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ARTICLE

Ecology of mixed-species flocks of birds across gradients in the Neotropics

Lia Nahomi Kajiki[1,6], Flavia Montaño-Centellas[2], Giselle Mangini[3], Gabriel J. Colorado Z.[4] & María Elisa Fanjul[5]

[1] Laboratório de Comportamento Animal, Departamento de Zoologia, Universidade de Brasília, Brasília, DF, Brazil.
[2] Department of Wildlife Ecology and Conservation, University of Florida, Florida, United States of America.
[3] Instituto de Bio y Geociencias del NOA, Salta, Argentina.
[4] Universidad Nacional de Colombia, km 2, via Tarapaca, Leticia, Amazonas, Colombia.
[5] Fundación Miguel Lillo & Universidad Nacional de Tucumán, Tucumán, Argentina.
[6] Corresponding author: lia.nahomi@gmail.com

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ABSTRACT: Mixed-species flocks of birds have been studied for more than a century, but investigation efforts are historically unbalanced towards certain types of habitats, such as woodlands and lowland forests. Here we provide a first glance of bird flocks' patterns across different gradients in recent studies conducted within the Neotropics. We summarize a symposium where a series of independent studies that approached the topic, some of them making use of techniques that were seldom applied in previous decades in Neotropical systems. We discuss bird flocks' patterns across a latitudinal gradient, social network patterns in bird flocks' across elevational gradients in local and regional scale, and, finally, patterns of flocking response to different levels of human disturbance. Altogether, these studies offer a larger and diverse panorama of possible patterns of response and diversity of mixed-species flocks of birds in the Neotropical region, and provide a rich ground where future studies with bird flocks in the Neotropics may rely on.

KEY-WORDS: altitude, anthropogenic disturbance, facilitation, habitat fragmentation, mixed parties of birds, positive interactions.

INTRODUCTION

More than a century ago, every naturalist and ornithologist who penetrated the tropical humid forests would be mesmerized by the "mixed parties of birds", to judge from the fascinating description of Bates in 1863 (p. 334–335): "*One may pass several days without seeing many birds; but now and then the surrounding bushes and trees appear suddenly to swarm with them. There are scores, probably hundreds of birds, all moving about with the greatest activity (…) in a few minutes the host is gone, and the forest path remains deserted and silent as before*". Bird flocks may account of more than a hundred individuals (Diamond 1987), and these "bird waves" have been the focus of many investigations.

Mixed-species flocks of birds (MSF henceforth) are associations of individual birds from different species in which participants actively maintain a connection over time, move together searching for resources and foraging (Morse 1970, Sridhar *et al.* 2009, Harrison & Whitehouse 2011). They are a prevailing social system in almost every terrestrial ecosystem on earth, from tropical forests – where many passerine birds detected in an area can be observed in MSFs and the aggregation is prevalent year-round (Goodale *et al.* 2009), to temperate forests – where flocking species primarily integrate mixed-species flocks during winter, when resources are scarce and birds are typically outside the breeding season (Morse 1970). MSF members are hypothesized to benefit from joining these associations by two main mechanisms: (*i*) improve feeding efficiency and/or (*ii*) reduce risk of predation (Morse 1977, Sridhar & Shanker 2014, Goodale *et al.* 2015). The benefits, however, may vary among species (Hino 2000), and be dependent of habitat context and group organization (Sridhar *et al.* 2012).

From an ecological perspective, MSFs represent "community modules" (*sensu* Holt 1997), in which competition and positive interactions are highly concentrated in space and time (Sridhar *et al.* 2012). Because of the intricate biological interactions acting upon MSFs, they are considered among the most complex multi-specific associations of terrestrial vertebrates (Munn 1985). Furthermore, they have been proposed as an ideal study system to test for community assembly hypotheses and community responses to disturbance in ecological time scales (Graves & Gotelli 1993, Sridhar *et al.* 2012, Zuluaga & Rodewald 2015). A new interest for the study of these social systems has recently raised, potentially triggered by a new venue for statistical analyses, new computational power and access to large-scale datasets

(Sridhar *et al.* 2009, Sridhar *et al.* 2012, Mokross *et al.* 2014).

