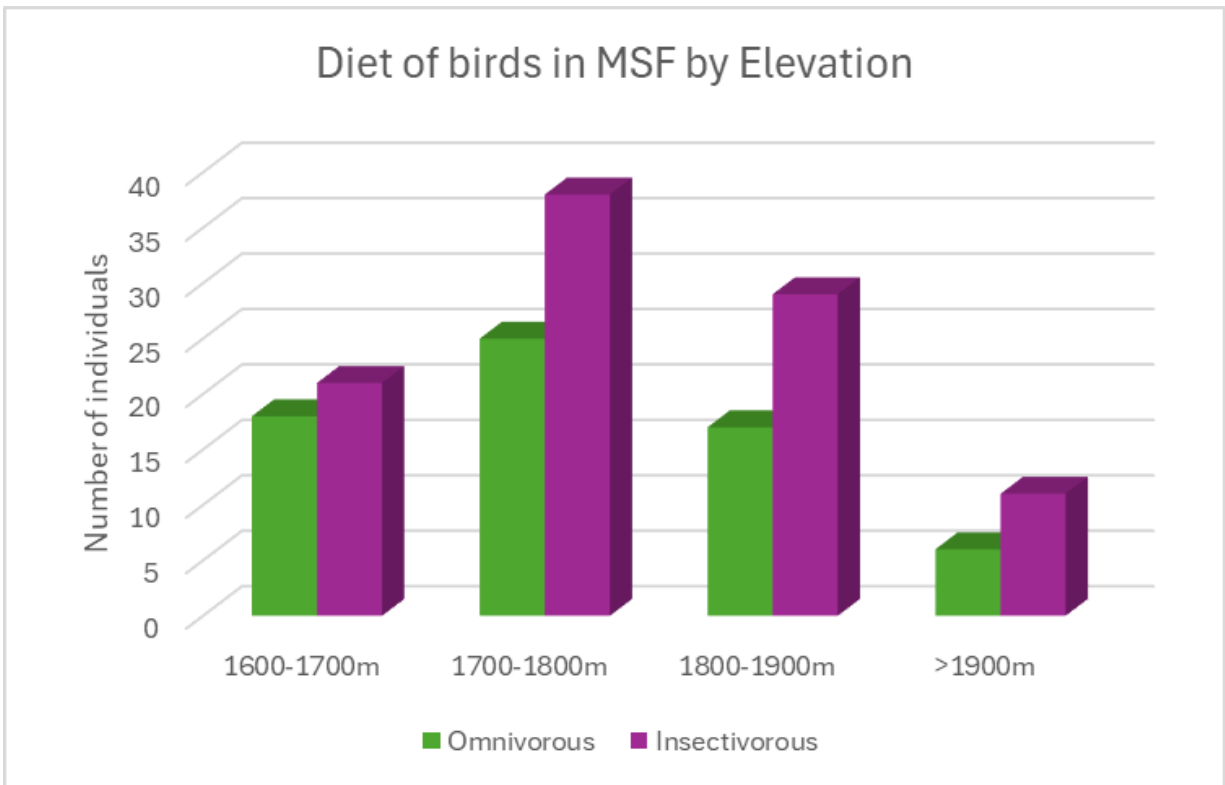


Figure 7: Bar chart of the number of birds for each diet in MSFs by altitude.

3.3 Behavioural Analyses

Comparing foraging height by major family with a one-way ANOVA test showed a significant difference between the foraging heights, with a p-value = 0,0203 but not between the different families (p-value = 0,2028). Percentages of the heights used also show a certain similarity between families (Figure 8).

