



RESEARCH ARTICLE

# The response of mixed-species bird flocks to anthropogenic disturbance and elevational variation in southwest China

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## ABSTRACT

Avian mixed-species flocks (MSFs) are an important example of species interactions threatened by the biodiversity crisis. They are found throughout the world in forested habitats but are generally reduced in size or frequency by human disturbance. In southern China, a unique MSF system is led by several species of closely-related fulvetts (*Alcippe morrisonia*, *A. hueti*, and *A. davidi*). Our objective was to understand how this system is distributed across elevational gradients, especially moving west into the Hengduan Mountains, and how it responds to human disturbance. We sampled leadership and composition of 375 MSFs over 2 yr in and surrounding 5 nature reserves in Guangxi Zhuang Autonomous Region and Yunnan Province, with transects placed in different land use types—protected forest, buffer areas, or agriculture—and ranging from 400 to 3,200 m. We also sampled birds outside of MSFs. We found MSFs led by fulvetts (*A. fratercula* and *A. davidi*) in forests across the region up to 2,900 m. Elevation was not a significant influence on MSF size or prevalence in models that also included land use. We found that MSFs were encountered at only one-third of the frequency in agriculture as in forest, and had strongly different composition and leadership. Although MSFs in buffer areas were more similar to those in forest, birds in buffer areas had lower flocking propensity, different flock leaders, and less complex social networks. In particular, buffer transects that were seeded pine had low numbers of fulvetta-led MSFs and forest specialists in MSFs. In the future, it is important to understand which vegetational characteristics allow MSFs, particularly fulvetta-led MSFs, to persist in buffer habitats.

**Keywords:** bird conservation, community ecology, conservation biology, group living, social network, species interaction network

中国西南地区鸟类混合群对人为干扰和海拔梯度变化的响应

## 摘要

鸟类混合群广布全球，常见于森林，是研究物种间相互作用的重要案例之一，人类的干扰通常导致混合群大小及遇见率降低。有研究显示中国南部地区存在由雀鹛（包括 *Alcippe davidi*, *A. fratercula*, 和 *A. hueti*）领导的特有鸟类混合群。为了探究该特有鸟类混合群及群内领导关系如何响应海拔变化及不同程度的人为干扰，尤其是对横断山脉西侧的鸟类混合群的探究，我们采用样线法，在云南及广西两省的5个保护区内外沿不同海拔梯度（400–3200米）在森林、缓冲区及农作物种植区三种土地利用类型内对鸟类及其混合群进行了观察并记录。三年间（2015–2017年）共记录到375个鸟类混合群且在海拔2900米的森林内也发现了由雀鹛（*A. fratercula* 和 *A. davidi*）领导的混合群。结果表明：1）农作物种植区内鸟类混合群的遇见率仅为森林的三分之一，混合群的鸟种组成及领导关系也与森林内显著不同；2）缓冲区内鸟类混合群组成与森林内相似，但鸟类混合群倾向却显著低于森林，其社会关系网复杂性也显著低于森林，在缓冲区内领导混合群的主要领导种也与森林内的不同，特别是由雀鹛领导的混合群和森林特有种在人工针叶林缓冲区内鲜有记录。因此，目前对鸟类混合群（尤其是由雀鹛领导的）存在的缓冲区的植被类型及植被特征进行了解就显得尤为重要。

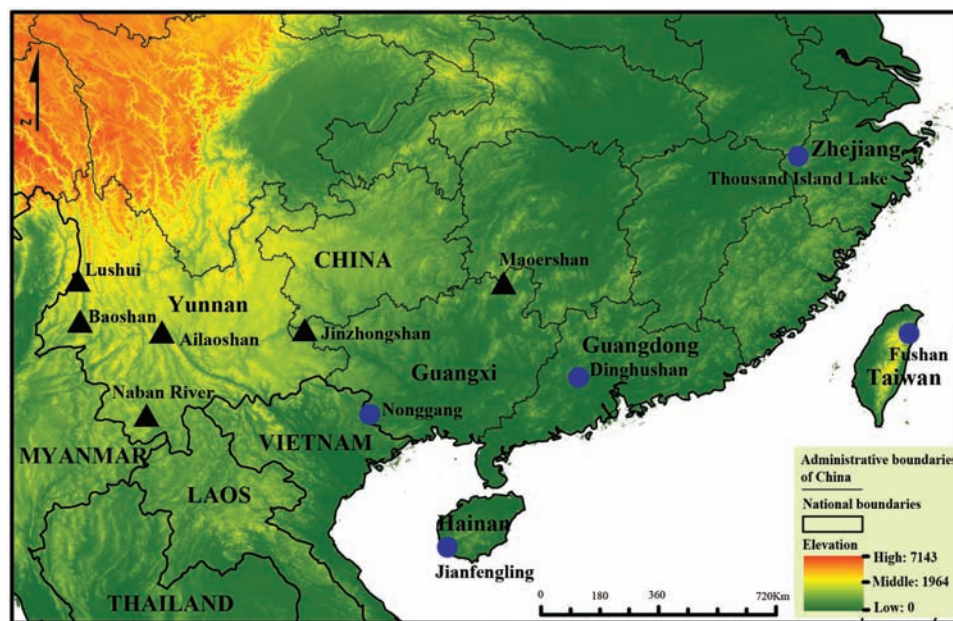
**关键词：**鸟类保护，群落生态学，保护生物学，群居生活，物种关系网

## INTRODUCTION

In the current era of biodiversity loss (Pimm et al. 2014, Ceballos et al. 2017), species interaction networks can be even more sensitive to disturbance than the species themselves, even to the point of potential coextinction of mutualists (Dunn et al. 2009, Magrath et al. 2014, Valiente-Banuet et al. 2015). An important example of species interaction networks is mixed-species animal groups (Goodale et al. 2017). In birds, forest mixed-species flocks (MSFs) are found worldwide but are particularly prevalent in tropical rainforests, where in some forests more than 50% of birds can be interacting in them at any one time (e.g., Eguchi et al. 1993, Latta and Wunderle 1996). These communities have similar rules of inclusion and organization worldwide, usually consisting of insectivorous non-terrestrial species (Thiollay 1999) and certain “nuclear” species that tend to be gregarious, active, and vocal, and are hence important for MSF initiation or cohesion (Moynihan 1962, Goodale and Beauchamp 2010, Pagani-Núñez et al. 2018). MSFs are ecologically significant because they provide benefits to their participants in increased foraging efficiency and decreased predation risk (Morse 1977, Colorado 2013), and can increase survival of their members (Jullien and Clobert 2000, Srinivasan 2019). Studies of MSF response to land use change have been conducted in limited geographic areas and land use types. A recent meta-analysis of these limited data suggested that MSFs are more sensitive to anthropogenic disturbance than the overall avifauna, through

altered predation, foraging opportunities, and species pools (Zou et al. 2018).

