



REVIEW

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# The structure of mixed-species bird flocks, and their response to anthropogenic disturbance, with special reference to East Asia

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## Abstract

Mixed-species flocks of birds are distributed world-wide and can be especially dominant in temperate forests during the non-breeding season and in tropical rainforests year-round. We review from a community ecology perspective what is known about the structure and organization of flocks, emphasizing that flocking species tend to be those particularly vulnerable to predation, and flocks tend to be led by species that are able to act as sources of information about predators for other species. Studies on how flocks respond to fragmentation and land-use intensification continue to accumulate, but the question of whether the flock phenomenon makes species more vulnerable to anthropogenic change remains unclear. We review the literature on flocks in East Asia and demonstrate there is a good foundation of knowledge on which to build. We then outline potentially fruitful future directions, focusing on studies that can investigate how dependent species are on each other in flocks, and how such interdependencies might affect avian habitat selection in the different types of human-modified environments of this region.

**Keywords:** Biodiversity crisis, Biological networks, Community assembly, Competition, Interspecific communication, Keystone species, Mutualism, Predation

## Introduction

Mixed-species flocking of birds (hereafter referred to as “flocking”) is a well-studied, broadly distributed biological phenomenon. It occurs in many different kinds of ecosystems, including pelagic, wetland, and grassland systems, and in many different groups of birds including waterfowl, wading birds, and granivores (see review of Harrison and Whitehouse 2011). Most research, however, has concentrated on flocks in forested systems, for which there are flock descriptions from all continents other than Antarctica (Fig. 1; see review by Powell 1985; and meta-analysis by Sridhar et al. 2009), and such forest flocks will be the focus of this review. Mixed-species flocks must be distinguished from assemblages that gather at a localized resource in that they are always moving (Powell 1985), and most species involved in forest flocks

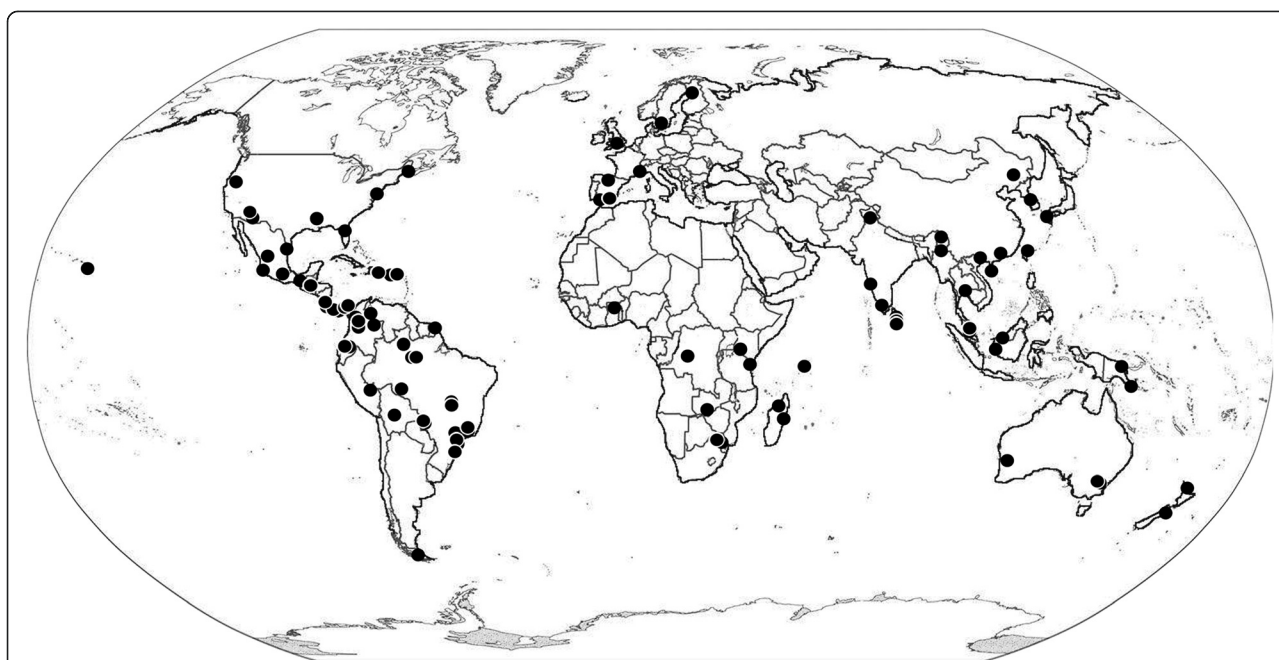
are insectivorous, with some exceptions (Munn 1985; Powell 1985). In some habitats, such as temperate forests in winter and lowland tropical forests, mixed-species flocks dominate entire bird communities (for example, in some areas more than half of all birds are found within them; Eguchi et al. 1993; Latta and Wunderle 1996; Goodale et al. 2009).

