Plantation forestry of Alder-leaf Birch (*Betula alnoides*) affects composition but not interactions of mixed-species bird flocks in southwestern China

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ABSTRACT

Human disturbance impacts mixed-species bird flocks ("flocks"). Unfortunately, the impact on flocks by one large-scale disturbance, plantation forestry, has remained little explored. We examined how plantation forestry of a widespread yet understudied timber species, Alder-leaf Birch (*Betula alnoides*, "birch"), affects the composition and interactions of flocks in the Indo-Burma biodiversity hotspot in southwestern China. We conducted transect surveys to sample flocks in birch plantations and natural forests of two age classes (mature and young). While flock size and species richness per flock were similar across land-use types, rarefied species richness accounting for unequal sampling effort was noticeably higher in mature forests. Furthermore, flock composition differed across land-use types, with differences related to species' morphological characteristics, dietary preferences, and foraging substrates. Specifically, mature forests supported flock participants with large bodies, poor dispersal ability, and a fruit-eating diet. Birch plantations offered equal support to invertivores as both natural forests, and additional support to bark foragers. Lastly, interactions among flocking species quantified by social network metrics were similar across land-use types, suggesting that birch plantations perserved the flocking behavior itself. Our study reveals the conservation potential of birch plantations in supporting invertivorous birds and preserving interactions in flocks. More importantly, it highlights the irreplaceability of mature forests because of their unique species composition. We recommend promoting birch planting without compromising local economies and protecting remnant mature forests through education programs and continued research.

1. Introduction

Interaction networks among different species regulate species distributions (Svenning et al., 2014), provide ecosystem services (Free, 1970), and maintain biodiversity (Bascompte et al., 2006). As important as they are to ecological communities, these networks are challenging to protect because they are vulnerable to human disturbance (Valiente-Banuet et al., 2015). At the same time, because interaction networks involve more than one species, protecting them is an opportunity to protect multiple species at once (Zou et al., 2018). Presenting both a challenge and an opportunity, conserving interaction networks is a crucial component of biodiversity conservation that deserves research

priority (Fuzessy et al., 2022; Leimberger et al., 2022; Tylianakis et al., 2008).

One type of interaction network that has been a conservation focus occurs in mixed-species bird flocks ("flocks"). By participating in flocks, birds gain anti-predation and foraging benefits (Sridhar and Shanker, 2014), which often translate into higher body condition and survival (Dolby and Grubb Jr, 1998). Despite their importance, flocks are often sensitive to human disturbance (Zou et al., 2018). In the Amazonian rainforest, flocks avoid disturbed secondary forests and edge habitats (Mokross et al., 2018), both of which decrease the association frequency among flock members and gradually break down their interaction networks (Mokross et al., 2014). Furthermore, obligate flock participants

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often disappear quickly from disturbed habitats because they are particularly vulnerable to disturbance (Rutt et al., 2020; Van Houtan et al., 2006). Similar to the Amazonian flocking system, flocks in the Western Ghats of India and Sri Lanka also show vulnerability to human disturbance (Mammides et al., 2015). Compared with these regions, flocks in some other parts of the world are more resilient to human disturbance. In the Colombian Andes, for example, even though generalist species replace forest specialists in smaller fragments, the flocking behavior itself persists (Jones and Robinson, 2020). Also, flock participants tend to have higher colonization and lower extinction rates in an array of islands in eastern China that mimic a fragmented landscape (Martínez et al., 2023).

While attention to flock conservation is increasing, our understanding of this topic remains limited concerning one type of human disturbance, plantation forestry. The area of plantation forests has been rapidly increasing worldwide to satisfy the need for timber products (McEwan et al., 2020; Payn et al., 2015). To maximize wood production and reduce management effort, most plantation forests consist of single-species, even-aged stands with oversimplified vegetation structure (Kelty, 2006). Apart from producing timber, plantation forests also contribute to ecosystem service and carbon sequestration (Paquette and Messier, 2010). In contrast, they typically contribute little to biodiversity conservation, especially when compared with natural forests (Stephens and Wagner, 2007). For instance, a recent global meta-analysis has shown that bird species richness and abundance are generally lower in plantation forests than in natural forests (Castaño-Villa et al., 2019). Furthermore, monocultures of exotic timber species are particularly poor habitats because of the reduced vegetation complexity (Bremer and Farley, 2010; Hua et al., 2016). Given their insufficient support for biodiversity, plantation forests may also disrupt interaction networks such as flocks (Zhang et al., 2013).

