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Research

Interspecific competition and facilitation coexist in mixed-species bird flocks of montane coniferous forests in Taiwan

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Besides competition, positive interactions also play an important role in shaping the social structure of mixed-species bird flocks. This study aimed to illuminate the interspecific interactions of competition and facilitation in mixed-species bird flocks. We recorded the foraging behavior and microhabitat use of flocking species in montane coniferous forests of Taiwan under different social contexts. Foraging niche breadth and niche-overlap with other flocking species were compared between individuals inside and outside of mixed flocks. For the three microhabitat variables (foraging locations, vertical strata and horizontal strata), relationships between niche-overlaps of heterospecific pairs of these flocking species and their corresponding interspecific associations were determined using a simple linear regression. While in mixed flocks, two understory species, Taiwan fulvetta *Fulvetta formosana* and yellowish-bellied bush warbler *Horornis acanthizoides*, shifted their foraging from shrubs upwards into coniferous trees. Meanwhile, flamecrests *Regulus goodfellowi* moved downwards vertically within the canopy, and black-throated tits *Aegithalos concinnus* spread out horizontally along branches. In addition, flamecrests applied many more sally-hovers inside of mixed flocks than outside of flocks. All four species are insectivores which might find it more difficult to obtain sufficient food during the colder winters when food resources become scarcer. Therefore, they may be using the increased vigilance afforded by the flock to expand their foraging niches and thus to increase their foraging opportunities inside mixed flocks. Furthermore, niche-overlaps of heterospecific pairs of the 11 common flocking species were positively correlated with their corresponding interspecific associations on all three microhabitat variables. These results indicate that a greater foraging niche-overlap between two flocking species would result in higher coexistence of the two species in mixed flocks. Consequently, facilitative interactions occurred in these mixed-species flocks in addition to competitive interactions.

Keywords: coniferous forest, flamecrests, foraging behavior, niche-overlap, positive interaction, tits

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Introduction

A mixed-species bird flock is defined as two or more bird species that forage and move together in a concordant manner for a considerable period of time (Moynihan 1962, Morse 1970, Hutto 1987). Two main hypotheses have been proposed for the formation of mixed-species bird flocks (mixed flocks from hereon): enhanced foraging efficiency and reduced predation risk (Morse 1977, Diamond 1981, Greenberg 2000). Many studies have tested these hypotheses over the last few decades, but the outcomes vary from study to study (Gaddis 1980, Suhonen et al. 1993, Thiollay and Jullien 1998, Dolby and Grubb 1999, Sridhar et al. 2009). One reason may be that each participant species joins mixed flocks for somewhat different benefits (Eguchi et al. 1993).

Because the phenomenon of mixed flocks is widespread in avian communities, the benefits of flock participation likely outweigh the costs in many circumstances (Thiollay 2003). In temperate and subtropical forests, mixed flocking is especially prominent in winters when food resources become scarcer or breeding territories do not need to be defended anymore (Morse 1970, 1978, Austin and Smith 1972, Berner and Grubb 1985), and this trend may also be applicable for tropical areas (McClure 1967, Croxall 1976). In Andean foothill forests, larger flocks were observed during the colder winter (Mangini and Areta 2018). Cold weather is indeed a stimulus for mixed flock formation in regions with clear seasonality, and flocking is considered an effective adaptation to overcome such difficult conditions (Morse 1970, Fogden 1972, Poulsen 1996, Mangini and Areta 2018). Therefore, increasing foraging efficiency appears to be an important benefit for most participating species, and changes in foraging behavior might be more easily observed during this period of time.

Mixed flocks have recently become a prime research model for positive interaction studies because both enhanced foraging efficiency and reduced predation risk involve positive interactions among flock members; consequently, several recent publications have focused on just these two kinds of interactions (Fallow and Magrath 2010, Hsieh and Chen 2011, Sridhar and Shanker 2014, Goodale et al. 2020). For example, Hino (1998) found an increase of interspecific overlaps in various foraging variables for flocking species in Madagascar rain forests, with foraging locations of these species becoming more similar when in mixed flocks. Jones et al. (2020) also found that foraging niche-overlaps among flocking species in Florida were significantly higher than expected by chance although each species had a distinctly different foraging niche. Hsieh and Chen (2011) observed that attendant species that have higher foraging niche-overlaps with the nuclear species also have greater flocking frequencies. Thus, these studies all suggest that flocking participants might receive more benefits than costs in mixed flocks, especially for species with similar foraging guilds, which would facilitate activity matching among flocking species (Hutto 1988, Sridhar et al. 2012).

