

**THE ROLE OF FACILITATION IN THE STRUCTURE OF TROPICAL BIRD
COMMUNITIES: A CASE STUDY OF MIXED-SPECIES FLOCKS**

by

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B.Sc., Universidad de Antioquia, 2011

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

May 2016

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Abstract

Understanding the influence of species interactions on community structure is a long-standing goal in ecology. While many studies have focused on negative biotic interactions, the role of other mechanisms has received less attention, in particular, facilitation. In birds, a striking case of facilitation occurs in mixed-species flocks, in which individuals of different species move and forage as a group to obtain benefits from the association. These associations of species in mixed flocks have been described in different habitats during the last century; however, there is still much debate regarding the prevalence of this foraging strategy and the role it plays in Neotropical bird communities. In this study, I integrated data from mixed species flocks observations and species occurrence to investigate how facilitative interactions influence the structure of Neotropical bird communities across a 3000-m elevational gradient on the eastern slope of the Andes in Peru. First, I examine how the structure of mixed flocks changes across elevations. Second, I quantify the stability of these multispecies groups over time. Third, I evaluate the association of several key habitat variables with flock diversity. Finally, utilizing a dataset for the entire forest bird community, I assess the prevalence and importance of mixed-species flocks across the gradient. The results showed that flocks were highly organized and stable across elevations. Flocks across the gradient exhibited a similar general structure, composed of a stable core group of species and a more dynamic component of attending species. This spatial and temporal analysis suggests that the stability of mixed-species flocks in the Andes is similar to what has been previously described in the Amazonian lowlands, with flocks exhibiting stable home ranges and core member composition over time. Vegetation structure

explained 63% of variation in flock richness along the gradient, with number of trees and canopy height as primary predictors. Importantly, this study demonstrates that mixed-species flocks are used by more than a third of bird species present in the community, suggesting that these facilitative interactions are an important and underappreciated component of tropical bird communities.

Preface

The research questions and project design were carried out collaboratively between my supervisor, Jill Jankowski, and me. I carried out the fieldwork for this project; however some data on species occurrence along the gradient were obtained from the Manu project database. I conducted all the analysis and writing of this thesis. Dr. Jankowski provided helpful feedback.

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List of Symbols and Abbreviations

~	approximately
dbh	diameter at breast height
FI	flocking index
m	meters
m ²	square meters
masl	meters above sea level
NPP	net primary productivity
SE	standard error

Acknowledgements

I would like to thank my supervisor, Jill Jankowski, for her guidance, advice, support and patience throughout my graduate work. I feel very privileged to have the opportunity to work with her. Thank you to my committee members Leticia Aviles and Darren Irwin for their thoughtful comments and ideas.

I feel very fortunate to be part of Manu project during the last years and I would like to thank Gustavo Londoño for his encouragement and support during all these years, and also to the Manu project volunteers in particular 2013 crew Mario Loaiza, Juliana Soto, Camilo De los Rios, Julian Heavyside, Wendy Valencia, Jeremia Kennedy. I would like to thank Paula Morales, Laura Gomez whose positivity tenacity and enthusiasm under challenging conditions were key to have successful field seasons. For insightful comments and discussions on this project I would like to thank Gustavo Londoño, Scott Robinson and Patrick Kelley.

I offer my enduring gratitude to the professors, staff and fellow students at Biodiversity Research Center, who have inspired me enlarging my vision of science. Thank you to Alice Liou, the Zoology Department graduate secretary, for her patience and help.

For their support, encouragement, positivity, patience and inspiration during this endeavor, I am indebted to my family mom, dad and brother, but especially to Santiago David.

This work was funded by the HESSE Research Award in Ornithology 2013-2014, Wendy Fan Memorial Scholarship, BRITE Fellowship, Dennis H.CHITTY Memorial Graduate Scholarship in Ecology.

A Alfonso, mi decisión de hacer lo que me hace feliz y mi amor por la selva lo herede de ti, esa es mi mejor herencia

A Lucina, en cada centímetro, de cada cosa que hago, tu eres mi inspiración.

A Jader, somos diferentes, pero siempre contarás conmigo.

A mis amigos, que son la familia que he ido encontrando.

A Camilo, lamentó no haber contruido un mundo mejor en el que te quisieras quedar.

A ti.

Chapter 1: General introduction

1.1 Introduction to facilitation

Understanding the influence of biotic interactions on community structure and species' range limits has been a long-standing goal in ecology and biogeography (Terborgh 1971; Terborgh and Weske 1975; Araújo and Luoto 2007; Gross et al. 2009; Sexton et al. 2009; Wisz et al. 2013). Among the various forms of interactions (e.g., competition, predation, parasitism, mutualism, facilitation) negative interactions, such as competition and predation, have received the most attention. Competitive interactions can influence distributional limits of species and community assembly, resulting in distributions limited by the presence of a competitor (Connell 1961; Terborgh and Weske 1975; Tilman 1994; Remsen and Graves 1995; Bullock et al. 2000; Jankowski et al. 2010). However, recent studies also suggest that the effect of positive interactions, particularly facilitation, can be just as important as negative interactions in structuring ecological communities and reinforcing range limits (Bertness and Callaway 1994; Bertness and Leonard 1997; Hacker and Gaines 1997; Stachowicz 2001; Cavieres et al. 2002). For example, experimental studies have shown that species involved in facilitative interactions can expand their elevational range to match their facilitator's range (Afkhami et al. 2014; Crotty and Bertness 2015).

In a broad sense, facilitation can be defined as an interaction between species that benefits the average individual fitness of at least one species without negatively affecting the other species (Hacker and Gaines 1997; Stachowicz 2001). Facilitation can occur when the presence of one species makes the local environment more favourable for another species, by enhancing,

directly or indirectly, its growth, reproduction or survival (Stachowicz 2001; Bruno et al. 2003). The outcome of facilitation to any participating organism (the facilitator and facilitated species) can be either neutral or beneficial, but not detrimental. Following this definition, mutualisms would be the subset of those facultative interactions in which participating species have reciprocally beneficial interactions (see Pugnaire et al. 1996).

Facilitation among species in communities has been the subject of increasing interest for community ecologists during the last decades (Michalet and Pugnaire 2016). Although this concept was introduced in the plant community literature a century ago (Pearson 1914; Clements 1916), it was largely neglected in ecological theory by most community ecologists, compared with the attention focused on other mechanisms (but see Bronstein 1994). Several relatively recent attempts have been made to include facilitation as an important mechanism in ecological theory (e.g., Boucher 1985; Bertness and Callaway 1994; Bruno et al. 2003; Michalet et al. 2006; Liancourt et al. 2012; Valiente-Banuet and Verdú 2013), which could highly impact the framework of many fundamental models in population and community ecology.

Incorporating facilitation into ecological theory can influence several fundamental concepts in ecology (Bruno et al. 2003). Among those, the niche concept, which predicts where a species can live, is of particular interest. Given that facilitation can allow a species, in the presence of a facilitator, to tolerate conditions that it would otherwise not be able to tolerate (Crotty and Bertness 2015), it can result in the expansion of the realized niche beyond the range predicted by its fundamental niche (Bruno et al. 2003), widening the distribution of the species (e.g., Afkhami et al. 2014; Crotty and Bertness 2015).

The occurrence and prevalence of facilitation along environmental gradients have attracted relative attention during the last two decades, after Bertness and Callaway (1994) proposed that the importance of facilitation should increase as environmental or biotic conditions become more stressful for species. Many studies focused in plant communities have found support for this stress gradient hypothesis, and some studies in animal communities confirm similar results (e.g. Callaway 2007). However recent studies inspired by this stress gradient hypothesis have suggested different outcomes (e.g. Maestre et al. 2009; Holmgren and Scheffer 2010), and it is now accepted that no single theoretical model may explain the occurrence of facilitation. The prevalence and role of positive interactions in response to environmental gradients remains highly debated and is especially poorly explored in animal communities.

Facilitation is ubiquitous in communities, with facilitative partners found in plants (Callaway 1995), fungi (Afkhami 2012), algae (Hay 1981), coral reefs, sessile invertebrates (Bertness 1989; Bracken et al. 2007), fishes (Pereira et al. 2013), birds (Sridhar et al. 2012), and mammals, ranging from diffuse and indirect interactions to highly integrated and coevolved associations between organisms. Some well-studied examples of facilitation include associational growth in plants (i.e., via increased access to nutrients, Pugnaire et al. 1996), associational defense (mutual protection from natural enemies, Hay et al. 2004), protection to plants by ants (protection from natural enemies for food reward, Rico-Gray and Oliveira 2007), nutritional symbiosis, and more generally, pollination (Pellmyr 2002) and seed dispersal (Levey et al. 2002). Nevertheless, despite the widespread examples of facilitative interactions across taxonomic groups, most studies have focused on the ecological consequences of facilitation on plant communities (i.e., plant-pollinator, plant-disperser, plant-herbivore); the role of facilitation as a mechanism

structuring communities in other taxonomic groups remains poorly explored. Among the studies describing the facilitation in vertebrate communities (e.g., animal-animal interactions), examples include fish schools (e.g., Pereira et al. 2013), mammal troops (Terborgh 1990) and flocking in birds (Thompson et al. 1991; Thomson et al. 2003; Sridhar et al. 2012). However, much remains to be learned about the consequences and importance of these interactions in ecological community structure and distribution of vertebrate species.

1.2 Facilitation in bird communities

In birds, facilitation occurs among species that participate in mixed-species flocks (Powell 1985; Sridhar et al. 2012; Palmer et al. 2015). Mixed-species flocks are roving groups of individuals of two or more bird species that obtain benefits from their association with other species (Swynnerton 1915; Morse 1970; Morse 1977; Powell 1985). Birds in mixed-species flocks may benefit directly or indirectly from this association, through shared social information (Satischandra et al. 2007; Goodale et al. 2010), increased foraging efficiency (Hino 1997; Dolby and Grubb 1998; Satischandra et al. 2007) and reduced predation risk (Moynihan 1962; Morse 1977; Thiollay 1999; Sridhar et al. 2009). Therefore, mixed-species flocks may allow a species to persist in high-predation or low-resource environments, or other harsh conditions where without facilitation by flocks, it would not otherwise persist (Morse 1970).

Species joining mixed-species flocks may accrue benefits through a variety of mechanisms (reviewed in Colorado 2013). Reduced predation risk can arise from mechanisms such as the risk-dilution effect (decreased probability to be singled out by a predator; Foster and Treherne 1981), the many-eyes effect (larger groups are more effective in detecting approaching predators; Pulliam 1973; Powell 1974), confusion effect (reduced attack-to-kill ratio of a

predator as a result of sensory inability to single out a prey in a group; Krause and Ruxton 2002) and collective defense against predators (mobbing behavior; Vieth et al. 1980), including nest predators (Martinez unp. data). Additionally, increased foraging efficiency for flocking individuals can arise from kleptoparasitism (Brockmann and Barnard 1979), copying (Krebs 1973), easier location of food (Powell 1985) and feeding on insects flushed by other birds (beating effect; Winterbottom 1943). Furthermore, mixed-species flocks can provide unique benefits by gaining information from other bird species, including taking advantage of the complementary anti-predator abilities across species (Powell 1985) and alarm calls of heterospecifics (Lea et al. 2008). Alternatively, individuals can incur costs associated with participation in mixed-species flocks, such as competition for resources (Goss-Custard 1980; Hutto 1988), kleptoparasitism by other flock members (Brockmann and Barnard 1979; Munn 1986; Satischandra et al. 2007), and increased conspicuousness to predators as a group (Hutto 1988).

Facilitation occurring among species in flocks varies along a continuum in the benefits that each species provides to others, from mutually beneficial interactions (+, +), to commensal interactions (+, 0), which are likely to be specific to species pairs. One of the scenarios implies both species in the interaction facilitating each other, and obtaining a benefit (i.e., species A and B simultaneously decreasing the risk of predation because the dilution effect). Alternatively, species A in the flock can facilitate an attendant species B without incurring a cost (i.e., flushing insects that other birds feed on). Other scenarios, where species A incurs a cost in the short term when facilitating species B (i.e., alarm call when a predator is close) are also possible. In the long term, however, it is expected that species participating frequently in mixed-species flocks

will be those for which the potential fitness benefits of flocking outweigh the costs (Brawn et al. 1995; Jullien and Clobert 2000; Jullien and Thiollay 2001).

1.3 Tropical mixed-species bird flocks

Among mixed-species bird flocks, Neotropical mixed-flocks have attracted the attention of ecologists for more than a century. Neotropical flocks exhibit some unique features, such as multi-species defense territoriality (Munn and Terborgh 1979), communal roosting sites (Buskirk et al. 1972), stability over long time scales (Martínez and Gomez 2013) and strong facilitative relationships among member species. Based on isolated evidence, several authors have suggested that mixed flocks may play an important and underappreciated role in tropical bird communities (e.g., Powell 1989; Jullien and Thiollay 2001; Lee et al. 2005; Harrison and Whitehouse 2011). Several studies have suggested that flocks influence birds from the individual to the community level; flock participation might have a positive effect on individual fitness (Jullien and Clobert 2000), influence population density of the participants and generate interdependence among them (Powell 1989). Furthermore, flocks have been proposed as a factor promoting high species diversity in Neotropical avifauna, leading to higher species packing within communities (Powell 1989).

Mixed-species flocks are widespread in the Neotropics, occurring virtually in all the habitats from the Amazon to the high Andes. However, comparative studies of flocks across local scales within a region are rare. Most studies collect data at one locality or small spatial scales (e.g. Buskirk et al. 1972; Poulsen 1996; Jullien and Thiollay 1998). Studying flocks at a regional scale presents an opportunity to address questions in community organization. To the

best of my knowledge, no study has examined the structure and the ecological importance of these flocks along a broad elevational gradient in the Neotropics.

1.4 Study goals

The aim of this research is to study facilitative interactions in tropical mixed-species bird flocks along a broad elevational gradient. I use observational data to describe the structure and stability of flocks across elevations, including tropical lowlands, lower montane forest and cloud forest. I examine the habitat factors that influence flock diversity. Finally, I examine the importance of these multi-species flocks for individual species and for the bird community across the gradient.

Chapter 2: Mixed-species flocks along an elevational gradient and their importance for bird communities.

2.1 Introduction

Tropical ecosystems exhibit the highest species diversity in the world for the large majority of higher-level taxa, including birds (MacArthur 1969; Gaston 2000; Hillebrand 2004). Tropical bird communities exhibit both high species richness and beta diversity (MacArthur and MacArthur 1961; Jankowski et al. 2013) and host numerous endemic species (Myers et al. 2000). For example, a 100 m elevation band in the Andean foothills may contain nearly 300 species of breeding birds (Terborgh 1977), and a single survey plot in the Amazon lowlands can host over 100 species with overlapping foraging territories (Terborgh 1971). Such heightened diversity on several scales potentially allows for more frequent and complex interactions among species (Schemske et al. 2009).

Many complex interspecific interactions have been described in the tropics, including specialized pollinator systems (Bawa 1990), mutualistic defenses in ant-plant symbioses (Davidson and Mckey 1993) and antbirds parasitizing foraging army ants (Wrege et al. 2005). Among the numerous interspecific interactions in the tropics, one striking interaction found in bird communities is the association of individuals of multiple bird species in mixed flocks (hereafter mixed-species flocks). Mixed-species flocks are among the most complex multi-species aggregations found in terrestrial vertebrates (Munn 1985) and have attracted broad interest from tropical ecologists over the last century (e.g. Davis 1946; Buskirk et al. 1972;

Buskirk 1976; Munn and Terborgh 1979; Hutto 1987; Graves and Gotelli 1993; Jullien and Thiollay 1998; Greenberg 2000; Sridhar et al. 2009). These multispecific flocks of birds are roving groups of individuals of two or more species that group to forage together and share heterospecific information (Morse 1970). These flocks are distinguished from aggregations of birds that accidentally form when feeding in a localized resource (Powell 1985).

Mixed-species flocks occur in temperate, subtropical and tropical areas (e.g. Powell 1985; Goodale et al. 2009; Sridhar et al. 2012; Goodale et al. 2015), in all terrestrial habitats across the world, but reach their maximum diversity and complexity in tropical forest (Munn 1985). In some tropical forests, mixed-species flocks dominate entire bird communities, where as many as one third of local species join these flocks (Latta and Wunderle 1996; Jullien and Thiollay 2001). These tropical flocks can consist of up to 80 species and more than 100 individuals (Munn 1985). Moreover, these flocks are not randomly drawn from the community. Instead, species tend to associate in flocks with other species that are phenotypically similar, for example in body size and foraging behaviour (Sridhar et al. 2012).

The pervasiveness of mixed flocks in the tropics (Greenberg 2000) and the broad range of species utilizing this flocking strategy at local scales may indicate that they play an important role in higher-order ecological patterns such as community structure and distributional patterns of birds (e.g. Powell 1985; Powell 1989; Jullien and Clobert 2000; Jullien and Thiollay 2001; Harrison and Whitehouse 2011). Other features of tropical flocks that make them interesting to study, particularly for the partitioning of ecological roles, include interspecific alarm calls and responses (Munn 1986), multi-species territorial defense (Munn and Terborgh 1979), communal roosting sites (Buskirk et al. 1972), collective defense against predators (e.g., nest predator

defense, Martinez unp. data), mobbing behaviour (Courter and Ritchison 2012), and stability over long time scales (e.g. decades; Martínez and Gomez 2013).

Despite the great interest in mixed-species flocks over the last century and the recognition of these flocks as prevalent characteristic of tropical communities, our knowledge of their ecological importance is still quite limited. Information of flocks has been collected at relatively narrow elevational spatial scales (e.g., Arbeláez-cortés and Marín-gomez 2012), discontinuous elevations (e.g., Goodale et al. 2009; Marín-Gómez and Arbeláez-Cortés 2015), short periods of time, and individuals that have not been colour banded (Goodale et al. 2015). Therefore, assessments of the ecological consequences and importance of flocks for broader tropical bird communities are restricted to small spatial and short temporal scales (e.g. Powell 1989).

Furthermore, whereas numerous studies have examined different ecological aspects of tropical flocks at low elevations (i.e., composition, structure, stability over time; (Willis 1958; Munn and Terborgh 1979; Munn 1985; Graves and Gotelli 1993; Stouffer and Bierregaard 1995; Develey and Peres 2000; Jullien and Clobert 2000; Maldonado-Coelho and Marini 2000; Ragusa-Netto 2002; Martínez and Zenil 2012), less is known about these aspects of flocks at higher elevations (but see Davis 1946; Buskirk et al. 1972; Powell 1979; Merkord 2010; Arbeláez-Cortés and Marín-Gomez 2012). Previous studies of lowland mixed-species flocks have documented cohesive groups that exhibit high diversity and long-term stability (i.e., core-member composition, home range boundaries), sometimes over decades (Martínez and Gomez 2013); by comparison, studies at higher elevations suggest a tendency for montane flocks to be less diverse (Moynihan 1962; Arbeláez-Cortés and Marín-Gomez 2012), more dynamic, and in

some cases, they do not appear to hold permanent territories (e.g., non-Amazonian flocks; Stotz 1993; Hart and Freed 2003). Although there is some evidence in the literature suggesting temporal stability in montane flocks (e.g., Buskirk et al. 1972; Powell 1979; Merkord 2010), the overall lack of data available for tropical montane mixed-flocks, and the limited information on the effects of elevation (but see Goodale et al. 2009; Marín-Gómez and Arbeláez-Cortés 2015) and other environmental variables (i.e. vegetation structure), have led to the idea that stable, complex tropical mixed-species flocks are mainly a low elevation phenomenon.

2.2 Research questions

In this study, I examine how mixed-species bird flocks influence the structure of bird communities across a broad forested Neotropical elevational gradient within one of the world's foremost biodiversity hotspots, Manu National Park, Peru. First, I examine how mixed-species flocks structure change across the elevational gradient. Second, I quantify the stability of these multispecies groups over time (i.e., for three different temporal periods) across the gradient, using data on species composition and home range locations for colour-banded flocks. Third, I evaluate the association of several key environmental variables (i.e. canopy height, vegetation density) with flock diversity along the gradient. Finally, utilizing a dataset for the entire forest bird community, I assess the prevalence and importance of mixed-species bird flocks for the bird community across the gradient.