The phenomenon of MSF has been studied under many different perspectives, from the comprehension of composition and structure (Bates 1863, Goodale *et al.* 2009, Goodale *et al.* 2015) to understanding species roles and dynamics through experimental studies (*e.g.*, Dolby & Grubb-Jr. 1998, Forsman *et al.* 1998, Krams 2001). Nevertheless, studies are not equally distributed throughout the globe. Historically, much more attention has been given to forested habitats, such as temperate broadleaf forests and to tropical rainforests, whereas fewer studies have been conducted in other environments, such as savannah and dry shrublands (Alves & Cavalcanti 1996, Jones & Bock 2003, Amaral & Ragusa-Netto 2008, Zarco & Cueto 2017).

This directional tendency of studies originated mainly two kinds of biases: between (temperate *vs.* tropical ecosystems) and within climatic regions (*e.g.*, lowland *vs.* highland in the Neotropics). The first is noticeable when comparing flock diversity: in temperate ecosystems, flocks show a lower species diversity compared to tropical flocks, and species in temperate flocks tend to join seasonally and perform well-defined functions within the mixed flocks (Morse 1970, Farley *et al.* 2008). This condition allows researchers to test for specific hypotheses on benefits and consequences of species loss on the overall flock. However, in tropical systems, investigations may increase in complexity, because some species do not have clear established functions within MSF (Greenberg 2000, Zuluaga 2013, Fanjul 2016). The second bias is especially evident in the Neotropical region by the fact that most of our understanding of tropical flocks comes from lowland ecosystems, particularly from the Amazonia, where MSFs seem to be more stable in space and time (*e.g.*, Graves & Gotelli 1993, Martínez & Robinson 2016), and are dominated by certain groups of species (*e.g.*, antbirds).

Additionally, within the Neotropics there are comparatively fewer studies in other non-forested environments such as grasslands, shrublands and mangroves (but see Zarco & Cueto 2017, Ferrari & Motta-Junior 2018), and studies investigating how the structure of mixed flocks vary across natural gradients (*e.g.*, elevational gradient in Andean ecosystem) are even more scarce (but see Marín-Gómez & Arbeláez-Cortés 2015). Finally, MSFs may be affected by several kinds of anthropogenic disturbances, from fragmentation to urbanization, but the first was far more investigated (Maldonado-Coelho & Marini 2000, Mokross *et al.* 2014, Cordeiro *et al.* 2015, see further references in Goodale *et al.* 2015), in detriment of studies on the impacts of deforestation and habitat degradation, or the combination of both. Thus, similar to the Wallacean shortfalls in biodiversity, it is clear that we face basic knowledge shortfalls on mixed-species flocks of birds in the Neotropics.

The importance of the Neotropical region is undeniable: it encompasses a great latitudinal extension, including 181 terrestrial ecoregions and 11 biomes (Olson *et al.* 2001), that ranges from extremely moisture habitats to deserts and xeric shrublands. A major physiographic feature of the region is the mountain ranges that run from south to north along the west, which separates the Pacific from the Amazon Basins. The Neotropical region not only harbors the largest remnant of tropical rainforest in the globe, but also the driest desert, the desert of Atacama, plus one of the rainiest places, the Choco Biogeographic Region to the west. MSF are widespread in the Neotropics, occurring virtually in all its ecoregions. Additionally, MSF have been proposed as systems that promote high species diversity in Neotropical avifauna, leading to higher species packing within communities (Graves & Gotelli 1993). Unfortunately, a considerable part of the pristine environments in the Neotropical region had already been altered (Gibson *et al.* 2011) and is still under pressure of forest loss and habitat change due to human activities (Wright *et al.* 2009). Additionally, climate change effects highlight the need of further understanding of the ecology and dynamics of the highly diversified Neotropical biota (Joly 2008).