Competition has long been considered the prominent influence in shaping community structure (Morse 1970, 1978, Austin and Smith 1972, Alatalo 1981, Eguchi et al. 1993, Jabłoński and Lee 2002); however, observed niche separation among species of mixed flocks might not be solely due to competition. Suhonen et al. (1993) found that foraging site selection by the dominant species in a mixed-species tit flock was a trade-off between competition and predation, and the dominant species preferred to stay at safer locations instead of locations with more abundant food. Based on the competition theory, if two bird species have a similar foraging niche and therefore a high niche-overlap, both should avoid each other. Consequently, the probability to coexist in a mixed flock is expected to be low. In contrast, if two species with high niche-overlap frequently occur in the same mixed flock, a benefit different from obtaining food may be of importance. In such cases, positive interaction or facilitation is very likely to occur, and the benefits (e.g. reduced predation risk) received probably outweigh the costs due to food competition or interspecific aggression (Herrera 1979, Eguchi et al. 1993, Bertness and Callaway 1994, Goodale et al. 2010, Hsieh and Chen 2011). As a result, niche-overlap among flocking species could be a valuable index to determine the extent of competition or facilitation within a mixed flock. However, the two might not be mutually exclusive in mixed flocks (Jones et al. 2020).

This study aimed to illuminate the influence of competition and facilitation in mixed flocks. We first tested the hypothesis of increased foraging efficiencies by examining changes in foraging niche breadths and niche-overlaps of flocking bird species inside versus outside of mixed flocks in coniferous forests of Taiwan. Furthermore, we correlated foraging niche-overlaps of common attendant species to their corresponding interspecific associations to determine whether competition or facilitation prevails in these mixed flocks.

Methods

Fieldwork was carried out in the Tataka (23° 29’ 15”N, 120° 53’ 30”E), Hehuanshan (24° 09’ 44”N, 121° 17’ 14”E) and Dasyueshan (24° 15’ 19”N, 121° 0’ 30”E) areas, Taiwan, during both the non-breeding (September–February) and the breeding (March–August) seasons in 2015 and 2016. Mixed-species flocks were regularly formed from September to February when cold weather prevails. We focused on flocking members of mixed flocks and recorded their foraging behavior and microhabitat use. Extensive trails within each study site were used for searching birds. A two-person team worked together and followed targeted bird species closely for as long as possible to collect data on each individual’s foraging behavior. Different social contexts (mixed-species flock, monospecific flock, solitary or in pairs) were noted whenever a flocking species was encountered. All the species in a mixed flock were identified, and the number of individuals of each participant species was determined with the aid of binoculars. After the flock disappeared, both observers double-checked and compared the numbers of all species identified in the flock. If the recorded numbers for the individuals of a particular

species were not the same between the two observers, we used the larger one, the reason being that one of the observers might have had a better view of the flock or was situated at the right spot to count the birds when they crossed a trail (Chen and Hsieh 2002, Kotagama and Goodale 2004). The proportion of all flocks taken together occupied by each flocking species was then calculated as the flocking frequency of each species; in other words, we calculated a mean proportion across all the data from the 81 flocks (Hutto 1994). We also collected foraging data of flocking species both inside and outside of the mixed flocks. The foraging behavior and categories for microhabitat use of a foraging bird as defined by Remsen and Robinson (1990) were used. The main foraging behaviors included gleaning, hanging, probing, sally-striking and sally-hovering. Reaching and pecking occurred very rarely; thus, we lumped them with gleaning and probing. We made only one observation from each individual in a mixed flock to maintain the independence of our behavioral data. To achieve this, we always shifted to another species whenever observations of one individual had been completed. In some cases, we observed more than one individual of a particular species if we were able to assure that both individuals were not the same one. For example, we occasionally moved on to another individual of the same species which was located somewhere away from the previously targeted bird, or we switched to an individual of the opposite sex which we could distinguish by its distinctive sex-specific plumage.

Microhabitat use was divided into three parts: foraging locations, vertical strata and horizontal strata. Foraging location was the type of vegetation on which foraging occurred, including trees, shrubs or herbs, and the ground. If the foraging observation occurred on a tree, we further recorded the vertical stratum and horizontal stratum where the bird foraged. Vertical strata were divided equally into three sections according to the tree height. Lower stratum included the trunk from the ground to the lower edge of the crown, and the middle and upper strata occupied the lower and upper sections of the tree crown, respectively. Horizontal strata were also divided into three parts along a branch starting from the trunk to the edge of the tree crown. The inner stratum consisted mainly of large branches, and the outer stratum was defined as the very fine and outer twigs and needle leaves of a conifer tree.