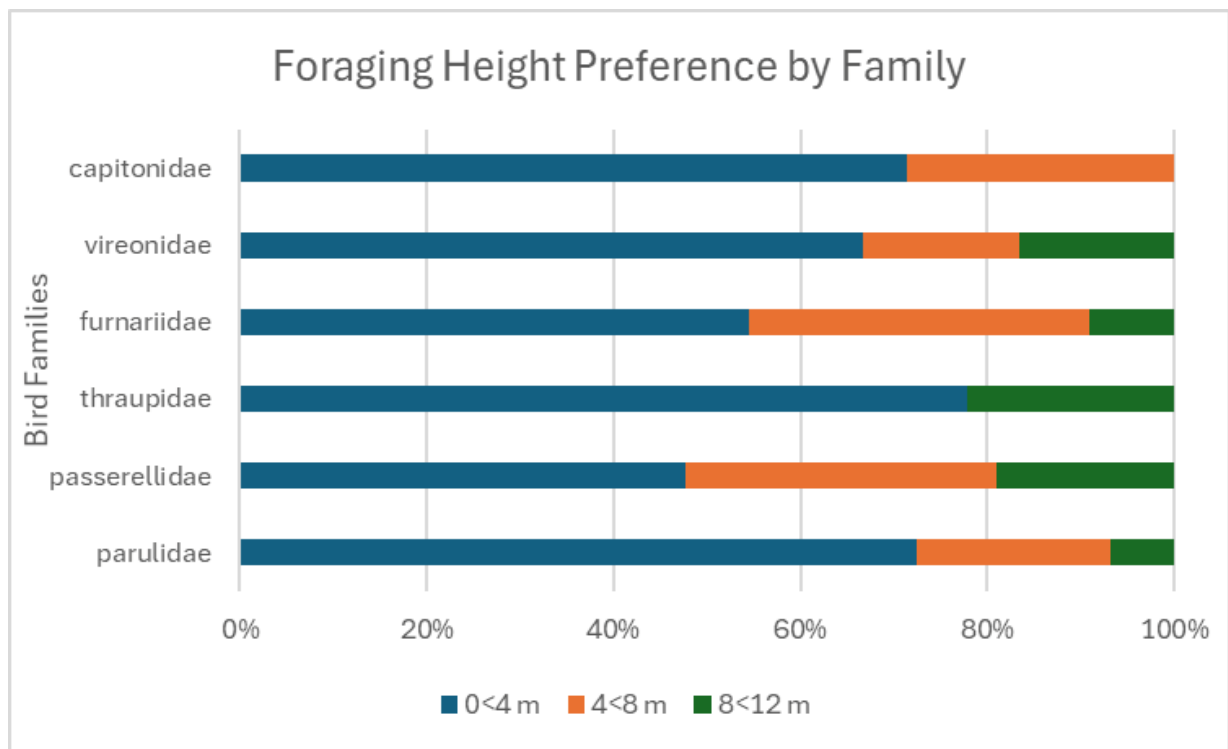
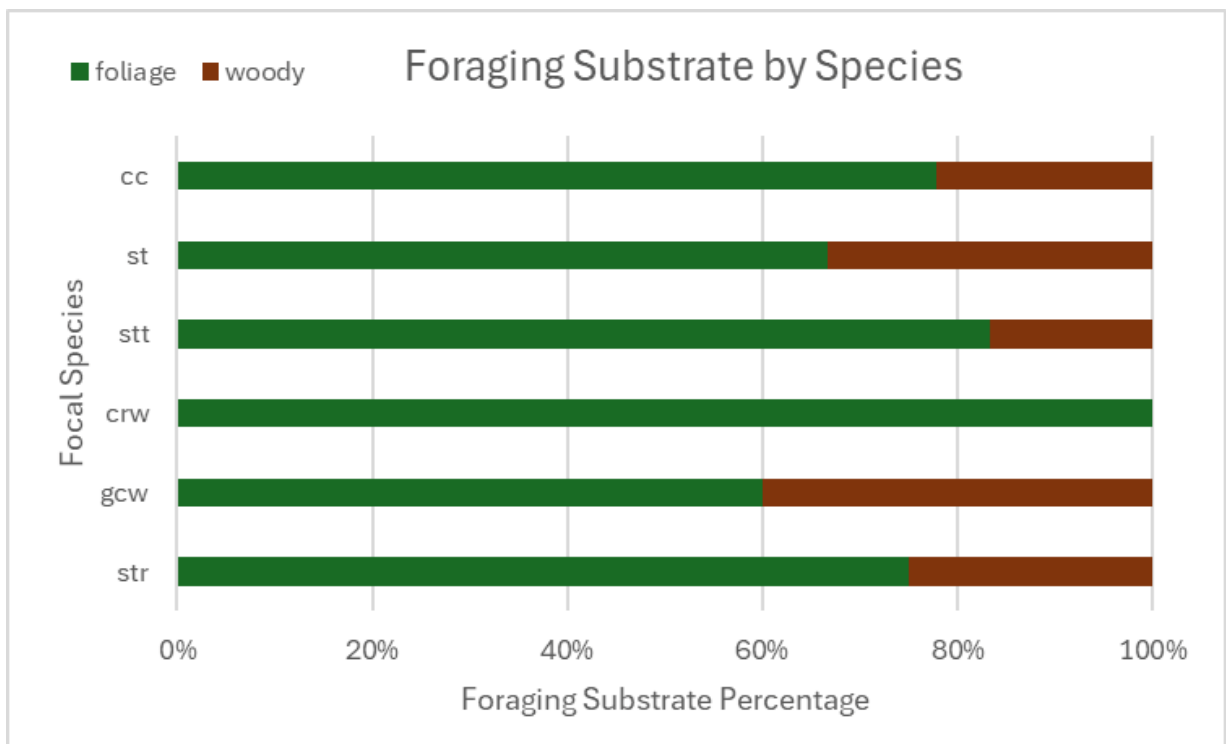
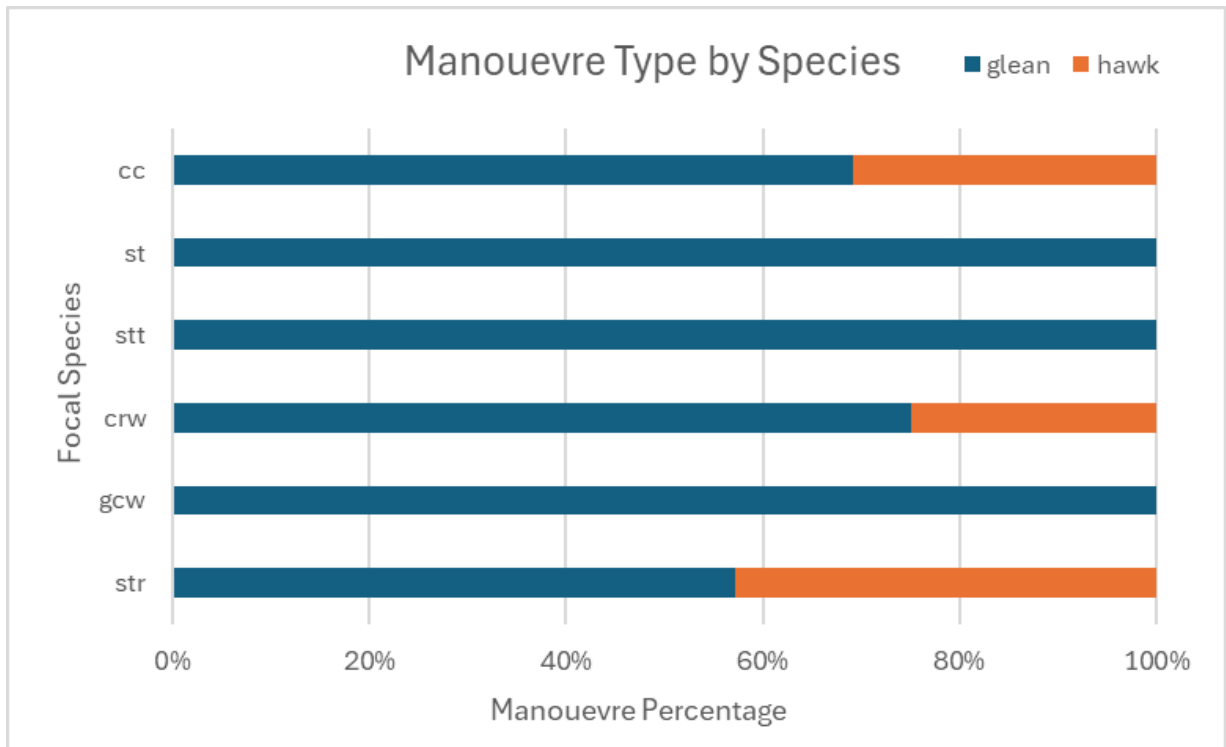