Here we explore how MSFs respond to anthropogenic change and elevational variation in southwest China. This is an interesting area to explore global change, as it is on the northern border of the tropics, where tropical montane species might be especially vulnerable to climate change (Pounds et al. 1999, Freeman and Freeman 2014, Sreekar et al. 2017). There have been several reports of MSF systems in southern China (Chen and Hsieh 2002, Jiang 2007, Zou et al. 2011, Zhang et al. 2013; Figure 1). In these flocks a highly gregarious fulvetta (*Alcippe* spp.) appears to be the most important nuclear species (sensu Morse 1970, Contreras and Sieving 2011). The fulvetta in these flocks represents a recently split complex of Morrison’s Fulvetta (*Alcippe morrisonia*) in Taiwan, Huet’s Fulvetta (*Alcippe hueti*) in Guangdong and Hainan, and David’s Fulvetta (*Alcippe davidi*) in Guangxi (Zou et al. 2007). It is not known how this system changes over elevational gradients, especially moving west into the Hengduan Mountains. Also, although Zhang et al. (2013) described fulvetta-led MSF dissolution in early successional lands of planted pine, how MSFs change in a wide range of human-modified land types is not well understood for the region. Lastly, it is important to ask how wide-ranging and crucial are fulvettas to MSFs. There have been some calls to target nuclear species in conservation plans (Maldonado-Coelho and Marini 2004, Zou et al. 2018), but for such a strategy to be generally effective, the nuclear species needs



**FIGURE 1.** Map of previous studies on MSFs in southern China (circles; the study in Zhejiang Province, by A. Martínez and colleagues, is unpublished), and the 5 reserves in which we sampled (triangles) in southern (Guangxi) and southwest China (Yunnan). Road construction forced us to move the location of the lower-elevation transects in the Gaoligongshan National Nature Reserve halfway through the study from the Luishui region to the Baoshan region.

to be consistently important to MSFs across a wide area. Yet most MSF studies in Asia tend to be conducted at one or a few closely situated sites, and not widely spaced across environmental gradients (but see [Sridhar and Sankar 2008](#), [Goodale et al. 2014](#)).

To address these questions, we surveyed birds, both inside and outside MSFs, along an elevational gradient rising gradually from east (Guangxi Zhuang Autonomous Region, technically in southern China) to west (Yunnan Province in southwest China), in 5 National Nature Reserves. In each reserve we sampled from relatively undisturbed protected forest inside the reserve, buffer habitats of degraded natural forests or agroforests near the reserve border, and agriculture surrounding the reserve. Across elevations and land use, we analyzed the following MSF metrics: flock leadership, species richness, numbers of individuals, encounter rate, propensity (the percentage of individuals in MSFs), and social networks.

## METHODS

### Study Sites

Four of the reserves sampled in this study were in the latitudinal range between 24° and 26°, from east to west: Maoershan National Nature Reserve (25°48'N, 110°20'E; transects between 400 and 2,100 m elevation), Jinzhongshan National Nature Reserve (24°04'N, 104°46'E; transects between 900 and 1,700 m), Ailaoshan National Nature Reserve (24°31'N, 101°01'E; transects between 1,400 and 2,500 m), Gaoligongshan National Nature Reserve (25°56.799'N, 98°44.962'E; transects between 1,000 and 3,200 m; [Figure 1](#), [Supplementary Material Table S1](#)). These reserve forests are mostly subtropical, becoming temperate above ~2,500 m ([Zhu 2016](#)). Composition and structure of natural forests change with elevation from broadleaf evergreen forests to forests incorporating some fir (*Abies* spp.) above 2,900 m. In addition, we also worked in tropical forest ([Zhang and Cao 1995](#)) at a more southern site in Yunnan, Naban River Watershed National Nature Reserve (22°04'N, 100°32'E; transects between 900 and 1,700 m). All of these sites had a similar pattern of greater human disturbance at lower elevations.

In these 5 reserves we placed 1 km transects in 3 different land use types ([Figure 2](#)). Twenty transects were placed in relatively undisturbed forest inside protected reserves, 17 transects in buffer zone of agroforest or degraded natural forest at the border of reserves, and 15 transects in areas of intensive agriculture ([Supplementary Material Table S1](#); see [Figure 2](#) for some representative photographs of the different land uses). Undisturbed forests were primary forests, sometimes with disturbance created by making a road (see below). Degraded natural forests were either secondary forests or those affected by non-systematic removal of valuable trees. In comparison, agroforests were

seeded *Pinus* spp. Agricultural crops consisted primarily of maize and wheat.

As transects, we chose preexisting paths or roads that were relatively straight and located at a homogeneous elevation. Because of the inaccessibility of some of the forests, in 38% of the transects (20 of 52) we were forced to use lightly traveled tar roads (in particular, there was greater use of such roads in Gaoligongshan Reserve, which may have affected our sampling of forest there, making those forest transects more disturbed). We attempted to place a transect for every 200 m of elevation change, >1 km away from each other. The transects in Gaoligongshan National Nature Reserve were first located in the Lushui region, but in November 2016 road construction forced us to relocate most of the low-elevation transects to a different part of the reserve, closer to Baoshan ([Figure 1](#)); the elevation and forest structure of the Baoshan transects were quite similar to those that they replaced.