China has an extensive area of plantation forests, which was last measured to be roughly 46 million ha (FAO, 2020). While covering a massive area, most of these artificial forests provide poor support for biodiversity (Hua et al., 2016). Recently, however, the Alder-leaf Birch (*Betula alnoides*, "birch") has been suggested to possess conservation potential (Williams, 2015). This fast-growing pioneer species occurs naturally in southern China, Indochina Peninsula, and northern Indian Peninsula (Zeng et al., 2006). In addition to its natural occurrence, birch has also been widely planted for commercial timber production, especially in western Yunnan (Dao et al., 2013). Despite its high popularity in the timber industry, birch has not attracted much attention from conservation scientists. Besides one study of mycorrhizal fungi (Jing et al., 2020) and a few studies of plants (Chen et al., 2006; Dao et al., 2013; Wang et al., 2011), we do not know how much biodiversity birch plantations support. With its congeners showing support for biodiversity (Holmes and Robinson, 1981; Patterson, 1993), birch may be a candidate for conservation gains in plantation forestry. Furthermore, because birch generates higher economic value and better protects the soil than many alternative timber species (Lu et al., 2006), it may conserve biodiversity without compromising timber production or ecological restoration as would some alternatives. As plantation forests continue expanding (McEwan et al., 2020), assessing their conservation value becomes crucial, especially for understudied yet promising species such as birch.

Here we study how plantation forestry of birch affects the composition and interactions of flocks in the Indo-Burma biodiversity hotspot in southwestern China. Flocks in this region are particularly interesting because many phylogenetically distant flock members show similar plumage characteristics (Zhou et al., 2022). This plumage convergence may imply a long history of co-evolution among different flocking species (see supplementary figures in Kimball et al., 2023 for example species with convergent plumage). To determine whether such highly coevolved interaction networks disintegrate or persist in birch plantations, we ask 1) how flock size (number of individuals per flock) and species richness differ between birch plantations and natural forests, 2) whether birch plantations and natural forests support distinct flocking species, 3) if flock composition differs between birch plantations and natural forests, which functional traits are associated with these differences, and 4) whether interaction patterns among flocking species persist or change from natural forests to birch plantations.

2. Methods

2.1. Study system

We conducted fieldwork in one landscape centered around Tongbiguan Township (24°36′44.9″N 97°39′25.0″E) in Dehong Prefecture in Yunnan, China. Some of our sampling sites were within the Tongbiguan Provincial Nature Reserve. This region falls into the "tropical and subtropical moist broadleaf forests" biome (Olson et al., 2001). The annual rainfall averages roughly 1500 mm, with a distinct rainy season from May to October (China Meteorological Administration). Furthermore, being part of the Indo-Burma biodiversity hotspot (Myers et al., 2000), this region harbors rich biodiversity across taxa (Fan, 2011). For example, by 2007, 390 species of birds had already been recorded in the Tongbiguan Provincial Nature Reserve alone (Hu and Han, 2007). Despite its tremendous biodiversity, this region is facing a series of threats including plantation forestry (Yang et al., 2004). Sustainably managing plantation forests in this biologically hyperdiverse region carries great importance to conservation.

Studying birch in Dehong is particularly relevant because of its enormous area of birch plantations. While birch planting in this region only started in mid-1990s, the total area of birch plantations reached 0.8 million ha by 2020, a number higher than any other region in China (Dao et al., 2013). Despite the lack of official data, the area of birch plantations in Dehong has substantially surpassed that of many other timber plantations in this region (E. Zhang, pers. comm.). These alternative timber species include Nepalese Alder (*Alnus nepalensis*), Simao Pine (*Pinus kesiya*), and Teak (*Tectona grandis*). While plantations of Chinese Fir (*Cunninghamia lanceolata*) cover a similar area as birch plantations in Dehong (E. Zhang, pers. comm.), this timber species often fails to provide sufficient support to biodiversity (Cai, 2017; Su et al., 2021; Williams, 2017).