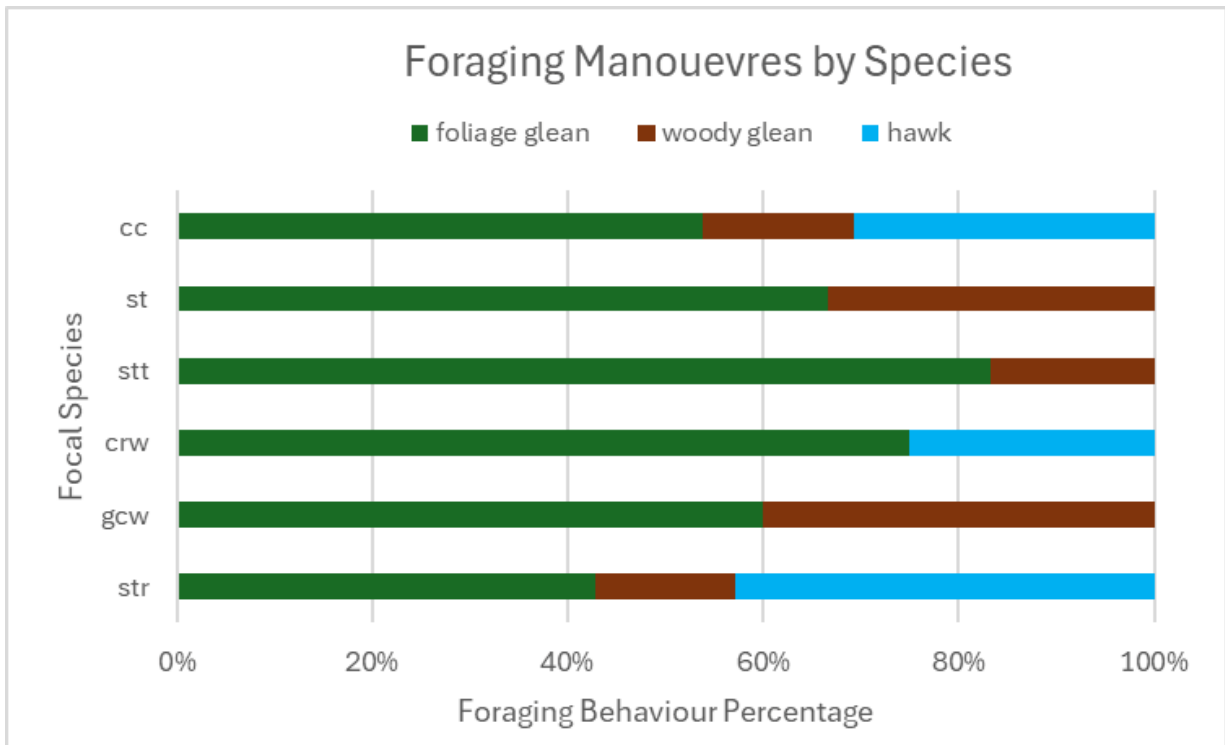
Figure 8: Bar chart of the percentages of foraging height (FH) ranges by the families in MSFs.

Comparing the foraging height, a significant difference was found between the lower height (0<4m) and both the higher ones (4<8m and 8<12m), with respective p-values of 0,0422 and 0,0306.

The same analysis was performed for the three main warbler species and the two main Thraupidae species (within family), leading to a significant result only for the warblers' foraging heights (p-value = 0,0073), with a similar result of the same analysis between families, finding the significant p-values of 0,0378 (0<4m against 4<8m) and 0,0131 (0<4m against 8<12m).

Comparing the foraging manoeuvres, manoeuvre types and substrate type by focal species using a chi-square test, no significant values were found, the proportions of these aspects are represented by the Figures 9, 10 and 11.





Figures 9,10 and 11: Bar charts from the top left to the bottom left of the percentages of manoeuvre types, substrate types and foraging manoeuvres (respectively); Species acronyms: Common Chlorospingus (cc); Speckled Tanager (st); Silver-throated Tanager (stt); Costa Rican Warbler (crw); Golden-crowned Warbler (gcw); Slate-throated Redstart (str).

Performing the same analysis only for foraging behaviour in the different families participating in MSF gave a significant result with a p-value of 0,0019 for woody glean, the significant difference was then found to reside between the Furnariidae family and all the other families using the Bonferroni correction, this difference in behaviour is also evident in Figure 12.

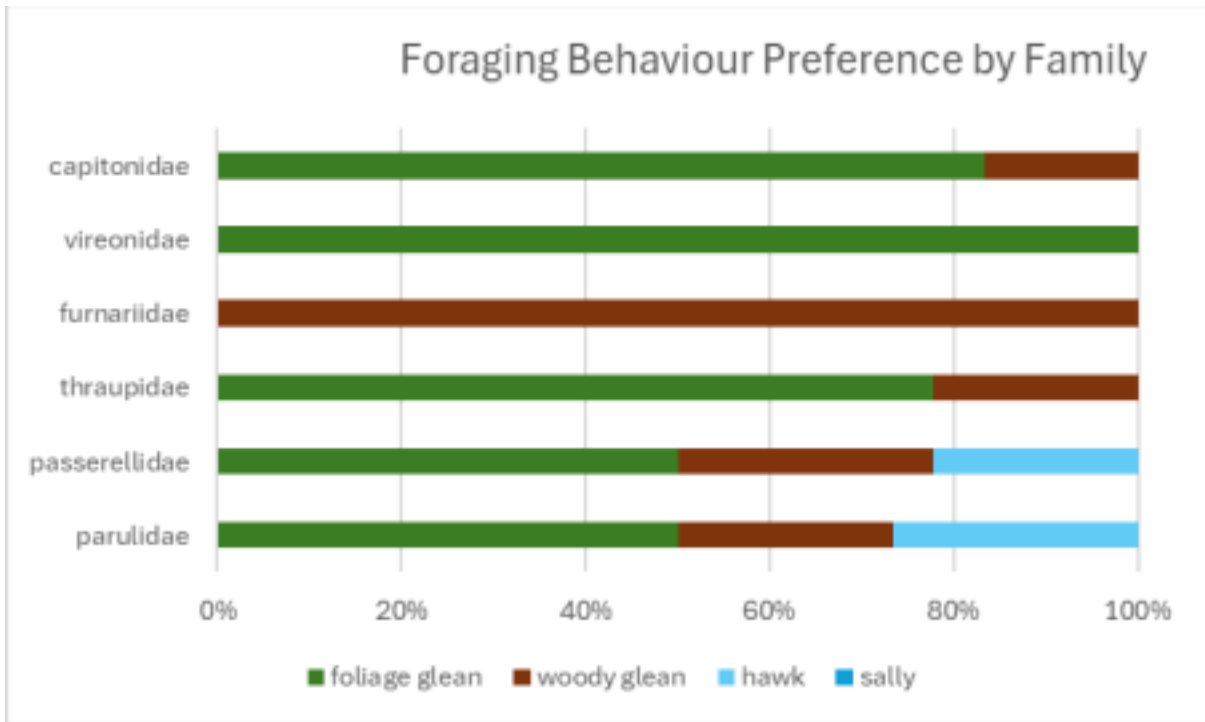


Figure 12: Bar chart of the percentages of FM by the families in MSFs.