2.3 Materials and methods

2.3.1 Study site

This research was conducted along an elevational gradient on the eastern slope of the Andes in the buffer zone of Manu National Park, Peru. The gradient encompassed elevations between 400-3500 m, extending from lowland forest (<800 m, floodplain forest, *terra firme*), through premontane forest (800-1200m), cloud forest (1200-2200m) and upper montane forest to *puna* grassland (2200-3400m). The forest present in the area is mainly primary forest, with small patches of older secondary forest adjacent to the unpaved, narrow Manu road, which runs along the southern border of the park from treeline to the lowlands. The forest is a patchwork of different canopy heights even at similar elevations, created by the geography of the terrain, windswept ridges, landslides and the presence of bamboos patches. Annual temperatures means along the elevational gradient ranged from 11.2 °C in the montane forest to 23.2 °C in the lowland forest (Londoño unp. data).

2.3.2 Data collection mixed-species flocks

A mixed-species flock was defined as a group of individuals of at least two species foraging and moving together within 15 m distance from their nearest neighbor for at least 10 minutes (Stotz 1993). Mixed-species flock data was collected over two field seasons from July to October 2013 and August to October 2014. Systematic searches for flocks were conducted daily from dawn until dusk along the elevational gradient (400-3300m), following trails in areas of primary forest and in some cases older secondary forest. Once a flock was detected, it was followed as closely as possible (i.e., 10-40 m) for at least 30 minutes until all species were

identified (i.e., no new species were detected for 10 min) up to a maximum of 60 minutes. One hour was, in general, enough time to fully characterize even larger flocks and is within the time window previously suggested by other observational studies to characterize flocks (Goodale et al. 2009).

Data collected from each flock included songs and calls, species composition, and when possible, flock structure (i.e., number of individuals per species) and individual colour band identification (see section below). For all flocks, I registered the latitude/longitude location and elevation with a GPS unit (Garmin 62s) every 15 min. Flocks that were not fully characterized or that were lost by the observer more than 15 min out of 60 min were excluded from analyzes. To assign flock independence, I assumed flock territories to be circular with a diameter of 400m and 800m, for the lowlands and montane flocks, respectively (based on Jullien and Thiollay 1998, Martínez and Gomez 2013, pers.obs). Therefore, flocks observed >400 (i.e., lowland flocks) or >800 m (i.e., montane flocks) from previously observed flocks in sequential or non-sequential observations were considered independent. Neighboring flocks found closer than this defined circular territory were included only if it was certain that it was a new flock (i.e., by citing colour banded individuals in the flocks).

2.2.3 Colour marking

This study was conducted as part of a larger project that evaluates the factors that determine species range limits along an elevational gradient. As part of this study, banding data were collected along the elevational gradient in four field seasons from August to December, 2011-2014. Nets were located at ground level in 50 netting stations along the gradient. Each

netting station was run for three days, at least twice each year (within the five-month field season). Individual birds of focal forest species participating in flocks were captured with mist-nets and uniquely colour-marked. The colour-banded scheme consisted of one metal numbered band in one leg and two celluloid colour bands on the other leg. Colour banding of individuals allowed me to identify individual flocks and to monitor the same flock over time. As I was not able to mark all individuals in each flock, I considered a flock to be the same if it was detected within the flock's territory and if at least 1-2 individuals of different species within the flock were colour banded. A total of 6553 individuals were just metal banded, and 882 individuals were metal and colour banded. During the banding process, we collected morphometric measurements including body mass, tarsus, bill length, and wing chord.

2.3.3 Species participation in mixed-species flocks

Bird species were classified into four categories using their observed participation in flocks and based on detections from census points and mist netting at the study site (Jankowski *unpubl data*). Each bird species was categorized as an accidental, occasional, regular, or obligate participant of mixed-species flocks using a combination of two metrics occurrence and propensity to calculate a Flocking Index that weights the participation of each species in flocks by their abundance in the study site:

$$\text{Flocking Index} = (\text{Occurrence} * \text{Propensity})$$

Occurrence is the frequency in which a species occurs in flocks, calculated as the number of times a species was observed foraging in mixed-species flocks divided by the total flocks of

that type sighted (e.g., lowland flocks, low montane flocks), as follows: Occurrence = (# detection sp. A in flocks/ # total flocks of that type). Occurrence values range from 0-1, where 0 indicates a species that was never observed in flocks and 1 indicates a species observed in all flocks. For occurrence calculation, the presence of a species was considered as a time, the number of individuals was not considered.

Propensity is the frequency in which a species uses the flocking strategy. It was calculated as the number of times a species was observed foraging in mixed-species flocks divided by the number of times the species was detected overall (i.e. in mixed-flocks, monospecific-flocks and solitary combined). For this calculation each individual of a species detected was considered as a time. Propensity was calculated using data from flock observations and previous point count surveys, using the formula: Propensity = (# times sp. A observed in flocks/ # times sp. A detected).

To establish the final categories of species based on the Flocking Index, I used the following groups:

a) *Obligate flocking species* were species that permanently associate in flocks, having a Flocking Index >0.6. These species exhibit a high occurrence and propensity. Groups of two or more obligate participants in flocks form the "core" of the flock.

b) *Regular flocking species* often follow flocks beyond their territories but also forage independently of mixed flocks. They may leave the flock several times during the day.

These species exhibit a Flocking Index between 0.30-0.59.

c) *Occasional flocking species* were species commonly detected outside the flocks and found in flocks only briefly and for short distances. These species exhibit a Flocking Index between 0.05-0.29.

d) *Accidental flocking species* were mostly found outside the flocks and detected within flocks for short periods of time and on very few occasions, probably passing through the flock territory. These species exhibit a Flocking Index <0.049 .

2.3.4 Foraging guild classification

Bird species were classified into foraging categories using their observed and documented diet (Del-Hoyo et al. 1992, 1994, 1997, 1999). Each bird species was categorized as frugivorous, insectivorous, nectarivorous or omnivorous.

2.3.5 Flock stability

Temporal flock stability was defined as the proportion of species that are consistent in a given flock between two observations separated by a time period. Temporal flock stability was measured at three different time scales, comparing the species composition of a flock between two observations separated by 3-5 hours, 6-15 days and one year. For example, I compared the species composition of a given flock in 2013 with its composition in 2014. Similarly, I compared the species composition of a flock observed in day 1 with its composition 8 days later.

I identified individual flocks using colour-banded individuals, which allowed me to compare the same flock over time. The calculation of stability was limited to flocks that contained at least one colour-banded individual from each of two different species in the same

home range, or if the home range was not known, less than 200 m from its first observed location. To collect data on flock composition, flocks were followed as closely as possible during 60 min intervals. During this interval time, I collected data on species composition, number of individuals, colour banded individuals, songs, and flock movement.

2.3.6 Home range characterization

Home range of focal flocks ($n=7$) across the gradient was characterized using a one-day sample. Each of the focal flocks was followed from dawn (6:00 am) to dusk (5:00 pm). I collected data on species composition, number of individuals and individual identity (when colour-banded) for 60-minute intervals. The exact location of the flock was georeferenced every 15 minutes. The home range of each mixed flock was mapped using a minimum of 30 georeferenced locations, and the area was measured using the minimum convex method in QGIS version 2.8.2 (ESRI 2012).

2.3.7 Vegetation structure

Vegetation structure was characterized using a protocol adapted from Martin et al. (1997). Vegetation structure, including vertical and understory structure, was measured within each mixed-species flock territory, in the location where the flock was first encountered. Forest vertical structure was characterized in a 20 x 20 m plot at each flock territory using five variables: canopy height, number of trees, and percent cover of canopy, bamboo and epiphytes. Canopy height was measured using a rangefinder (Nikon Prostaff 3) and calculated as the average of canopy height in the center of the plot. Number of trees was estimated by counting

trees >10 cm diameter at breast height (d.b.h.). Canopy, bamboo and epiphyte cover was calculated as a percentage of cover over the total area of the plot using ocular estimation (i.e., <25%, 25-50%, 50-75%, 75-100%). Forest understory structure was characterized in a 10 x 10 m plot at each flock territory by the number of small stems (≤ 2.5 cm d.b.h.; >1m height).

2.3.8 Prevalence of flocking at the community level

I compiled a database of the bird community along the Manu elevational gradient (i.e., species found across all elevations in the study area) using data from previous point count surveys and mist netting data collected from 2006 to 2014 (Jankowski unpubl. data). I collected additional data of species occurrence from July to Nov 2012-2014, using automated field scan recorders (Songmeter SM2), flock observations and occasional detections. The automated field scan recorders recorded songs for 20 minutes every hour from dawn to dusk every day. Recorders were placed in forest locations separated by 100 m in elevation and were moved to new locations along the gradient every three days to cover all elevations. The species identified follow the most recent updated taxonomy from the current version of the South American Classification Committee (Remsen 2015).

I combined bird species presence data collected by the different sampling methods to create an elevation by species presence matrix for the community. For the purpose of this analysis, the community was divided into 100-m elevational zones along the gradient (e.g., 300-399, 400-499 masl) from 500 to 3400 elevation, and the community composition in each elevational zone was calculated. In addition, I calculated the number of species observed in mixed flocks in each elevational zone (e.g., 300-399, 400-499 masl).

To examine the prevalence of flocking (FP) at the community level, I calculated the proportion of species in the community joining flocks at each elevation. Flocking prevalence (FP) in the community ranges from 0-1, where 0 indicates zones in which no species participated in flocks and 1 indicates zones in which all species present in that community joined flocks.

$$\text{Flocking prevalence(FP)} = \frac{\text{\#spp detected in flocks within a given elevational zone}}{\text{\# spp detected within a given elevational zone}}$$

2.3.9 Data analysis

To group mixed-species flocks along the gradient into different flock types, I performed a Cluster analysis in R package ‘vegan’ (Oksanen et al. 2011). I used the average linkage agglomerative method (UPGMA) to perform a hierarchical clustering analysis of flocks (Mirkin 2011). The hierarchical cluster distance was based on the Jaccard dissimilarity Index, commonly used for presence-absence based community comparisons (Krebs 2014). The Jaccard index ranges from 0 (similar) to 1 (dissimilar). The hierarchical cluster analysis based on flock composition dissimilarity was used to inform the division of flocks into distinguishable groups (i.e., flock types) along the gradient.

To test for differences among flock types in mean richness and size, I fit a generalized linear model (GLM) to the data and performed an ANOVA test (type=III), F-test. In this analysis, flock type was included as a factor (fixed effect), using a quasi-Poisson error distribution (i.e., given the overdispersion of the variance) and a log link function (Ver Hoef 2007).

Temporal flock stability (i.e., flock similarity over time) was examined using the Jaccard dissimilarity index to compare species composition of a given flock between two observations (29 flocks between 2013 and 2014; 17 flocks observed 6-15 days later; 6 flocks in a given hour to their composition 3 hours later). Data were plotted using 1-Jaccard dissimilarity index to show the similarity of each flock over time. To test for differences in stability among time periods, I fit a generalized linear model (GLM) to the data and performed an ANOVA test (type=III, F-test). In this analysis, flock time period (i.e., years, days, hours) was included as a fixed effect, using a binomial error distribution and a logit link function. To examine the effect of elevation on flock stability, I performed a Generalized Linear Model (GLM) with time period (i.e., years, weeks, days) as fixed effect, using a binomial error distribution and logit link function.

The home range area of each mixed flock was estimated using the minimum convex method in QGIS version 2.8.2 (QGIS Development Team, 2012). The percentage of overlapping home range area between 2013 and 2014 was calculated in ArcMap.

To examine the effect of elevation and vegetation structure (i.e., canopy height, number of trees) on flock species richness, I fit a Generalized Linear Model (GLM) with quasi-Poisson error distribution and log link function (Ver Hoef and Boveng 2007). To evaluate and compare the relative fit of alternative models to the data (e.g., canopy height, canopy height + elevation, canopy height + elevation + trees), I used the modified version of Akaike's Information Criterion for overdispersed count data, (QAIC) Quasi-Akaike Information Criterion (Burnham and Anderson 2002; Bolker 2016) where the quasi likelihood adjustment is calculated. I fit each model twice, once with a Poisson error distribution and once with a quasi-Poisson error distribution, and then extracted the over dispersion parameter manually. For each of the models,

I calculated the *QAIC*'s value in R package 'AICcmodavg' (Mazerolle 2012), and then used those quantities to calculate the *QAIC* weights (range 0-1) for each fitted model. The best model was selected considering the lowest *QAIC*'s. The relative importance of each predictor was evaluated by summing the *QAIC*_w for each model in which that variable appears. These summed weights were used to rank the various predictors.

To examine avian foraging guilds participation in mixed species flocks across elevations, I fit a Generalized linear model with quasi-Poisson error distribution and log link function, with foraging guild included as a fixed effect. To examine the proportion of species participating in flocks by foraging guild I fit a GLM with binomial error distribution and logit link function. Finally I fit a Generalized linear model with quasi-Poisson error distribution and log link function to examine the prevalence of flocking at the community level.

For each model used for analysis, I assessed the model assumptions of overdispersion, influential observations and autocorrelation of the data. All analyses were done in R (R Development Core Team 2015)

2.4 Results

2.4.1 Spatial distribution of mixed-species flocks

Mixed-species bird flocks were found across the elevational gradient. I obtained a total of 210 independent mixed-species flock observations over two years, with 99 observations from the first field season (July to October 2013) and 111 from the second (August to October 2014). Cluster analysis based on flock composition dissimilarity identified three major distinguishable

clusters (hereafter flock types; Fig. 2.1). Each of the flock types was represented by a distinct species composition and was broadly associated with a different forest type. The flock types identified were lowland flocks (300-1100 m, n=95), low montane flocks (1100-1900 m, n=55) and high montane flocks (2300-3500 m, n=50). Transitions between flock types occurred in the elevational zones of 1000-1100, 1900-2000, and 2200-2300 m.a.s.l. respectively. A potential fourth type of flock was identified in the range of 1850-2200 m.a.s.l., these data could not be included in the analysis. Additionally, the cluster representing lowland flocks identified three subgroups: understory flocks in *terra firme* forest, understory flocks in bamboo forest and canopy flocks in both *terra firme* and bamboo forest. Here I focus on the three flock types identified in the three main clusters: lowland, low montane, and high montane flocks.

Mixed-species flock richness (number of species) and size (number of individuals) differed among flock types (ANOVA $p=0.002$, $n=210$, $F=6.13$, Fig. 2.2; $p<0.001$, $F=9.96$, Fig. 2.3). Low montane flocks were larger (20.6 ± 10.7 individuals) and more diverse (12.3 ± 5.6 species) than lowland flocks (14.2 ± 9.4 individuals; 9.3 ± 5.7 species) and high montane flocks (18.9 ± 8.5 individuals; 9.39 ± 4.21 species). However, when considering the three different subgroups of lowlands flocks, lowland canopy flocks were larger and more diverse than any other flock type (21.4 ± 13.1 individuals; 14.0 ± 7.7 species; Table 2.1). Flock richness and size were strongly and positively correlated (Kendall's Tau= 0.789, $p<0.001$, Fig. 2.4). The number of species per flock exhibited as much variation within a given elevation as was found across elevations.

2.4.2 Species participation in mixed-species flocks

A total of 273 species associated with mixed flocks to some degree. Using the Flocking Index, I identified 19 spp. as obligate participants of flocks, with a high Index (0.6; Table 2.2), 40 spp. as regular species, 169 spp. as occasional species, and 45 spp. as accidental species or species with too few registers to be informative (Appendix A).

The species identified, as accidental flock followers were those detected mostly outside the flocks and detected within flocks for short periods of time, on very few occasions, when the flock was passing through their territory. Accidental followers included species with small territories, such as manakins and flycatchers, and it was uncertain whether their presence was merely accidental. The species classified as occasional participant of flocks, were species seen in flocks only briefly and for short distances such as tanagers and wood-creepers. These occasional participants were commonly detected outside flocks in the study area. The 40 species classified as regular flocking species often follow flocks beyond their own territories but also forage independently of mixed flocks. They leave the flock several times during the day and in some cases used different flocks. This was the case with species known to occupy larger territories and utilize patchily distributed resources (i.e., fruits), including species from genera such as *Chlorornis*, *Cotinga*, *Buthraupis*, *Monasa*, *Tangara*, *Turdus*, and *Xiphorinchus*.

The 19 species classified as obligate participants permanently associated in mixed-species flocks and were rarely detected foraging solitarily, even during the breeding season. These species exhibited a high occurrence or propensity to forage in flocks, and usually both. Groups of two or more obligate participants in flocks formed the "core" of the flock that showed

high stability in composition over time (Table 2.2). The core group of species for each mixed-species flock types identified were:

- a. Lowland *terra firme* flocks: *Thamnomanes ardesiacus*, *Thamnomanes schistogynus*, *Myrmotherula axillaris*, *Myrmotherula menetriesii*
- b. Lowland Bamboo flocks: *Thamnomanes schistogynus*, *Microrhophias quixensis*, *Anabazenops dorsalis*
- c. Lowland Canopy flocks: *Lanio versicolor*, *Myrmotherula axillaris*, *Tachyphonus rufiventer*, *Tangara schrankii*, *Tangara chilensis*
- d. Low montane flocks: *Myioborus miniatus*, *Chlorospingus flavigularis*, *Leptopogon superciliaris*, *Chlorochrysa calliparaea*, *Tangara arthus*
- e. High montane flocks: *Myioborus melanocephalus*, *Mecocerculus stictopterus*, *Hemispingus atropileus*.

2.4.3 Foraging guild participation in flocks

Analysis of individual foraging guilds revealed that flocks across the gradient were composed mainly by insectivorous birds species (Fig. 2.5a). The same pattern of high representation of insectivorous birds was observed for the overall avian community in Manu elevational gradient (Fig. 2.5b). Similarly, the representation of omnivores, frugivores and nectarivores in mixed-species flocks followed the pattern of species representation of each guild in the overall avian community (Fig. 2.6; Appendix F). Moreover the relative participation of foraging guilds revealed that insectivorous and omnivorous species participated in mixed-species

more than other guilds at low elevations and frugivorous species participate relatively more at high elevations (Fig. 2.7).

2.4.4 Flocks stability

Flock stability over time was estimated for 52 independent colour-banded flocks. I compared the composition of 29 flocks observed in 2013 to their own composition in 2014, the composition of 17 flocks observed in a given day to their composition 6-15 days later, and the composition of 6 flocks in a given hour to their composition 3-5 hours later.

Temporal flock stability showed that flocks have an average similarity index over time of 0.34 ± 0.12 , suggesting that flocks maintained 34 % of the species consistent between observations. Flock similarity ranged from 0.14 to 0.64 (mean 0.36 ± 0.12 , $n=29$) across years, 0.14 to 0.55 (mean 0.29 ± 0.11 , $n=17$) across weeks, and 0.14 to 1 (mean 0.51 ± 0.19 , $n=6$) across hours (Fig.2.8). Flock similarity did not differ across time scales or flock types (ANOVA, $n=52$, $p=0.17$, $F=1.86$; $p=0.12$, $F=2.21$). Furthermore, flock similarity did not show a clear trend with elevation (Fig. 2.9), suggesting that high montane flocks are as stable and cohesive over time as low montane and lowland flocks (Fig. 2.10, Fig 2.11).

Flocks at any elevation across the gradient were composed of two identifiable parts: a core subset of a few species that is retained over time, and a non-core group of several attendant species that changes in composition over time and generates fluctuations in flock composition.

2.4.5 Home range and territoriality

Using information from colour-banded individuals, I found that mixed-species flocks along the gradient maintained the same home ranges over time. Home ranges of lowland (n=3), low montane (n=2) and high montane flocks (n=2) that were extensively characterized in one day sample (i.e., >30 georeferenced locations), overlapped from 71- 89 % (80.42 ± 5.96) between 2013 and 2014 (Fig. 2.12), whereas the home ranges of these flocks overlapped on slightly with neighboring flocks. Home ranges of most mixed-species flocks were not fully characterized (i.e., 2-3 georeferenced locations) and for these flocks the overlap between years cannot be described. However, most of these color-banded flocks were spotted < 200 m from their initial observed location, days later (n=74) and a year later (n=53), suggesting that these flocks likely maintain the same home range over time, both within and between years.