Given this broad distribution and dominance of mixed-species flocks in some areas, any study of bird community organization must incorporate them in some way. Mixed-species flocks qualify as “community modules” (sensu Holt 1997) in which biotic interactions such as competition, mutualisms, and predation are highly concentrated in space and time and, therefore, are especially amenable to scientific investigation, and naturally interesting to community ecologists. One approach derived from community ecology is to analyze flocks as a subset of the avifauna, and to try to understand and predict which species should be in flocks and what roles different species play (Goodale et al. 2010). A second and

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**Fig. 1** The worldwide distribution of studies on forest (or savannah) mixed-species bird flocks, as of 2014. Only studies which have largely complete information on the composition of flocks are included. Some studies in which multiple sites were widely dispersed were removed (e.g., Colorado and Rodewald 2015), whereas others were estimated by one dot (e.g., Hutto 1987; Gram 1998) or two (King and Rappole 2000) for this course-grained analysis. Multiple studies in one place (e.g., Barro Colorado Island, Panama) represented by overlapping dots.  $N = 87$  species, 93 sites; see [www.animal-ecology-guangxi.com](http://www.animal-ecology-guangxi.com) for details

perhaps more difficult approach is to ask how flocks affect the overall bird community. A recent review (Harrison and Whitehouse 2011) argued that, in an evolutionary sense, the behavior of some species in mixed-species flocks has created unique ecological niches for other species. But the role of species in creating niches for others is also relevant in ecological time, to understand the importance of flocking to conservation. If the presence of flocks alters the fitness and distribution of the species that participate in them (e.g., Jullien and Clobert 2000), then any factors that cause flocks to break down could alter the entire composition of communities. This issue is of special concern given the mounting evidence that a wide array of anthropogenic threats negatively affects flocks (Van Houtan et al. 2006; Mokross et al. 2014; see also section below on this topic). Potentially, the loss of a few crucial members of mixed-species flocks as a result of anthropogenic habitat alteration (e.g., habitat fragmentation, silviculture) could reduce the fitness of many other species.

The purpose of this review is to examine the ecological organization of mixed-species flocks, to understand how the structure of these communities might influence their response to human disturbance, and then to outline future directions of research on these issues, especially in East Asia, where human disturbance is pervasive. The review is organized as follows. In the first section, we describe what is known about flock community assembly:

what determines which species do and do not join flocks and what are the characteristics of species that lead flocks. In the second section, we review how human habitat modification affects flock structure, and discuss whether participating in flocks causes organisms to be particularly vulnerable or resistant to such disturbance. In the third section, we review studies of flocks in East Asia, which have not before been summarized, and ask what foundation we have to build upon. In the fourth section, we propose some lines of research that fill the gaps in knowledge identified in the previous sections. We suggest that East Asia presents unique opportunities to understand the level of interdependence of the species that participate in flocks and the implications of mixed-species flocking for conservation.

While the benefits of mixed-species flocking to birds is not the focus of this review, it remains an important backdrop to the issues we discuss, and hence a quick review is necessary. There are two main hypotheses underlying the benefits of flocks: improved foraging efficiency and increased predator avoidance (Morse 1977; Sridhar et al. 2009). These two hypotheses apply to both mono-specific and multi-species flocks and are not mutually exclusive; indeed, they interact because reduced individual investment in vigilance can lead to increased investment in foraging (Caraco et al. 1980; Sullivan 1984; Sridhar et al. 2009). Although there is strong evidence

that conspecific groupings allow animals to find food through social information sharing (Galef and Giraldeau 2001; Aplin et al. 2012), the evidence that birds learn about food from heterospecifics in flocks is limited (Krebs 1973; Waite and Grubb 1988), with the exception of a class of sallying birds that catch insects disturbed by other species or even kleptoparasitize them (Hino 1998; Satischandra et al. 2007; Sridhar and Shanker 2014). In contrast, the evidence that birds reduce their predation risk in flocks through a variety of mechanisms is strong and continues to accumulate (Thiollay and Jullien 1998; Thiollay 1999a; Sridhar et al. 2009). The reader is referred for further reading to a series of reviews over several decades: Morse (1977), Diamond (1981), Powell (1985), Greenberg (2000), and Colorado (2013).

## Review

### A. The structure of mixed-species flock communities

#### *Explaining patterns in flock participation*

Perhaps the most basic question about flocks is why are some species found in flocks and some not. As explained above, many flocking species tend to be insectivorous because that diet is most amenable to the constant movement of a flock, compared to other diets such as frugivory that require active searching for a clumped resource. Beyond diet, predation-related ecology, competition and use of space may influence species' participation in flocks, and we address these issues here in turn.