2.2. Data collection

2.2.1. Flock surveys

We sampled flocks on 17 transects totaling 12 km across three different land-use types: four in mature forests, five in young forests, and eight in birch plantations (See Table A1 in Appendix for transect information). While mature forests were intact forests that had been protected ever since the Tongbiguan Provincial Nature Reserve was established in 1986 (Fan, 2011), young forests and birch plantations were regenerating forests of roughly 20 years old (Fig. 1). All transects were within the 1000–1700 m elevational band, which is within the natural range of birch in Dehong (800–2000 m, Dao et al., 2013). To avoid mixing different land-use types, we placed transects at least 100 m from any detectable edges or different land-use types. We also separated transects by at least 250 m to ensure their independence (Zuluaga and Rodewald, 2015). Due to landscape constraints, these transects varied from 400 m to 1000 m in length. Nevertheless, transects in each land-use type added up to 4 km, allowing total distance sampled to be equal among land-use types.

In 2021 and 2022, we conducted transect surveys during mornings (8:30–12:00) and afternoons (15:30–18:00) from January to mid-March, a portion of the non-breeding season when flock activity is the highest (Jiang et al., 2020). We avoided sampling flocks around noon because birds are generally less active during this time. During a transect survey, one observer (WZ) searched for flocks by walking at a slow pace of roughly 650 m per hour (Zhou et al., 2019). We defined a flock as a group of birds consisting of two or more species that were <25 m from

Fig. 1. Illustrative photographs demonstrating the typical vegetation structure of a mature forest (A), young forest (B), and birch plantation (C).

each other and moved together for at least 5 min (Hutto, 1987; Latta and Wunderle Jr, 1996). When we encountered a flock, we started observing it until we had detected no new species in the last 5 min of observation. This procedure allowed us to record complete flock composition, thereby accounting for imperfect detection of different species in recorded flocks (Jones and Robinson, 2021). During each flock observation, we recorded all species detected and estimated the number of individuals per species. We identified species by sight and sound. While we recorded flocks during both the initial and return walks along a transect following Jones and Robinson (2021), we only walked one roundtrip to avoid recording the same flocks repeatedly. Whenever possible, we evenly spread out our visits during the sampling period and alternated these visits between the three land-use types to avoid any temporal biases. Lastly, we ensured >15 flocks were recorded in each transect. While one previous study chose five flocks as the minimum requirement for analyses (Mammides et al., 2015), we believed a higher value would more accurately represent the characteristics of flocks on each transect.

2.2.2. Trait data acquisition

We obtained functional trait data from the AVONET database (Tobias et al., 2022). These included two continuous variables, body mass and hang-wing index, and one categorical variable, diet. To prepare for the subsequent analysis of trait-environment interactions (see section *2.3.3.*), we log-transformed body mass to better fit a normal distribution. We also slightly modified the diet categories according to the research platform "Birds of the World" (Billerman et al., 2022), the Elton trait database (Wilman et al., 2014), and our field observations. By doing this, we reduced diet to three categories: invertivore, frugivore, and omnivore. While "insectivore" occurs more frequently in the ornithological literature, we chose "invertivore" because many insect-eating birds in our study also consume non-insect invertebrates such as arachnids (spiders) and annelids (worms). Apart from diet, we also gathered data on species' preferred foraging substrates according to Birds of the World (Billerman et al., 2022) and our field observations. We then assigned species into four foraging substrate categories: aerial, bark, foliage and twig, and general. Among these functional traits, body mass is related to energy and area requirements (Kendeigh, 1970; Pe'er et al., 2014), hang-wing index is linked to dispersal ability (Ausprey et al., 2023; Claramunt, 2021; Sheard et al., 2020), and diet and foraging substrate are associated with ecological niche (Remsen and Robinson, 1990). Because of their ecological relevance, these functional traits may explain species' vulnerability to human disturbance (Newbold et al., 2013).