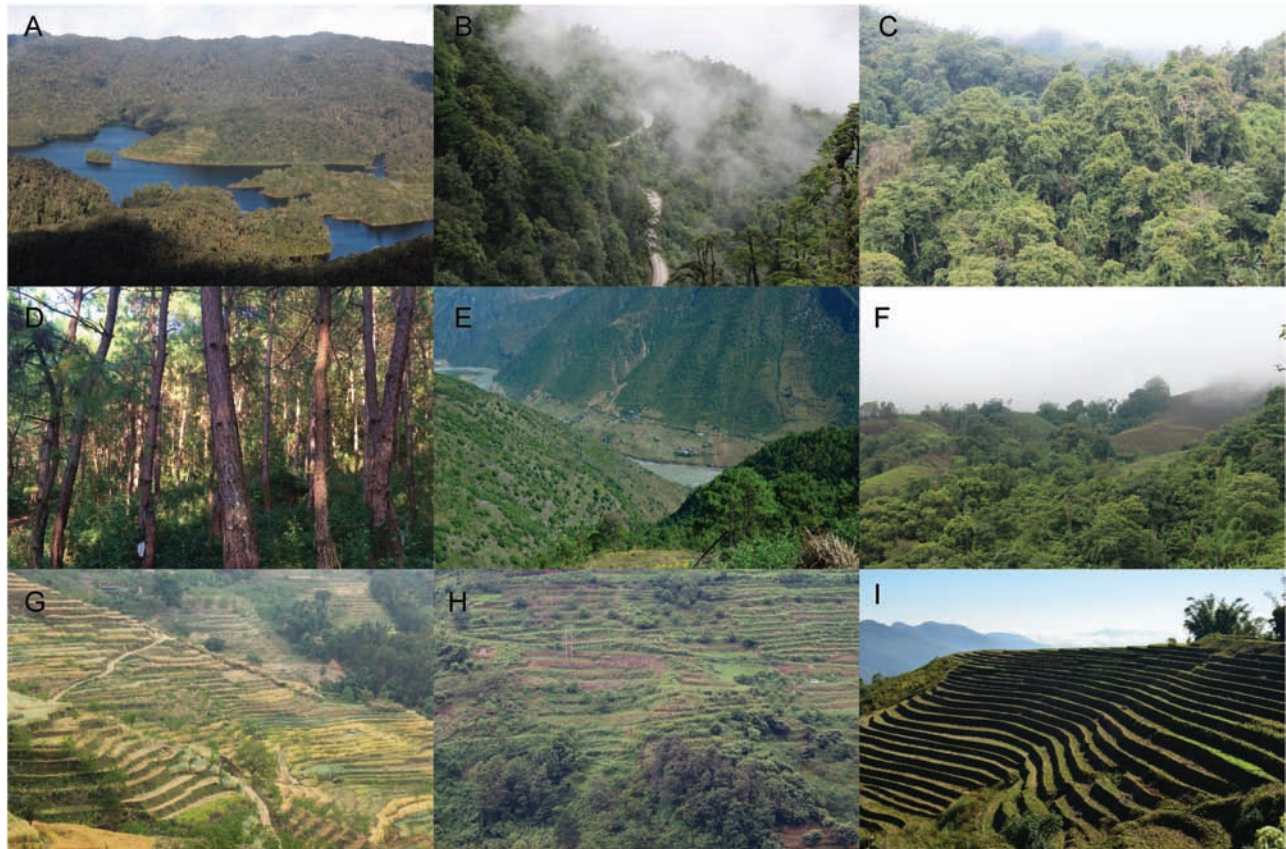
### Sampling

We visited these transects, working in 2 teams: (1) The XTBG team, consisting of L.Z., the bird observer, sometimes assisted by a field assistant who took notes, and (2) the GXU (Guangxi University) team, consisting of I.P., the bird observer, and either D.J. (who helped I.P. identify birds at the beginning of the sampling work) or H.G. (toward the end of the work) taking notes. Both teams visited Ailaoshan and Gaoligongshan, working on the same transects, which allows for the evaluation of observer effects. The XTBG team completed the survey of Naban River by itself, and the GXU team completed the survey of Maoershan and Jinzhongshan by itself; in Gaoligongshan, the relocated transects were only visited by the XTBG team. All observers had at least 3 months' experience with bird identification upon starting the fieldwork, and we all worked together at the beginning of the project to standardize data collection protocol.

For each of the 5 reserves, we ensured that most transects were visited 3 times in the nonbreeding season (August through March), between October 2015 and January 2017 (for Gaoligongshan, each pair of original transect and replacement transect, considered together, was visited 3 times). The majority of our observations (83% of transect walks) were from the start of October through the end of January. On each visit, the transect was walked twice, once in the morning (between 0730 hours and 1100 hours), and once in the afternoon (between 1500 hours and 1800 hours) on a different day, and hence most transects were walked 6 times. We avoided working in a constant rain, although misty conditions were unavoidable.

On a visit to the transect, the observers walked the transect at a slow pace (~1.5 hr for 1 km). All birds seen or heard (except for flyovers and raptors) within 50 m were noted. Birds were recorded as inside or outside of a MSF, where





**FIGURE 2.** Representative photographs of the different land uses. Top panels (**A, B, C**) are forest in the reserves in Yunnan Province: Ailaoshan, Gaoligongshan, and Naban River, respectively. Middle panels (**D, E, F**) are buffer habitats, and bottom panels (**G, H, I**) are agriculture on the border of the same 3 reserves and surrounding them. Land use types in Guangxi were similar. Photographs by Liping Zhou.

a MSF was defined as >2 bird species moving in the same direction for at least 5 min (Goodale et al. 2009). When a MSF was encountered, it was observed for >5 min, but not more than 15 min (as we wanted to continue walking the transect). Bird taxonomy follows the Clements checklist (<http://www.birds.cornell.edu/clementschecklist/>).

We used a fixed radius approach for the analyses in this study because we were primarily interested in MSFs, in which most of the participants are seen together and thus different detectabilities do not highly confound results. We avoided detectability adjustments of different species outside of MSFs because the diversity of land types, elevations, and species meant that we had very few species with large sample sizes from similar transects. We used out-of-flock data in calculations of propensity, following Thiollay (1999), but propensity is correlated with MSF encounter rate (the number of MSFs per km,  $r = 0.73$ ) and the findings for the 2 variables were similar.

#### Leadership Data

We took 2 types of leadership data: (1) at the whole MSF level and (2) at the level of individual birds within the

MSF. For the whole MSF level data, we observed whether one species consistently led the MSF over openings or comprised the majority of the individuals on the front edge of the MSF during the entire observation; if we could not identify one such species, no leader was identified. To compare this method to previously published techniques, we also gathered individual-level leadership data, similar to the method of Morse (1970:126). In this approach, we recorded the species identity of 2 birds that were noticed to directly follow each other (specifically, we required the follower to move within 5 s at least 3 m in the same direction as the leader, although these 2 birds were not necessarily at the very front of the MSF). We then tallied what percent of the individuals of each species was seen in the leadership position, and what percent was seen in the following position. When fieldwork focused on collecting this individual-level leadership data only, we followed large MSFs up to 35 min to try to get data from different individuals. Leadership data were taken between September 2016 and December 2017, again in the nonbreeding season, and only at Ailaoshan and Gaoligongshan.

We defined as forest specialists those species described as exclusive to forest in *Handbook of the Birds of the World* ([www.hbw.com](http://www.hbw.com)).