We used the chi-squared test to determine homogeneity in frequencies between inside and outside mixed flocks on each of the four foraging variables for the 11 common flocking species for which we had made at least 20 independent foraging observations (Table 1). A post hoc chi-squared test was used to identify the significant level for each frequency through a Bonferroni correction in the 'chisq.posthoc.test' package. Regarding vertical strata, we lumped the observations of the ground, herbs and shrubs into the category 'lower stratum.'

To determine the foraging niche breadth, we used the formula given in Levins (1968). We also calculated foraging niche-overlap (Pianka 1973) between all heterospecific pairs of the 11 common flocking species for both inside and outside the mixed flock. Niche-overlaps range from 0 to 1, and a value close to 1 indicates a high niche-overlap between

Table 1. Flocking frequency (in %), mean number of individuals per flock, and guild of 23 flocking species in 81 mixed-species bird flocks observed in montane coniferous forests of Taiwan. Species are ordered by flocking frequency and then by the mean number.

Bird species	Scientific name[a]	Flocking frequency	Mean number	Guild[b]
Flamecrest	*Regulus goodfellowi*	75.3	10.8 ± 12.4	TI
Coal tit	*Periparus ater*	56.8	7.5 ± 8.8	TI
Green-backed tit	*Parus monticolus*	51.9	2.2 ± 1.0	TI
Taiwan fulvetta	*Fulvetta formosana*	46.9	6.7 ± 8.7	SI
Black-throated tit	*Aegithalos concinnus*	45.7	24.0 ± 16.1	TI
Yellowish-bellied bush warbler	*Horornis acanthizoides*	34.6	2.2 ± 0.9	SI
Eurasian nuthatch	*Sitta europaea*	19.8	1.8 ± 0.7	BI
Rufous-capped babbler	*Cyanoderma ruficeps*	18.5	2.9 ± 1.3	SI
Collared bush-robin	*Tarsiger johnstoniae*	18.5	1.4 ± 0.5	GI
Morrison's fulvetta	*Alcippe morrisonia*	17.3	15.7 ± 11.0	SI
White-whiskered laughingthrush	*Trochalopteron morrisonianum*	14.8	5.0 ± 5.3	SO
Taiwan yuhina	*Yuhina brunneiceps*	9.9	7.3 ± 2.3	TH
Golden parrotbill	*Suthora verreauxi*	7.4	40.8 ± 16.9	SI
Taiwan barwing	*Actinodura morrisoniana*	6.2	14.4 ± 16.7	BI
Ferruginous flycatcher	*Muscicapa ferruginea*	4.9	2.8 ± 0.8	FI
Steere's liocichla	*Liocichla steerii*	3.7	2.3 ± 0.5	SO
Eurasian wren	*Troglodytes troglodytes*	3.7	1.3 ± 0.5	GI
Rufous-faced warbler	*Abroscopus albogularis*	2.5	3.0 ± 0.0	TI
Fire-breasted flowerpecker	*Dicaeum ignipectus*	1.2	2.0 ± 0.0	TH
White-browed bush-robin	*Tarsiger indicus*	1.2	1.0 ± 0.0	GI
Vivid niltava	*Niltava vivida*	1.2	1.0 ± 0.0	FI
Eyebrowed thrush	*Turdus obscurus*	1.2	1.0 ± 0.0	TO
Yellow-browed warbler	*Phylloscopus inornatus*	1.2	1.0 ± 0.0	TI

[a] Scientific names follow Clements et al. (2019).
[b] Ecological guilds based on this study and Ding et al. (2008): ground insectivore, GI; shrub insectivore, SI; shrub omnivore, SO; tree insectivore, TI; tree omnivore, TO; tree herbivore, TH; bole insectivore, BI; fly-catching insectivore, FI.

the two species. We then applied Wilcoxon signed-rank test to determine the difference in niche-overlaps between inside and outside mixed flocks for each flocking species on the three microhabitat variables (location, vertical and horizontal strata).

Finally, to detect whether the flocking species associated with one another by chance alone, we calculated a coefficient of interspecific association for each pair of species using the modified Cole's coefficient (Cole 1949, Péron and Crochet 2009, Arbeláez-Cortés and Marín-Gomez 2012). The equation for calculating the coefficient was: $(A,B) = \frac{a \times d - b \times c}{\sqrt{(a+b)(a+c)(d+c)(d+b)}}$, where a represented the number of flocks where both species were found, b the number of flocks in which only species A was found, c the number of flocks in which only species B was found and d the number of flocks in which neither was found. The coefficient ranges from −1 for complete exclusion to +1 for obligate association for any two flocking species (Cole 1949, Péron and Crochet 2009). We further correlated the coefficient of interspecific association of the 11 common flocking species to their corresponding niche-overlaps of the three microhabitat variables by using a simple linear regression. All statistical analyses and figure plotting were performed in R ver. 4.0.3 (<www.r-project.org>).