Here, we examine the ecological response of mixed-species flocks to natural and anthropogenic gradients in the Neotropical region. We do not intend to conduct a comprehensive bibliographic review, but to discuss current advances in studies with flocks in the Neotropics, and to provide guidelines for further progress on this topic. The studies summarized here were presented during the Symposium "Mixed-species flocks of birds: ecology and evolution" at the XII Ornithological Congress of the Americas, held at Puerto Iguazú, Argentina, from 8 to 11 August 2017. This document is organized in two sections. First, we describe the three most important gradients in the Neotropical region: the latitudinal gradient, the elevational gradient and the gradient of human disturbances. Second, we present a section with conclusions and guidelines for future research largely inspired in the discussion following the symposium and in the interaction among participants.

Mixed-species flocks and latitudinal gradients

A well-documented biogeographic pattern is the change of richness and diversity along latitudinal gradients, which shows a progressive decrease from the tropics to the temperate regions (Pianka 1966, Ruggiero 2001, Willig *et al.* 2003, Hillebrand 2004). Rabinovich & Rapoport (1975) observed that the spatial variation of bird richness is explained by climatic and topographic variables. Most studies point to climate regimes as the main drivers of latitudinal gradients of bird diversity, which affect various aspects of the ecology of the species directly or indirectly, including diets, use of available microhabitats and behavior (Ruggiero & Lawton 1998, Ruggiero 2001, Salisbury *et al.* 2012).

There are numerous studies that evaluate patterns in structure, composition and social role of the species that participate in flocks in the Neotropics (Munn & Terborgh 1979, King & Rappole 2000, Tubelis 2007, Amaral & Ragusa-Netto 2008, Knowlton & Graham 2011, Fanjul & Echevarria 2015), but virtually none of them investigates latitudinal effects. The subtropical mountain forest of the Yungas in Argentina is distributed from northern Salta (limit with Bolivia) to the north of Catamarca province encompassing approximately 700 km of extension. A pattern of decreasing diversity along latitude was observed in this forest in different *taxa*, including birds (Nores 1989, Blendinger & Alvarez 2009), mammals (Ojeda *et al.* 2008) and trees (Morales *et al.* 1995, Blundo *et al.* 2011). This pattern would be related mainly to latitudinal climatic impoverishment caused by the decrease in temperature and precipitation that influence the structure of the local vegetation (Brown *et al.* 2001, Ojeda *et al.* 2008, Blundo *et al.* 2011, Bellard *et al.* 2012). Considering these findings, Fanjul (2016) examined the potential role of the latitudinal gradient on the composition and structural variables of MSF (number of flocks, number of species and individuals participating) along the Yungas Forest of Argentina.

In this symposium, Fanjul demonstrated that whereas there was an effect of the latitudinal gradient on the composition of species, there was no effect on structural variables of MSF. However, species composition changed along the latitudinal gradient, dividing the Argentine Yungas in three sectors (north, center and south).

The structure and composition of mixed flocks are intimately related to the type of environment where flocks occur (Mokross *et al.* 2014), varying between regions, localities and habitats (Powell 1985). Although there is a turnover of individuals and species within a flock across space and time, most flocks' general structure will not change, unless the environment is altered (Zhang *et al.* 2013, Marín-Gómez & Arbeláez-Cortés 2015). In such case, these results could indicate that flocks maintain their structure independently of an inherent species turnover across the latitudinal gradient.