Home ranges of flocks differed along the elevational gradient. Lowland flocks used a smaller area ($7.3 \text{ ha} \pm 0.8$, n=3), compared with the larger areas used by low montane flocks ($16.4 \pm 1.2 \text{ ha}$, n=2) and high montane flocks ($17.1 \pm 1.6 \text{ ha}$, n=2). The boundaries of the home ranges, in general, did not appear to be defined by topographic features of the landscape, although in some of the low and high montane flocks, the boundaries of home ranges were sometimes coincident with large rivers (e.g., Rio Kosñipata, Rio Piñi-Piñi), small creeks, and trails.

Flocks exhibited territorial disputes with other flocks along most of the elevational gradient. Direct territorial interactions (i.e., aggressive flights) were frequently observed between congeners of neighboring flocks in lowlands, and sometimes in low montane flocks up to 2200 m.a.s.l., but were never observed directly in high montane flocks. Mixed-species territorial

disputes in low montane flocks, much like those in lowland flocks, included close approaches, songs, calls, and aggressive flights back and forth, sometimes lasting for up to 20 minutes.

Flocks at different elevations along the gradient exhibited communal roosting sites in the flock's home range. In these areas, individual members of the flock began their activities in the morning and coalesced every day. The roosting sites in low montane flocks and high montane flocks extended in an area up to 1200 m², whereas lowland flock roosting sites were more compact. The flock's roosting area (n=10) was maintained from 2013 to 2014 (e.g., Fig. 2.12).

Coalescence of the flocks in the roosting sites occurred in the predawn and initiated with loud vocalizations of several individuals from one or two species, followed by calls and songs of several other species. Lowland flock coalescence was initiated by vocalizations of individuals from *Thamnomanes schistoginus*, *T. asdesiacus*, *Myrmotherula axillaris* and *Chlorothraupis carmioli* (if present) in *terra firme* forest, and *Thamnomanes schistoginus* and *Microrhophias quixensis* in bamboo forest. Low montane flock coalescence was initiated by vocalizations of individuals from *Chlorospingus flavigularis* and *Tangara arthus* and *Chloroceryza calliparaea*, and in high montane flocks, coalescence was initiated by calls of individuals from the *Hemispingus* genus. Following these initial vocalizations, the vocal activity in the area increased and was maintained for around 10 minutes.

2.4.6 Elevation and vegetation structure

Mixed flock species' richness along the gradient was best explained by a model that included canopy height and number of trees ($QAICcWt=0.63$, Table 2.3). However, a model including three predictors (i.e., elevation, canopy height, and number of trees) had a *Delta*

QAICc value of 2.13, so essentially as good as the best model. Among these predictors, number of trees was the most important variable ($\sum QAICcWt=1$) and appears in all the top models. Canopy height was the second most important variable ($\sum QAICcWt=0.85$), and elevation ranked last ($\sum QAICcWt=0.30$). As a general pattern, mixed-species flock richness increased with an increase in the number of trees and with increasing canopy height; elevation explained little variation in flock species richness (Fig. 2.13).

2.4.7 Prevalence of flocking at the community level

The Manu regional bird community consisted of 550 species, which were detected along the elevational gradient by one or more survey methods (i.e., mist-netting, recordings, survey points). A subset of 273 species participated in mixed flocks to some extent (~49% of species in the Manu region). Species richness decreased with increasing elevation in the overall bird community ($r=-0.6$ $p<0.001$) and in flocks ($r=-0.4$, $p<0.001$; Fig. 2.14). Analysis of flock participation by elevational zones showed three peaks of high prevalence of flocking: for the lowlands (400 - 500 m.a.s.l.); cloud forest (1600 - 1700 m.a.s.l.); and high montane forest (2600 - 2800 m.a.s.l.; Fig. 2.15).

2.5 Discussion

Here I present the first study of mixed-species flocks across a continuous forested elevational gradient in the Neotropics. These results showed structured mixed-species flocks occurring across elevations, from Amazon lowland rainforest to Andean treeline. Mixed flocks exhibited relatively high stability in species composition over time at low elevations, with a portion of the

flock maintaining the same membership, as previously suggested by other studies (e.g., Martínez and Gomez 2013), but also in mid and high elevations. Furthermore, flocks exhibited stability in home range boundaries over time and communal flock territoriality across the elevational gradient. Vegetation structure explained 63% of the variation in flock richness along the gradient, with number of trees and canopy height as predictors, where number of trees had a higher relative importance. Overall, mixed-species flocks were widely utilized as a foraging strategy for birds across elevations, by ~40% bird species in lowland Amazon forest, as previously documented, but also within low (~39%) and high montane forest (~35%), where flocks are just as prevalent in the community as in low elevations. These results highlight the importance of these multi-species interactions for tropical bird communities across elevations.

2.5.1 Spatial distribution of flocks

Flocks occurring along the elevational gradient in Manu fell into three main types based on cluster analyses: lowland, low montane and high montane. Lowland flocks were further differentiated between habitats and forest strata, in bamboo and *terra firme* understory and canopy flocks. Each flock type features a distinct group of species, mainly determined by the core obligate members. Interestingly, the locations along the gradient where flock types transitioned (i.e., 1100-1200, 1700-1800, 2200-2300), were largely consistent with the elevations that exhibit peaks of high turnover in both bird and tree communities (e.g., 1100-1200; 1700-2000, 2000-2250 m.a.s.l) (Jankowski et al. 2013).

The lowest elevation flock transition occurred in the lower limit of montane forest (1100-1200 m.a.s.l), in foothill elevations. At this elevation both lowland and low montane flocks can be observed within 100m of each other, without overlapping territories. This change in flock composition might be determined by shifts in vegetation, specifically the high turnover in tree composition that occurs at this elevation (Jankowski et al. 2013). At this elevation there is also high bird species turnover of the overall community, possibly responding to this change in vegetation composition. The second region of flock transition occurs in montane cloud forest (1700-1800 m). At this elevational zone there is again a high turnover in tree species composition that notably matches the transition in flock composition. Finally, the third region of transition of flocks occurs at 2200 - 2300 m, the peak of bird species turnover in the overall community may also drive the transition at this particular elevation.

The congruence in the location of turnover peaks along the gradient between the overall bird community and mixed-species flock suggests that flock composition is strongly aligned with overall transitions in the bird community, which has been shown to be associated with changes in vegetation structure and tree composition. It has been suggested elsewhere that species composition of mixed flocks changes with the composition of the overall bird community (Hutto 1994; Goodale et al. 2009; Péron and Crochet 2009). One recent study of high elevation flocks in Colombia, however, did not find shifts in flock composition with elevation (Arbeláez-Cortés and Marín-Gomez 2012), but this could be due to the relatively narrow range of elevations surveyed (3000-3450m). It is also possible that mixed-species flocks, birds and vegetation communities are responding in a similar fashion to other factors of the gradient that vary with elevation, such as temperature and productivity (Tilman et al. 1997). Broader sampling of other gradients and

taxonomic groups will be required to better understand community transitions and separate these alternative factors.

2.5.2 Species participation in mixed-species flocks

Flocks along the gradient exhibited a similar general structure, with a group of core species that was permanently associated with the flock, and a more dynamic group of attendants that changed over time. This structure was similar to what has been documented for other Neotropical flocks, including Munn and Terborgh (1979) and Graves and Gotelli (1993) in Peru, Powell (1985) in Costa Rica, Hutto (1994) in Mexico, and Jullien and Thiollay in French Guiana (2001). The core of the flocks was usually composed of three to five species pairs or small groups that stayed constantly in the same flock over time, even between years, as evidenced by colour banded individuals. The dynamic component of the flocks was composed of dozens of species pairs or individuals that join for varying lengths of time each day and included regular, occasional and accidental flock participants.

The obligate participants that formed the core of the flock exhibited several behavioural and morphological features described for nuclear species (i.e., species that maintain the cohesion of the flocks). For example, most of these species were conspicuous and vocal, which also tended to forage in intraspecifically gregarious groups within the mixed flock: *Chlorospingus flavigularis*, *Hemispingus atropileus*, *Thamnomanes ardesiacus*, *Thamnomanes schistogynus*, *Myrmotherula axillaris*, *Myrmotherula menetriesii*, *Lanio versicolor*, *Tachyphonus rufiventer*, *Tangara chilensis*, *Tangara arthus*, *Myioborus melanocephalus*, *Myioborus miniatus* and *Microrhopias quixensis*. Other obligate participants were not evidently intraspecifically

gregarious, nor conspicuously vocal, such as, *Leptopogon superciliaris*, *Mecocerculus stictopterus*, *Anabazenops dorsalis*, *Chlorochrysa calliparaea*., and their role as nuclear species maintaining the cohesion of the flock was less evident.

The foraging behavior of the obligate flock participants ranged from active searching foragers to less active foragers (i.e., sit-wait), and most of the species were insectivorous or omnivorous that foraged in the mid to high forest strata and towards the ends of branches in trees and vegetation. One exception to this pattern was the nectarivorous species, *Digglosa cyanea*. Morphologically, these obligate species have a smaller body mass than the average for all flocking species (data not show) and exhibited plumage coloration with any combination of yellow, green, gray and brown, with one exception being *Tangara chilensis*, which exhibits brilliant colouration. Similar patterns of resembles in color among the species of the black, yellow and brown (social mimicry), has been described in plumages of other obligate flocking species by Moynihan (1968) in Panama, as a potential adaptation that allow positive interactions within the flock (e.g risk-dilution effect).

2.5.3 Mixed-species flocks richness and foraging guild participation

The number of species per flock was highly variable, exhibiting as much variation within a given elevation as was found across elevations. Thus, flock size variation was not explained by elevation itself. However, when analyzing flock types, low montane flocks were in average larger and more diverse compared with flocks at other elevations. This result differs from the existing body of work on mixed-species flocks, which suggests lowland flocks are larger and more diverse (Reviewed in Goodale 2009). The larger size in montane flocks could be driven by

a peak in bird diversity found at the lower montane forest (Jankowski, *unpublished data*). However, it can also be related to the high productivity at this elevational range in Manu gradient, compared with other elevations, as described by Marthews et al. (2012). High productivity might allow a higher diversity of bird species from different foraging guilds to join the flocks without incurring costs from higher competition.

In terms of guild structure, we found that insectivorous species participate in flocks more than any other guild across elevations. Similar patterns have been described for the structure of tropical flocks at smaller spatial scales by Moynihan (1962) , Munn (1985) and Srinivasan et al. (2012). However, we also observed the same pattern of higher number of insectivores birds compared with other foraging guilds for the overall bird community in Manu (Fig. 2.10.b) as previously suggested by Jankowski *et al.* (2013) and described in other tropical gradients (e.g., Terborgh 1971). Thus foraging guild composition in flocks appeared to be merely reflecting the overall availability of bird species in the Manu community.

However, after controlling the observed patterns of guild participation by the number of species in the community, the results suggested that a higher proportion of insectivorous and omnivorous species joined flocks at low elevations compared with other guilds. This could suggest that at low elevations (i.e < 2000 m) the strategy of joining flocks is more important for species utilizing evenly distributed resources, such as insects, compared with more localized and patchy fruit and nectar resources. Interestingly, I found that at high elevations (i.e >2000) a higher proportion of frugivorous species joined flocks compared with other guilds. Overall our results suggested that flock guild composition is not merely reflecting the proportions of the guilds in

the community as a large, instead is a specialized foraging strategy used mainly by insectivorous and omnivorous species at lower elevations and by frugivores species at higher elevations.

2.5.4 Flock stability

In this study, I showed that flocks along the gradient from the lowland Amazon to the high Andes exhibited highly stable member species composition and home range boundaries over time. These results are consistent with previous studies of lowland mixed-species flocks (e.g., Munn and Terborgh 1979; Jullien and Thiollay 1998), including recent research that demonstrated long term stability (i.e., over two decades) of territories and species composition in lowland flocks in French Guiana (Martínez and Gomez 2013) and a similar study over eight years in Panama (Greenberg and Gradwohl 1986). Importantly, the results of my study show that the high stability in core member composition and home range boundaries in flocks occurring at low elevations in the Amazon, as previously suggested by the studies mentioned above, extends to mid- and high-elevation flocks in the Andes.

The stability of Andean mixed-species flocks in both member species composition and home range boundaries, similar to Amazonian lowland flocks, is in contrast to other studies. For example, Hart and Freed (2003) found that flocks at middle elevations in Hawaii exhibited unstable membership. Work by Stotz (1993) in the Atlantic forest in Brazil described that non-Amazon flocks observed in the same location on different days were very different in composition, and did not appear to hold permanent territories, suggesting that stability was a feature of Amazon flocks. Similarly Poulsen (1996) described Andean flocks in Ecuador as more dynamic and unstable than Amazonian flocks. Overall my study highlights that the stability in

species composition, home range boundaries and roosting sites are a widespread feature of Neotropical mixed-species flocks along the gradient and are not a distinctive feature of Amazonian flocks. This stability also differentiates Neotropical mixed-species flocks from mixed flocks in the Old World Tropics where a study along an elevational gradient by Goodale (2009) found no evidence of interspecific territoriality or stability over time.

The temporal stability of flocks, in both member composition and home range boundaries, might have important implications for the core species that associate permanently in the same flock. For instance, stability in flocks may promote interdependence among species, thus allowing for the potential rise of evolutionary stable strategies. Complex behaviors among species can arise from such stable flocks, given sufficient periods of time for selection to act on species' traits. Some complex behaviors that have been described in flocks indicate interdependence among species, including multi-species territory defense (Munn and Terborgh 1979), interspecific alarm calls and responses (Munn 1986) and collective defense against predators (mobbing behaviours, Courter and Ritchison 2012). In this study I found that these complex behaviors are common in flocks from the Amazon basin to the high Andes, and also found evidence that other strategies, such as cooperative breeding of the species, can arise from such stable associations in mixed-species flocks (Munoz *personal observation*). Furthermore, the stability in flock home ranges should have important implications for the population density (flock- density dependent), at least for core species that associate permanently in flocks, actually in the same flock, potentially for their entire lives. Moreover home range stability may limit the density of obligate flock participants allowing greater species packing and potentially promote high species richness in Neotropical avifaunas as suggested by Powell (1989).

2.5.5 Elevation and vegetation structure

The variation in the number of species per flock was best explained by vegetation structure complexity, including canopy height and number of trees. Although elevation was included in some of the top models, it explained little variation in flock richness along the gradient. Among the predictors, elevation had the least relative importance in the model, and the model with elevation as a sole variable performed worse than any other model.

I found that flocks tended to be larger and more diverse in areas with a higher density of trees and with higher forest canopy. Together, these variables may offer a more structurally complex forest, with opportunities for species to partition resources and foraging locations across forest strata, increasing the capacity for overall group size of the flocks. A similar pattern with larger flocks occurring in areas with more diverse and dense vegetation was described in a smaller scale study in Andean flocks by Moynihan (1979) and by Lee et al. (2005) who also found a decrease in diversity per flock in areas with simpler vegetation structure. Other habitat variables, such as vegetation composition and resource availability (Srinivasan and Quader 2012), are also expected to be important in determining flock richness. It will be of great interest to further investigate these habitat factors in conjunction and their contribution to support flock diversity.

2.5.6 Prevalence of flocking at the community level

The results of this study showed that flocks are an important characteristic of bird communities along the gradient, where around 40 % of species at any given elevation utilized

flocks as a foraging strategy. The relatively high proportion of species participation in these flocks is consistent with other studies at smaller scales in tropical regions, including the Atlantic forest, where >50% of the bird community joined flocks (Aleixo 1997), the Colombian Andes (40%; Arbeláez-Cortés et al. 2011), Hispaniola Island (>80%, Latta and Wunderle 1996) and French Guiana (38%; Jullien and Thiollay 2001). However, the idea that mixed-species flocks are a predominant feature of bird communities across elevations, from the Amazon lowlands to the high Andes, has not been well documented before. This research makes an important step towards filling that knowledge gap by demonstrating that facilitation plays an important and underappreciated role in structuring bird communities across various tropical habitats and elevations.

The prevalence of the flocking strategy at the community level peaks at three different elevations along the gradient 400 to 500 m.a.s.l., 1600 to 1700 m.a.s.l., and 2600 to 2800 m.a.s.l. In this study we did not test the factors that could explain these peaks of high species participation in flocks at those particular elevations. However, historically patterns of participation in flocks have been attributed to predation pressure (Thiollay 1999) and resource availability (Berner and Grubb 1985). Interestingly, the peaks of flocking prevalence occurring at 400 to 500 m.a.s.l., and 1600 to 1700 m.a.s.l. match the elevations where peaks of net primary productivity (NPP) have been described along the Manu elevational gradient by Marthews et al. (2012) and Huasco et al. (2014). In addition, the peak observed from 400 to 500 m.a.s.l., is also consistent with the peak in raptor diversity (the main predators of adult passerines) reported by Valdez (1999). I hypothesize that an interaction between these factors could be driving this pattern.

Finally, I point out that the prevalence of mixed-species flocks across elevations indicates that facilitation plays an important and underappreciated role as a mechanism structuring Neotropical bird communities. Although much information has been documented over the last century about flock presence in different habitats in the tropics, emphasis should be now shifted towards broad scale patterns and implications for bird communities.

Table 2.1 Mixed-species flock types identified across the elevational gradient. Mean number of species (Mean \pm SD) and mean number of individual birds for each flock type is presented. Sample size and range of values are shown in bold.

Flock type	Elevations m.a.s.l.	Mean number of species \pm SD (n)	Mean number of individuals	Range	
Lowland terra-firme	300-1100	8.4 \pm 4.5 (50)	12.9 \pm 7.5	3-21	5-38
Lowland Bamboo	300-1100	6.8 \pm 2.0 (31)	10.1 \pm 3.2	4-12	6-19
Lowland Canopy	300-1100	14.0 \pm 7.7 (23)	21.4 \pm 13.1	6-35	7-51
Low-montane	1100-1900	12.3 \pm 5.6 (55)	20.6 \pm 10.8	4-29	7-54
High-montane	2250-3500	9.4 \pm 4.2 (51)	19.1 \pm 8.5	3-20	6-41

Table 2.2 Species with high tendency to flock. The core component of each flock type, Flocking Index (Occurrence*Propensity) and number of flocks observed are presented. Species that were intraspecifically gregarious are indicated with an asterisk (*).

Species	n	Flocking index	Flock type
<i>Myioborus melanocephalus</i> *	37	0.93	High montane
<i>Mecocerculus stictopterus</i>	31	0.78	High montane
<i>Hemispingus atropileus</i> *	30	0.75	High montane
<i>Diglossa cyanea</i>	40	0.66	High montane
<i>Myioborus miniatus</i> *	41	1.00	Low montane
<i>Chlorospingus flavigularis</i> *	40	0.98	Low montane
<i>Leptopogon superciliaris</i>	37	0.90	Low montane
<i>Chlorochrysa calliparaea</i>	36	0.88	Low montane
<i>Tangara arthus</i> *	25	0.61	Low montane
<i>Thamnomanes schistogynus</i> *	27	1.00	Lowlands bamboo
<i>Microrhophias quixensis</i>	24	0.89	Lowlands bamboo
<i>Anabazenops dorsalis</i>	16	0.59	Lowlands bamboo
<i>Lanio versicolor</i> *	10	0.83	Lowlands canopy
<i>Myrmotherula axillaris</i> *	10	0.83	Lowlands canopy
<i>Tachyphonus rufiventer</i> *	10	0.83	Lowlands canopy
<i>Tangara schrankii</i>	9	0.75	Lowlands canopy
<i>Tangara chilensis</i> *	8	0.67	Lowlands canopy
<i>Myrmotherula axillaris</i> *	35	1.00	Terra firme/Flooded
<i>Myrmotherula menetriesii</i>	23	0.66	Terra firme/Flooded
<i>Thamnomanes ardesiacus</i> *	23	0.66	Terra firme/Flooded
<i>Thamnomanes schistogynus</i> *	23	0.66	Terra firme/Flooded

Table 2.3 Model selection results from generalized linear models for flock richness across the elevational gradient. Explanatory variables include elevation (Elev), mean canopy height (Canopy), and number of trees (Trees). For each fitted model the number of parameters (k), change in corrected quasi-Akaike from the model with the lowest QAIC value ($\Delta QAICc$), QAIC weights ($QAICcWt$) are shown.