Results

The complete compositions of 81 mixed flocks were recorded in montane coniferous forests of Taiwan during the study period (39 flocks from Tataka, 33 from Dasyueshan and 9 from Hehuanshan), and 23 species were observed participating in the mixed flocks (Table 1). The average flock consisted of 4.4 (± 1.9 [SD], range 2–11) species and 40.3 (± 28.4 [SD], range 7–122) individuals. The mean number of the conspecific group size was much larger for nuclear species, which actively led the flocks alternatively (Supporting information; Goodale and Beauchamp 2010); for example, 10.8 for flamecrest, 24.0 for black-throated tit and 7.5 for coal tit. In contrast, attendant species such as the green-backed tit or the Eurasian nuthatch had relatively smaller conspecific group sizes (mean 2.2 and 1.8, respectively; Table 1).

Seven out of the 11 common flocking species behaved differently in at least one foraging variable when we compared their foraging behavior for inside versus outside of mixed flocks. While in flocks, individuals of two understory species, Taiwan fulvetta and yellowish-bellied bush warbler, moved upward into trees more frequently (χ^2-test, $p < 0.05$; Table 2). When foraging by itself, the Taiwan fulvetta is an understory species that seldom forages beyond three meters above ground in coniferous forests (Liu 2012). It usually foraged on shrubs, bamboo thickets and saplings. However, Taiwan fulvettas often went upward into coniferous trees when foraging in mixed flocks. As a result, they also expanded their foraging vertically into middle stratum (χ^2-test, $p < 0.05$; Table 2), and increased their foraging niche breadth. A similar change was observed for the yellowish-bellied bush warbler. When foraging by itself, it mainly foraged in grass and bamboo thickets, but in mixed flocks it occasionally foraged on saplings which were located above these thickets, expanding its niche breadth from 1.17 to 2.78 (Table 2).

In contrast, individuals of a canopy species, flamecrest, often moved downward along vertical strata (χ^2-test, $p < 0.001$; Table 2). The flamecrest foraged on the crown of conifers when foraging by itself. However, it moved downward into the middle and lower strata of coniferous trees in mixed flocks and thus also showed a niche expansion from 1.71 to 2.48. On the other hand, individuals of the black-throated tit spread out their foraging along the horizontal strata more evenly in mixed flocks (χ^2-test, $p < 0.05$; Table 2). The black-throated tit is a mid-story species when foraging by itself, but it extended its foraging range horizontally along branches in mixed flocks. While in mixed flocks, individuals of these four species expanded their foraging niche breadth. In contrast, individuals of the white-whiskered laughingthrush and Taiwan yuhina moved upwards and reduced their foraging niche breadth when in mixed flocks (χ^2-test, $p < 0.05$ and $p < 0.01$; Table 2).

In terms of foraging behavior, individuals of the flamecrest applied many more sally-hovers in mixed flocks than outside of flocks and thus increased their foraging niche breadth by shifting from mainly gleaning outside of flocks to more diverse maneuvers in mixed flocks (χ^2-test, $p < 0.001$; Table 2). In contrast, individuals of the coal tit decreased their foraging niche breadth while in mixed flocks because they concentrated their foraging more on gleaning (χ^2-test, $p < 0.05$; Table 2).

Regarding niche-overlaps in foraging location, individuals of the Taiwan fulvetta and the yellowish-bellied bush warbler had greater niche-overlaps with individuals of other flocking species inside mixed flocks than outside of flocks (Wilcoxon signed-rank test, $p < 0.05$; Table 3). Individuals of the flamecrest and coal tit also showed greater niche-overlaps with individuals of other flocking species in vertical strata use inside mixed flocks than outside of flocks (Wilcoxon signed-rank test, $p < 0.01$; Table 3). The same trend was observed for individuals of the black-throated tit in horizontal strata (Wilcoxon signed-rank test, $p < 0.05$; Table 3).

Significantly positive correlations were found between the interspecific associations of the 11 common attendant species (Supporting information) and their corresponding niche-overlaps for all three microhabitat variables (foraging location, $r^2 = 0.09$, $p < 0.05$, vertical strata, $r^2 = 0.40$, $p < 0.001$ and horizontal strata $r^2 = 0.22$, $p < 0.01$; Fig. 1).