3.4 Seasonality and Vegetation

The two different seasons (rainy and dry) were represented by different numbers of surveys, 20 for the dry season and 31 for the rainy season, with a total of 21 and 34 MSF respectively (Figure 13).

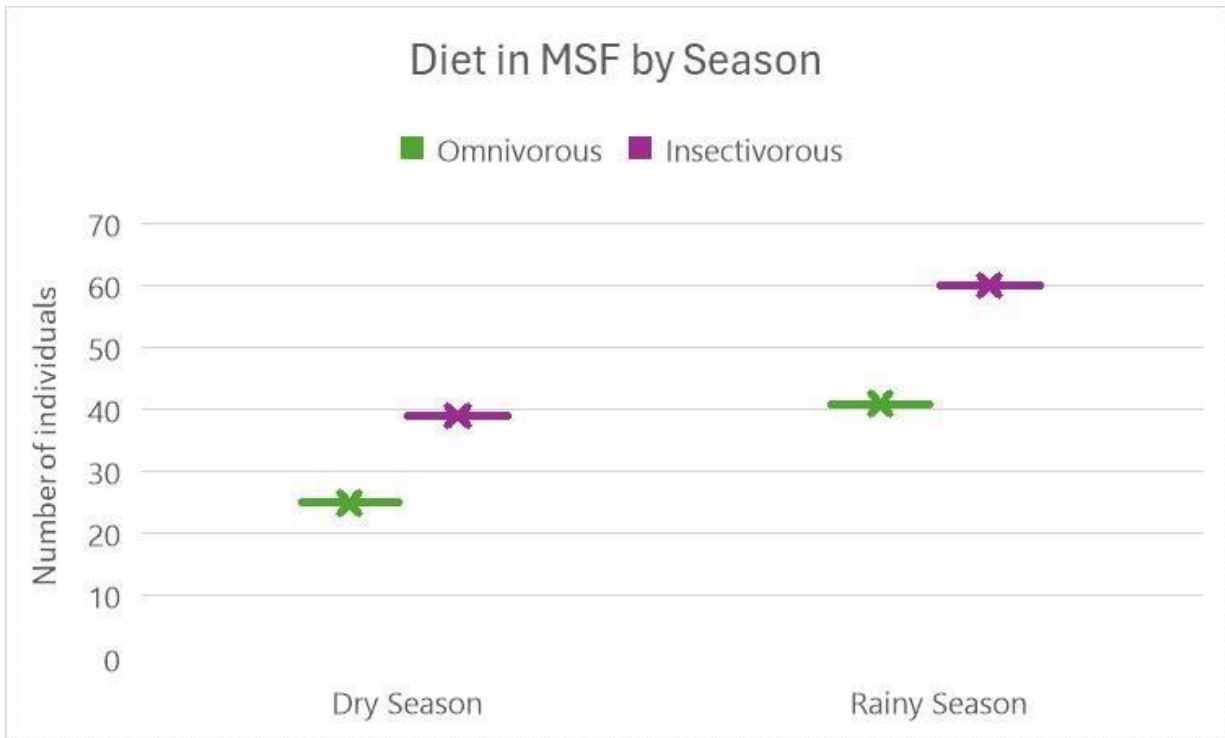


Figure 13: Boxplot of the number of MSFs split by diet for the two seasons.

Analysing the number of birds and number of species between seasons using an equal number of flocks with linear mixed effect denotes the results obtained were not significant, respectively p-values of 0,5859 and 0,6733.

The vegetation was accounted for using a QGIS map that was created to highlight areas with lower tree density and areas with higher concentration of MSF creating a heatmap with the GPS points of the flocks recorded and extracting the Normalized difference vegetation index (NDVI) values from Sentinel2 imagery, then visually comparing the two resulting concentrations (Figure 14).