Response variable	Model	k	$QAICc$	$\Delta QAICc$	$QAICcWt$
Num_species	Canopy+Trees	4	435.19	0.00	0.63
	Elevation+Canopy+Trees	5	437.32	2.13	0.22
	Elevation+Trees	3	439.24	4.04	0.08
	Trees	4	439.52	4.33	0.07
	Canopy	3	447.33	12.14	0.00
	Elevation+Canopy	4	448.35	13.15	0.00
	Intercept	2	452.71	17.52	0.00
	Elevation	3	454.21	19.02	0.00

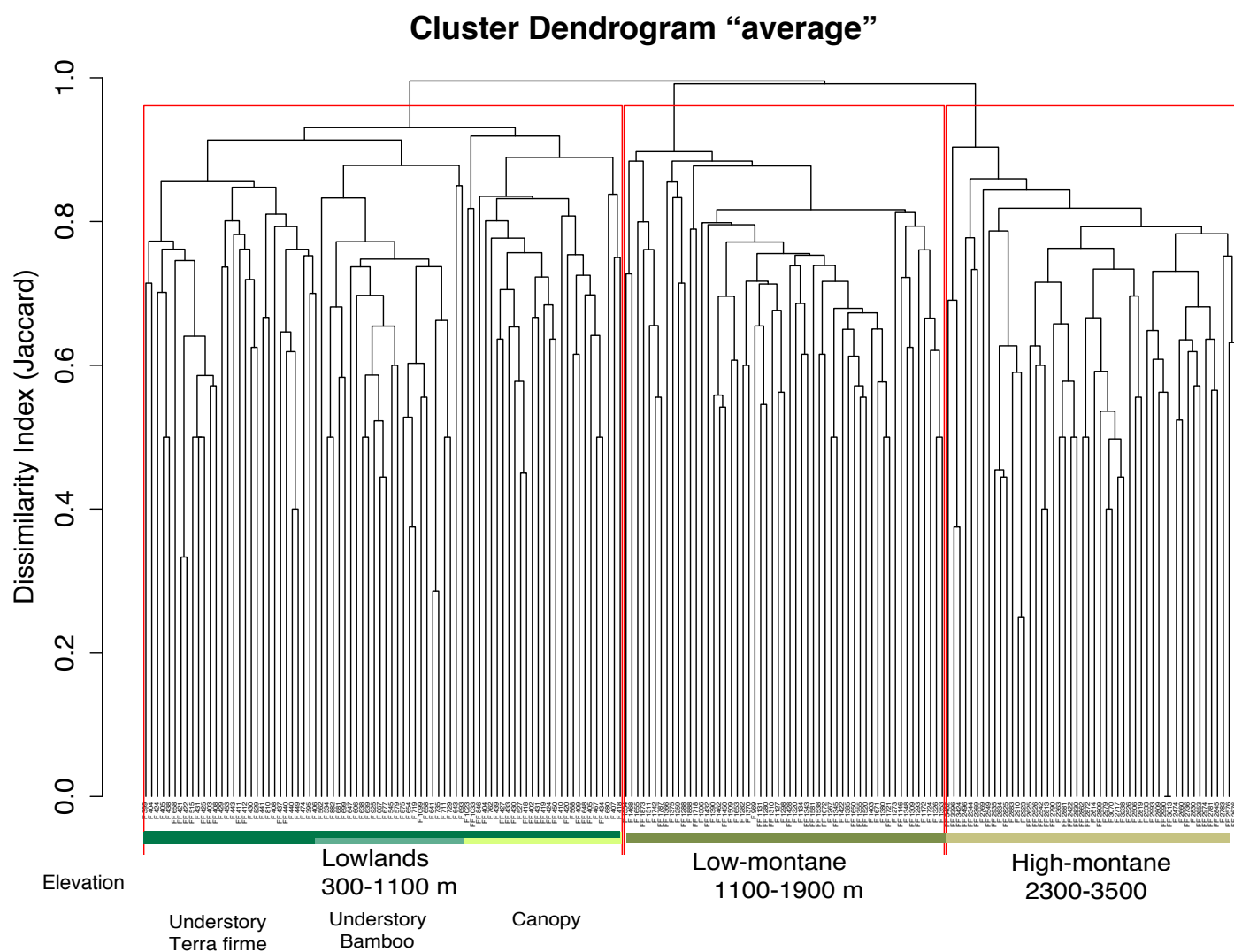


Figure 2.1 Dendrogram for average linkage cluster of mixed-species flocks along an elevational gradient. Clustering distance is based on Jaccard dissimilarity index of species composition of flocks. Each flock name indicates the elevation where it was observed. Red lines indicate clusters of the main flock types.

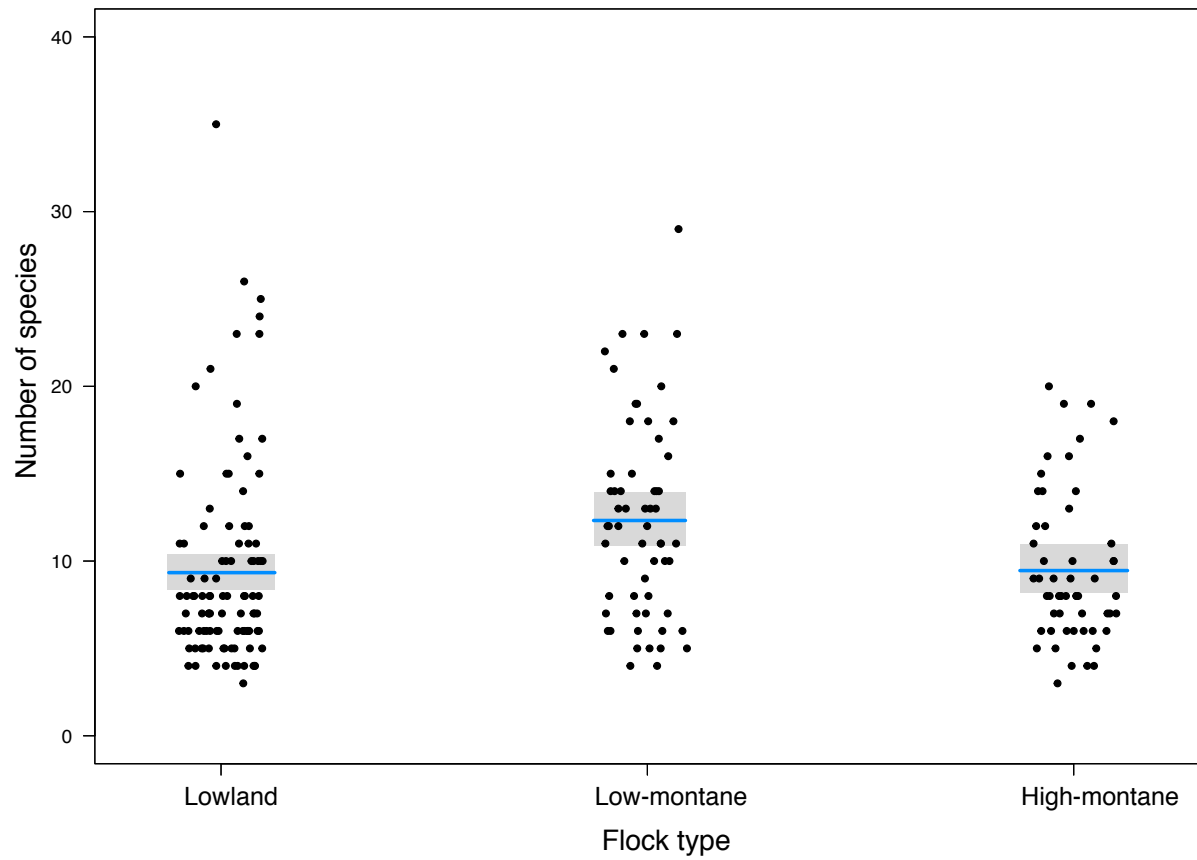


Figure 2.2 Mixed-species richness for Lowland, Low-montane and High-montane flocks in the Manu region, Peru. Number of species per flock is shown. Each dot represents an independent flock. The grey shading indicates the confidence intervals.

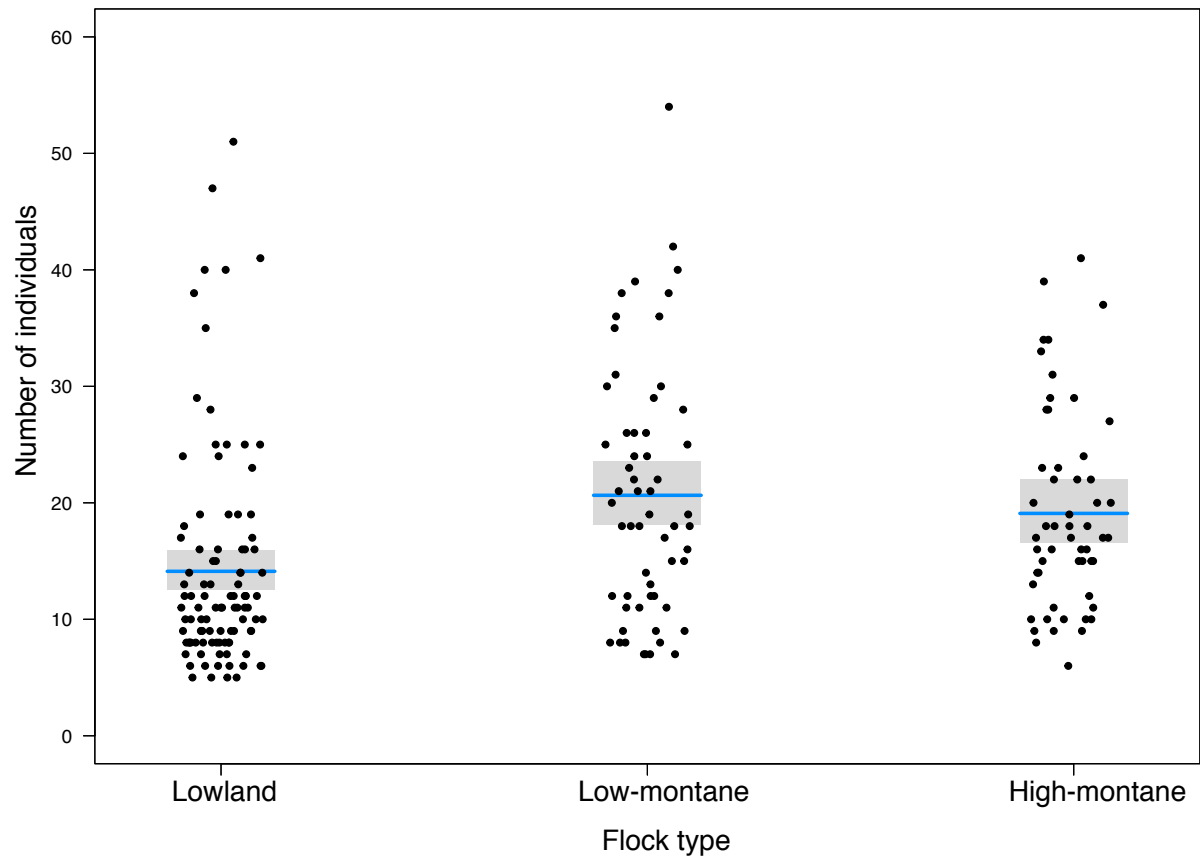


Figure 2.3 Mixed-species flock size for Lowland, Low-montane and High-montane flocks in the Manu region, Peru. Number of individuals per flock is shown.. Each dot represents an independent flock. The grey shading indicates the confidence intervals.

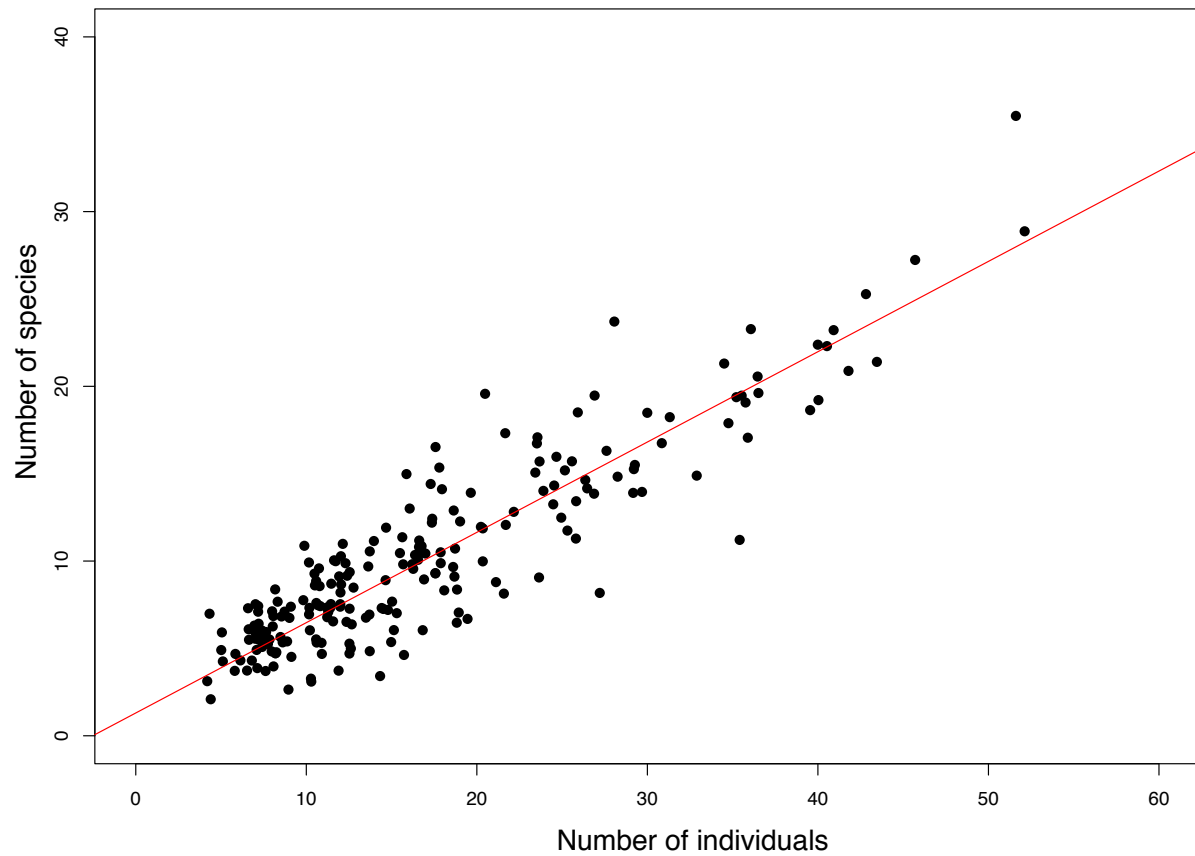


Figure 2.4 Regression of number of species and number of individuals foraging in mixed-species flocks in Manu region, Peru (Kendall's Tau= 0.789, $p < 0.001$).

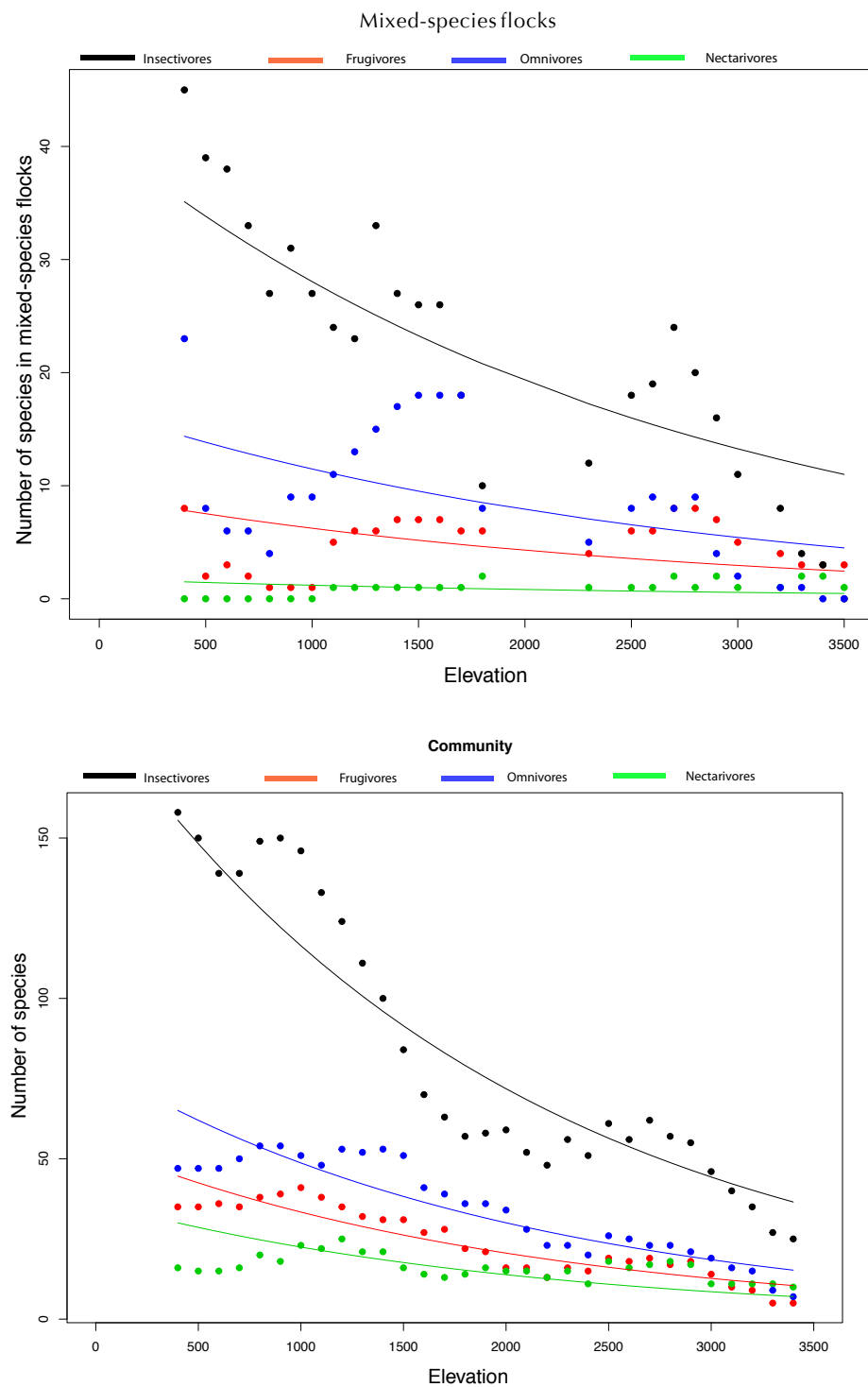


Figure 2.5 Species richness of avian foraging guilds across the Manu elevational gradient for (a) Mixed-species flocks (b) overall community. Each guild is represented by a different colour including: insectivores (black), frugivores (red), nectarivores (green) and omnivores (blue). Each dot represents the total number of species at a given elevational zone (e.g. 400-500; 501-600; 601-700). The solid lines are the predicted values of species as a function of elevation.