Discussion

Through observations of bird species and mixed flocks in the montane coniferous forests of Taiwan, we were able to show that four out of the 11 common flocking species (namely, Taiwan fulvetta, yellowish-bellied bush warbler, flamecrest

Table 2. Foraging niche shifting of common flocking species between foraging in mixed-species flocks (MSF) and outside of flocks (non-MSF) on four foraging variables in montane coniferous forests of Taiwan.

Bird species[a]	Social status	n	Foraging location[b]			Niche breadth	χ^2-test
			Ground	Shrubs	Trees		
TF	Non-MSF	75	3	58	14	1.58	$p < 0.05$[c]
	MSF	26	0	15	11	1.95	
WWL	Non-MSF	143	94	28	21	2.03	$p < 0.05$[c]
	MSF	7	2	5	0	1.69	
TY	Non-MSF	68	0	**46**	**22**	1.78	$p < 0.01$
	MSF	19	0	**4**	**15**	1.50	
YBBW	Non-MSF	38	0	35	3	1.17	$p < 0.05$[c]
	MSF	5	1	2	2	2.78	
			Vertical strata[b]				
			Lower	Middle	Upper		
FC	Non-MSF	117	**2**	**31**	**84**	1.71	$p < 0.001$
	MSF	126	**20**	**67**	**39**	2.48	
TF	Non-MSF	75	71	4	0	1.11	$p < 0.05$[c]
	MSF	26	21	4	1	1.48	
			Horizontal strata				
			Inner	Middle	Outer		
BTT	Non-MSF	19	2	11	6	2.24	$p < 0.05$
	MSF	54	21	15	18	3.06	
			Foraging behavior[b]				
			GN	HG	PB	SH	SS		
FC	Non-MSF	117	**93**	12	2	**8**	2	1.54	$p < 0.001$[c]
	MSF	126	**78**	7	0	**41**	0	2.03	
CT	Non-MSF	25	15	6	1	**2**	1	2.34	$p < 0.01$[c]
	MSF	71	60	9	2	**0**	0	1.37	

[a] Species codes: black-throated tit (BTT), coal tit (CT), flamecrest (FC), Taiwan fulvetta (TF), Taiwan yuhina (TY), white-whiskered laughingthrush (WWL), yellowish-bellied bush warbler (YBBW).
[b] Bolded values represent significant differences ($p < 0.05$) in post hoc chi-squared tests (with the Bonferroni correction) by using the 'chisq.posthoc.test' package in R.
[c] Columns were collapsed due to small sample sizes.

and black-throated tit) expanded their foraging niche in different aspects while foraging in mixed flocks when compared to foraging outside of flocks (Table 2). In general, understory species expanded their foraging range upwards while one canopy species expanded its foraging range downwards when foraging in mixed flocks. This type of niche expansion was also observed in mixed flocks in the Malaysian rainforest (Mansor et al. 2020). In addition, the black-throated tit was found to expand its foraging along branches in mixed flocks.

Interestingly, all of these four species are insectivores. Presumably, insectivores experience more difficulties in winter to obtain sufficient prey within their regular foraging

Table 3. Differences in interspecific niche-overlaps for categories of three foraging microhabitat variables for the 11 common flocking species between inside and outside flocks in montane coniferous forests of Taiwan. Species codes as in Table 2 and Supporting information.

Species	Foraging location			Vertical strata			Horizontal strata		
	MSF	Non-MSF	p-value[a]	MSF	Non-MSF	p-value[a]	MSF	Non-MSF	p-value[a]
FC	0.7 ± 0.4	0.6 ± 0.4	0.2	0.7 ± 0.3	0.3 ± 0.3	< 0.01	0.6 ± 0.3	0.6 ± 0.3	0.89
CT	0.7 ± 0.4	0.6 ± 0.4	0.14	0.7 ± 0.2	0.5 ± 0.3	< 0.01	0.7 ± 0.3	0.6 ± 0.3	0.48
BTT	0.8 ± 0.3	0.7 ± 0.2	0.28	0.7 ± 0.3	0.6 ± 0.2	0.51	0.8 ± 0.1	0.5 ± 0.3	< 0.05
GBT	0.7 ± 0.4	0.6 ± 0.4	0.14	0.6 ± 0.4	0.5 ± 0.3	0.2	0.8 ± 0.2	0.7 ± 0.1	0.05
EN	0.7 ± 0.4	0.6 ± 0.4	0.16	0.5 ± 0.4	0.5 ± 0.3	0.45	0.7 ± 0.2	0.6 ± 0.3	0.16
TB	0.7 ± 0.4	0.6 ± 0.4	0.16	0.8 ± 0.1	0.7 ± 0.3	0.39	0.7 ± 0.3	0.5 ± 0.4	0.05
TF	0.7 ± 0.1	0.5 ± 0.3	< 0.05	0.6 ± 0.3	0.6 ± 0.4	0.72	0.8 ± 0.2	0.6 ± 0.4	0.07
WWL	0.3 ± 0.4	0.3 ± 0.1	0.96	0.5 ± 0.4	0.6 ± 0.4	0.14	NA	0.6 ± 0.4	NA
TY	0.8 ± 0.3	0.6 ± 0.2	0.24	0.7 ± 0.2	0.7 ± 0.3	0.51	0.7 ± 0.2	0.5 ± 0.3	0.26
YBBW	0.7 ± 0.1	0.4 ± 0.4	< 0.05	0.7 ± 0.3	0.6 ± 0.4	0.72	0.6 ± 0.3	0.4 ± 0.4	0.4
GP	0.3 ± 0.4	0.4 ± 0.4	0.06	0.5 ± 0.4	0.6 ± 0.4	0.14	NA	0.5 ± 0.4	NA