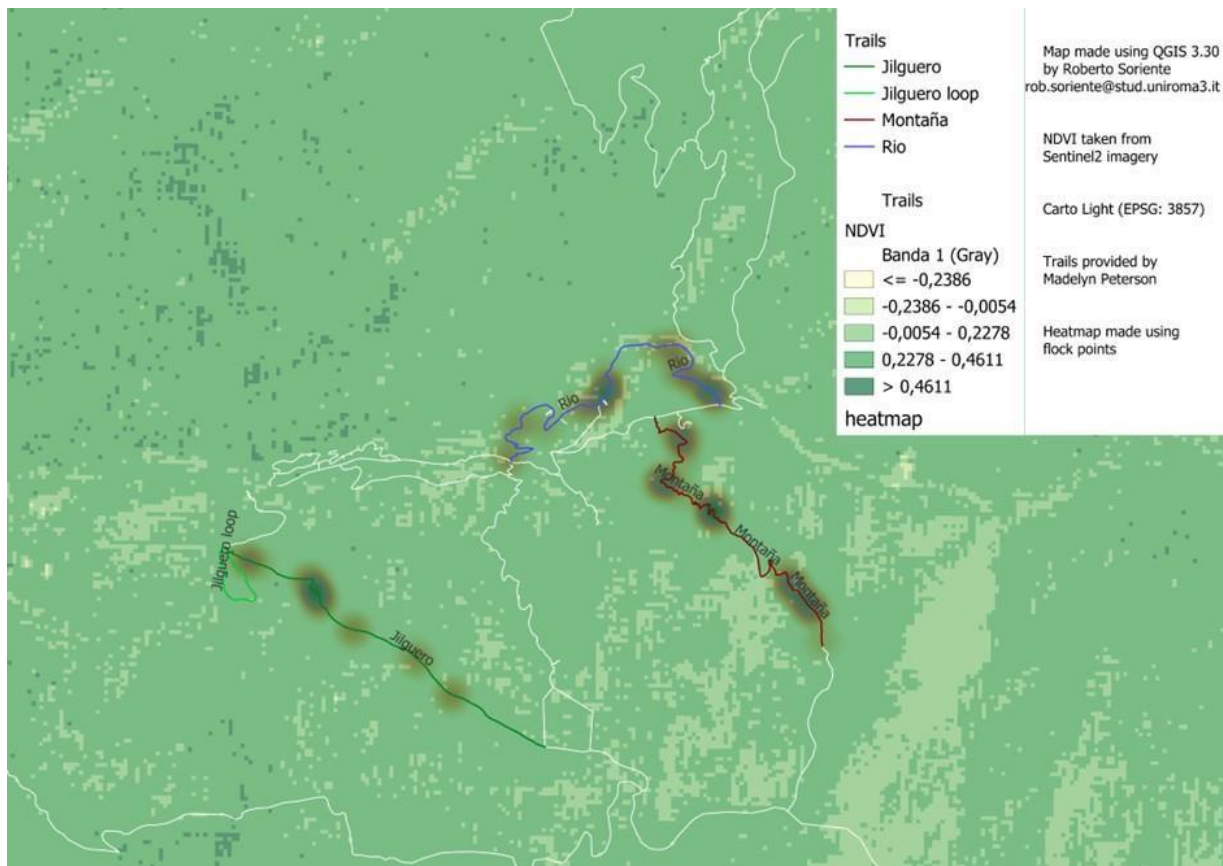


Figure 14: Map presenting the concentration of MSF (dark areas) and the tree density (NDVI) with the used transects in Cloudbridge.

4. DISCUSSION

4.1 Flocks Composition

The most common family in MSF in Cloudbridge was found to be Parulidae, which represented a third of the species present in each flock. The following family being Passerellidae, comprising mostly Common Chlorospingus (*Chlorospingus flavopectus*), while the most common warbler was the Slate-throated Redstart (*Myioborus miniatus*). Parulidae were found in most of the groups, while some associations were centred around big groups of *C. flavopectus*. In particular, Furnariidae and Capitonidae members were found with them, and tanagers of both Thraupidae and Cardinalidae families were commonly found together. The

presence of brushfinches (Passerellidae), thrushes (Turdidae) and wrens (Troglodytidae) with other families highlights the absence of a separation between understory and tree foragers in MSFs. In fact, while in the taller lowland forests as in the Amazon, flocks are clearly differentiated into canopy and understory flocks (Powell 1979, Munn 1985, Terborgh et al. 1990). It is unlikely that in montane forests both canopy and understory birds flock together (Powell 1985), indicating that these results are different from previous studies.

4.2 Occurrence of mixed species flocks

Mixed species flocks were found to be less common on Jilguero trail, particularly the upper elevations. They were also less present in the medium elevation of the Montaña transect and near the river in Rio trail. Similar numbers were shown in Rio and Montaña. Previous studies have demonstrated that mixed-species flocks of birds differed along a discrete environmental gradient in *terra firme* forest, both in richness and species composition within the network (Kajiki et al., 2018), examining the effect of environmental variables (elevation and NDVI index) in species richness and structure of mixed species flocks with less than 130 m between highest and lowest point. In the present research, a similar low gradient is present (300m) in an environment, the cloud forest, where information on mixed flocks remains less developed, despite the well-known ecological and ornithological significance of such habitats as the Costa Rican montane cloud-forest (Slifkin 2019; Kajiki et al., 2018). For higher elevations Montaña

Centellas (2015) presented an example of flock variation along a well-preserved elevational gradient in Bolivia. In this study a significant correlation between altitude and presence of mixed species flocks was found as well, with a decrease at higher altitudes and a peak around 1700 masl. This result suggests that some parameters (biotic or abiotic) that change even in a 300m altitudinal range, could have an effect on the formation of such flocks.

A question that had to be answered is if time of day has any effect on the behaviour and if not the time instead, is responsible for the difference in MSF formation and thus frequency of encounter (or add up to other variables). The same analysis for the altitude provided an insignificant result, therefore the effect of time on the MSF formation should be excluded (at least for that time frame). A larger observational time period would be more indicative if a relative negative relation was present, but the two hour time frame was assumed to be enough to assure the lack of a relationship. A previous study (Szekely et al., 1991) found that flocking

is at its highest level in the morning; afterwards the number of flocking birds declines to a stable level up to dusk. Although it is better to be in a flock than to forage alone, the number of birds in flock as compared to foraging alone depends on time of day because of the time delay in finding a flock (Szekely et al., 1991). In another montane cloud forest in Colombia the daily pattern of the flock activity was reduced in the early morning and late afternoon (Bohórquez, 2003). This uneven distribution of flock activity suggests that birds join flocks during an optimal foraging time, advocating that feeding may be an important aspect of mixed-species flock formation (Bohórquez, 2003). The period of lowest flock activity could provide a time available to the species for reproductive activities.

Generally, avifaunal species richness increases with greater architectural complexity in vegetation in both dry (Kutt and Martin 2010), and wet forests (Hurlbert 2004), but in a study by Kutt and Vanderduys (2017) the peaks were at either end of the gradient, in the most complex and the least complex vegetation types. In Cloudbridge there's a significant difference in tree height between the three types of vegetation, which are distributed at different altitudes, but not a significant difference in the tree density (van der Laan, 2018). At the same time the little patches where NDVI (tree density) is lower, and the MSF concentration was higher seemed to occur next to each other (Figure 14). Another evidence is that the trail with the lowest number of MSF seen (Jilguero) was also the one with highest NDVI, with higher concentrations of MSF towards the forest edge (Jilguero loop). Various studies (Ulfstrand, 1975; Thiollay & Jullien, 1998; Thiollay, 1999) already suggest more frequent mixed flocks in open vegetation areas and forest edges which, as for the data collected in this study, could happen even with little differences.

4.3 Variations in the MSFs by altitude and seasonality

Numbers of birds and number of species variation with altitude were both insignificant, with similar numbers in the diet, showing that an altitudinal range of 300m in a cloud forest doesn't provide enough change in the richness and diversity of birds flocking in MSFs. In a much higher elevational gradient in a tropical forest, the number of species participating in flocks decreased with elevation, with an average of six species above 3250 m a.s.l. and an average of nine species at 2000 m a.s.l. (Kajiki et al., 2018). Moreover, as previously said on the number of birds present in mixed flocks, high abundances of montane passerines might compensate for the small areas

available at high elevations, and as a result they can maintain population sizes comparable to those of their lowland-forest counterparts (Ferenc et al., 2016).