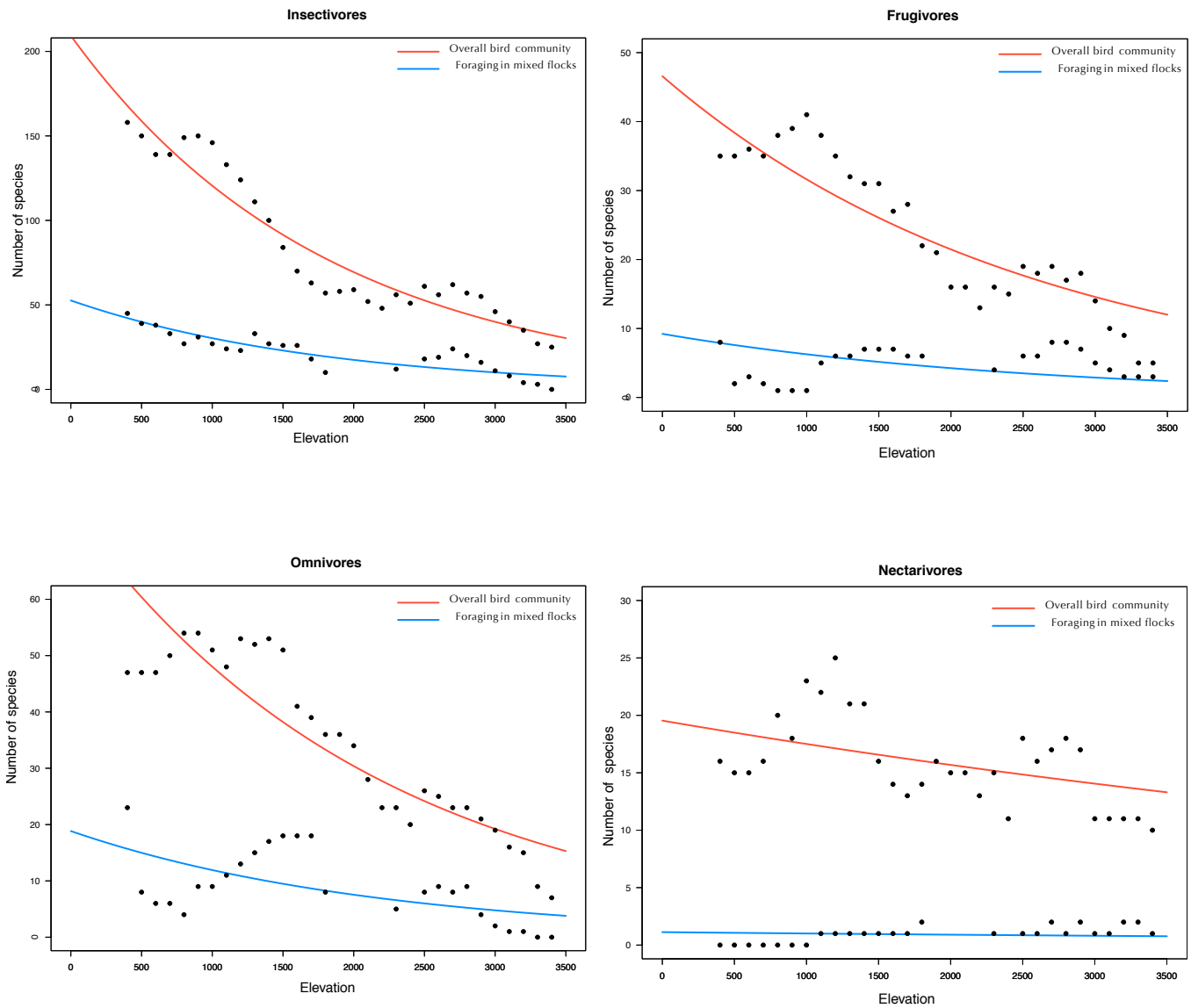


Figure 2.6 Species richness of avian foraging guilds across the Manu elevational gradient. Total number of species in the Manu gradient community (red) and number of species participating in flocks (blue) for each elevational zone are shown for (a) insectivores, (b) frugivores, (c) omnivores, (d) nectarivores. The solid lines are the predicted values of species richness as a function of elevation.

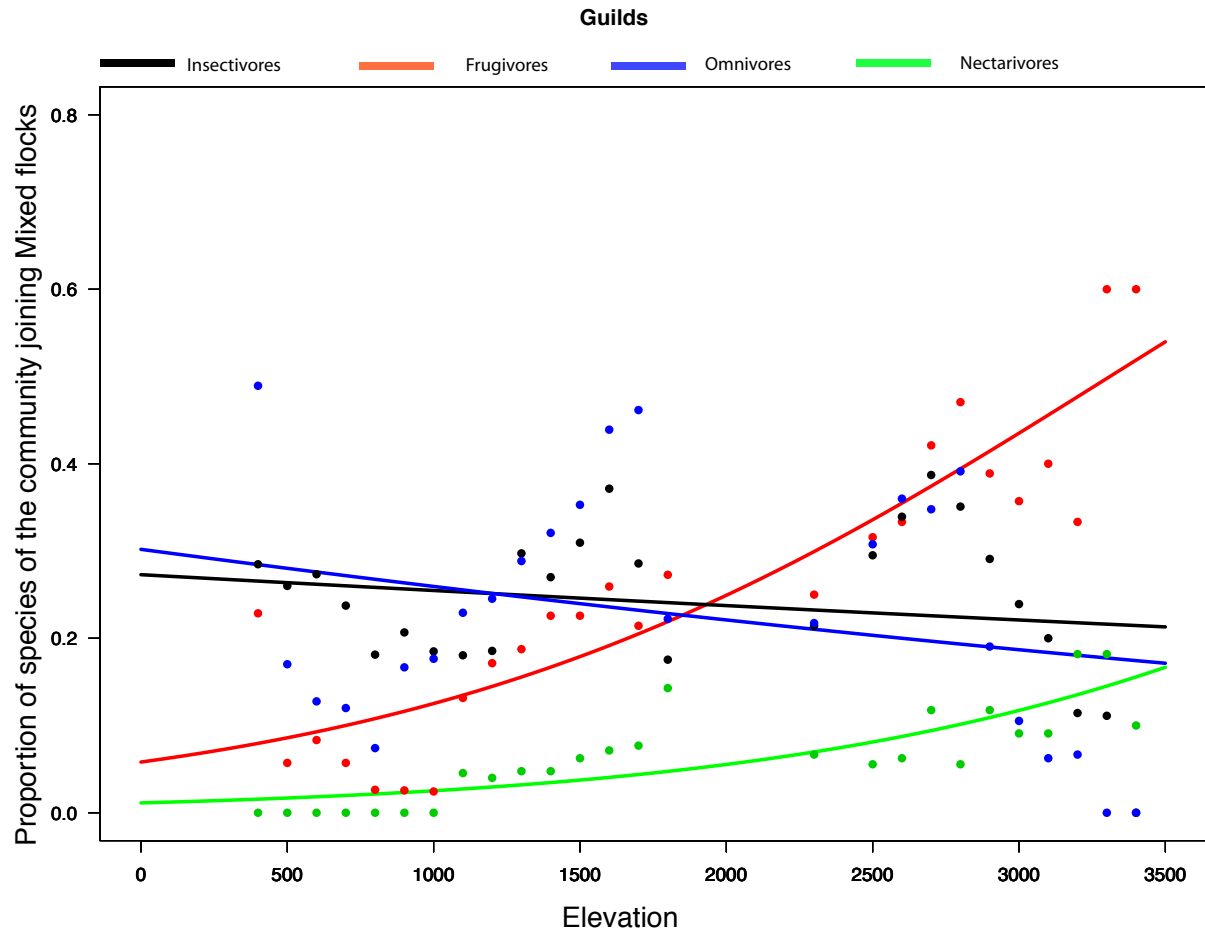


Figure 2.7 Proportions of species in the community joining mixed flocks for each foraging guild across elevation are shown. Each guild is represented by a different colour including: insectivores (black), frugivores (red), omnivores (blue) and nectarivores (green). Each dot represents the proportion of species joining flocks at a given elevational zone (e.g. 400-500; 501-600; 601-700). The solid lines are the predicted values as a function of elevation.

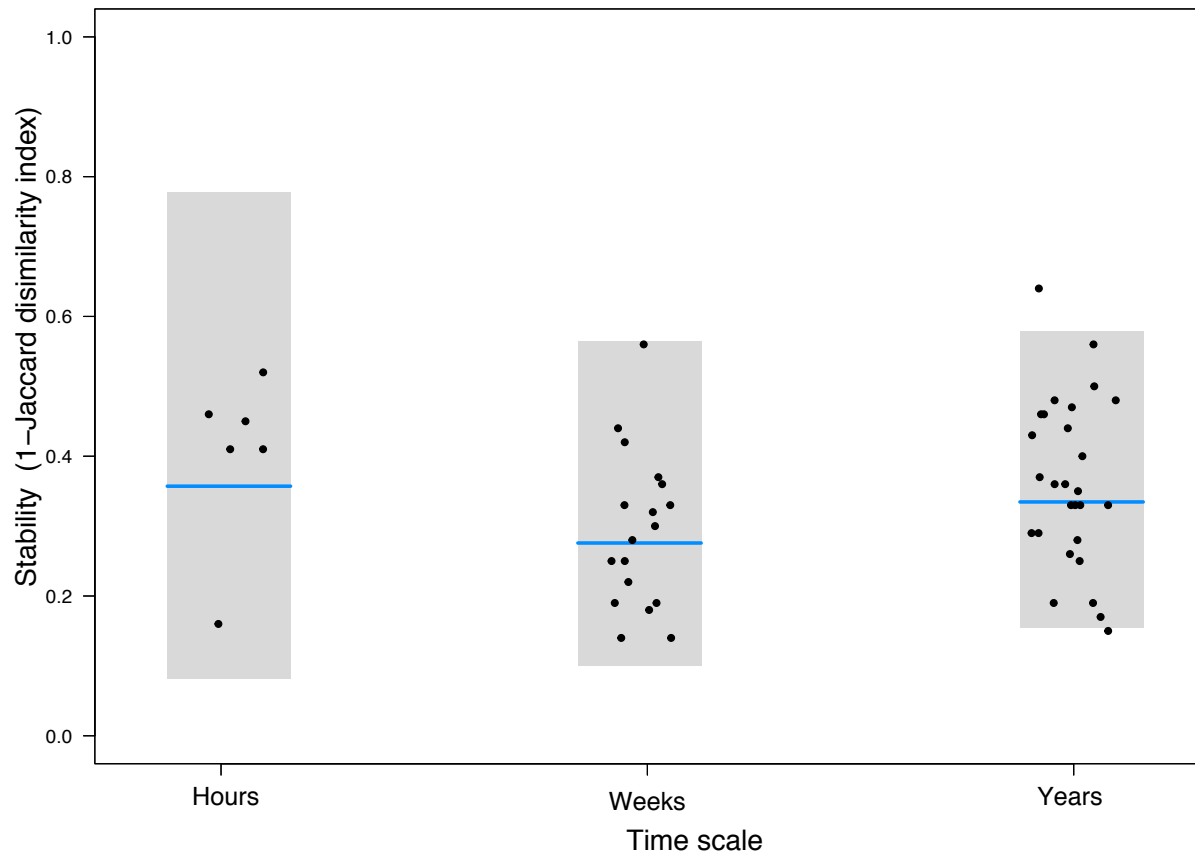


Figure 2.8 Stability of flocks over time. Similarity in species composition of flocks observed in (a) hours 1-2, (b) days 1-2 and (c) years 1-2 is shown. Each dot represents the calculated similarity index (1-Jaccard dissimilarity index) for each flock between observations. The grey shading shows the confidence intervals.

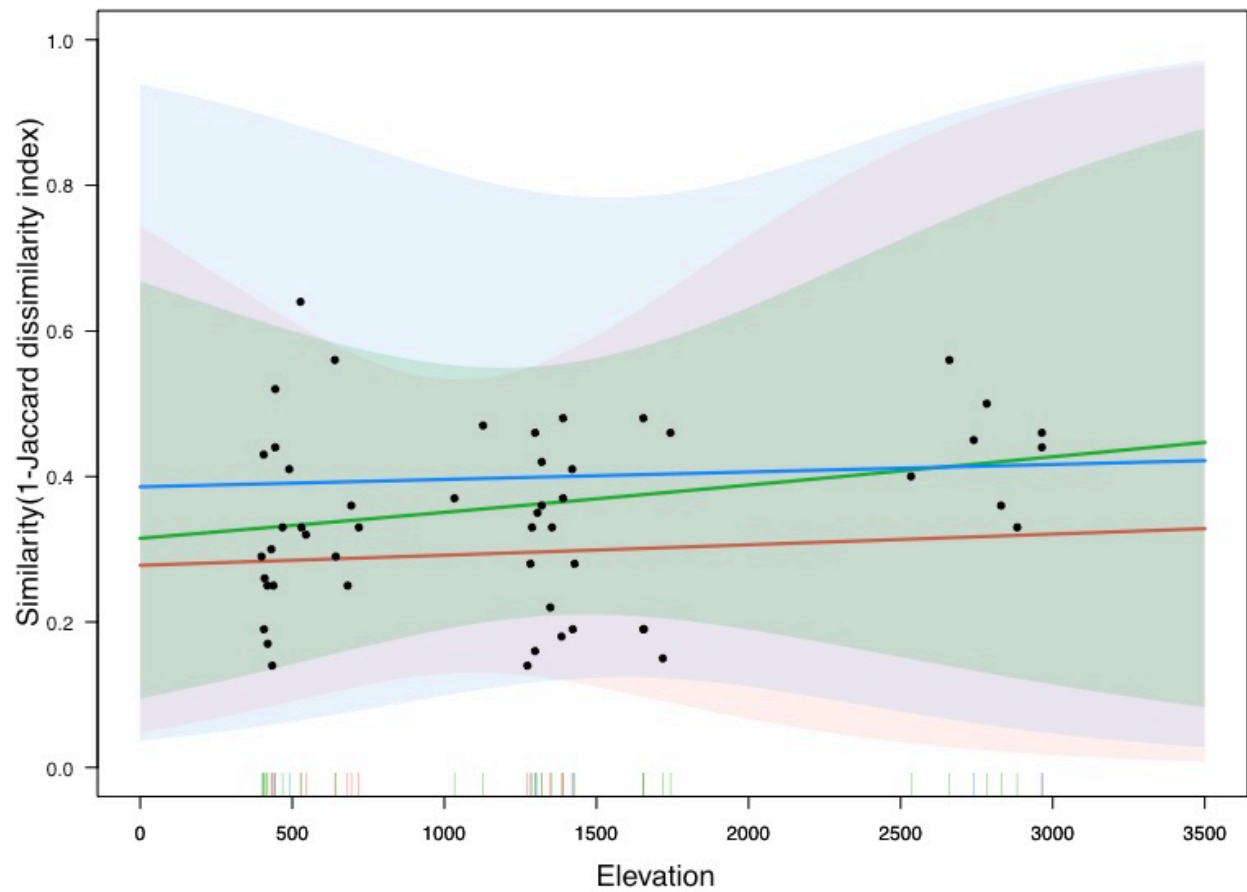


Figure 2.9 Temporal stability of flocks across elevation. Similarity in species composition of flocks across elevation at three different time scales. The solid lines are the predicted values of flock stability as a function of elevation between hours (blue), weeks (red) and years (green). The shading shows the confidence intervals based on the standard errors of the estimates. The lines along the x-axis indicate the elevation where each flock was observed.

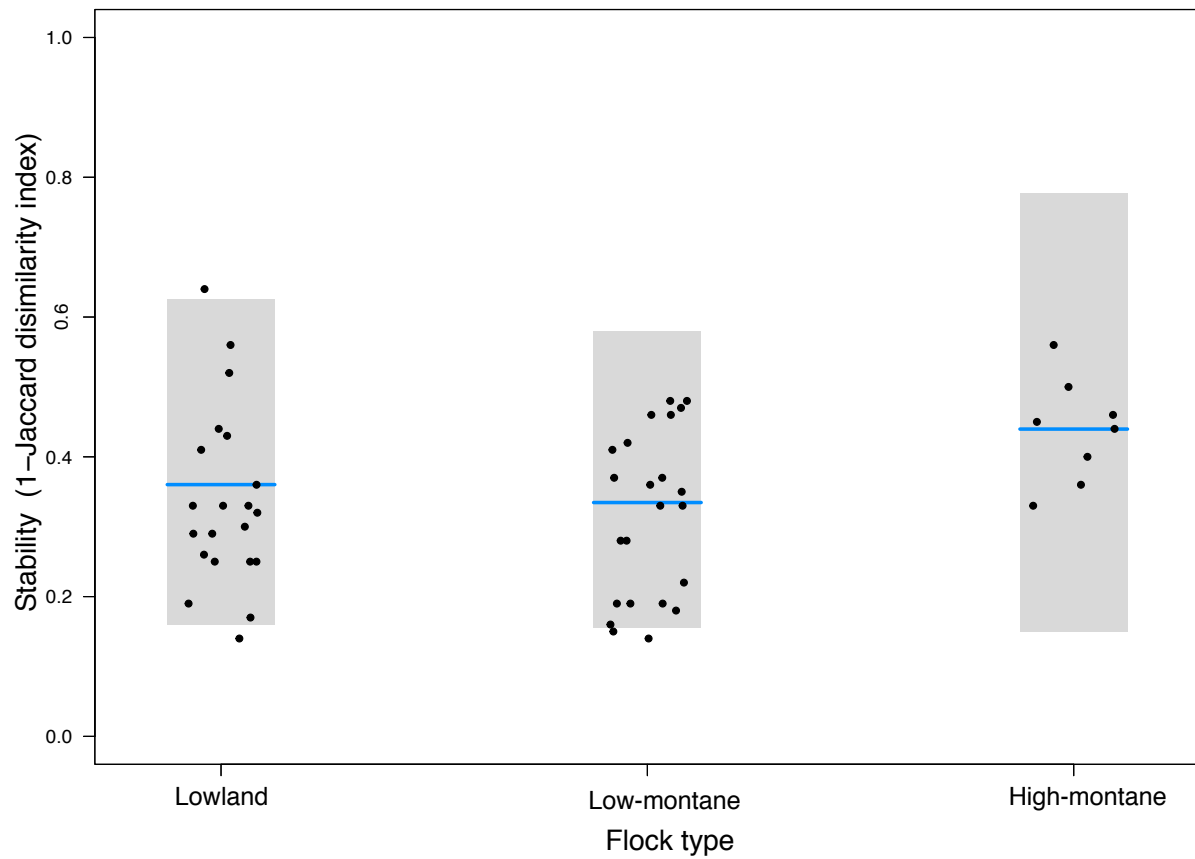


Figure 2.10 Stability of flocks over time. Similarity in species composition for a) Lowland flocks b) Low-montane flocks c) High-montane flocks. Each dot represents the calculated similarity index (1-Jaccard dissimilarity index) for each flock between observations.

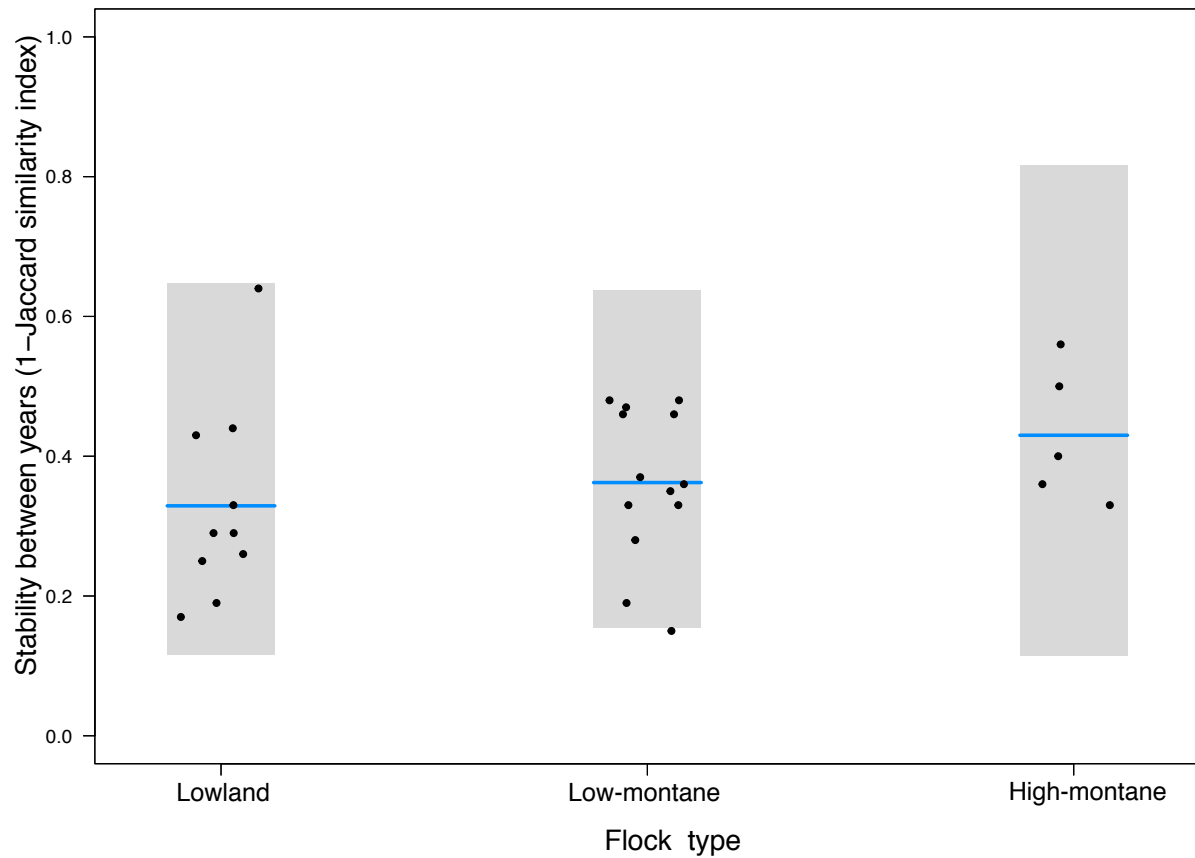


Figure 2.11 Stability of flocks across years. Similarity in species composition of flocks observed in 2013 and 2014 for a) Lowland flocks b) Low-montane flocks c) High-montane flocks. Each dot represents the calculated similarity index (1-Jaccard dissimilarity index) for each flock between observations.