### Statistical Analysis

**Generalized linear mixed models focused on land use and elevation.** The first step of our analysis was to compare observer teams, contrasting observations of the GXU team to that of the XTBG team at any transect where they both collected information (at Ailaoshan and Gaoligongshan). We determined with generalized linear mixed models (GLMMs), implemented in the R program (R Core Team 2017) library lme4 (Bates et al. 2017), whether 4 response variables (species richness, number of individuals per MSF, encounter rate [MSFs per transect visit], and propensity) differed due to observer team (the fixed factor) and the random factor of transect, nested in reserve ( $n = 2$ ). For species richness, number of individuals, and encounter rate (multiplied by 100 to be an integer), we used a Poisson distribution, and for propensity we used a binomial distribution on the matrix of individuals in MSFs and those out of MSFs. The 2 teams showed significant ( $\alpha = 0.05$  here and hereafter) differences in the size and encounter rate of MSFs, although not flocking propensity (Supplementary Material Table S2). These differences may have been because of some seasonal variation in when they visited the transects (e.g., differences between September and November) or some differences in observation technique (that one team saw larger, but fewer, MSFs suggests that they spent on average somewhat more time per MSF before considering the observation complete). To incorporate observer team differences in the rest of the analysis, we developed a set of mixed models that separated data collected in the same reserve by the 2 teams, hence concentrating on within-team variation caused by land use and elevation.

The general goal of our analysis was to understand how MSFs responded to land use type and elevation. GLMMs were conducted with the lme4 package as above, to investigate how the 4 response variables (each analyzed in a separate model) were affected by land use type, elevation, and the interaction between land use type and elevation (all fixed factors); transect nested in replicate ( $n = 7$ ; 5 reserves, including 2 visited by both teams) was added as the random factor. We progressively simplified models by removing interaction terms that were not significant (when judged from ANOVA tables), and then variables that were not significant. If we encountered overdispersion in the GLMMs, we added an individual-level random effect (Bolker 2018). We then repeated these analyses for the number of species and the number of individuals of forest specialist species in MSFs. Finally, because the sampling effort in Maoershan, Jingzhingshan, and Naban River was less than that for Ailaoshan and Gaoligongshan, and only conducted by one team, we did a further analysis that only

looked at MSFs in Ailaoshan and Gaoligongshan on transects where both teams collected data. In these GLMMs, again we included transects nested in replicate ( $n = 4$ ; 2 reserves conducted by 2 teams).

To investigate the composition of MSFs we conducted non-metric multidimensional scaling (NMDS) using the R package vegan (Oksanen et al. 2017). A first NMDS compared the different land types in the 5 different reserves; each data point represented the total number of individuals of different species seen in MSFs of a transect (i.e. an abundance matrix). A second NMDS compared the composition of MSFs led by different leaders (judged from the whole MSF level leadership data), again using the numbers of individuals of the different species, this time per MSF. To see whether visual patterns were statistically significant, we subjected NMDS scores to ANOVA and subsequent Tukey Honest Significant Difference (HSD) multiple comparison tests.

**Network analysis.** Our objective in the network analysis was to see if changes in MSFs due to land use or elevation might be more complex and nuanced than simply MSF size or encounter rate, and affect the interactions of species (Mokross et al. 2014). Due to the general lack of influence of elevation as a factor in other analyses (see Results), and because network analysis requires many co-occurrence data points, we pooled MSF observations among land use types within a reserve to make one network. However, we kept observations from different teams separate, and hence for Ailaoshan and Gaoligongshan there was the potential for 2 networks per land use type. We then used the asnipe package in R (Farine 2013) to construct the networks, as long as there were at least 4 MSFs recorded (Mammides et al. 2018), a process that resulted in 17 networks in total.

Following Mokross et al. (2014) and Kay et al. (2018), we calculated for each network the following 5 metrics: (1) mean normalized degree, an estimate of the average connectedness of the species in the network; (2) mean weighted degree, another measure of connectedness that incorporates the strength of associations between species; (3) skewness of the distribution of normalized degree across all the different species in the network; (4) global clustering coefficient, a measurement of the extent to which species tend to cluster together; and (5) modularity, a measurement of the number of subgroups and how exclusively they interact with each other (for more detail, see Supplementary Materials: Methods).

As before, we used linear mixed models (with replicate as a random factor,  $n = 7$ ) and Tukey HSD post hoc tests to assess whether the 5 network metrics differed between the 3 land use types. We log-transformed clustering to avoid violating the assumption of normality. In addition, to assess whether the patterns we observed were not due to non-social factors that affect co-occurrences (Farine 2017), we randomized each network 999 times (using the asnipe package; Farine 2013), and recalculated each time the land use types' pairwise post hoc coefficients for each network



metric (hereafter referred to as the “permutation analysis”). We then used the results to calculate the probability that the observed coefficients differed from what would be expected at random (Farine 2017). We considered a coefficient to be statistically significant if it was either smaller than the 0.025 quantile or larger than the 0.975 quantile of the corresponding permuted values (Farine 2017).

**Leadership analysis.** The analysis of leadership is generally qualitative in identifying which species were leaders in different land use types. However, we made comparisons between the 2 methods of leadership by comparing their results for different species. We calculated a ratio of the times a species was identified as a leader to the total times it was recorded in the dataset for both methods. Then species’ scores for the 2 methods were compared with Spearman correlations (as the data were not normal) for the different land use types separately.

## RESULTS

### Land Use and Elevation

We encountered 375 MSFs over the sampling period, recording 311 species (including 4 unidentified species) and collecting 18,849 individual detections of birds (Appendix 1 in Supplementary Materials). Of this total, 75 species were classified as forest specialists.

Species richness of MSFs was overall quite low, although there were many individuals (species richness:  $4.2 \pm 2.4$  SD, individuals:  $20.2 \pm 17.0$ ). Species richness of MSFs was marginally higher in forests than in agriculture ( $1.2\times$ ), but there were no differences between land use types in number of individuals (Figure 3A, B; Table 1). Elevation was never significant in a model that also included land use (Table 1).

In contrast, propensity and encounter rate were strongly affected by land use type (Figure 3C, D). Propensities in forest were higher than agriculture ( $3.6\times$ ; i.e. a larger percentage of individuals was in flocks) and propensities in buffer were also higher than agriculture ( $2.5\times$ ). Forest also had higher propensities than buffer ( $1.5\times$ ). Encounter rate showed similar results, with encounter rate in forest higher than agriculture ( $3.1\times$ ) and buffer higher than agriculture ( $2.1\times$ ), although the comparison between forest and buffer was nonsignificant.