Seasonality also showed no significant results in the number of birds and number of species, showing that the two seasons are not different enough to see a difference in the diversity at the Cloudbridge study site; even though some migratory species left that wasn't enough to leave a substantial numerical change. In general, flocking behaviour has been demonstrated to vary seasonally, even in environments that lack strong seasonality, such as the Amazon Rainforest (Mangini et al., 2018, Rutt et al., 2021). In fact, seasonal differences within flocks can exceed habitat-specific differences between flocks, illustrating that habitat effects could be misleading if seasonality is ignored (Rutt et al., 2021). Mixed-species flocks are generally more frequent and larger during the non breeding season (Moynihan 1962, Powell 1979). Nevertheless, all the non-migratory species seem to participate all year in mixed species flocks. This pattern could be related to the high rainfall. Even if both seasons were not equally surveyed, the mean numbers of MSF seen was not different in Cloudbridge, suggesting that it differs from other studies. Regarding the diet in such flocks, in other environments, like the Mexican dry forest, the abundance of omnivores was higher in the dry than in the rainy season (Almazán-Núñez et al., 2018). This result differs from other studies that reported greater abundance of omnivorous birds in the rainy season (e.g., Borghesio & Laiolo 2004, Tinoco 2009). In this montane cloud forest however there doesn't seem to be any difference in diet by season looking at the graphical visualization.

4.4 Behaviour of the flocks' members

The behaviour of the birds was analysed to look for any difference in how they use the vegetation resource (foraging height) and any difference in how they catch prey (manoeuvres and substrates) while participating in mixed species flocks. The foraging height was found to be differently used, preferring the lower parts (0 to 4 m) to the higher parts (4 to 8 and 8 to 12m). This could be partly due to birds preferences, because where more MSF were found (1700m) less tall trees are present, which allows for the possibility that many times MSF birds still preyed at canopy level but were more difficult to observe higher up on a tree (researcher error). These differences were only found between heights and not between families or individuals belonging to the same species, suggesting that a similar behaviour is present in all

the birds. Other researchers have found that flocking species with similar foraging behaviours forage at different heights in a variety of systems (Greenberg 1984, Hutto 1988, Eguchi et al. 1993, Greenberg et al. 2001).

Comparing the foraging manoeuvres, manoeuvre types and substrate type by focal species no significant values were found, suggesting here that species of the flocks are behaving similarly; unfortunately the data was scarce, so the results could be insignificant because of it. In Newell et al. (2014) resource partitioning was found between four species of migratory warblers in foraging behaviour and foraging height in a Venezuelan shade coffee. Though, the only significant difference in the present study for these behaviours was to be found between the total foraging behaviour of the Furnariidae against the other families, this family has in fact a different behaviour, foraging only by woody gleaning as opposed to foliage gleaning (the preferred method of the other families). Resource partitioning may also occur through use of different foraging manoeuvres and substrates (Robinson and Holmes, 1984), but none of these were found in this study. The lack of hawking observed is probably correlated to the difficulty of observing such behaviour and recognizing it as such, instead of identifying it as flying from tree to tree. Various studies have indicated that birds alter their foraging behaviour when participating in MSFs compared to when foraging with conspecifics or alone (Latta and Wunderle, 1996; Hino, 2000; Jullien and Clobert, 2000; Chen and Hsieh, 2002; Thiollay, 2003; Satischandra et al., 2007; Zou et al., 2011; Hsieh and Chen, 2011). This research didn't analyse the behaviour of birds in and out of the flocks, so no conclusions can be made on that.

5. CONCLUSIONS

In this research it was found that the major families present in MSF at Cloudbridge were Parulidae, Passerellidae and Turdidae. It was also found that even with a discrete altitudinal gradient there was a difference in the occurrence of MSF and that at least in a two hour frame the flocks were encountered with a similar frequency. NDVI was also found to be less where more MSF are present, meaning tree density and vegetation complexity could in fact play a role in the formation of these flocks. These vegetation traits and altitude could either have a synergic effect or be coincidental (more open vegetation at 1700 masl and lower altitudes). This research also tried to see if species varied their foraging strategies to better use resources. The foraging height was found to be differently used, preferring the lower parts (0 to 4 m) to the upper parts

(4 to 8 and 8 to 12m) but this was a preference of all the birds and no differences were found between them. All in all, behaviours seemed alike, having only Furnariidae adopting woody gleaning instead of foliage gleaning, so no resource partitioning seemed to be present within families. In general, birds were consistent with the expected behaviour: Furnariidae woody gleaning, Capitonidae foliage gleaning, and so on.

The effect of vegetation could be further investigated with a study analysing biotic and abiotic factors and/or taking only the more open areas at different altitudes, these studies could better identify the causes of the MSF occurrence in a montane cloud forest like Cloudbridge. Abundance and diversity of birds in MSF didn't show any difference with altitude or season, as normally it would be expected that less birds participate during the breeding season. The researcher's ability to find flocks could also have increased over time leading to a lower number of MSF spotted in the dry season than the current one. Further research could find out if this environment sees a similar pattern of differing behaviours or instead differs from other studies. The study was able to widen our understanding of mixed species flocks in a montane cloud forest and open some new perspectives on future research on this topic.

References

- Almazán-Núñez, R. C., Alvarez-Alvarez, E. A., Pineda-López, R., & Corcuera, P. (2018). Seasonal variation in bird assemblage composition in a dry forest of Southwestern Mexico. *Ornitología Neotropical*, 29, 215-224.
- Beauchamp, G. (2005). "Does group foraging promote efficient exploitation of resources?" *Oikos* 111: 403-407.
- Bohórquez, C. I. (2003). Mixed-species bird flocks in a montane cloud forest of Colombia. *Ornitología Neotropical*, 14, 67-78.
- Centellas, F. A. M. (2018). *Disentangling Driving Forces of Avian Community Assembly along Altitudinal Gradients* (Doctoral dissertation, University of Florida).
- Chen, C. C., & Hsieh, F. (2002). Composition and foraging behaviour of mixed-species flocks led by the Grey-cheeked Fulvetta in Fushan Experimental Forest, Taiwan. *Ibis*, 144(2), 317-330.