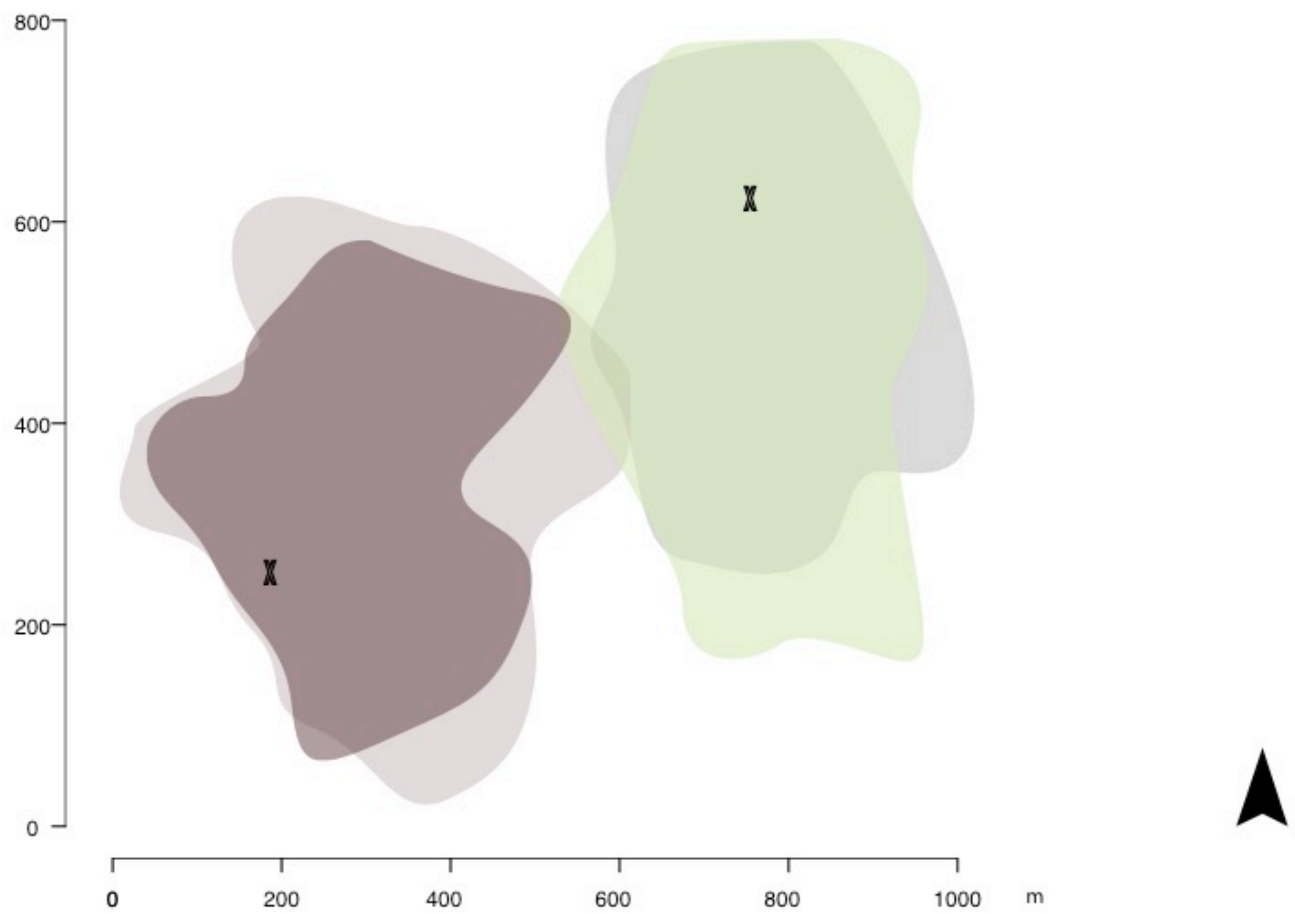


Figure 2.12 Home range of two mixed-species bird flocks at Low-montane elevation (1240-1260 masl). Light colours indicate the 2013 home range for each flock; dark colours indicate the 2014 home range. Roosting site is indicated for each flock.

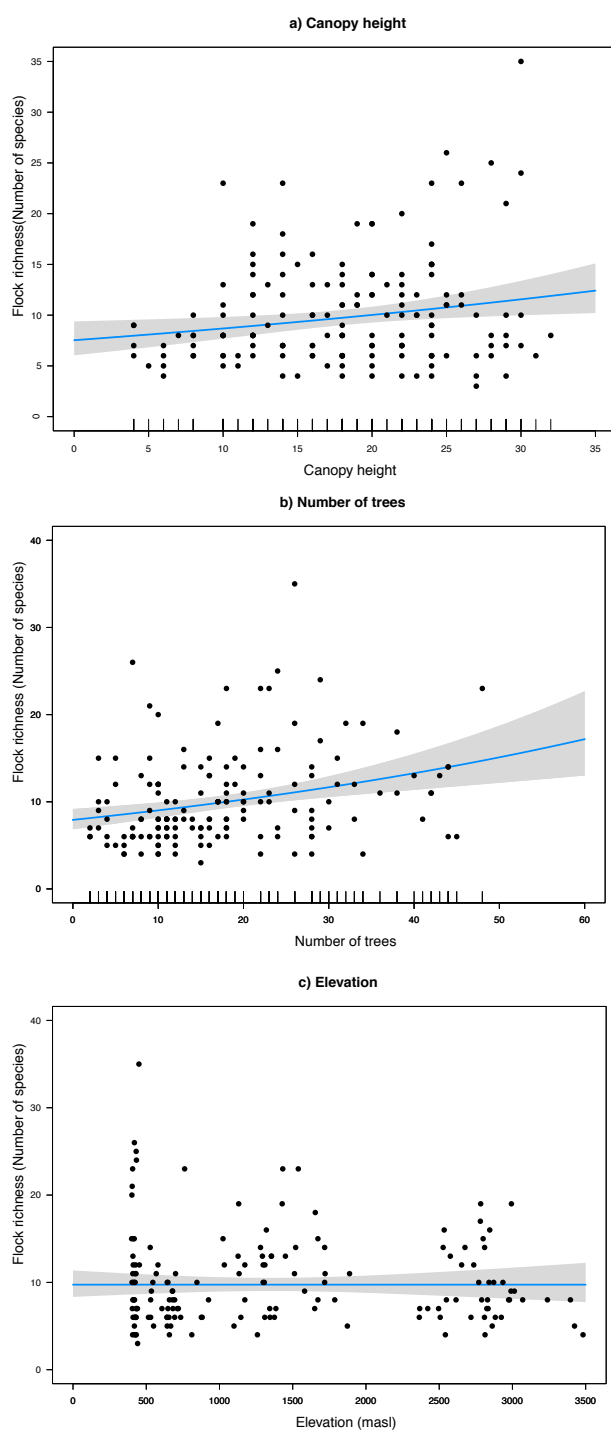


Figure 2.13 Mixed-species flock richness in the Manu study region varying by (a) canopy height, (b) number of trees and (c) elevation. Best-fitted model was used to plot canopy height and number of trees. Second best-fitted model was used to plot elevation. The solid line is the predicted value of flock richness as a function of each variable, filling in the other explanatory variables to the median. Each dot represents a observed flock. The grey shading shows the confidence intervals based on the standard errors of the estimates.

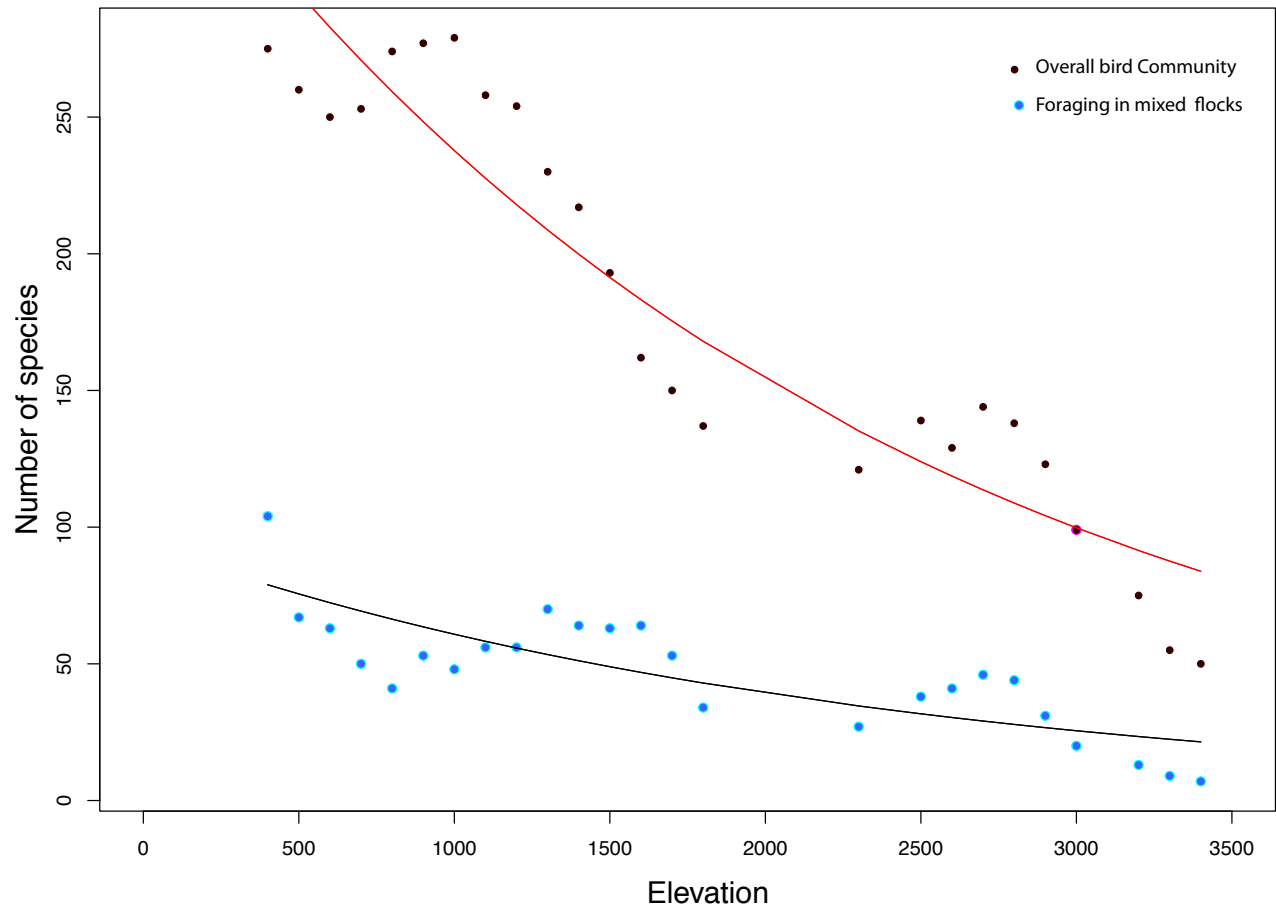


Figure 2.14 Bird species richness per elevational band. Total number of species in the Manu gradient community (black) and number of species participating in flocks (blue) for each elevational zone are shown (e.g. 400-500; 501-600; 601-700). The solid line is the predicted value of species richness as a function of elevation.

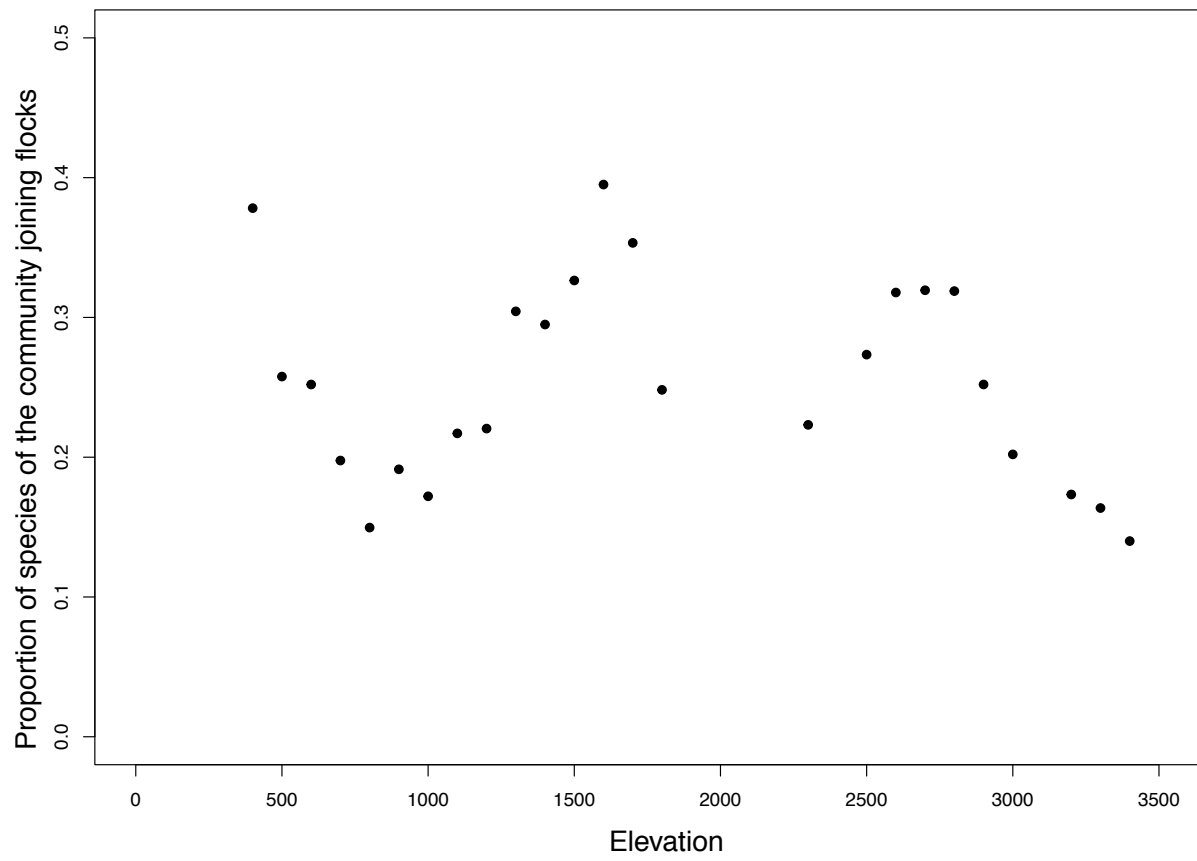


Figure 2.15 Prevalence of flocking across elevations. Proportion of species of the community joining flocks for each elevation band is shown.

Chapter 3: Conclusions

3.1 General conclusions

This study examined the structure and dynamics of one of the most striking examples of facilitation among multiple species, mixed-species bird flocks. This is the first study that describes these multi-species groups of birds across a large-scale, continuous elevational gradient in the Neotropics. I demonstrated that mixed-species flocks are a common feature of Neotropical bird communities at all elevations, within different habitats of the Amazonian lowlands (*terra firme* and bamboo forest) to the high Andes (lower montane and cloud forest). These flocks exhibit an extraordinary degree of organization and stability. My analysis of flock structure called attention to three distinguishable types of flocks occurring across the gradient, with transitions that are associated with changes in the overall bird community. Andean flocks can be differentiated from Amazonian flocks by their larger home range size and higher diversity of participating species, compared to the smaller and slightly less diverse lowland flocks. Flocks across the gradient exhibited a similar general structure, composed of a highly stable core group of species and a more dynamic component of attendant species. The core component of the flocks was restricted to 3-5 species of obligate participants per flock type, represented by twelve genera from three families: Thaupidae, Tyrannidae and Thamnophilidae.

The analysis of temporal and spatial stability showed that Andean mixed-species flocks were just as stable as those occurring in the Amazonian lowlands, with flocks exhibiting stable home ranges and consistency in core member composition over time, even across years. Finally,

I showed that some species are specialized to forage within mixed-species flocks and appear to be behaviourally restricted to these subunits of the community. Furthermore, this study demonstrates that mixed-species flocks are used by over one third of species present at any elevation across the gradient, representing an important component of tropical bird communities. It is still unclear from these results, however, whether any attributes or behaviours can be used to reliably predict species participation in flocks.

There are two key insights from this study that contribute to our understanding of how flocks influence the structure of tropical bird communities. First, the stability of these multispecies associations across elevations suggests that flocks function as small subunits within bird communities. In these flocks, obligate participants, in their role as nuclear species, may be responsible for the cohesion and maintenance of these multi-species groups. Importantly, if these species were removed from the community, they could have a disproportionate effect on many other species due to their influence on flock formation. Second, this study highlights the high proportion of species participating in these multi-species associations, suggesting that such facilitative interactions are remarkably important in Neotropical bird communities. The facilitation occurring among bird species in these flocks may relax competition in the community and thus allow the coexistence of a higher number species. Furthermore the potential strong interdependence of some flock members may limit their densities, promoting higher species packing in Neotropical communities.

3.2 Future research

A number of questions remain to be explored in how facilitative interactions of mixed-species flocks influence bird communities. One key avenue will be to examine the interdependence of obligate flock participants in aspects such as co-occurrence patterns and elevational ranges. One may expect that species with sufficiently strong interdependent interactions may co-occur more often than expected by chance and exhibit coincident elevational range boundaries. Long-term associations with mixed species flocks may have consequences for individual species traits and behaviours. As such, it will be of great interest to explore whether certain life-history traits or behaviours (e.g., lower BMR, higher survival, cooperative breeding) emerge more frequently in species associated with mixed-species flocks. Other relatively unexplored area of research is the evaluation of factors that explain the prevalence of flocking across elevations. Predation risk, as well as resource availability and patchiness, may be particularly good predictors to explain variation in flocking prevalence. Finally, with the increased availability of information on evolutionary relationships among avian species, it will be very interesting to evaluate the phylogenetic structure of mixed flocks across elevations, to evaluate whether these groups tend to be composed of more closely or distantly related species. Traditional studies of mixed-species flocks have intentionally avoided repeated observations of the same flock (e.g. Satischandra et al. 2007); however, I recommend that future studies repeat detailed surveys of the same flock at different time intervals to specifically examine the stability of association among species.

Given the various gaps remaining in this topic, and the challenges involved in conducting experiments with this taxonomic group in particular, advancing the frontier of our knowledge on mixed species flocks will require several comprehensive and comparable data sets across large

scales to more effectively address the question of how these facilitative interactions structure communities. This thesis represents a first step towards the exploration of this question using broad spatial scales.

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Appendices

Appendix A List of species

Bird species participating in mixed-flocks in Manu gradient, Peru. Flock type and sample size is shown for each species.