Mixed-species flocks of birds and elevational gradients

Species diversity and community composition are known to change with elevation in a somehow predictable fashion: overall species diversity decreases with elevation, not necessarily following a linear pattern (McCain 2009, McCain & Grytnes 2010). Elevational gradients result in significant changes in many environmental conditions (*e.g.*, temperature, precipitation, oxygen levels), with lower temperatures and more seasonal climatic regimes characterizing higher elevations. Because environmental characteristics change within relatively short distances in mountains, they have been used as model systems to evaluate the relative importance of ecological and evolutionary processes in community structure (Sundqvist *et al.* 2013, Graham *et al.* 2014, Read *et al.* 2014). Harsh conditions at higher elevations are expected to act as a filter, allowing only species that are well adapted to these conditions to persist. On the other hand, at lower elevations, biological interactions (*e.g.*, species interactions) are expected to be a more important force shaping communities (Weiher *et al.* 2011). In a much smaller scale, topography may also cause variation in vegetation composition and determine overall species distribution (Cintra & Naka 2012) within a relatively small area.

Despite the great ubiquity of mixed-species flocks and their early recognition as good study models to test ecological hypotheses (Graves & Gotelli 1993), research focusing on ecological structure of flocks along elevational gradients are still scarce. This gap is clear when conducting a bibliographic search on ISI Web of Science v.5.27 (10 December 2017) with "mixed species flocks" AND "elevation" OR "altitude" as key words in the article topic: results returned only 19 studies between 1900 and 2017. Further examination on each of these studies indicates that only six of them focus on elevation, either testing for MSF composition changes with elevation (Greenberg *et al.* 2001, Arbeláez-Cortés & Marín-Gomez 2012, Marín-Gómez & Arbeláez-Cortés 2015, O'Donnell 2017), or including elevation as a predictor while testing for the effect of other habitat characteristics on flocks (Brandt *et al.* 2009, Goodale *et al.* 2009). Therefore, we attempted to analyze the effect of small and large amplitude of elevational variation in flock's network properties.

In this symposium, Montaño-Centellas presented an example of flock variation along a well-preserved elevational gradient in Bolivia. This study used network theory to test for the effect of elevation on the structure of social networks in mixed-species flocks of birds, along a continuous transect (2000–3550 m a.s.l.) that largely lacks human presence and dissects a protected area (Montaño-Centellas & Garitano-Zavala 2015). She found that species composition, species richness in flocks, as well as network-level metrics vary with elevation. As expected, the number of species participating in flocks decreased with elevation, with an average of six species above 3250 m a.s.l. and an average of nine species at 2000 m a.s.l. (Montaño-Centellas *in prep.*). At the species-level metrics, she found that whereas there were no significant differences in degree (the number of connections each species maintains with other species), weighted degree (the sum of the frequency of interspecific associations for each node) changed across elevations. These results suggest that the overall role of any given species within flocks might change across elevations as well as its position within the network. At the network-level metrics, she found that networks at higher elevations were less modular (*e.g.*, had less community structure), had lower strength (*e.g.*, average of the weighted degrees) and had lower skewed degree distributions than networks at lower elevations. Overall, these findings suggest that networks at higher elevations are less complex, more evenly distributed as they do not include "sub-units" within the flocks, and are potentially less resilient, as long tail degree distributions are characteristic of networks that are more resilient (Thébault & Fontaine 2010).

This study exemplifies the examination of flocks as components of the community along a broad environmental gradient, where abiotic characteristics (*e.g.*, temperature) strongly correlate with elevation and are important predictors of community changes. However, elevation may also affect communities at smaller scales, modifying local environmental characteristics and creating natural gradients within otherwise climatically "homogeneous" and stable habitats (*i.e.* non-seasonal when compared with temperate regions), such as the Amazonian lowland *terra firme* Forests (Karr & Freemark 1983, Cintra & Naka 2012). This idea would not be conceivable for lowland forests, where species richness was once believed to show a remarkable constancy in a variety of Amazonian sites (Cohn-Haft *et al.* 1997).