- Cintra, R., & Naka, L. N. (2012). Spatial variation in bird community composition in relation to topographic gradient and forest heterogeneity in a central Amazonian rainforest. *International Journal of Ecology*, 2012.
- Cody, M. L. (1971). "Finch flocks in the Mohave desert". *Theoretical Population Biology* 2: 141-158.
- Cuartas-Hernández, S. E., & Gómez-Murillo, L. (2015). Effect of biotic and abiotic factors on diversity patterns of anthophyllous insect communities in a tropical mountain forest. *Neotropical entomology*, 44, 214-223.
- Dale S, Mork K, Solvang R, Plumptre AJ (2000) Edge effects on the understory bird community in a logged forest in Uganda. *Conserv Biol* 14:265–276
- Borghesio, L., & Laiolo, P. (2004). Seasonal foraging ecology in a forest avifauna of northern Kenya. *Journal of Tropical Ecology*, 20(2), 145-155.
- Bubb, P., May, I. A., Miles, L., & Sayer, J. (2004). *Cloud forest agenda* (pp. 32-32). Cambridge, UK: UNEP World Conservation Monitoring Centre.
- Eguchi, K., S. Yamagishi, and V. Randrianasolo. 1993. The composition and foraging behavior of mixed-species flocks of forest-living birds in Madagascar. *Ibis* 135: 91– 96.
- Farine, D. R., & Milburn, P. J. (2013). Social organisation of thornbill-dominated mixed-species flocks using social network analysis. *Behavioral Ecology and Sociobiology*, 67, 321-330.
- Ferenc, M., Fjeldså, J., Sedláček, O., Motombi, F. N., Djomo Nana, E., Mudrová, K., & Hořák, D. (2016). Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: space limitation in montane forest selects for higher population densities. *Oecologia*, 181, 225-233.
- Foster, W. A., and J. E. Treherne (1981). Evidence for the dilution effect in the selfish herd from dish predation on a marine insect. *Nature* 293: 466-467.
- George, Gregory A. (2009). *Foraging ecology of male Cerulean Warblers and other Neotropical migrants*. West Virginia University.
- Givnish, T. J. (1999). On the causes of gradients in tropical tree diversity. *Journal of ecology*, 87(2), 193-210.

- Greenberg, R. (1984). The winter exploitation systems of Bay-breasted and Chestnut-sided Warblers in Panama. *University of California Publications in Zoology* 116: 1–107.
- Greenberg, R., C. E. Gonzales, P. Bichier, and R. Reitsma. (2001). Non-breeding habitat selection and foraging behavior of the Black-throated Green Warbler complex in southeastern Mexico. *Condor* 103: 31–37.
- Greenberg, R. S. (2001). Birds of many feathers: the formation and structure of mixed species flocks of forest birds. *On the move: how and why animals travel in groups*.
- Grytnes, J. A., & McCain, C. M. (2007). Elevational trends in biodiversity. *Encyclopedia of biodiversity*, 2, 1-8.
- Hamilton, W. D. (1971). "Geometry of the Selfish Herd". *Journal of Theoretical Biology* 31: 295-311.
- Hino, T. (2000). Intraspecific differences in benefits from feeding in mixed-species flocks. *Journal of Avian Biology*, 31(4), 441-446.
- Hsieh, F., & Chen, C. C. (2011). Does niche-overlap facilitate mixed-species flocking in birds?. *Journal of Ornithology*, 152, 955-963.
- Hurlbert, A. H. (2004). Species–energy relationships and habitat complexity in bird communities. *Ecology Letters*, 7(8), 714-720.
- Hutto, R. L. (1988). Foraging behavior patterns suggest a possible cost associated with participation in mixed-species bird flocks. *Oikos* 51: 79–83.
- Inman, A. I., and J. R. Krebs (1987). "Predation and group living". *Trends in Ecology and Evolution* 2: 31-32.
- Jullien, M., & Clobert, J. (2000). The survival value of flocking in Neotropical birds: Reality or fiction?. *Ecology*, 81(12), 3416-3430.
- Kajiki, L. N., Montaño-Centellas, F., Mangini, G., Colorado Z, G. J., & Fanjul, M. E. (2018). Ecology of mixed-species flocks of birds across gradients in the Neotropics. *Revista Brasileira de Ornitologia*, 26, 82-89.
- Khursigara, A. J., Roberts, A. P., Burggren, W., & Hamilton, T. J. (2023). Behavior and ecotoxicology.

- Kotagama, S. W., & Goodale, E. (2004). The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. *Forktail*, 20, 63-70.
- Krebs, J. R. (1973). "Social learning and the adaptive significance of mixed-species flocks of chickadees". *Canadian Journal of Zoology* 51: 1275-1288.
- Kutt, A. S., & Martin, T. G. (2010). Bird foraging height predicts bird species response to woody vegetation change. *Biodiversity and Conservation*, 19, 2247-2262.
- Kutt, A. S., & Vanderduys, E. P. (2017). Bird assemblage changes along a savannarainforest gradient in north-eastern Australia. *Australian Zoologist*, 38(4), 552-561.
- Latta, S. C., & Wunderle Jr, J. M. (1996). The composition and foraging ecology of mixed-species flocks in pine forests of Hispaniola. *The Condor*, 98(3), 595-607.
- Lee TM, Soh MCK, Sodhi N, Koh LP, Lim SLH. (2005). Effects of habitat disturbance on mixed species bird flocks in a tropical sub-montane rainforest. *Biol Conserv* 122:193–204
- Maldonado-Coelho M, Marini MA. (2004). Mixed-species bird flocks from Brazilian Atlantic forest: the effects of forest fragmentation and seasonality on their size, richness and stability. *Biol Conserv* 116:19–26
- Mangini GG, Areta JI. (2018). Bird mixed-species flock formation is driven by low temperatures between and within seasons in a Subtropical Andean-foothill forest. *Biotropica* 50, 816–825. (doi:10.1111/btp. 12551)
- Mangini GG et al. (2023). A classification scheme for mixed-species bird flocks. *Phil. Trans. R. Soc. B* 378: 20220100. <https://doi.org/10.1098/rstb.2022.0100>
- McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18(3), 346-360.
- McCain, C. M., & Grytnes, J. A. (2010). Elevational gradients in species richness. *eLS*.
- Montano-Centellas, F. A., & Garitano-Zavala, Á. (2015). Andean bird responses to human disturbances along an elevational gradient. *Acta Oecologica*, 65, 51-60.
- Moynihan, M. H. (1962). The organization and probable evolution of some mixed species flocks of neotropical birds.