Flock type	Habitat	Species	n
Lowland (Bamboo)	Bamboo forest	<i>Anabazenops dorsalis</i>	16
Lowland (Bamboo)	Bamboo forest	<i>Automolus infuscatus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Automolus melanopezus</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Automolus ochrolaemus</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Basileuterus chrysogaster</i>	13
Lowland (Bamboo)	Bamboo forest	<i>Campylorhamphus trochilirostris</i>	13
Lowland (Bamboo)	Bamboo forest	<i>Cercomacra manu</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Chlorophanes spiza</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Chlorothraupis carmioli</i>	7
Lowland (Bamboo)	Bamboo forest	<i>Cranioleuca gutturata</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Cyanerpes caeruleus</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Cyanerpes cyaneus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Cyanocompsa cyanoides</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Cymbilaimus sanctaemariae</i>	5
Lowland (Bamboo)	Bamboo forest	<i>Dacnis cayana</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Dacnis lineata</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Dendrocincla fuliginosa</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Dendrocincla merula</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Dryophila devillei</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Dysithamnus mentalis</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Epinecrophylla erythrura</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Epinecrophylla ornata</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Euphonia rufiventris</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Euphonia xanthogaster</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Galbula cyanescens</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Glyphorynchus spirurus</i>	12
Lowland (Bamboo)	Bamboo forest	<i>Herpsilochmus rufimarginatus</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Hyloctistes subulatus</i>	1

Flock type	Habitat	Species	n
Lowland (Bamboo)	Bamboo forest	<i>Hylophilus hypoxanthus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Hylophilus ochraceiceps</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Hypocnemis subflava</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Lanio versicolor</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Lathrotriccus euleri</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Leptopogon amaurocephalus</i>	11
Lowland (Bamboo)	Bamboo forest	<i>Microrhopias quixensis</i>	24
Lowland (Bamboo)	Bamboo forest	<i>Mionectes oleagineus</i>	6
Lowland (Bamboo)	Bamboo forest	<i>Mionectes olivaceus</i>	8
Lowland (Bamboo)	Bamboo forest	<i>Myioborus miniatus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Myrmeciza fortis</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Myrmeciza goeldi</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Myrmoborus leucophrys</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Myrmotherula brachyura</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Myrmotherula longipennis</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Myrmotherula menetriesii</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Myrmotherula schistoginus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Pachyramphus minor</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Pernostola lophotes</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Piaya cayana</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Pipra erythrocephala</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Ramphotrigon fuscicauda</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Saltator grossus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Saltator maximus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Simoxenops ucayalae</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Tachyphonus rufiventer</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Tangara chilensis</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Tangara gyrola</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Tangara mexicana</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Tangara punctata</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Tangara schrankii</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Terenura callinota</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Thamnomanes schistogynus</i>	27
Lowland (Bamboo)	Bamboo forest	<i>Thamnophilus palliatus</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Thamnophilus schistaceus</i>	7
Lowland (Bamboo)	Bamboo forest	<i>Trogon curucui</i>	2
Lowland (Bamboo)	Bamboo forest	<i>Vireo olivaceus</i>	3
Lowland (Bamboo)	Bamboo forest	<i>Xenopipo holochlora</i>	1

Flock type	Habitat	Species	n
Lowland (Bamboo)	Bamboo forest	<i>Xenops minutus</i>	1
Lowland (Bamboo)	Bamboo forest	<i>Xiphorhynchus elegans</i>	9
Lowland (Bamboo)	Bamboo forest	<i>Xiphorhynchus guttatus</i>	5
Lowland	Terra firme/Flooded	<i>Anabazenops dorsalis</i>	1
Lowland	Terra firme/Flooded	<i>Ancistrops strigilatus</i>	1
Lowland	Terra firme/Flooded	<i>Arremon taciturnus</i>	2
Lowland	Terra firme/Flooded	<i>Automolus infuscatus</i>	6
Lowland	Terra firme/Flooded	<i>Automolus melanopezus</i>	2
Lowland	Terra firme/Flooded	<i>Automolus ochrolaemus</i>	13
Lowland	Terra firme/Flooded	<i>Automolus rufipileatus</i>	2
Lowland	Terra firme/Flooded	<i>Automolus sp</i>	1
Lowland	Terra firme/Flooded	<i>Bucco capensis</i>	1
Lowland	Terra firme/Flooded	<i>Campephilus melanoleucos</i>	1
Lowland	Terra firme/Flooded	<i>Campephilus rubricollis</i>	1
Lowland	Terra firme/Flooded	<i>Campylorhamphus trochilirostris</i>	1
Lowland	Terra firme/Flooded	<i>Capito auratus</i>	6
Lowland	Terra firme/Flooded	<i>Celeus gramicus</i>	1
Lowland	Terra firme/Flooded	<i>Celeus grammicus</i>	1
Lowland	Terra firme/Flooded	<i>Cercomacra manu</i>	1
Lowland	Terra firme/Flooded	<i>Cercomacra sp</i>	1
Lowland	Terra firme/Flooded	<i>Chlorophanes spiza</i>	3

Flock type	Habitat	Species	n
Lowland	Terra firme/Flooded	<i>Chlorothraupis carmioli</i>	12
Lowland	Terra firme/Flooded	<i>Cnemotriccus fuscatus</i>	1
Lowland	Terra firme/Flooded	<i>Coccyzus americanus</i>	1
Lowland	Terra firme/Flooded	<i>Coccyzus melacoryphus</i>	1
Lowland	Terra firme/Flooded	<i>Conopophaga peruviana</i>	1
Lowland	Terra firme/Flooded	<i>Cranioleuca gutturata</i>	2
Lowland	Terra firme/Flooded	<i>Cyanerpes caeruleus</i>	3
Lowland	Terra firme/Flooded	<i>Cyanerpes cyaneus</i>	2
Lowland	Terra firme/Flooded	<i>Cyanocompsa cyanoides</i>	1
Lowland	Terra firme/Flooded	<i>Cymbilaimus lineatus</i>	4
Lowland	Terra firme/Flooded	<i>Deconychura longicauda</i>	1
Lowland	Terra firme/Flooded	<i>Dendrocincla fuliginosa</i>	3
Lowland	Terra firme/Flooded	<i>Dendrocolaptes picumnus</i>	1
Lowland	Terra firme/Flooded	<i>Drymophila devillei</i>	5
Lowland	Terra firme/Flooded	<i>Epinecrophylla erythrura</i>	14
Lowland	Terra firme/Flooded	<i>Epinecrophylla leucophthalma</i>	10
Lowland	Terra firme/Flooded	<i>Epinecrophylla ornata</i>	1
Lowland	Terra firme/Flooded	<i>Eubucco richardsoni</i>	2
Lowland	Terra firme/Flooded	<i>Eubucco tucinkae</i>	3
Lowland	Terra firme/Flooded	<i>Euphonia rufiventris</i>	2

Flock type	Habitat	Species	n
Lowland	Terra firme/Flooded	<i>Euphonia sp</i>	1
Lowland	Terra firme/Flooded	<i>Euphonia xanthogaster</i>	2
Lowland	Terra firme/Flooded	<i>Furnaridae sp</i>	3
Lowland	Terra firme/Flooded	<i>Glyphorynchus spirurus</i>	29
Lowland	Terra firme/Flooded	<i>Gymnoderus foetidus</i>	1
Lowland	Terra firme/Flooded	<i>Habia rubica</i>	3
Lowland	Terra firme/Flooded	<i>Hemithraupis flavicollis</i>	4
Lowland	Terra firme/Flooded	<i>Hemithraupis guira</i>	2
Lowland	Terra firme/Flooded	<i>Hyloctistes subulatus</i>	4
Lowland	Terra firme/Flooded	<i>Hylophilus hypoxanthus</i>	7
Lowland	Terra firme/Flooded	<i>Hylophilus ochraceiceps</i>	6
Lowland	Terra firme/Flooded	<i>Icterus cayanensis</i>	1
Lowland	Terra firme/Flooded	<i>Isleria hauxwelli</i>	2
Lowland	Terra firme/Flooded	<i>Lanio versicolor</i>	22
Lowland	Terra firme/Flooded	<i>Lathrotriccus euleri</i>	1
Lowland	Terra firme/Flooded	<i>Lepidothrix coronata</i>	1
Lowland	Terra firme/Flooded	<i>Leptopogon amaurocephalus</i>	11
Lowland	Terra firme/Flooded	<i>Leptopogon superciliaris</i>	1
Lowland	Terra firme/Flooded	<i>Melanerpes cruentatus</i>	1
Lowland	Terra firme/Flooded	<i>Metopothrix aurantiaca</i>	1

Flock type	Habitat	Species	n
Lowland	Terra firme/Flooded	<i>Mionectes macconnelli</i>	5
Lowland	Terra firme/Flooded	<i>Mionectes oleagineus</i>	8
Lowland	Terra firme/Flooded	<i>Mionectes olivaceus</i>	1
Lowland	Terra firme/Flooded	<i>Monasa morpheus</i>	3
Lowland	Terra firme/Flooded	<i>Monasa morphoeus</i>	7
Lowland	Terra firme/Flooded	<i>Monasa nigrifrons</i>	2
Lowland	Terra firme/Flooded	<i>Monasa sp</i>	1
Lowland	Terra firme/Flooded	<i>Myiarchus tyrannulus</i>	1
Lowland	Terra firme/Flooded	<i>Myiobius barbatus</i>	2
Lowland	Terra firme/Flooded	<i>Myiodinastes maculatus</i>	1
Lowland	Terra firme/Flooded	<i>Myiopagis gaimardii</i>	1
Lowland	Terra firme/Flooded	<i>Myrmoborus leucophrys</i>	1
Lowland	Terra firme/Flooded	<i>Myrmoborus myotherinus</i>	10
Lowland	Terra firme/Flooded	<i>Myrmotherula axillaris</i>	35
Lowland	Terra firme/Flooded	<i>Myrmotherula brachyura</i>	13
Lowland	Terra firme/Flooded	<i>Myrmotherula longipennis</i>	16
Lowland	Terra firme/Flooded	<i>Myrmotherula menetriesii</i>	23
Lowland	Terra firme/Flooded	<i>Myrmotherula multostriata</i>	1
Lowland	Terra firme/Flooded	<i>Pachyramphus minor</i>	5
Lowland	Terra firme/Flooded	<i>Parula pitiayumi</i>	1

Flock type	Habitat	Species	n
Lowland	Terra firme/Flooded	<i>Phillydor erythropterum</i>	2
Lowland	Terra firme/Flooded	<i>Philydor erythrocerum</i>	4
Lowland	Terra firme/Flooded	<i>Piculus leucolaemus</i>	1
Lowland	Terra firme/Flooded	<i>Pipra chloromeros</i>	1
Lowland	Terra firme/Flooded	<i>Pipra fascicauda</i>	3
Lowland	Terra firme/Flooded	<i>Pipra fasciicauda</i>	1
Lowland	Terra firme/Flooded	<i>Poecilotriccus albifacies</i>	1
Lowland	Terra firme/Flooded	<i>Pygmytila stellaris</i>	13
Lowland	Terra firme/Flooded	<i>Ramphotrigon fuscicauda</i>	3
Lowland	Terra firme/Flooded	<i>Saltator grossus</i>	2
Lowland	Terra firme/Flooded	<i>Saltator maximus</i>	4
Lowland	Terra firme/Flooded	<i>Sclerurus mexicanus</i>	1
Lowland	Terra firme/Flooded	<i>Simoxenops ucayalae</i>	1
Lowland	Terra firme/Flooded	<i>Sittasomus griseicapillus</i>	1
Lowland	Terra firme/Flooded	<i>Tachyphonus cristatus</i>	1
Lowland	Terra firme/Flooded	<i>Tachyphonus luctuosus</i>	7
Lowland	Terra firme/Flooded	<i>Tachyphonus rufiventer</i>	18
Lowland	Terra firme/Flooded	<i>Tangara callophrys</i>	1
Lowland	Terra firme/Flooded	<i>Tangara chilensis</i>	12
Lowland	Terra firme/Flooded	<i>Tangara gyrola</i>	9

Flock type	Habitat	Species	n
Lowland	Terra firme/Flooded	<i>Tangara mexicana</i>	2
Lowland	Terra firme/Flooded	<i>Tangara schrankii</i>	22
Lowland	Terra firme/Flooded	<i>Tangara velia</i>	1
Lowland	Terra firme/Flooded	<i>Tangara xanthogastra</i>	5
Lowland	Terra firme/Flooded	<i>Terenotriccus erythrurus</i>	2
Lowland	Terra firme/Flooded	<i>Thamnomanes ardesiacus</i>	22
Lowland	Terra firme/Flooded	<i>Thamnomanes schistogynus</i>	22
Lowland	Terra firme/Flooded	<i>Thamnophilus aethiops</i>	1
Lowland	Terra firme/Flooded	<i>Thamnophilus schistaceus</i>	11
Lowland	Terra firme/Flooded	<i>Thraupis palmarum</i>	1
Lowland	Terra firme/Flooded	<i>Thripophaga fusciceps</i>	1
Lowland	Terra firme/Flooded	<i>Tityra semifasciata</i>	1
Lowland	Terra firme/Flooded	<i>Todirostrum chrysocrotaphum</i>	1
Lowland	Terra firme/Flooded	<i>Tolmomyias assimilis</i>	2
Lowland	Terra firme/Flooded	<i>Trogon collaris</i>	2
Lowland	Terra firme/Flooded	<i>Trogon curucui</i>	1
Lowland	Terra firme/Flooded	<i>Trogon melanurus</i>	1
Lowland	Terra firme/Flooded	<i>Trogon violaceus</i>	2
Lowland	Terra firme/Flooded	<i>Trogon viridis</i>	1
Lowland	Terra firme/Flooded	<i>Vireo leucophrys</i>	4

Flock type	Habitat	Species	n
Lowland	Terra firme/Flooded	<i>Vireo olivaceus</i>	2
Lowland	Terra firme/Flooded	<i>Xenopipo holochlora</i>	1
Lowland	Terra firme/Flooded	<i>Xenops minutus</i>	8
Lowland	Terra firme/Flooded	<i>Xenops rutilans</i>	3
Lowland	Terra firme/Flooded	<i>Xenops tenuirostris</i>	7
Lowland	Terra firme/Flooded	<i>Xiphocolaptes promeropirhynchus</i>	1
Lowland	Terra firme/Flooded	<i>Xiphorhynchus elegans</i>	21
Lowland	Terra firme/Flooded	<i>Xiphorhynchus guttatus</i>	17
Lowland	Terra firme/Flooded	<i>Xyphorinchus picus</i>	1
Low-montane	Cloud forest	<i>Anabacerthia striaticollis</i>	18
Low-montane	Cloud forest	<i>Anisognathus somptuosus</i>	1
Low-montane	Cloud forest	<i>Atlapetes melanolaemus</i>	2
Low-montane	Cloud forest	<i>Automolus infuscatus</i>	1
Low-montane	Cloud forest	<i>Automolus ochrolaemus</i>	8
Low-montane	Cloud forest	<i>Basileuterus bivittatus</i>	1
Low-montane	Cloud forest	<i>Basileuterus chrysogaster</i>	1
Low-montane	Cloud forest	<i>Basileuterus coronatus</i>	5
Low-montane	Cloud forest	<i>Basileuterus signatus</i>	1
Low-montane	Cloud forest	<i>Basileuterus tristriatus</i>	16
Low-montane	Cloud forest	<i>Chiroxiphia boliviana</i>	2
Low-montane	Cloud forest	<i>Chlorochrysa calliparaea</i>	36
Low-montane	Cloud forest	<i>Chlorophanes spiza</i>	2
Low-montane	Cloud forest	<i>Chlorophonia cyanea</i>	5
Low-montane	Cloud forest	<i>Chlorospingus flavigularis</i>	40
Low-montane	Cloud forest	<i>Chlorospingus ophthalmicus</i>	9
Low-montane	Cloud forest	<i>Chlorospingus parvirostris</i>	3
Low-montane	Cloud forest	<i>Cissopis leverianus</i>	1
Low-montane	Cloud forest	<i>Coereba flaveola</i>	1
Low-montane	Cloud forest	<i>Colaptes punctigula</i>	1
Low-montane	Cloud forest	<i>Colaptes rubiginosus</i>	3

Flock type	Habitat	Species	n
Low-montane	Cloud forest	<i>Conopias cinchoneti</i>	2
Low-montane	Cloud forest	<i>Contopus fumigatus</i>	1
Low-montane	Cloud forest	<i>Cranioleuca curtata</i>	1
Low-montane	Cloud forest	<i>Creurgops dentatus</i>	7
Low-montane	Cloud forest	<i>Cyanerpes caeruleus</i>	1
Low-montane	Cloud forest	<i>Cyanerpes cyaneus</i>	1
Low-montane	Cloud forest	<i>Cyanocorax yncas</i>	1
Low-montane	Cloud forest	<i>Dacnis cayana</i>	1
Low-montane	Cloud forest	<i>Dendrocolaptes picumnus</i>	1
Low-montane	Cloud forest	<i>Diglossa cyanea</i>	1
Low-montane	Cloud forest	<i>Diglossa glauca</i>	5
Low-montane	Cloud forest	<i>Dysithamnus mentalis</i>	1
Low-montane	Cloud forest	<i>Elaenia albiceps</i>	1
Low-montane	Cloud forest	<i>Elaenia pallatangae</i>	1
Low-montane	Cloud forest	<i>Elaenia parvirostris</i>	1
Low-montane	Cloud forest	<i>Entomodestes leucotis</i>	5
Low-montane	Cloud forest	<i>Eubbuco versicolor</i>	12
Low-montane	Cloud forest	<i>Euphonia mesochrysa</i>	6
Low-montane	Cloud forest	<i>Euphonia xanthogaster</i>	20
Low-montane	Cloud forest	<i>Galbula cyanescens</i>	1
Low-montane	Cloud forest	<i>Hemispingus melanotis</i>	16
Low-montane	Cloud forest	<i>Hemithraupis guira</i>	2
Low-montane	Cloud forest	<i>Hemitriccus rufigularis</i>	1
Low-montane	Cloud forest	<i>Herpsilochmus axillaris</i>	2
Low-montane	Cloud forest	<i>Iridophanes pulcherrimus</i>	3
Low-montane	Cloud forest	<i>Iridosornis analis</i>	12
Low-montane	Cloud forest	<i>Lathrotriccus eulerei</i>	2
Low-montane	Cloud forest	<i>Legatus leucophagius</i>	1
Low-montane	Cloud forest	<i>Lepidocolaptes lacrymiger</i>	5
Low-montane	Cloud forest	<i>Leptopogon superciliaris</i>	37
Low-montane	Cloud forest	<i>Malacoptila fulvogularis</i>	1
Low-montane	Cloud forest	<i>Mionectes olivaceus</i>	2
Low-montane	Cloud forest	<i>Mionectes striaticollis</i>	19
Low-montane	Cloud forest	<i>Myarchus cephalotes</i>	1
Low-montane	Cloud forest	<i>Myioborus miniatus</i>	41
Low-montane	Cloud forest	<i>Myiophobus fasciatus</i>	1
Low-montane	Cloud forest	<i>Myiophobus inornatus</i>	1
Low-montane	Cloud forest	<i>Myiometetes cayanaensis</i>	1

Flock type	Habitat	Species	n
Low-montane	Cloud forest	<i>Myrmotherula longicauda</i>	2
Low-montane	Cloud forest	<i>Myrmotherula schisticolor</i>	4
Low-montane	Cloud forest	<i>Odontorchilus branickii</i>	6
Low-montane	Cloud forest	<i>Pachyramphus poliopterus</i>	1
Low-montane	Cloud forest	<i>Pachyramphus versicolor</i>	1
Low-montane	Cloud forest	<i>Parula pitiayumi</i>	8
Low-montane	Cloud forest	<i>Philydor erythrocerum</i>	1
Low-montane	Cloud forest	<i>Philydor ruficaudatum</i>	1
Low-montane	Cloud forest	<i>Phyllomyias cinereiceps</i>	10
Low-montane	Cloud forest	<i>Phylloscartes ophthalmicus</i>	10
Low-montane	Cloud forest	<i>Phylloscartes poecilotis</i>	1
Low-montane	Cloud forest	<i>Phylloscartes ventralis</i>	2
Low-montane	Cloud forest	<i>Piaya cayana</i>	5
Low-montane	Cloud forest	<i>Pipraeidea melanonota</i>	1
Low-montane	Cloud forest	<i>Piranga leucoptera</i>	1
Low-montane	Cloud forest	<i>Piranga olivacea</i>	1
Low-montane	Cloud forest	<i>Poecilatriccus plumbeiceps</i>	1
Low-montane	Cloud forest	<i>Premnoplex brunnescens</i>	1
Low-montane	Cloud forest	<i>Pyrrhomyias cinnamomeus</i>	7
Low-montane	Cloud forest	<i>Ramphocelus carbo</i>	6
Low-montane	Cloud forest	<i>Rhynchocyclus fulvipes</i>	1
Low-montane	Cloud forest	<i>Saltator maximus</i>	5
Low-montane	Cloud forest	<i>Sclerurus mexicanus</i>	1
Low-montane	Cloud forest	<i>Synallaxis azarae</i>	1
Low-montane	Cloud forest	<i>Tachyphonus rufiventer</i>	3
Low-montane	Cloud forest	<i>Tangara arthus</i>	25
Low-montane	Cloud forest	<i>Tangara chilensis</i>	9
Low-montane	Cloud forest	<i>Tangara chrysotis</i>	3
Low-montane	Cloud forest	<i>Tangara cyanicollis</i>	18
Low-montane	Cloud forest	<i>Tangara cyanotis</i>	1
Low-montane	Cloud forest	<i>Tangara gyrola</i>	10
Low-montane	Cloud forest	<i>Tangara nigroviridis</i>	6
Low-montane	Cloud forest	<i>Tangara parzudakii</i>	1
Low-montane	Cloud forest	<i>Tangara punctata</i>	12
Low-montane	Cloud forest	<i>Tangara ruficervix</i>	6
Low-montane	Cloud forest	<i>Tangara xanthocephala</i>	6
Low-montane	Cloud forest	<i>Thamnophilus doliatus</i>	1
Low-montane	Cloud forest	<i>Thamnophilus palliatus</i>	2