[a] Wilcoxon signed-rank test.

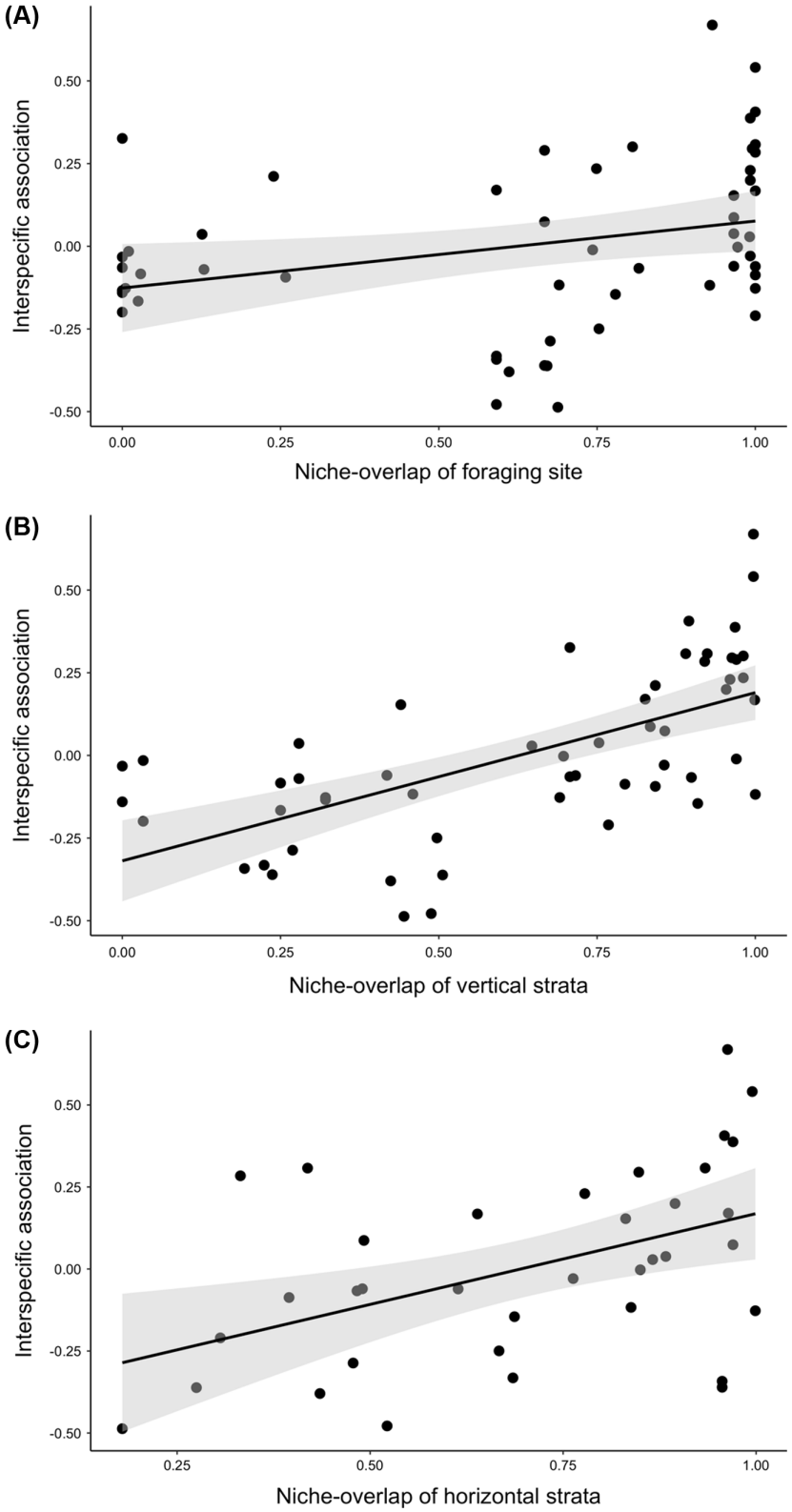

Figure 1. Simple linear regressions between interspecific association (quantified with the modified Cole's coefficient) and niche-overlap among the 11 common attendant species for foraging location (A), vertical strata (B) and horizontal strata (C) in mixed flocks of montane coniferous forests, Taiwan.

niche because prey availability decreases during this period of the year (Chen and Tsai 2005, Mangini and Areta 2018). Therefore, they are more likely to join mixed flocks and expand their foraging niche to increase their foraging opportunities (Morse 1970, Fogden 1972, Poulsen 1996, Mangini and Areta 2018). Joining flocks likely allows participants to expand their foraging outward to reach more food resources possibly because of the corporate vigilance of flock mates (Sullivan 1984, Roberts 1996, Limparungpatthanakij et al. 2019). Mixed flocking is especially noticeable for insectivorous species during the colder winters because they face more challenging conditions than other species which feed, for example, on plant matter (Mangini and Areta 2018).

The two omnivorous species, the white-whiskered laughingthrush and the Taiwan yuhina, reduced their foraging niche breadths instead when foraging in mixed flocks. This may partly be because these two species shift their diet from insects to plant materials during the winter (Chen and Chou 1999, Yu and Yuan 2000). For example, Taiwan yuhinas shift their diet from insects to nectar during the winter, and thus they forage on flowers in blossoming trees most of the time in winter. As a result, they concentrate their foraging on trees regardless of whether they are within a mixed flock or not. Therefore, the decrease in foraging niche breadth of these two species is considered mainly due to their seasonal shifts in food resources, which happens mostly independent of the presence of flocks; accordingly, the flocking frequencies of these two species are rather low (< 15%) anyway when compared to those of the insectivorous species (> 30%). We therefore assume that these two omnivorous species are not as dependent as insectivores on mixed flocks for foraging during the winter.