- Munn, C. A. (1985). Permanent canopy and understory flocks in Amazonia: species composition and population density. *Ornithological monographs*, 683-712.
- Neill, S. R. J., and J. M. Cullen (1974). "Experiments on whether schooling of prey affects hunting behaviour of cephalopods and fish predators". *Journal of Zoology* 172: 549-569.
- Newell, Felicity L., Tiffany-Ahren Beachy, Amanda D. Rodewald, Carlos G. Rengifo, Ian J. Ausprey, and Paul G. Rodewald. (2014). Foraging behavior of migrant warblers in mixed-species flocks in Venezuelan shade coffee: interspecific differences, tree species selection, and effects of drought. *Journal of Field Ornithology* 85, no. 2 : 134-151.
- Péron, G., & Crochet, P. A. (2009). Edge effect and structure of mixed-species bird flocks in an Afrotropical lowland forest. *Journal of Ornithology*, 150(3), 585-599.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2007). Linear and nonlinear mixed effects models. R package version, 3(57), 1-89.
- Powell, G. V. (1979). Structure and dynamics of interspecific flocks in a Neotropical midelevation forest. *The Auk*, 96(2), 375-390.
- Powell, G. V. (1985). Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. *Ornithological Monographs*, 713-732.
- Pulliam, H. R. (1973). "On the advantages of flocking". *Journal of Theoretical Biology* 38: 419-422.
- Rabinovich, J. E., & Rapoport, E. H. (1975). Geographical variation of diversity in Argentine passerine birds. *Journal of Biogeography*, 141-157.
- Remsen, J. V., & Robinson, S. K. (1990). A classification scheme for foraging behavior of birds in terrestrial habitats. *Studies in avian biology*, 13(1), 144-160.
- Robinson, S. K., & Holmes, R. T. (1982). Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology*, 63(6), 1918- 1931.
- Robinson, S. K., & Holmes, R. T. (1984). Effects of plant species and foliage structure on the foraging behavior of forest birds. *The Auk*, 101(4), 672-684.

- Ruggiero, A., & Lawton, J. H. (1998). Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean passerine birds?. *Biological Journal of the Linnean Society*, 63(2), 283-304.
- Ruggiero, A. (2001). Size and shape of the geographical ranges of Andean passerine birds: spatial patterns in environmental resistance and anisotropy. *Journal of Biogeography*, 28(10), 1281-1294.
- Rutt CL, Stouffer PC. (2021). Seasonal dynamics of flock interaction networks across a human-modified landscape in lowland Amazonian rain forest. *Ecol. Appl.* 31, e02235. (doi:10.1002/eap.2235)
- Salisbury, C. L., Seddon, N., Cooney, C. R., & Tobias, J. A. (2012). The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecology Letters*, 15(8), 847-855.
- Satischandra, S. H. K., Kudavidanage, E. P., Kotagama, S. W., & Goodale, E. B. E. N. (2007). The benefits of joining mixed-species flocks for greater racket-tailed drongos *Dicrurus paradiseus*. *Forktail*, 23, 145.
- SIG y Unidad de Climatología, Departamento de Desarrollo, Instituto Meteorológico Nacional San José, Costa Rica, 2023
(<https://www.imn.ac.cr/documents/10179/29808/PerspClimaCR-202402/0fe8265d-f9644732-aeba-2e02a2739ec8>)
- Slifkin, J. (2019). Surveys of Mixed Species Feeding Flocks in Cloudbridge Nature Reserve, Costa Rica: A Progress Report.
- Sridhar, H., Beauchamp, G., & Shanker, K. (2009). Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour*, 78(2), 337-347.
- Srinivasan, U., & Quader, S. (2012). To eat and not be eaten: modelling resources and safety in multi-species animal groups.
- Stouffer, P. C., & Bierregaard Jr, R. O. (1995). Use of Amazonian forest fragments by understory insectivorous birds. *Ecology*, 76(8), 2429-2445.
- Szekely, T., Sozou, P. D., & Houston, A. I. (1991). Flocking behaviour of passerines: a dynamic model for the non-reproductive season. *Behavioral Ecology and Sociobiology*, 28, 203-213.

- Terborgh, John. (1977). Bird species diversity on an Andean elevational gradient. *Ecology* 58, no. 5: 1007-1019.
- Terborgh, J., Robinson, S. K., Parker III, T. A., Munn, C. A., & Pierpont, N. (1990). Structure and organization of an Amazonian forest bird community. *Ecological Monographs*, 60(2), 213-238.
- Jullien, M., & Thiollay, J. M. (1998). Multi-species territoriality and dynamic of neotropical forest understory bird flocks. *Journal of Animal Ecology*, 67(2), 227-252.
- Thiollay, J. M. (1999). Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: an intertropical comparison. *Journal of Avian Biology*, 282-294.
- Thiollay, J. M. (2003). Comparative foraging behavior between solitary and flocking insectivores in a Neotropical forest: does vulnerability matter. *Ornitologia neotropical*, 14, 47-65.
- Tinoco, BA. (2009). Estacionalidad de la comunidad de aves en un bosque deciduo tumbesino en el sur occidente de Ecuador. *Ornitologia Neotropical* 20: 157–170.
- Tubelis, D. P. (2007). Mixed-species flocks of birds in the Cerrado, South America: a review. *Ornitología Neotropical*, 18(1), 7.
- Ulfstrand, S. (1975). Bird flocks in relation to vegetation diversification in a South Swedish coniferous plantation during winter. *Oikos*, 65-73.
- Waite, T. A., and T. C. Grubb. (1988). "Copying of foraging location in mixed-species flocks of temperate-deciduous woodland birds: an experimental study". *Condor* 90: 132-140.
- Winterbottom, J. M. (1943). On woodland bird parties in northern Rhodesia. *Ibis*, 85(4), 437-442.
- van der Laan, C. (2018). Forest assessment of planted, naturally regenerated and primary tropical cloud forest.
- Vazquez G., and Givnish. (1988). Altitudinal Gradients in Tropical Forest Composition, Structure, and Diversity in the Sierra de Manantlan." *Journal of Ecology* 86, no. 6: 999–1020.

- Zhang, Q., Holyoak, M., Goodale, E., Liu, Z., Shen, Y., Liu, J., ... & Zou, F. (2020). Trait–environment relationships differ between mixed-species flocking and nonflocking bird assemblages. *Ecology*, 101(10), e03124.
- Zou, F., Chen, G., Yang, Q., & Fellowes, J. R. (2011). Composition of mixed-species flocks and shifts in foraging location of flocking species on Hainan Island, China. *Ibis*, 153(2), 269-278.
- Zuluaga, G. J. C., & Rodewald, A. D. (2015). Response of mixed-species flocks to habitat alteration and deforestation in the Andes. *Biological Conservation*, 188, 72-81.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R (Vol. 574, p. 574). New York: springer.