Flock type	Habitat	Species	n
Low-montane	Cloud forest	<i>Thamnophilus schistaceus</i>	1
Low-montane	Cloud forest	<i>Thamnophilus unicolor</i>	1
Low-montane	Cloud forest	<i>Thlypopsis ruficeps</i>	1
Low-montane	Cloud forest	<i>Thraupis episcopus</i>	2
Low-montane	Cloud forest	<i>Thraupis palmarum</i>	2
Low-montane	Cloud forest	<i>ThricHothraupis melanops</i>	2
Low-montane	Cloud forest	<i>Thripadectes melanorhynchus</i>	8
Low-montane	Cloud forest	<i>Tityra semifasciata</i>	1
Low-montane	Cloud forest	<i>Tolmomyias assimilis</i>	1
Low-montane	Cloud forest	<i>Trichothraupis melanops</i>	5
Low-montane	Cloud forest	<i>Trogon personatus</i>	2
Low-montane	Cloud forest	<i>Trogon personatus</i>	1
Low-montane	Cloud forest	<i>Turdus nigriceps</i>	2
Low-montane	Cloud forest	<i>Xenopipo unicolor</i>	1
Low-montane	Cloud forest	<i>Xenops minutus</i>	1
Low-montane	Cloud forest	<i>Xenops rutilans</i>	1
Low-montane	Cloud forest	<i>Xiphocolaptes promeropirhynchus</i>	4
Low-montane	Cloud forest	<i>Xiphorhynchus ocelatus</i>	2
Low-montane	Cloud forest	<i>Xiphorhynchus triangularis</i>	12
Low-montane	Cloud forest	<i>Zimmerius bolivianus</i>	6
High-montane	Montane/ Puna	<i>Ampelion rubrocristatus</i>	2
High-montane	Montane/ Puna	<i>Anisognathus igniventris</i>	19
High-montane	Montane/ Puna	<i>Arremon torquatus</i>	1
High-montane	Montane/ Puna	<i>Atlapetes melanolaemus</i>	16
High-montane	Montane/ Puna	<i>Basileuterus luteoviridis</i>	9
High-montane	Montane/ Puna	<i>Basileuterus signatus</i>	2
High-montane	Montane/ Puna	<i>Buthraupis montana</i>	14
High-montane	Montane/ Puna	<i>Cacicus chrysonotus</i>	3
High-montane	Montane/ Puna	<i>Catamblyrhynchus diadema</i>	1
High-montane	Montane/ Puna	<i>Chlorophonia cyanea</i>	1
High-montane	Montane/ Puna	<i>Chlorornis riefferii</i>	17
High-montane	Montane/ Puna	<i>Chlorospingus ophthalmicus</i>	1
High-montane	Montane/ Puna	<i>Chlorospingus parvirostris</i>	1
High-montane	Montane/ Puna	<i>Cinnycerthia fulva</i>	3
High-montane	Montane/ Puna	<i>Cnemoscopus rubrirostris</i>	5
High-montane	Montane/ Puna	<i>Colaptes rivolii</i>	1

Flock type	Habitat	Species	n
High-montane	Montane/ Puna	<i>Conirostrum albifrons</i>	9
High-montane	Montane/ Puna	<i>Conirostrum ferrugineiventris</i>	2
High-montane	Montane/ Puna	<i>Conirostrum sitticolor</i>	1
High-montane	Montane/ Puna	<i>Conirostrum sitticolor</i>	4
High-montane	Montane/ Puna	<i>Cranioleuca marcapatae</i>	3
High-montane	Montane/ Puna	<i>Creurgops dentatus</i>	1
High-montane	Montane/ Puna	<i>Cyanolyca viridicyanus</i>	4
High-montane	Montane/ Puna	<i>Delothraupis castaneoventris</i>	3
High-montane	Montane/ Puna	<i>Dendrocincla tyrannina</i>	2
High-montane	Montane/ Puna	<i>Diglossa brunneiventris</i>	1
High-montane	Montane/ Puna	<i>Diglossa caerulescens</i>	1
High-montane	Montane/ Puna	<i>Diglossa cyanea</i>	40
High-montane	Montane/ Puna	<i>Diglossa mystacalis</i>	3
High-montane	Montane/ Puna	<i>Diglossa sittoides</i>	4
High-montane	Montane/ Puna	<i>Drymotoxeres pucherani</i>	1
High-montane	Montane/ Puna	<i>Elaenia albiceps</i>	1
High-montane	Montane/ Puna	<i>Elaenia gigas</i>	1
High-montane	Montane/ Puna	<i>Elaenia obscura</i>	1
High-montane	Montane/ Puna	<i>Elaenia pallatangae</i>	20
High-montane	Montane/ Puna	<i>Entomodestes leucotis</i>	1
High-montane	Montane/ Puna	<i>Hemispingus atropileus</i>	30
High-montane	Montane/ Puna	<i>Hemispingus parodii</i>	2
High-montane	Montane/ Puna	<i>Hemispingus superciliaris</i>	8
High-montane	Montane/ Puna	<i>Hemispingus trifasciatus</i>	6
High-montane	Montane/ Puna	<i>Hemispingus xanthophthalmus</i>	7
High-montane	Montane/ Puna	<i>Hemitriccus granadensis</i>	10
High-montane	Montane/ Puna	<i>Iridosornis jelskii</i>	8
High-montane	Montane/ Puna	<i>Knipolegus signatus</i>	1
High-montane	Montane/ Puna	<i>Lepidocolaptes lacrymiger</i>	4
High-montane	Montane/ Puna	<i>Leptopogon superciliaris</i>	2
High-montane	Montane/ Puna	<i>Margarornis squamiger</i>	21
High-montane	Montane/ Puna	<i>Mecocerculus leucophrys</i>	14
High-montane	Montane/ Puna	<i>Mecocerculus stictopterus</i>	31
High-montane	Montane/ Puna	<i>Mionectes striaticollis</i>	4
High-montane	Montane/ Puna	<i>Myiarchus tuberculifer</i>	3

Flock type	Habitat	Species	n
High-montane	Montane/ Puna	<i>Myioborus melanocephalus</i>	37
High-montane	Montane/ Puna	<i>Myioborus miniatus</i>	1
High-montane	Montane/ Puna	<i>Myiophobus ochraceiventris</i>	1
High-montane	Montane/ Puna	<i>Myrmotherula axillaris</i>	1
High-montane	Montane/ Puna	<i>Ochthoeca rufipectoralis</i>	1
High-montane	Montane/ Puna	<i>Pachyramphus versicolor</i>	4
High-montane	Montane/ Puna	<i>Phylloscartes ventralis</i>	1
High-montane	Montane/ Puna	<i>Pipraeidea melanonota</i>	1
High-montane	Montane/ Puna	<i>Pipreola intermedia</i>	1
High-montane	Montane/ Puna	<i>Piranga flava</i>	1
High-montane	Montane/ Puna	<i>Premnornis guttuligera</i>	1
High-montane	Montane/ Puna	<i>Pseudocolaptes boissonneautii</i>	8
High-montane	Montane/ Puna	<i>Pyrrhomyias cinnamomeus</i>	8
High-montane	Montane/ Puna	<i>Synallaxis azarae</i>	6
High-montane	Montane/ Puna	<i>Tangara nigroviridis</i>	1
High-montane	Montane/ Puna	<i>Tangara vassorii</i>	9
High-montane	Montane/ Puna	<i>Thlypopsis ornata</i>	1
High-montane	Montane/ Puna	<i>Thlypopsis ruficeps</i>	10
High-montane	Montane/ Puna	<i>Thraupis bonariensis</i>	1
High-montane	Montane/ Puna	<i>Thraupis cyanocephala</i>	19
High-montane	Montane/ Puna	<i>Troglodytes solstitialis</i>	3
High-montane	Montane/ Puna	<i>Trogon personatus</i>	2
High-montane	Montane/ Puna	<i>Veniliornis nigriceps</i>	2
High-montane	Montane/ Puna	<i>Vireo leucophrys</i>	1
High-montane	Montane/ Puna	<i>Xiphorhynchus triangularis</i>	3

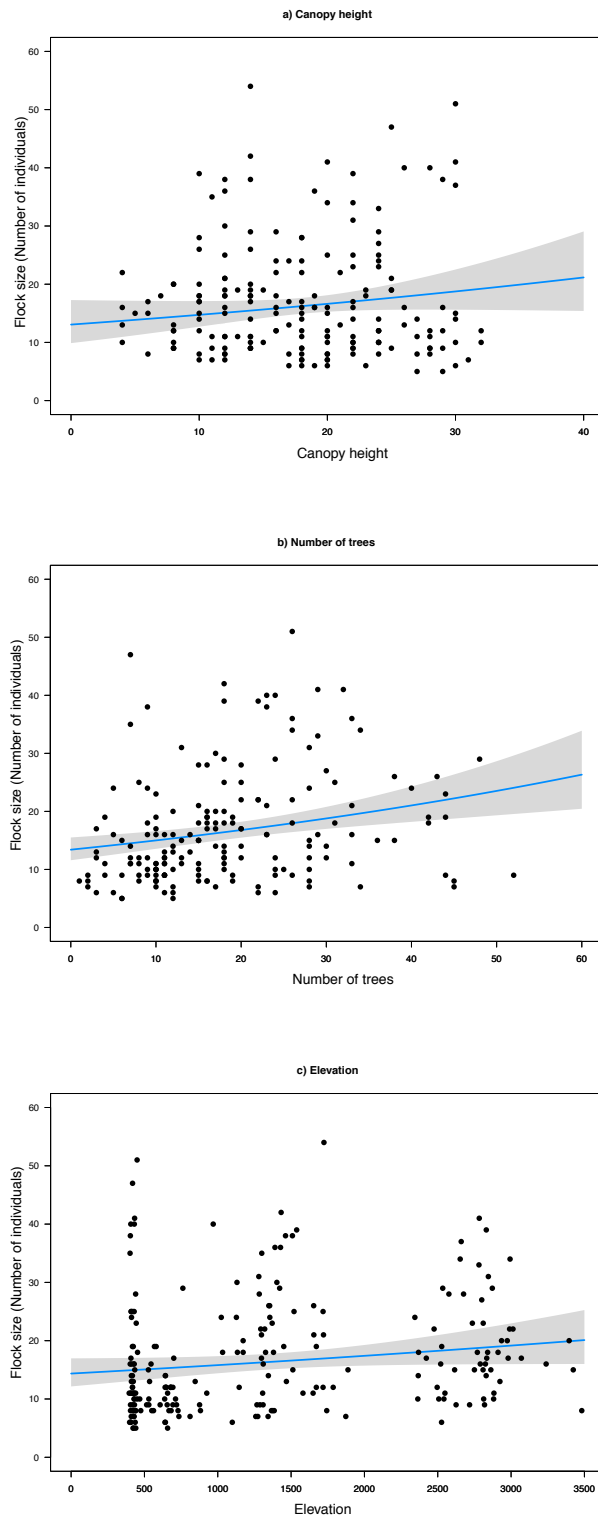
Appendix B Model selection

Model selection results from generalized linear models for flock size (Num of individuals) across the elevational gradient. Explanatory variables include elevation (Elev), mean canopy height (Canopy), and number of trees (Trees). For each fitted model the number of parameters (k), change in corrected quasi-Akaike from the model with the lowest QAIC value ($\Delta QAICc$), QAIC weights ($QAICcWt$) are shown.

Response variable	Model	k	$QAICc$	$\Delta QAICc$	$QAICcWt$
Num_individuals	Elevation+Canopy+Trees	5	352.42	0.00	0.84
	Elevation+Canopy	4	357.66	5.24	0.06
	Elevation	3	358.31	5.89	0.04
	Elevation+Trees	4	359.10	6.67	0.03
	Canopy + Trees	4	359.22	6.79	0.03
	Canopy	3	368.76	16.34	0.00
	Intercept	2	372.33	19.90	0.00
	Trees	3	372.53	20.11	0.00

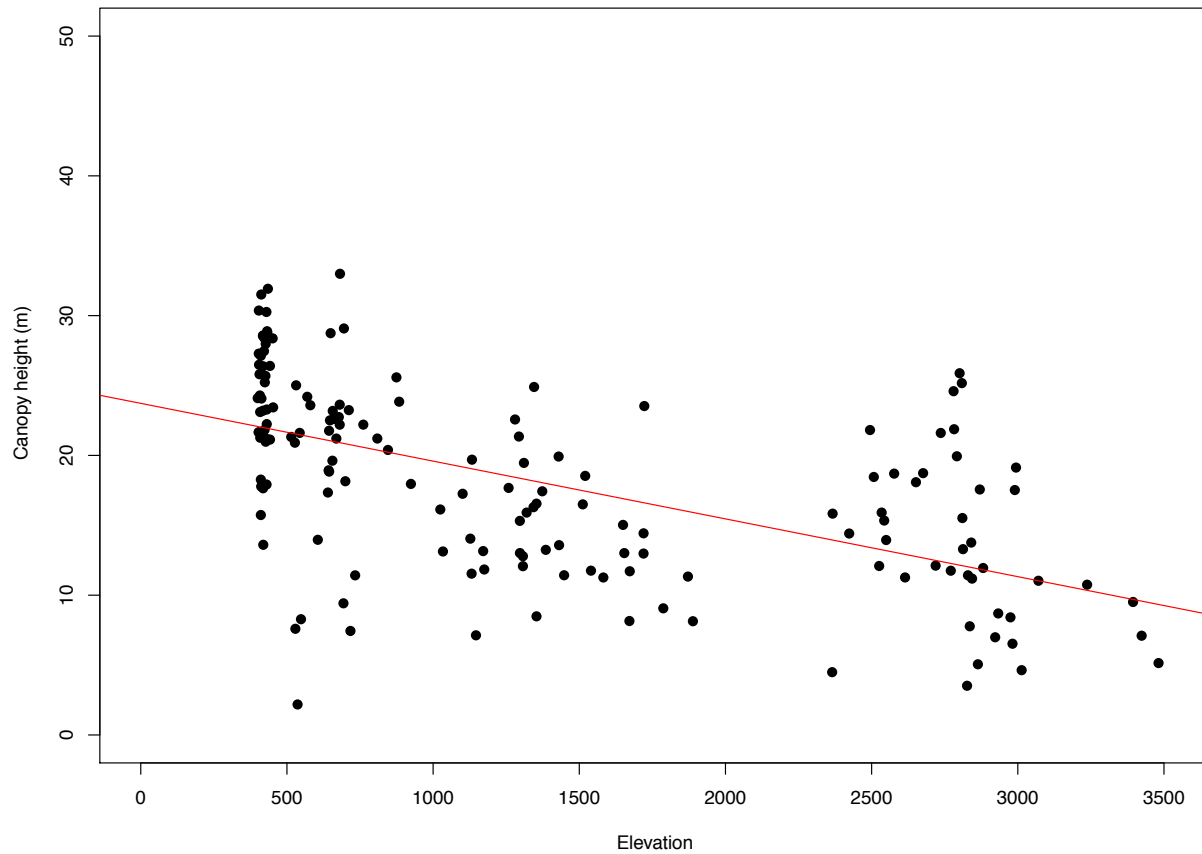
Appendix C Model flock size

Mixed-species flock size in the Manu study region varying by (a) canopy height, (b) number of trees and (c) elevation. Best-fitted model was used to plot canopy height, number of trees and elevation. The solid line is the predicted value of flock size as a function of each variable, filling in the other explanatory variables to the median. Each dot represents a observed flock. The grey shading shows the confidence intervals based on the standard errors of the estimates.



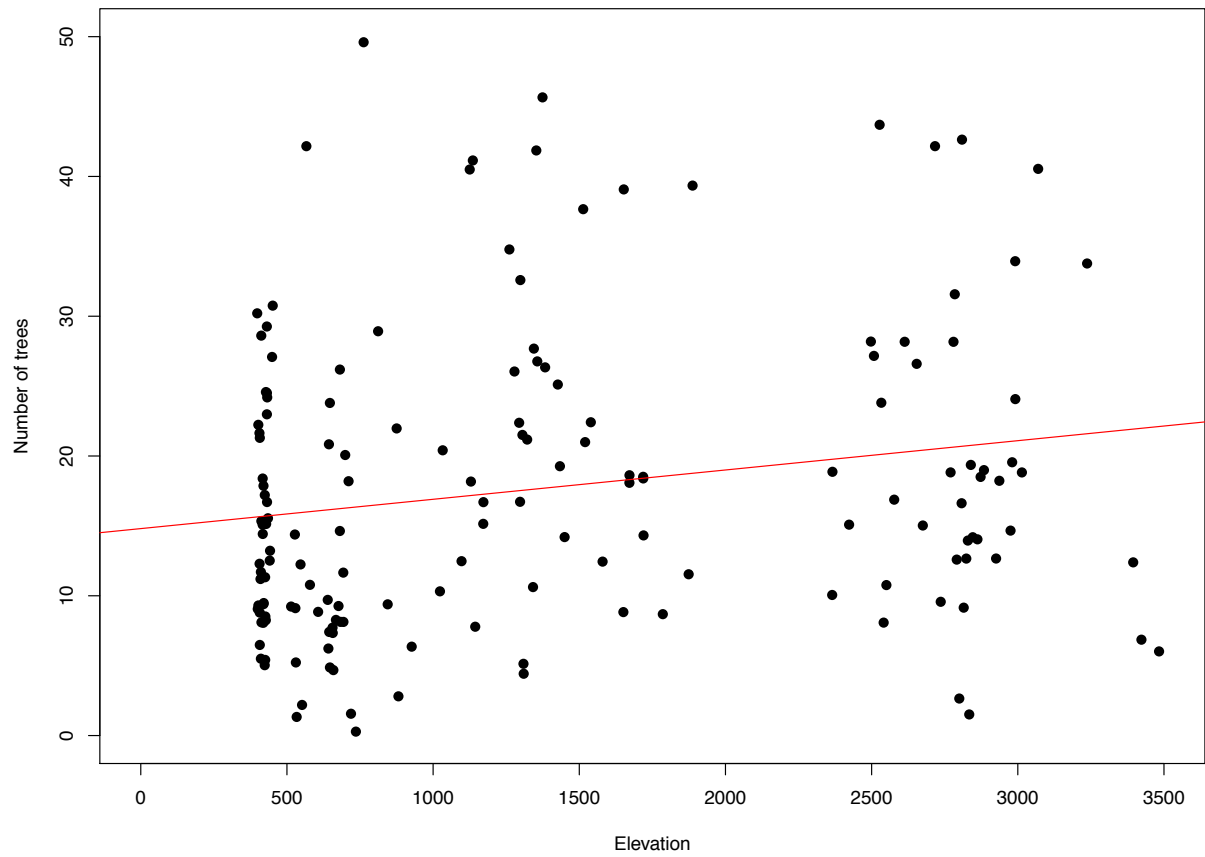
Appendix D Regression canopy height

Regression of Canopy height and Elevation in Manu region, Peru.



Appendix E Regression

Regression of Number of trees and Elevation in Manu region, Peru.



Appendix F Foraging guilds

Proportion of species of the community joining mixed flocks for each foraging guild across elevation is shown.