When we focused solely on forest specialist species in MSFs, land use type and elevation showed a significant interaction (Supplementary Material Table S3). At middle (1,300–1,700 m) or higher (1,800–3,200 m) elevations, the number of forest specialist species gradually rose from agriculture to forest, but at lower elevations buffer had the highest number of forest specialists (and this result also occurred for the number of individuals of forest specialists in middle elevations). Nevertheless, as in the other models, land use was more significant than elevation.

Results were similar when analyzed for the heavily sampled reserves (Ailaoshan and Gaoligongshan) only, with land use being more important than elevation in all cases. The exact results showed some differences with the main analysis described above (Supplementary Material Results; Tables S4 and S5; Figure S1). In particular, land use significantly affected the number of individuals per MSF, as well as species richness. Also, there was no interaction between land use and elevation for the forest specialist result; rather, MSFs in forest had significantly higher numbers of forest specialist species and individuals than MSFs in buffer or agriculture (Supplementary Material Results; Table S4).

In the NMDS of MSF composition, both land use and elevation changed dramatically across axis one, and did not clearly vary on axis two (Supplementary Material Figure S2). Buffer transects were particularly widely distributed across the NMDS space.

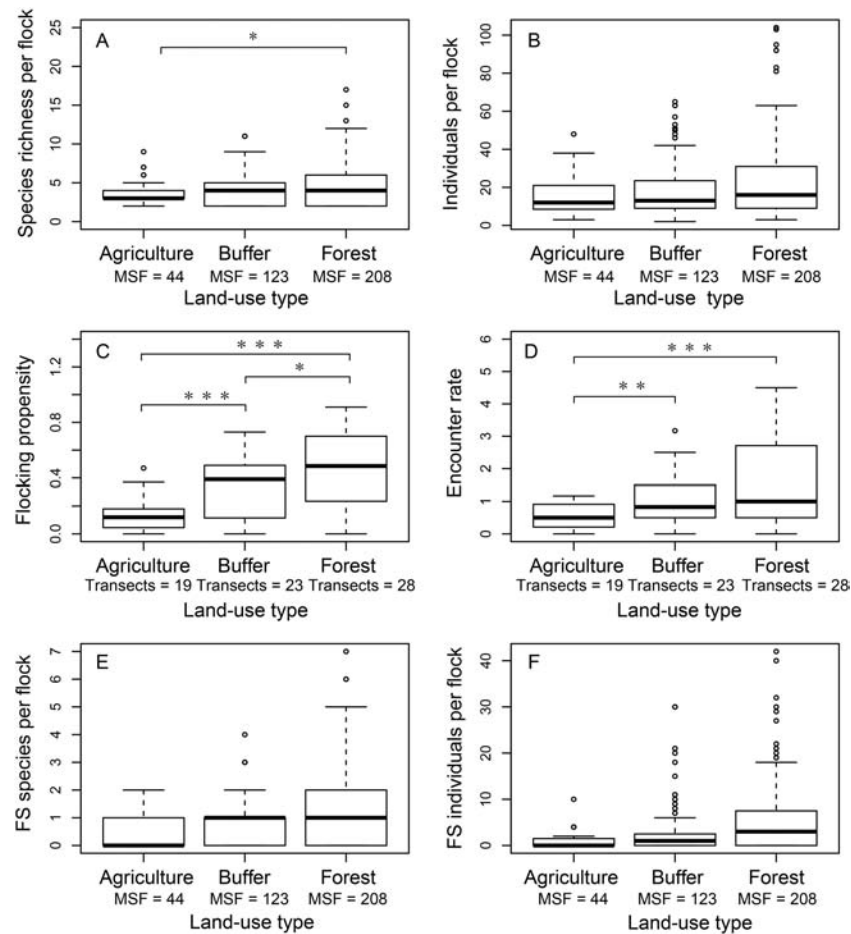
### Network Analysis

Our results showed only a few differences between land use types in the characteristics of social networks (Figure 4 and Supplementary Material Table S6). The mean normalized degree (i.e. the average number of connections between species) was higher in forest than in agriculture ( $P = 0.001$ ) and marginally higher in forest than in buffer ( $P = 0.06$ ). Contrastingly, clustering was higher in agriculture than in buffer ( $P = 0.04$ ) and marginally higher in agriculture than in forest ( $P = 0.06$ ). The results of the permutations (Supplementary Material Table S6) confirmed that these patterns were due to social factors and not due to other factors that affect co-occurrences (Farine 2017).

### Leadership Analysis

At the whole MSF level, we observed leadership for 218 MSFs (142 Ailaoshan, 76 Gaoligongshan), but in only 116 were we able to define one species as the leader. At the individual level, we took 597 observations (321 Ailaoshan, 276 Gaoligongshan).

Yunnan Fulvetta (*Alcippe fratercula*; in Guangxi, flocks were led by *A. davidi*, but we had no systematic leadership data from there) was the most frequent leader in forest and among the most frequent leaders in buffer, but was not present in agriculture (Table 2). Yunnan Fulvetta was not always a leader, however: it was found in 10 MSFs led by another species, and in 14 additional MSFs in which we were unable to designate a clear leader. Other gregarious species, including the Chestnut-tailed Minla (*Actinodura strigula*) and the Black-faced Warbler (*Abroscopus schisticeps*), also led MSFs fairly frequently in forests, particularly in Ailaoshan. There were 3 species that led MSFs in disturbed areas: Blue-winged Minla (*Actinodura cyanouroptera*), Black-throated Tit (*Aegithalos concinnus*), and Japanese White-eye (*Zosterops japonicus*) collectively led a total of 24 MSFs in buffer and agricultural land use types (Table 2).



**FIGURE 3.** The effects of land use type on MSF metrics and composition. (A) MSF species richness, (B) numbers of individuals, (C) flock propensity (% of individuals in MSFs), (D) MSF encounter rate, (E) number of forest specialist [FS] species in MSF, (F) number of FS individuals. Boxplots show the median value (middle line), the 25th and 75th percentile (bottom and top of the box), with whiskers representing approximately 5% and 95% percentiles, and circles any outlying points. Statistical significance: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ ,  $P < 0.10$ . Statistics are not shown for panels (E) and (F) because of the presence of an interaction with elevation. Sample sizes are shown below each column.

The NMDS of leadership shows that the composition of the MSFs led by Yunnan Fulvetta, Chestnut-tailed Minla, and Black-faced Warbler were considerably different than MSFs led by Blue-winged Minla, Black-throated Tit, and Japanese White-eye (Figure 5). NMDS scores on axis one were significantly higher for the 3 forest-dwelling leaders than for the 3 leaders in disturbed land use types (Tukey HSD, all  $P$ -values  $< 0.001$ ). However, the composition of Yunnan Fulvetta-led MSFs was generally similar to those led by the other forest leaders (Chestnut-tailed Minla and Black-faced Warbler).