2.3. Data analyses

2.3.1. Flock size and species richness

To compare the average flock size and species richness per flock among land-use types, we constructed Generalized Linear Mixed Models

(GLMMs) using the *glmer.nb* function from the lme4 package (Bates et al., 2015). These models treated transect as the random intercept to account for transect-level differences. We then fitted each model with a negative binomial distribution (log link) to account for data overdispersion (Lindén and Mäntyniemi, 2011). Using the *glht* function from the multcomp package (Hothorn et al., 2008), we performed post-hoc TukeyHSD tests to examine all pairwise comparisons among the three land-use types. Apart from comparing species richness per flock, we also compared rarefied species richness in each land-use type through a rarefaction analysis following previous studies (Lee et al., 2005; Montaño-Centellas, 2020; Zhang et al., 2013). Unlike these studies, we constructed sample-based, not individual-based, rarefaction curves because our sampling unit was one flock, not one individual. We completed this step using the *iNEXT* function from the iNEXT package (Hsieh et al., 2022). This rarefaction method allowed us to compare species richness with unequal sampling effort. Lastly, we performed a non-parametric Spearman's correlation test to examine the correlation between flock size and species richness per flock.

2.3.2. Species composition

We performed a non-metric multidimensional scaling analysis (NMDS) to determine whether flock composition differed by land-use types. This ordination method organizes transects with similar species composition close to each other in a two-dimensional ordination space. We first constructed a Bray-Curtis dissimilarity matrix using our transect-by-species abundance matrix. In this step, we used the *avgdist* function from the vegan package (Oksanen et al., 2022). Similar to the rarefaction analysis, this method rarified the abundance matrix to account for unequal sampling effort. We then used the *metaMDS* function from the vegan package to calculate the two-dimensional ordination position of each transect on an NMDS plot. To determine if flocking composition was statistically different across the three land-use types, we performed a permutational multivariate analysis of variance (PerManova) with 1000 permutations using the *adonis2* function from the vegan package (Oksanen et al., 2022). To determine if pairwise comparison was significant, we also performed a pairwise permutational multivariate analysis of variance (pairwise PerManova) with 1000 permutations using the *pairwise.perm.manova* function from the RVAideMemoire package (Hervé, 2022). We applied Bonferroni corrections to account for the increased probability of Type I error associated with conducting multiple pairwise comparisons (McCune and Grace, 2002).

2.3.3. Trait-environment interactions

With the compiled functional trait data described in Section 2.2.2, we performed a fourth corner and RQL analysis to determine which traits were associated with differences in species composition among land-use types. This analysis requires three matrices: a site-by-environment matrix (R), a species-by-trait matrix (Q), and a site-by-species abundance matrix (L). The fourth corner refers to the inferred environment-trait interaction (Legendre et al., 1997). To estimate the

environment-trait interaction coefficients, we used the *traitglm* function from the mvabund package (Wang et al., 2012). Following Brown et al. (2014), we applied to our negative binomial regression a least absolute shrinkage and selection operator (LASSO) penalty, which reduced overfitting by shrinking less important interactions.