Vulnerability to predation appears to be the best predictor of high flock propensity (that is, a high percentage of individuals in flocks; Buskirk 1976; Thiollay and Jullien 1998; Thiollay 1999a, 2003). Species with high propensity to flock either have a foraging technique or a microhabitat that makes them more exposed to predators (Thiollay 2003). Further, flocking behavior is more intense where predation pressure is higher (Thiollay 1999b). These hypotheses, which were derived from studies at both a regional (Thiollay and Jullien 1998; Thiollay 2003) and global (Thiollay 1999a) level, makes it possible to predict with reasonable accuracy which species will and will not be in flocks. At the same time, it should be realized that this body of literature did not incorporate phylogenetic relatedness into their analyses. Members of some families or genera tend to be usually found in flocks, and it is yet unclear whether evolutionary history, in addition to, or instead of, predation-related or foraging-related ecology, explains the presence of these birds in mixed-species flocks (Gómez et al. 2010).

Does competition also influence which species participate in flocks? Graves and Gotelli (1993) asked this question for data from Munn and colleagues' studies (Munn 1985; see also Pierpont 1986). They found that some close congeners exhibited a 'checkerboard' pattern in which one species was present when the other was absent. However, a re-analysis of this data that looked at all congeneric pairs

did not find a significant trend for congeners to avoid each other in Munn's data, and quite to the contrary, found evidence at the global scale that congeners were more likely to associate together than expected by chance (Sridhar et al. 2012). More generally, this meta-analysis found that a considerable proportion of studies indicated that species tend to associate in flocks with other species that share their body size and/or foraging behavior (Sridhar et al. 2012; but see Colorado and Rodewald 2015 for a regional study that does not show this pattern).

While competition may not usually restrict species from joining flocks, some species have been shown to change their foraging ecology or spatial position in flocks in a manner suggesting they are avoiding competition. Many studies, especially on tit-led temperate systems, have shown that tits may change where they feed in trees (Morse 1970; Alatalo 1981; Alatalo et al. 1985, 1987; Krams 2001; Jabłoński and Lee 2002) or their foraging technique (Pomara et al. 2003) to avoid dominant species in flocks. At the same time, however, other studies have demonstrated that species might actually move their foraging location to be close to other species, particularly leaders (Latta and Wunderle 1996; Hino 1998; Hsieh and Chen 2011; Farine and Milburn 2013), and sallying species adjust their location to capture insects disturbed by gleaners (Satischandra et al. 2007; Srinivasan and Quader 2012; Sridhar and Shanker 2014). Valburg (1992) described a primarily frugivorous species that was insectivorous in flocks. In summary then, studies to date suggest that facilitation (through reduced risk of predation or increased foraging efficiency) is as important as competition in determining spatially where in flocks species are present relative to other species, and is more important than competition in determining which species are present in flocks (Sridhar et al. 2012).

The participation of species in flocks can also be influenced by how different species use space. For example, in color-banded studies it has been shown that species with small territories drop out of flocks when they leave their territories, whereas species with very large territories may even move between different flocks (Munn and Terborgh 1979; Gradwohl and Greenberg 1980). Hence species with larger territories may be more consistently with flocks (Pomara et al. 2007). Unfortunately, our knowledge of this issue is limited by the very small number of studies on mixed-species flocks that have color-banded individuals, limited to Central America (Buskirk et al. 1972; Gradwohl and Greenberg 1980), Amazonian Peru and French Guinea (Munn and Terborgh 1979; Munn 1985; Jullien and Thiollay 1998), and Australia (Farine and Milburn 2013).

#### *Explaining patterns in flock organization and leadership*

A second important question about flocking is which species play important roles in flock organization.

Winterbottom (1943) and Moynihan (1962) were the first to identify “nuclear” species, which were hypothesized to stimulate the formation and cohesion of mixed-species flocks, and “associate” species that follow the nuclear species. Nuclear species can be identified by investigating which species lead flocks (Develey and Stouffer 2001; Goodale and Beauchamp 2010; Contreras and Sieving 2011), or their centrality in network analyses (Sridhar et al. 2013), or many species being positively associated with them (Srinivasan et al. 2010).

Nuclear species have several characteristic properties. Most obviously, they are often intraspecifically gregarious (Goodale and Beauchamp 2010); indeed many are cooperative breeders (Sridhar et al. 2009). This gregariousness makes them conspicuous in flocks, and the possibly kin-selected signals they use for intraspecific communication, especially those related to predation threats, can be eavesdropped on by other species (Goodale et al. 2010; Harrison and Whitehouse 2011). Nuclear species also tend to be generalists that range over a wide variety of foraging heights, and leaf-gleaning species that disturb insects as they move, making them attractive to follow for a wide-range of other species (Hino 1998; Hsieh and Chen 2011).

A separate class of species, known as “sentinel” species, may also be important to flocks because they provide information about predators, because they are sallying (fly-catching) species that frequently scan for insects (Greig-Smith 1981; Munn 1984; Terborgh 1990; Goodale and Kotagama 2005a). Such species may meet Moynihan’s (1962) criterion of being important for the cohesion or formation of flocks, although they are rarely gregarious, and they do not necessarily lead flocks (Goodale and Kotagama 2005a).