The correlation between the whole MSF level observations and the individual level observations was weak in agriculture ( $r = 0.11$ ,  $P = 0.81$ ,  $n = 7$  species), buffer ( $r = 0.24$ ,  $P = 0.30$ ,  $n = 20$  species), and forest ( $r = 0.16$ ,  $P = 0.43$ ,  $n = 27$  species). However, the top of the list of leading species was similar. Yunnan Fulvetta, Black-throated Tit, Chestnut-tailed Minla, and Blue-winged Minla were the 4

species seen to lead most MSFs in both datasets. The individual leadership table (Supplementary Material Table S7) is also interesting because it identifies some species that usually follow MSFs: for example, White-tailed Nuthatch (*Sitta himalayensis*, 17 observations, 0 leading), Black-headed Sibia (*Heterophasia desgodinsi*, 9 observations, 0 leading), and 2 fly-catching species, the Grey-headed Canary Flycatcher (*Culicicapa ceylonensis*, 8 observations, 0 leading) and White-throated Fantail (*Rhipidura albicollis*, 15 observations, 2 leading).

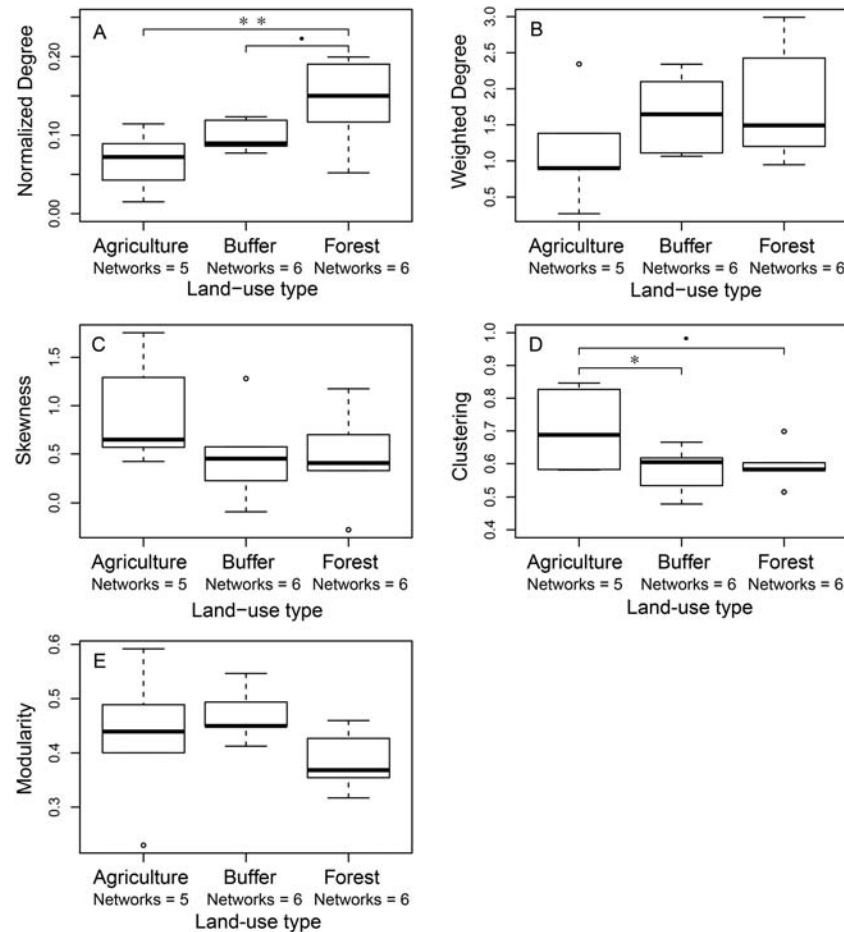
## DISCUSSION

The MSFs that we describe here are similar to a system that has been described before in southern China (Chen and Hsieh 2002, Jiang 2007, Zou et al. 2011, Zhang et al. 2013), in having fairly low diversity of species per flock, but high numbers of individuals. This is due to the presence

**TABLE 1.** Results of the main analyses in Figure 3. These data include MSF in all of the nature reserves ( $n = 7$  replicates in 5 reserves, considering 2 different observation groups). All models included 2 variables (elevation and land use) and an interaction term, and were sequentially simplified, removing nonsignificant (according to the ANOVA table) interactions and variables. Sample sizes, generalized linear mixed model distributions, and model fit ( $R^2$ , following Nakagawa and Schielzeth 2013) shown for each model. <sup>a</sup>An overdispersed model, for which we did corrections (see methods).

Response	Model	Family	$R^2_m$	$R^2_c$	Factor	$\chi^2$	df	$P$	Comparison	$Z$	$P$
Species richness	Full model	Poisson	0.03	0.14	Elevation	0.16	1	0.69			
					Land use	4.14	2	0.13			
	Minus Interaction	Poisson	0.02	0.15	Land use: Elevation	4.36	2	0.11			
Number of individuals	Land use only	Poisson	0.02	0.14	Elevation	0.08	1	0.78			
					Land use	3.34	2	0.19			
	Full model <sup>a</sup>	Poisson	0.03	0.23	Land use: Elevation	4.57	2	0.1	B vs. A F vs. A F vs. B	1.09 2.03 1.21	0.28 0.04 0.23
Propensity	Land use only <sup>a</sup>	Poisson	0.009	0.22	Elevation	0.33	1	0.56			
					Land use	2.29	2	0.32			
	Full model	Binomial	0.16	0.27	Land use: Elevation	4.67	2	0.1			
Encounter rate	Land use only	Binomial	0.15	0.23	Elevation	0.26	1	0.61			
					Land use	1.98	2	0.37			
	Full model	Binomial	0.16	0.25	Land use: Elevation	1.97	2	0.37			
Forest specialist (sp)	Land use only	Poisson	0.18	0.44	Elevation	1.26	1	0.26			
					Land use	28.51	2	<0.001			
	Full model	Poisson	0.18	0.45	Land use: Elevation	1.03	2	0.6			
Forest specialist (ni)	Land use only	Poisson	0.16	0.41	Elevation	1.25	1	0.26			
					Land use	28.22	2	<0.001			
	Full model	Poisson	0.16	0.41	Land use: Elevation	35.07	2	<0.001	B vs. A F vs. A F vs. B	3.64 5.92 2.29	<0.001 <0.001 0.02
Forest specialist (sp)	Land use only	Poisson	0.16	0.41	Elevation	1.05	1	0.3			
					Land use	15.03	2	<0.001			
	Full model	Poisson	0.18	0.44	Land use: Elevation	0.31	2	0.86			
Forest specialist (ni)	Land use only	Poisson	0.16	0.41	Elevation	1.05	1	0.3			
					Land use	15.00	2	<0.001			
	Full model	Poisson	0.16	0.41	Land use: Elevation	17.16	2	<0.001	B vs. A F vs. A F vs. B	2.69 4.13 1.43	0.007 <0.001 0.15
Forest specialist (sp)	Land use only	Poisson	0.16	0.41	Elevation	3.16	1	0.08			
					Land use	16.76	2	<0.001			
	Full model	Poisson	0.16	0.41	Land use: Elevation	8.71	2	0.01			
Forest specialist (ni)	Land use only	Poisson	0.16	0.41	Elevation	10.64	1	0.001			
					Land use	15.27	2	<0.001			
	Full model	Poisson	0.16	0.41	Land use: Elevation	12.43	2	0.002			