Because mixed-species flocks of birds represent "community modules" (*sensu* Holt 1997), flocks are expected to respond as communities to small changes, with little or no differences among MSF that occur in the same habitat. However, in this symposium, Kajiki demonstrated that mixed-species flocks of birds differed along a discrete environmental gradient in *terra firme* forest, both in richness and species position within the network. She examined the effect of environmental variables (elevation and NDVI index) in species richness and structure of mixed species flocks in a *terra firme* forest in the Brazilian Amazon, where elevation varied by less than 130 m between highest and lowest point. By employing network analysis to understand general network properties of flocks, she found that only weighted degree was affected by the environmental gradient: MSF at lower elevations presented higher frequencies of interspecific interactions. Furthermore, species richness was also affected by this gradient, with richer MSF in mid-elevation sites, which presented higher NDVI values. These results suggest that birds are responding to small-scale environmental heterogeneity (Cintra & Naka 2012) and that even small differences in elevation can result in different network properties.

Mixed-species flocks of birds' response to anthropogenic disturbances

Of the world's rapidly vanishing tropical forests, Neotropical forests are not an exception (Bierregaard-Jr. & Lovejoy 1989, Pimm & Raven 2000). This is of great concern because the Neotropics harbor several biodiversity hotspots (Myers *et al.* 2000), and a great amount of information on natural history of Neotropical species, as well as ecological data of these biological communities, are still missing. The main reason behind the rapid vanishing of tropical forest is the expansion and intensification of agricultural frontier, which leads to forest loss and fragmentation (Foley *et al.* 2005, Laurance *et al.* 2014). As fragmentation increases, the surface of native environments and the size of the remnant fragments decrease, with the subsequent increment in isolation. Removal of native forests and replacement by crops with different architecture and phenology result in changes in several environmental conditions in newly created landscapes. For instance, air temperature, temperature range within the day and albedo increase due to changes in the radiation balance within fragments, which leads to higher desiccation rates (Foley *et al.* 2005, Laurance *et al.* 2014). Higher radiation and desiccation levels in forest fragments may lead to decreased prey availability, reducing foraging opportunities for birds and alter their natural cycles (Saunders *et al.* 1991, Laurance 2004). Furthermore, fragmented landscapes limit movements of understory passerines (Tellería & Santos 1995, Develey & Stouffer 2001), increase nest predation (Kattan *et al.* 1994, Renjifo 1999, 2001) and facilitate the establishment of raptors associated with forest gaps (Thiollay 1999). These changes in forest configuration and the associated mechanisms reduce habitat quality for birds, causing an overall loss of biodiversity (Stouffer & Bierregaard-Jr. 1995, Maldonado-Coelho & Marini 2004).

Nevertheless, the consequences of deforestation and habitat degradation extend beyond the loss of bird diversity, and affect ecological interactions (Brandt *et al.* 2009, Mokross *et al.* 2014). Because MSF are an important functional component of bird communities it is imperative to better understand the complex social structure of this type of group association (Greenberg 2000). Furthermore, MSF may be a good predictor of habitat quality, as there is a positive relationship between habitat quality and flock attributes (*e.g.*, well-preserved habitats contain richer mixed flocks; Zuluaga & Rodewald 2015).

In this respect, Mangini showed in her presentation that for seasonal forests in Salta, northwest of Argentina, birds attended mixed-species flocks in both continuous and fragmented forests, following the same seasonal pattern, and reaching the highest number of recorded mixed flocks during the Austral fall and winter. However, some species with similar abundances in both types of forest configuration had a higher flocking propensity within forest fragments, while other species showed this pattern in continuous forest (Mangini *et al.* in prep.). Furthermore, the number of flocks, as well as their species richness and number of individuals, were smaller within forest fragments when compared with continuous forest.