Another possible reason for niche expansion is competition among flock members due to a significant increase in the number of individuals in mixed flocks (Morse 1970, Austin and Smith 1972). The mean flock size (41.5) of this study is much greater than those recorded in temperate regions (10–17 birds; summarized by Austin and Smith 1972, Lee and Jabłoński 2006). The relatively large flock size may be partly due to the fact that more bird species were participating in mixed flocks in Taiwan than in North America and Europe. Apart from tits, nuthatches and warblers, many oriental bird taxa which join mixed flocks in Taiwan are absent in the avian communities of temperate regions (Ding et al. 2008, Liao et al. 2022). In addition, the conspecific group size is much larger for the nuclear species in our study sites than those in Europe and North America (Austin and Smith 1972, Kotagama and Goodale 2004). As a result, when a couple of these nuclear species participated in mixed flocks, intraspecific and interspecific competitions might have increased several folds for flocking members compared to those foraging outside of flocks. The competitive pressure may then have forced flock participants to shift their foraging beyond their regular niche, especially for subordinate species (Suhonen et al. 1993, Jabłoński and Lee 2002). Accordingly, the foraging niche expansion observed in this study is more conspicuous for nuclear species than for attendant species such as the green-backed tit or the Eurasian nuthatch (Supporting information), both of them with small group sizes.

Nevertheless, the expansion of the foraging location into trees by the yellowish-bellied bush warbler, an understory species, might not result from intraspecific competition because its group size is quite small within a mixed flock (mean 2.2; Table 1). Rather, they are probably attracted by the foraging flock into an unfamiliar space, in this case the subcanopy. Instead of being pushed out from their regular foraging niche due to competition, we assume that they actively move out so that they can benefit from being inside the flock, either for enhanced foraging efficiency or for reduced predation risk, or for both (Diamond 1981, Sridhar et al. 2009, Zou et al. 2011).