**FIGURE 4.** The effects of land use type on MSF networks. (A) Mean normalized degree, (B) mean weighted degree, (C) skewness, (D) clustering, (E) modularity. For a description of the boxplot attributes and statistical abbreviations, see Figure 2.

of several gregarious species, especially the fulvetta leader. We extend the known range of this system by more than 1,000 km to the west of the most western previous report (Jiang 2007), into the edge of the Hengduan Mountains and up to an elevation of 2,900 m (the highest previous report, that of Zou et al. 2011, was at 1,100 m). While there is strong genetic variation within this leading superspecies complex (Zou et al. 2007), the behavior of the northeast Guangxi birds (*Alcippe davidi*) and western Yunnan birds (*A. fratercula*) was quite similar in the field, and the superspecies leads MSFs across our study area. The number of species in this system ranges from 5.8 species (Chen and Hsieh 2002) and 6.0 species (Jiang 2007) in the most southern sites, to 2.5 species in Zhejiang (an unpublished study by A. Martínez and colleagues, far to the northeast of other sampling points; see Figure 1). The high number of individuals per MSF has been seen previously as a characteristic of MSFs in Asia (Goodale et al. 2009, 2015), at least compared to the Neotropics, in which there are often only a few individuals of each species per MSF (Powell 1985). The large distribution of the system places

it among a few systems worldwide that is widespread, including an Amazonian system (Munn and Terborgh 1979, Martínez and Gomez 2013), and parid-led systems that are widespread in the Holarctic (Morse 1970, 1973; Lee and Jabłoński 2006).

We show that this fulvetta-led system breaks down in agricultural lands. While changes in the average size of MSFs are relatively minor in agriculture compared to the other land uses, there is a steep decline in the encounter rate of MSFs and flocking propensity. Some previous studies have also shown a collapse in the density of MSFs in human-degraded areas (Sridhar and Sankar 2008) and particularly those including intense agriculture (Goodale et al. 2014). The dramatic difference between forest and agriculture is not unexpected because of the obvious differences in vegetation structure between these land use types. Vegetation structure modifies predation risk and predation risk is a major driver for mixed-species flocking (Terborgh 1990, Zou et al. 2018).

MSFs in buffer were more similar to those in forest, but not equivalent to them. There was a substantial difference

in propensity between buffer and forest, and the number of connections per species in social networks (mean normalized degree) was higher in forest than in buffer, although this difference was only marginally significant, and was not seen when the analysis was weighted for the number of co-occurrences for each species pair (mean weighted degree). In addition, at middle and high elevations (above 1,400 m), forest specialists were more abundant in forest MSFs than in buffer MSFs (as shown by the Ailaoshan and Gaoligongshan subanalysis). In these elevations, buffer transects primarily consisted of seeded pine, which did not have many forest specialists. At lower elevations in Guangxi and Naban River, buffer transects were more complicated mixtures of plantations and degraded forest, and had a similar number of forest specialists in MSFs as forests. This heterogeneity of buffer transects probably explains why they are so widely distributed in the NMDS of MSF composition (Supplementary Material Figure S2).

Leadership also changes in anthropogenically disturbed areas. Buffer forest had specific leaders, such as Blue-winged Minla and Black-throated Tit, that infrequently led in forest. The primary leader of forest MSFs, Yunnan Fulvetta, was rare in buffer. The 4 MSFs that this species led in buffer (Table 2) were all on one transect of degraded broadleaf forest in Ailaoshan. Seeded pine forest appears to be poor habitat for such fulvetta-led MSFs. In agricultural areas, Yunnan or David's fulvettas were absent, and loose MSFs were led by Japanese White-eyes. Social network analysis showed that MSFs in agriculture had high clustering, which indicates that a small number of species repeatedly interacted together. These results are similar to the findings of Zhang et al. (2013), who showed breakdown of a fulvetta-led system and replacement by white-eyed MSFs in early successional pine forest in Guangdong. Thus, such shifts in MSF frequency and composition due to anthropogenic disturbance can be found in a variety of land use types over the wide range of this MSF system.

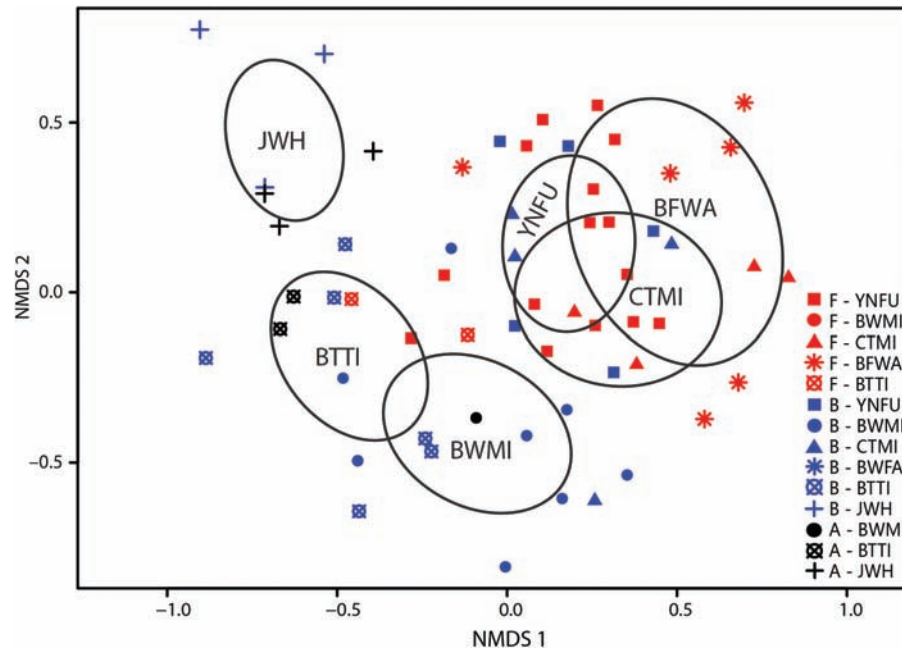
This system appears to be more threatened by land use change than climate change, since elevation plays a less important role in influencing MSF metrics and composition compared to land use. Indeed, flocks led by David's or Yunnan fulvetta could be seen from 900 m (the start of forest in Maoershan) to 2,900 m. MSFs did change dramatically over 3,000 m in Gaoligongshan, our highest-elevation site, as the forest begins to give way to bamboo thickets with a very different structure. This could provide an obstacle for the MSF system in responding to global warming (if the bamboo does not also shift upwards; its distribution may be defined by ridge microclimates).