Species that are laggards in flocks may be those whose foraging speed is not completely compatible with the flock’s; such incompatibilities may represent a cost of flocking for some species (Hutto 1988; Darrah and Smith 2013). For example, species that spend a long time foraging in one place, such as woodpeckers and parakeets, are the last species to cross open areas in Sri Lankan flocks, as they appear to need to fly long distances to catch up to the flock (Kotagama and Goodale 2004). Incompatibilities between the rate of movements of leading species and potential followers may explain why some intraspecifically gregarious species do not attract followers when foraging (Greenberg 2000; Chen and Hsieh 2002; Zhang et al. 2013).

#### ***The dependence of species on flocks and nuclear species***

While many benefits to mixed-species flocking have now been suggested, the actual fitness benefits of participating in flocks have rarely been measured. In a meta-analysis, Jullien and Clobert (2000) showed that obligate

flock species (those that forage exclusively in flocks) have higher survival rates than solitary or pair-feeding species. Dolby and Grubb (1998) found that an attendant species had poorer body condition following the removal of a flock leader. Nevertheless, there is a clear need for further studies of the extent to which species depend upon flocks for their fitness.

#### **B. The response of flocks to anthropogenic disturbance**

##### ***Why study the responses of flocks to disturbance?***

There are three main reasons that have been proposed for focusing on mixed-species flocks when studying how communities respond to habitat alteration, as compared to the whole bird community. First, flocks are particularly easy to locate and observe and can serve as a surrogate for the whole community (Lee et al. 2005). Second, conservation strategists are increasingly calling for the protection of species interactions and aspects of community structure, above and beyond the protection of species themselves (Tylianakis et al. 2009; Kiers et al. 2010; Valiente-Banuet et al. 2015), and flocks are an important type of mutualism. Third, flocking birds may be especially vulnerable to disturbance, and the loss of flocks could have ramifications for the overall bird community. Indeed, important early work on avian responses to habitat alteration in Amazonia showed flocking species were particularly affected (Thiollay 1992; Stouffer and Bierregaard 1995). In the accumulating body of literature about how flocks respond to anthropogenic disturbance, most papers simply document how flock qualities change along the disturbance gradient, but a few also tackle the question of why flock species might be expected to be particularly sensitive.

##### ***Empirical studies of how flocks respond to anthropogenic disturbance***

Two main aspects of anthropogenic disturbance have been studied primarily in flock studies so far. The first is fragmentation (Stouffer and Bierregaard 1995; Fernández-Juricic 2000, 2002; Maldonado-Coelho and Marini 2000, 2004; Tellería et al. 2001; Van Houtan et al. 2006; Sridhar and Sankar 2008; Cordeiro et al. 2014; Mokross et al. 2014). The general result of this literature is that flock qualities (size in individuals, species richness, encounter rate and even network characteristics; see Mokross et al. 2014 about networks) decrease as fragmentation increases, with fragments below 10 ha being especially effected (Maldonado-Coelho and Marini 2004; Mokross et al. 2014). The second gradient is land-use intensity, including the effects of selective logging (Thiollay 1992, 1999b), various kinds of agriculture or agroforestry (Sidhu et al. 2010; Zhang et al. 2013; Goodale et al. 2014; McDermott and Rodewald 2014; Colorado and Rodewald, in press), livestock grazing and firewood/



charcoal collection (Knowlton and Graham 2011), and urbanization (Lee et al. 2005). Again, flock structure decreases as intensity of land degradation increases, most likely due to changes in the structural complexity of different habitats (Lee et al. 2005; Zhang et al. 2013; Colorado and Rodewald, in press), or the percentage of forest cover near the site at a landscape level (Colorado and Rodewald, in press).

In addition to these two major types of gradients, Devey and Stouffer (2001) have found that roads can stop the movement of mixed-species flocks, and Tubelis et al. (2006) and Péron and Crochet (2009) have studied how flocks change at a forest-savannah edge, suggesting that flocks may help forest-interior species move closer to non-forest habitats (see below).

#### ***Are flocking species especially sensitive or resistant to human disturbance?***

In studying how flocks respond to anthropogenic disturbance, several studies have tried to distinguish between how disturbance affects flocks and how it affects the pool of birds at an area available to flock, by taking into account data on the overall abundance of birds in the community (Fernández-Juricic 2002; Sridhar and Sankar 2008; Sidhu et al. 2010; Goodale et al. 2014). While Fernández-Juricic (2002) found that the total bird density in fragments was a good predictor of the probability of encountering flocks, the other studies found that flocking propensity decreased in highly modified environments (very small fragments in Sridhar and Sankar 2008; and areas of intense agriculture for the studies of Sidhu et al. 2010; Goodale et al. 2014). In these highly disturbed areas, flocks often do not persist and flocking species are more affected than other species. That mixed-species flocks breakdown in non-forested habitats is perhaps not surprising given that they are considered to be an adaptation to the vertical structural complexity provided by forest habitat (Terborgh 1990). Indeed, the driving force behind flock breakdown in non-forested environments may be the lack of complex vegetation (Lee et al. 2005).