2.3.4. Interactions among flock participants

We performed a social network analysis to determine whether interactions among flocking species differed across land-use types. We built social networks of flocks using the "Gambit of the Group" method, which assumes interactions among co-occurring individuals (Franks et al., 2010). In building networks, we used two functions from the asnipe package (Farine, 2013): the *get_group_by_individual* function to create flock-by-species matrices based on presence-absence data of each transect, and the *get_network* function to create pair-wise association matrices. The latter function calculates the simple ratio index, which ranges from 0 to 1, with a higher value indicating a more frequent association between species pairs (Farine and Whitehead, 2015). Using the *graph.adjacency* function from the igraph package (Csardi and Nepusz, 2006), we converted these association matrices to igraph objects to calculate five network metrics: 1) mean normalized degree, which measures the average connectedness among species within a flock network; 2) mean weighted degree, which measures network connectedness while considering the interaction strength between species; 3) skewness, which measures the uneven distribution of connections; 4) clustering coefficients, which measure how much two interacting species are part of a highly connected group; and 5) modularity, which measures the formation of subnetworks within a flock network. These five metrics have been repeatedly used in the flock literature to quantify interactions among flocking species (Jones and Robinson, 2021; Mokross et al., 2014; Montaño-Centellas, 2020; Zhou et al., 2019). We performed Kruskal-Wallis tests to compare these network metrics among land-use types. We then performed post-hoc Dunn's tests for pairwise comparisons using the *dunnTest* function from the package FSA (Ogle et al., 2023). We applied Bonferroni corrections to account for increased likelihood of Type I error during multiple comparisons (McCune and Grace, 2002). Both Kruskal-Wallis and Dunn's tests are non-parametric and therefore robust to unequal variances and sample sizes.

Because network data are inherently non-independent (Farine, 2017), we performed 100,000 pre-network null model permutations to generate randomized networks using the *network_permutation* function from the asnipe package (Farine, 2013). We then calculated the same five network metrics from these randomized networks and used them for the Dunn tests. These steps allowed us to determine whether any observed differences in network metrics resulted from social preference or non-social factors (Farine, 2017). While 100,000 was much higher than 1000 or 5000 used by previous studies (Montaño-Centellas, 2020; Zhou et al., 2019), this number allowed our permuted network metrics to better approach normal distributions, which led to more accurate significance tests between our observed vs permuted values. We did not use a number higher than 100,000 because we had reached the maximum computing power that we could access.

We conducted all analyses in R 4.3.0 (R Core Team, 2023). Bird species names followed the Clements Checklist v2022 (Clements et al., 2022). We removed unidentified leaf warblers in the genus *Phylloscopus*, a group notoriously difficult to identify (Irwin et al., 2001). This removal was unlikely to skew our results because it represented only 2 % of all species detections.

3. Results

3.1. Flock size and species richness

We recorded a total of 498 flocks consisting of 113 species from 30 families (Table A2 in Appendix). The GLMM model for flock size

predicted an average of 28.04 (SE = 2.78), 26.00 (SE = 2.34), and 24.42 (SE = 1.81) individuals in mature forests, young forests, and birch plantations, respectively. The difference was statistically indistinguishable across land-use types (Fig. 2 left). According to the GLMM model for species richness per flock, mature forests averaged 7.10 species per flock (SE = 0.53), which was the highest among all three land-use types (Fig. 2 right). This average was significantly higher than the 5.50 species (SE = 0.39) in young forests (TukeyHSD, p = 0.03). However, it did not differ significantly from the 6.11 species (SE = 0.35) in birch plantations (TukeyHSD, p = 0.25). Additionally, flock size positively correlated with species richness per flock (r_s = 0.74, n = 498, p < 0.001; Fig. A1 in Appendix). Lastly, according to the sample-based rarefaction curves, which adjusted for unequal sampling effort, mature forests had more flocking species than both young forests and birch plantations (Fig. 3; see Fig. A2 in Appendix for similar results from individual-based rarefaction curves).

3.2. Flocking composition and trait-environment interaction

Flock composition differed across land-use types (PerManova, F = 3.99, p = 0.001, Fig. 4). These differences were statistically significant in each pairwise comparison (Table A3 in Appendix). Furthermore, land-use types and functional traits interacted in multiple cases, with mature forests showing strong interactions with three functional traits (Fig. 5). Specifically, mature forests positively correlated with body mass, negatively correlated with hand-wing index, and positively correlated with frugivore (interaction coefficient = 0.14, −0.18, and 0.10). These results indicated that mature forests supported large-bodied flock participants, poor dispersers, and fruit-eating species. Interaction between invertivore and any land-use types did not differ across land-use types, suggesting that birch plantations and natural forests equally supported invertivores. Lastly, birch plantations showed a weak but positive correlation with bark foragers (interaction coefficient = 0.06), suggesting that birch plantations provided additional support to bark foragers.