A general description of the fulvetta-led system is hampered by limitations of our data. Overall MSF size and density differed between observers due to some combination of observer effects and seasonal variation. However,

**TABLE 2.** Leadership at the whole MSF level by land use types. Using the whole MSF level leadership data, for each species in each land use type, we show 3 values: the number of times the species was clearly leading the MSF, the number of times it was present in a MSF that another species led (ASL), and the number of times it was present in a MSF for which there was not a clear leader (NCL). Data from Ailaoshan and Gaoligongshan only. We show only species that led MSF more than 3 times in a land use type.

Forest	Buffer				Agriculture			
	Species	Leader	ASL	NCL	Species	Leader	ASL	NCL
Yunnan Fulvetta ( <i>Alcippe fratercula</i> )		15	6	10	Japanese White-eye ( <i>Zosterops japonicus</i> )	9	4	1
Black-faced Warbler ( <i>Abroscopus schisticeps</i> ) <sup>a</sup>		6	8	18	6 other species	6	4	2
Chestnut-tailed Minla ( <i>Actinodura strigula</i> )		4	8	14	Yunnan Fulvetta ( <i>Alcippe fratercula</i> ) <sup>a</sup>	4	4	4
Rufous-capped Babbler ( <i>Cyanoderma ruficeps</i> )		4	5	3	Chestnut-tailed Minla ( <i>Actinodura strigula</i> ) <sup>a</sup>	4	4	2
Whiskered Yuhina ( <i>Yuhina flavicollis</i> )		3	1	6	14 other species	17	NA	NA
Yellow-browed Warbler ( <i>Phylloscopus inornatus</i> )		3	5	2	Total	40	NA	NA
Rufous-winged Fulvetta ( <i>Schoeniparus castaneiceps</i> ) <sup>a</sup>		3	6	8				
Stripe-throated Yuhina ( <i>Yuhina gularis</i> )		3	4	7				
19 other species		23	NA	NA				
Total		64	NA	NA				

<sup>a</sup>These species were only seen leading in this land use at Ailaoshan, which represents approximately two-thirds of the dataset. Differences between Ailaoshan and Gaoligongshan were probably because the transects in Ailaoshan were somewhat less disturbed, and MSFs there were easier to follow.



**FIGURE 5.** Non-metric multidimensional scaling of MSFs led by different species in Ailaoshan and Gaoligongshan Nature Reserves. Each point is a different MSF that was led by one of the species; with the symbols representing the different leading species (BFWA = Black-faced Warbler, BTTI = Black-throated Tit, CTMI = Chestnut-tailed Minla, BWMI = Blue-winged Minla, YNFU = Yunnan Fulvetta, JWH = Japanese White-eye). Colors represent land use types: red MSFs were on forest transects, blue on buffer transects, and black in agriculture. Ellipses represent one standard deviation from the centroid of each MSF type, defined by its leader.

we treated the data from these 2 observer groups in the same reserve separately, so that each dataset was incorporated as a different level of the random factor in the mixed models, and hence we were able to focus on the within-team variation that could be explained by the fixed factors of land use and elevation. We were not able to systematically study seasonal changes because surveying >50 transects did not allow us to visit transects as often as would be optimal. Seasonal changes included the participation of migratory species; however, because leading species (e.g., those species in Figure 4) were generally nonmigratory, we think migrants may not have influenced strongly the structure of the MSF communities.

MSF communities are also naturally complex. There appear to be some other, less widespread MSF systems in the area in addition to the fulvetta-led one. For example, between 2,300 and 2,900 m in Gaoligongshan, we found systems that were primarily composed of *Phylloscopus* spp. warblers. Multiple types of MSFs have been described on the southern border of the Himalayas, in Arunachal Pradesh (Srinivasan et al. 2012), and we expect more detailed studies to reveal such MSF types, especially across altitudinal gradients in Yunnan. Even within the dominant system, the central role of the Yunnan/David's Fulvetta is actually not black and white. Some MSFs can form when these fulvettas are not present, and some flocks with fulvettas are not led by them (Table 2). Further variation in leadership is shown by the individual-level leadership data,

where even species that generally follow MSFs, like the White-throated Fantail, occasionally lead (Supplementary Material Table S7). An open question is whether the different potential leaders give different benefits to the species that follow them.

In conclusion, our results mean that the benefits of flocking in terms of predator avoidance and potential foraging efficiency, which have been shown to affect participants' body condition and fitness (Dolby and Grubb 1998, Jullien and Clobert 2000, Srinivasan 2019), are not accruable for most birds in agriculture, and may change in buffer land use types, depending on the attributes of the leading species there. While our study indicates that seeded pine appears to be a poor habitat for fulvetta-led MSFs, further research, especially that on MSF movement (Mokross et al. 2018), would be useful to test exactly what vegetative aspects are required to keep MSFs, and particularly fulvetta-led MSFs, in buffer areas. We also hope more research will be done on the composition and leadership of MSFs to the south (southwestern Yunnan, Laos) and north (Sichuan) to understand how widely this fulvetta-led system is distributed.

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**Author contributions:** EG, RCQ, AJ, and MZ conceived the study and sought funding for it. The sampling procedure was designed by all authors. The data collection was spearheaded by LZ in Yunnan and, in Guangxi, by IP working with HG and DJ. Data analysis was primarily conducted by LZ, guided by EG, with CM overseeing the network component. The first draft of the paper was written by LZ and EG, and all authors contributed to subsequent drafts.

**Data depository:** Data on flock composition and flock propensity and encounter rate is available from [Zhou et al. \(2019\)](#).

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