Another potential mechanism that may cause flocking species to be more vulnerable to human disturbance and specifically fragmentation is their use of space. Van Houtan et al. (2006) worked in Amazonia with a system where flocks maintain multi-species territoriality.

(Munn and Terborgh 1979; Jullien and Thiollay 1998; Martínez and Gomez 2013), and found that the species that have higher flocking propensity in undisturbed habitat, and species that remain in flocks in disturbed habitat (as opposed to dropping out), are more likely to go extinct in fragmented areas. However, it is not clear that this mechanism operates in other areas, where flocks seem more like “waves” (McClure 1967), with birds joining and leaving at their own territory borders.

In contrast to the ideas above, it is also possible that flocking may benefit species in degraded landscapes because they help species adapt to hostile environments (Morse 1970) and forest-preferring birds might rely more on flocks when outside of forests. For example, experimental evidence has shown that forest birds are more likely to go into an open area in the presence of a nuclear flocking species (Dolby and Grubb 2000; Sieving et al. 2004). The edge studies discussed above suggest that flocking can encourage species to persist in open and hence risky areas: birds in mixed-species flocks traveled farther from forest than those that did not participate (Tubelis et al. 2006; Péron and Crochet 2009). Even where flocks do not persist at high densities in human disturbed environments, those flocks that do remain could be important refuges for forest-preferring species.

A final possible effect of flocks on participating species' vulnerability to anthropogenic habitat alteration could also be a result of species interactions and dependencies in flocks. If a species A is important to flocks, and a species B joins flocks to follow or derive benefits from A, then the habitat choices of A could alter the habitat preferences of B, a “within trophic cascade” analogous to trophic cascades in which top carnivores have large effects on communities (e.g., Terborgh et al. 2001). Several studies have implicated the absence of nuclear species as a strong contributor to the breakdown of flock structure (Maldonado-Coelho and Marini 2004; Sridhar and Sankar 2008; Zhang et al. 2013; Cordeiro et al. 2014). New analysis of Goodale and colleagues' data of flocks in Sri Lanka (Goodale et al. 2014) shows that at intermediate elevations, two different flock leaders, a babbler and a white-eye, vary in their sensitivity to land-use intensity, with babblers being more confined to forest (Mammides et al., unpublished manuscript). Other species show distinct preferences for one leader over the other, related to their body size, and this may affect their habitat selection; for example, several large threatened species are found mostly in babbler flocks and this may underlie their exclusivity to forest. Although a nuclear species, like this babbler in Sri Lanka, may be fairly common, it could be considered as a target of conservation if endangered species are dependent on it.

#### **C. The structure and composition of flocks in East Asian forests**

We next consider what foundation of knowledge we have on flocks in the East Asian region. In Table 1, we summarize the major studies of forest mixed-species flocks for the region, organized by latitude. Our search for literature included articles in Chinese, and reference books on Chinese birds (e.g., Zhuge 1990; Zhao 2001); unfortunately, we were not able to do a similar search in

**Table 1** Major flock studies in East Asia, with data on their species richness and leadership

| Authors (year of publication)                            | Province or Island | Latitude       | Longitude        | Habitat                 | Species richness |      |     | Leadership  |
|--|--------------------|----------------|------------------|-------------------------|------------------|------|-----|---|
|  |                    |                |                  |                         | >25%             | >10% | >5% |   |
| Zou et al. (2011)  | Hainan             | 18°23'–18°52'N | 108°36'–109°05'E | Mature                  | 4                | 11   | 21  | <i>Alcippe hueti</i>                                      |
| Jiang (2007)   | Guangxi            | ~22°28'N       | ~106°57'E        | Successional and mature | 6                | 16   | 25  | <i>Alcippe davidi</i>                                     |
| Zhang et al. (2013)                                      | Guangdong          | 23°09'–23°11'N | 112°30'–112°33'E | Mature                  | 6                | 12   | 17  | <i>Alcippe hueti</i>                                      |
| Zhang et al. (2013)                                      | Guangdong          | 23°09'–23°11'N | 112°30'–112°33'E | Successional            | 3                | 8    | 11  | <i>Zosterops japonicus</i> (but not “cohesive”)           |
| Chen and Hsieh (2002); Hsieh and Chen (2011)             | Taiwan             | ~24°34'N       | ~121°34'E        | Mature                  | 8                | 12   | 16  | <i>Alcippe morrisonia</i>                                 |
| Seki and Sato (2002)                                     | Kyushu             | ~32°49'N       | ~130°44'E        | Mature                  | n/a              | n/a  | n/a | <i>Aegithalos caudatus</i> ; 2 tits also dominant         |
| Suzuki (2012)  | Honshu             | 36°21'–36°22'N | 138°35'–138°36'E | Mature                  | <4               | <4   | <4  | Dominated by 3 tit species                                |
| Kubota and Nakamura (2000); Nakamura and Shindo (2001)   | Honshu             | ~37°08'N       | ~138°14'E        | Gardens and mature      | <4               | <4   | <4  | Dominated by 2 tit species and <i>Aegithalos caudatus</i> |
| Lee and Jabłoński (1999, 2006); Jabłoński and Lee (2002) | Seoul              | ~37°33'N       | ~126°58'E        | Mature                  | 4                | <8   | <8  | Dominated by 4 tit species and <i>Aegithalos caudatus</i> |
| Ogasawara (1965, 1970, 1975)                             | Honshu             | ~38°15'N       | ~140°53'E        | Gardens                 | n/a              | n/a  | n/a | Dominated by 4 tit species and <i>Aegithalos caudatus</i> |
| Hino (2005)  | Hokkaido           | ~43°10'N       | ~141°22'E        | Mature                  | n/a              | n/a  | n/a | Dominated by 2 tit species and <i>Aegithalos caudatus</i> |
| Gao (1987, 1991); Gao et al. (1993)                      | Jilin              | 44°01'–44°06'N | 126°00'–126°09'E | Mature                  | 4                | 8    | 10  | Dominated by 3 tit species and <i>Aegithalos caudatus</i> |