At a community scale, a mixed-species foraging flock can thus be considered as an example of 'niche construction,' in which the activity of the nuclear species and its attendant flock creates new niches that can be exploited by attendant species (Harrison and Whitehouse 2011). Although flocking species do not actively modify the physical environment, such as burrow building which is a typical example of physical niche construction (Odling-Smee et al. 1996, Laland et al. 2016), a moving flock does provide beneficial opportunities for attendant species to exploit. In other words, mixed flocks may allow the expansion of the fundamental niche of an attendant species to a larger realized niche (Odling-Smee et al. 2003, Martínez et al. 2018) and thus increase the foraging efficiency of some flocking species (Powell 1989, Bangal et al. 2021). This is one of several ways for attendant species to increase foraging efficiency (Gentry et al. 2019).

Though sally-hovering is an energetic and risky maneuver, flamecrests utilized this behavior five times more often in mixed flocks than outside of flocks. The reason may be that insects are more likely to be flushed or scared off by the moving flock through the beating effect (Moynihan 1962, Munn and Terborgh 1979, Hutto 1994) and thus become easier prey for species that can use aerial foraging maneuvers (Hino 1998, Satischandra et al. 2007, Thomson and Ferguson 2007). Under these circumstances, flamecrests more often resort to hovering, a more profitable foraging maneuver (Norberg 2021), to snatch prey from the peripheral fringes of a tree crown which are not easily reached by other perch gleaners, partly due to its small body size (9 cm in length). However, this conspicuous behavior may also attract a predator's attention and is thus unlikely to be applied frequently outside of flocks (Suhonen et al. 1993). Therefore, flamecrests might be afforded with a vigilance advantage in mixed flocks; otherwise, they likely would not try this conspicuous behavior at exposed sites so frequently (Sullivan 1984, Dolby and Grubb 2000, Thiollay 2003, Ridley et al. 2014). In contrast, the coal tit, a larger nuclear species (body length 10–12 cm), mostly applied perch gleaning and decreased its foraging niche breadth in the mixed flocks. This reduction indicates that the large number of individuals in a mixed flock, especially of the dominant species, not only produce interspecific competition on subordinate species but also exhibit competitive pressure on conspecific

individuals as well. Such interspecific and intraspecific competition might restrain the coal tits to concentrate on their most efficient foraging behavior (Morse 1970). On the other hand, mixed flocking might reduce intraspecific competition of the nuclear species through including more heterospecific species in the flocks (Cestari et al. 2020). This would greatly reduce the conflicts between conspecific individuals because adjacent neighbors of the nuclear species would be mainly heterospecific individuals.

The four flocking species that exhibited significantly higher niche-overlap with other flocking species were actually those with increased foraging niche breadth in mixed flocks. It is reasonable to assume that increasing foraging niche breadth likely increases niche-overlap with other flocking species as well (Hino 1998). On the other hand, the coal tit also showed greater niche-overlap with other flocking species in vertical strata while foraging in mixed flocks. This is because the coal tit is a generalist forager and has the greatest niche breadth in vertical strata. As a result, when other flocking species expand their foraging range in mixed flocks, it is very likely to result in an increased niche-overlap with the coal tit as well, especially in vertical strata. Hino (1998) noted that foraging locations used by flocking species usually become more similar while in mixed flocks, and he also observed an increase in niche-overlaps in various foraging variables for flocking species in Madagascar. In addition, Jones et al. (2020) found that foraging niche-overlaps of flocking species in Florida were significantly higher than expected by chance. These results further confirmed that flocking participants likely expand their foraging niche more in mixed flocks than outside of flocks.

Significantly positive correlations between the interspecific associations of heterospecific pairs of the 11 common flocking species and their corresponding niche-overlaps were observed for all three foraging microhabitat variables, especially in vertical strata. This implies that the greater the foraging niche-overlap of two flocking species is, the higher the chance is that both will appear together in the mixed flocks. As a result, foraging niche-overlaps with the nuclear species or other regular attendant species might be a prerequisite for attendant species to join mixed flocks (Jones et al. 2020). Similarity in foraging niche with other flocking species might result in more activity matching and foraging opportunities instead of competition, and thus a greater interspecific association (Sridhar et al. 2009, Hsieh and Chen 2011).

Based on this analysis, interspecific interactions among flock members are likely dominated by a facilitative relationship. The overall benefits received by flock participants very likely outweigh the overall costs; otherwise, a negative correlation between interspecific association and niche-overlap would occur. On the other hand, interspecific and intraspecific competition would induce flock participants to shift their foraging niches in order to avoid conflicts at a finer scale (Lee and Jabłoński 2006). This study suggests that facilitation and competition coexist in mixed-species bird flocks. Therefore, in addition to competition, facilitation and predation are also important factors in shaping the community structure of flocking birds (Suhonen et al. 1993).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.z08kprrdc> (Chen et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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