Even though fragmentation is a key factor for the loss of both biodiversity and interactions, flocks may be affected by factors acting simultaneously at different scales. As Colorado showed in his presentation, a multi-scale factor (*i.e.* landscape and local scale) seems to be affecting different attributes of mixed-species flocks recorded in one area. In this study conducted in several countries across the Andes, the remaining amount of forest at a regional level interacted with the type of habitat and microhabitat structure to shape the frequency of occurrence, richness and abundance of mixed flocks in a particular area (Zuluaga & Rodewald 2015). In general, deforestation, loss of habitat structure and conversion of high quality to poorer habitats (*e.g.*, silvopasture) resulted in the loss of some species and guilds (*e.g.*, understory specialists and insectivores) that do not exist in disturbed, less-complex habitats.

Along with the fragmentation process and habitat degradation mediated by anthropogenic causes, there is not only a biodiversity loss, but also a loss of poorly understood interactions such as those occurring in mixed-species flocks. Since mixed-species flocking is proposed as a behavior to improve the foraging efficiency and to enhance predation avoidance of their members (Miller 1922, Buskirk 1976, Morse 1977, Goldman 1980, Sridhar & Shanker 2014), the formation of mixed flocks can act as a mechanism to cope with difficult conditions (Morse 1970, Mangini & Areta 2018). Thus, MSF comprise social interactions that should not be understood as simple congregation of different species together in one place, and rather as a social interaction that allows bird species to obtain certain benefits. In this way, we do not know to what extent the loss of interactions, manifested by smaller and less diverse mixed flocks in degraded habitats will affect ecological dynamics of bird communities in mid to long-term.

Conclusion and future directions

Altogether, the presentations in this symposium demonstrate how mixed-species flocks respond to various environmental gradients in different scales. Environmental gradients affect not only general assembly patterns, such as species composition, but also network properties and species interactions within MSF. In general, MSF composition changed across the three gradients analyzed here, and structural properties of MSF (number of flocks, number of species and individuals within flocks) varied significantly across the elevational and the anthropogenic gradients. Furthermore, it was possible to detect changes in network properties of flocks across the elevational gradient, with less complex networks with fewer interspecific interactions at higher elevations. Interestingly, responses of MSF to environmental gradients were detected at different scales, suggesting flocks can be a good study system to further test ecological hypothesis.

The studies presented in this symposium represented a good overview of the current research on MSF in the Neotropics. Here we mention a number of opportunities for improvement. Studies were conducted in different environments and biomes: Yungas' foothill and montane forest, primary Andean montane Forest, Amazonian lowland Forest, and silvopasture. However, as a reflection of Wallacean shortfalls in biodiversity inventories in the Tropics, much of what we know on MSF is concentrated in certain regions, such as areas next to urban centers, populated municipalities, research institutes or environments that received more attention by their high biodiversity. Consequently, we still lack basic information on MSF in other environments such as subtropical forests, grasslands and shrublands that represent a significant amount of the geographic area in the Neotropical region.

In addition, advances in technology and computational power allowed the development of new equipment for tracking animal movements, and enabled the use of social network analysis with biological data. Population ecology explored these tools for a long time. However, only recently social network theory has been used to respond questions in MSF research through the analysis of emerging properties in MSF (see Farine 2014 and Mokross *et al.* 2014 for some examples). The method is powerful for assembling and depicting patterns of social interactions, which usually are not easy to detect or perceive. It enables inferences on the strength of those interactions, and analyses of species or individual's social functions within the group. Future investigations should consider including social network analysis in their methodological framework as a more accurate way of detecting social interactions and relationships among species. Furthermore, future studies should examine these interactions within mixed flocks and with their environment, integrating species-specific research and species-habitat relationships to disentangle the mechanisms that promote and maintain mixed flocks formations. Further experimental approaches to study the gain of benefits of joining MSF are also scarce in tropical areas and should be a fruitful arena for future research in the region. Finally, although much conservation attention is given for species as a unit, from a functional perspective, conservation efforts should be directed to preserve interactions rather than solely species, including those among birds in MSF.

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