Korean or Japanese, and we therefore could have missed studies in these countries. As yet, most studies have been descriptive, and so here we focus on just a few aspects of flocks: seasonality, species richness, and leadership. Taxonomy follows Gill and Donsker (2014).

As one might expect, there is a large difference between northern temperate flocks and tropical ones in seasonality. Ogasawara (1965) described in detail the seasonality of a temperate Japanese flock system, starting from June for some species after breeding, peaking in the early autumn and disbanding again in March. Such systems are also encountered in Korea (Lee and Jabłoński 1999) and northern China (Gao 1987); and contrast strongly with Chinese tropical flock systems such as those in Hainan, which do not have any noticeable differences between seasons (Zou et al. 2011). The seasonal variation in flocking in between these two extremes requires greater study. For example, in Guangdong, seasonal differences were low, although there is a noticeable decrease in flock size in April, May and June (Zhang et al. 2013), perhaps associated with the breeding season.

Species richness is also correlated with latitude. For example, in northern China and Korea, an average (from four studies; see Table 1) of 4 species were found in 25% of flocks, and 6.5 species in 5% of flocks. In comparison, in mature forest of South China, an average (from four studies; see Table 1) of 6 species were in 25% of flocks, and an average of 19.8 in 5%. However, presently we are unable to distinguish whether southern flocks are larger

simply because there are more species in these areas, or because the flocks are a larger percentage of the avifauna, as only two studies in the region (Zou et al. 2011; Zhang et al. 2013) have data on birds both inside and outside of flocks.

Compositional studies also show large differences between southern and northern China, especially in which species play nuclear roles for flocks. The fulvetta species *Alcippe davidi*, *A. hueti* and *A. morrisonia* are the nuclear species in forested habitats in southern China (see Table 1), and have been reported to lead flocks as far west as Yunnan (Wang 1983; where the species would likely be *A. fratercula*). These species are extremely gregarious, with between 21.2 and 32.5 individuals per flock. *Alcippe* species play important roles in flocks outside of East Asia, too: *A. poioicephala* plays a leading role in flocks in Malaysia and India (McClure 1967; Sridhar et al. 2013). Other members of the families Timaliidae, Pellorneidae, Leiothrichidae (Fregin et al. 2012; groups traditionally called “babblers”) are also frequently noted to be mixed-species flock participants in books on the Chinese avifauna, and especially in southern China (Zhuge 1990; MacKinnon and Phillipps 2000; Zhao 2001).

In contrast, the flocks of the northern part of the region are dominated by the tit (Paridae) and bushtit (Aegithalidae) families. The species *Parus major*, *Periparus ater*, *Poecile palustris*, *Sittiparus varius* and *Aegithalos caudatus* are all found in multiple flock systems, often together, and *Regulus regulus* (Regulidae) is another common participant (Song

1981; Gao 1987; Gao et al. 1993; Lee and Jabłoński 1999; Hino 2005). In addition, *Poecile montanus* has been described in flocks (Ogasawara 1965), and is potentially important in flock formation (Suzuki 2012). Among these different species, there is little information as to which species lead the flock, although Seki and Sato (2002) observed *Aegithalos caudatus* to be a leader when present. Following these species are a variety of nuthatches, creepers and woodpeckers.

Beyond these two clear flocking types, there may be other flock types, especially in areas of intermediate latitude or in early successional habitat. For example, on the tops of mountains in southeast China, *A. hueti* may be rare and other species, such as the Red-billed Leiothrix *Leiothrix lutea*, can lead flocks (A. Jiang, J. Zhao and Q. Zhang, personal communication). In Zhejiang Province, *Aegithalos concinnus* and *Pardaliparus venustulus* are described as flocking species (Zhuge 1990); another southern tit flock participant may be *Machlolophus spilonotus* (Zhao 2001). White-eyes (Zosteropidae) often form multispecies flocks in disturbed habitat (Kawakami and Higuchi 2003) and can serve as leaders of flocks with low cohesion in human-dominated ecosystems (Zhang et al. 2013; Mammides et al., unpublished manuscript on birds of South Asia; E. Goodale, personal observation in Xishuangbanna, Yunnan Province). *Phylloscopus* warblers may form multispecies flocks, especially close to migration time (Gao 1987), and members of the *Seicercus* genus have also been observed in flocks (Zhuge 1990).

A few generalizations can be made regarding the literature from this region. East Asian flocks are notable for the high numbers of individuals per flock, due to the presence of gregarious leading species, a characteristic also noted in South Asia (Goodale et al. 2009), and contrasting to tropical America, where most species have just a few individuals (Powell 1985). The gregarious nuclear species in these groups may consist of stable flocks of mated pairs such as parids (Smith 1991), or perhaps closely related family groups (although it should be noted that fulvetas do not appear to be cooperative breeders; Collar et al. 2013), and hence participate in seemingly altruistic behavior that benefit their kin or mates (Maynard Smith 1965). Sentinel species, represented by the drongos, are also present in some tropical and subtropical flocks (Chen and Hsieh 2002; Jiang 2007; Zou et al. 2011). Other fly-catching species could also serve as sentinels, as does the Grey-headed Canary Flycatcher (*Culicicapa ceylonensis*) in flocks of disturbed habitats in Xishuangbanna, Yunnan (E. Goodale, personal observation).

#### D. The future of studies of flocks in East Asia

##### *A need for more flock observations and research in East Asia*

While there is a strong foundation for flock studies in the region, there are some clear knowledge gaps that

need to be filled including the composition and structure of flocks at intermediate latitudes, particularly in central and western China, and in human-disturbed environments, as the pioneering Zhang et al. (2013) article is the only study yet to concentrate on how flocks in early successional forest compare to those in mature forest. It would be particularly interesting to see whether birds in any area have the choice of joining tit-led flocks as opposed to babbler-led flocks, or even joining another system like that of white-eyes or warblers.

Flock observations need not only be reserved for professional ornithologists because there is a new group of skilled bird-watchers in the region from whom it may be possible to gather information (Si and Ding 2011; Ma et al. 2013). Efforts are currently underway to have data compilers, such as eBird (ebird.org) or the Chinese-focused site, Chinese Bird Report (birdtalker.net), incorporate mixed-species flock data into their data collection protocols.

As East Asia has a great range of latitudes, elevations and natural ecosystems, and because anthropogenic stress on natural ecosystems is high, leading to many kinds of human-modified and human-dominated habitats, we also see a range of fruitful ways in which scientists in this region can investigate flocks. Based on our review of flock structure and response to human disturbance, there are some critical questions as yet unanswered: what enhances flock persistence in disturbed environments, how much space do flocks require and how dependent are species on each other in flocks? Here we discuss these questions in turn, also suggesting some observational and experimental approaches that can address them.

##### *Studies of flock persistence in human-modified habitats*

The question of whether flocking species are especially vulnerable to anthropogenic change still needs to be answered for a variety of regions and environments. Further, it is critical to know how important flocks are to the persistence of birds in a fragmented landscape. Studies of foraging ecology (measuring foraging rates, efficiency and head scans) would be useful over a gradient of human disturbance (Tellería et al. 2001; Pomara et al. 2003). Even better would be the ability to look at direct measures of birds' fitness, such as nest success in disturbed areas with and without flocks (although finding comparable areas is always difficult; see experimental approaches below).

Work on what habitat features enable flocks to persist in human-modified areas would also be a productive research direction. What vegetational characteristics are needed? Can flocks move through areas using "corridors" or "stepping stone" patches of forest habitat? An experimental paradigm involving translocation of birds

away from their territory and observations of what habitat they use on their way back (e.g., Gillies and St Clair 2010) might also be useful to use on nuclear species, although one might have to translocate groups of such species, since they are usually not naturally alone.

### **Studies of the use of space by flocks**

In order to determine how flocks can be conserved in human-modified areas, we need to better understand their movement patterns and how much space they require. As noted above, there is a clear lack of studies of color-banded flocks outside Central/South America and Australia. Such studies are really the only way to understand how individual birds are using space in flocks and outside of them, and are required both in natural habitats in Asia as well as in fragmented landscapes.

### **Flock interdependency: studies along gradients**

How co-evolved are flock systems, and how dependent are species on specific heterospecifics in flocks? One approach to this question is to study an environmental or disturbance gradient and see if the ranges of species with high propensity to flock begin and end randomly or coincide. Such studies have been used to investigate competition (e.g., Terborgh 1971; Jankowski et al. 2012). In the flocking context, if species that participate in flocks are all clumped together on such a gradient, it would provide evidence for the flock or a particularly important leader affecting the distribution of species along the gradient (Fig. 2). This gradient could be elevation, or fragmentation, or land-use intensification. For example, the Thousand Island Lake system in eastern China (Wang et al. 2011) could be an excellent system in which to look for fragmentation effects. The flock leading species *Alcippe hueti* is found on 35 of these 42 islands (Wang et al. 2011), so it would be interesting to see what

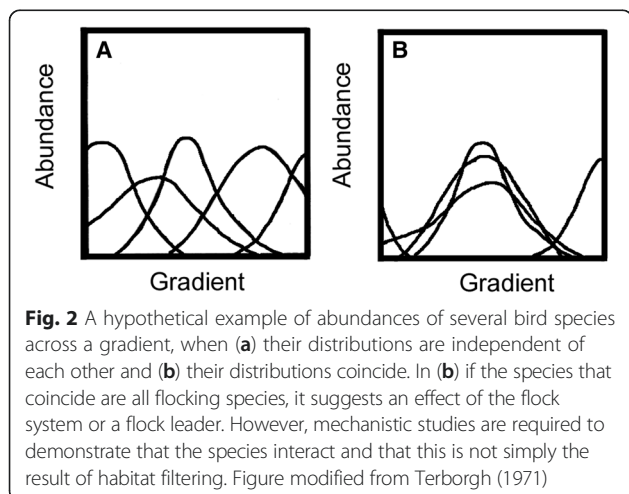
happens to flocks and the pool of bird species on the remaining seven islands.

As intuitive as this approach sounds, clumping of species in one area could also be evidence of habitat filtering, that is, birds with similar phenotypes responding to habitats in similar ways (Jankowski et al. 2012). Hence, this approach is best used in conjunction with mechanistic or experimental approaches (see below). Another way to investigate whether habitat filtering is responsible for community structure is a phylogenetic analysis, for if habitat filtering is occurring in an area, species are expected to be more phylogenetically similar than expected by chance (Webb et al. 2002), assuming that phylogenetically related species are more phenotypically similar. A recent study (Gómez et al. 2010) has taken such a phylogenetic approach, combined with models of trait evolution, to analyze antbird assemblages in mixed-species flocks in Amazonia and found evidence for phylogenetic clumping. Perhaps this clumping is due to relaxed competition, as expected in mutualisms (Sridhar et al. 2012). The result warrants replication, and further conceptual work should investigate whether facilitation has the same or different implications for these analyses as reduced competition.

### **Flock interdependency: experimental studies**

Experimental studies remain the most powerful way to determine how flocking affects fitness. For example, Grubb and colleagues were able to remove species from flocks that are found in small pockets of forest in an agricultural landscape, and then measure the effects on the body condition of the remaining birds (Cimprich and Grubb 1994; Dolby and Grubb 1998, 1999). One can imagine potential experiments on the Thousand Island Lake landscape (Wang et al. 2011), discussed above, where fulvetas could be removed from islands, or even added to islands where they were not before, with the one complicating problem that the resulting flocks would not only be different in the presence of this one species, but also in the number of individuals per flock (due to the species being highly gregarious).

As removal experiments are difficult to accomplish, however, playback can be used as another technique to measure interspecific relationships. For example, after observations of elevational gradients suggested interspecific interactions, playback trials were used to demonstrate interspecific aggression (Jankowski et al. 2010). In an analogous manner, several studies have used the playback of a species' vocalizations to simulate that species' presence and then measured approaches by heterospecifics to determine the importance of that species to the community (Mönkkönen et al. 1996), or specifically to other flocking species (Goodale and Kotagama 2005b; Goodale et al. 2012; Cordeiro et al. 2014). While these





kinds of experiments have their limitations (e.g., impossible or difficult to simulate non-vocal species or those with low-amplitude vocalizations, inability to measure exploitation competition), they can be used in conjunction with observations to understand the community structure of flocks.

## Conclusions

In the introduction, we summarized two different approaches to studying the community ecology of mixed-species flocks: 1) how are these subsamples of an avian community organized in terms of which species are included and which species play important roles, and 2) how does the flock phenomenon influence the structure of the overall community? Research on mixed-species flocks has so far focused on the more manageable first approach. Yet the set of questions involved in the second approach are, we believe, particularly important to understanding the implications of flocking for conservation. While the current research suggests that flocks are negatively affected by human disturbance, we still do not understand what happens to birds when flocks disappear or how can we enhance their persistence. The ecological breadth of the region, the vast amount of human-modified habitats, and the increase of skilled observers and potential students of flocking, afford tremendous opportunities for East Asia in the century to come.

## Competing interests

The authors declare that they have no competing interests.

## Authors' contributions

All authors contributed to developing the ideas and writing the manuscript. All authors have read and approved the final version of the manuscript.

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