3.3. Interactions among flock participants

All network metrics quantifying interactions were statistically indistinguishable across the three land-use types (Fig. 6). These results indicated that flocking species interacted with each other in a similar way regardless of the land-use type in which they occurred. While the higher mean weighted degree in mature than young forests approached
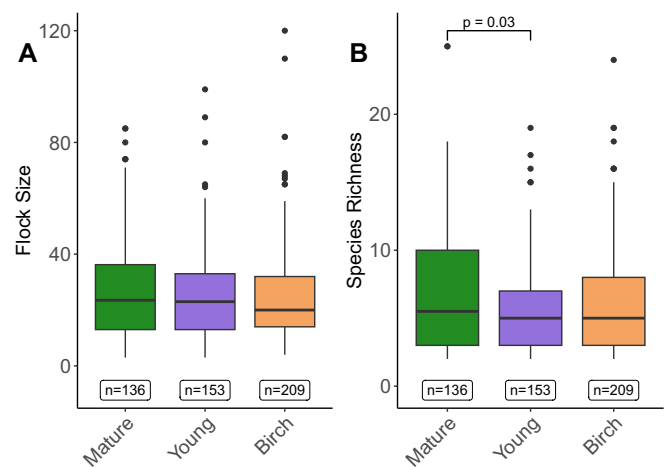
Fig. 2. Boxplots comparing flock size (left) and species richness per flock (right) among land-use types. The rectangular boxes above the x-axis show the sample size. The bracket shows the statistically significant difference in species richness per flock between mature and young forests (p = 0.03).
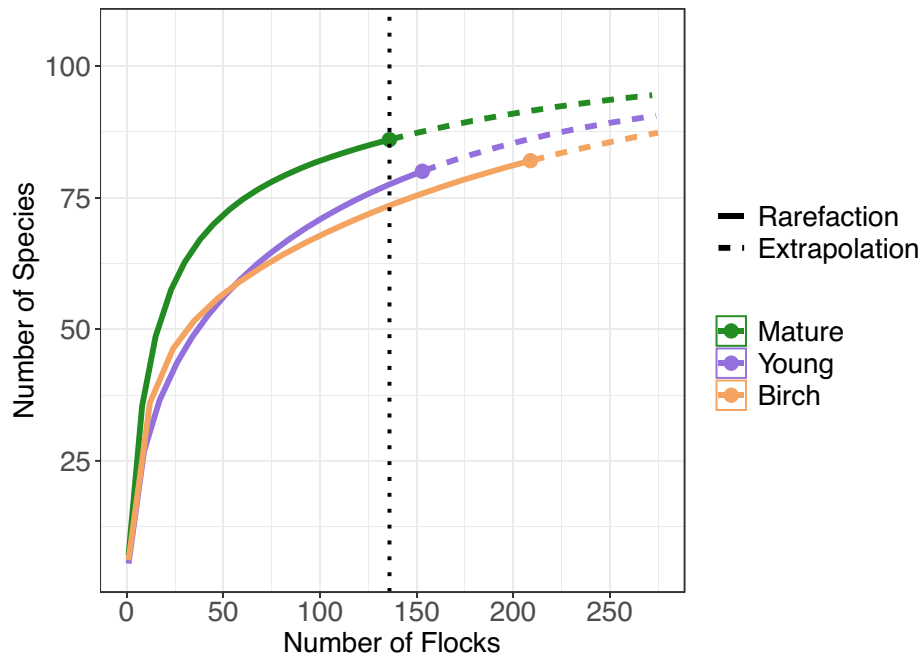
Fig. 3. Sample-based rarefaction curves comparing the rarefied flocking species richness of all three land-use types. The rarefaction component (solid line) of each curve represents the rarefied species richness with any given sampling effort. The extrapolation component (dashed line) of each curve represents the predicted species richness if sampling effort continued. The shaded areas represent the 95 % confidence intervals. The dotted vertical line represents the sampling effort with which species richness can be appropriately compared (n = 136).
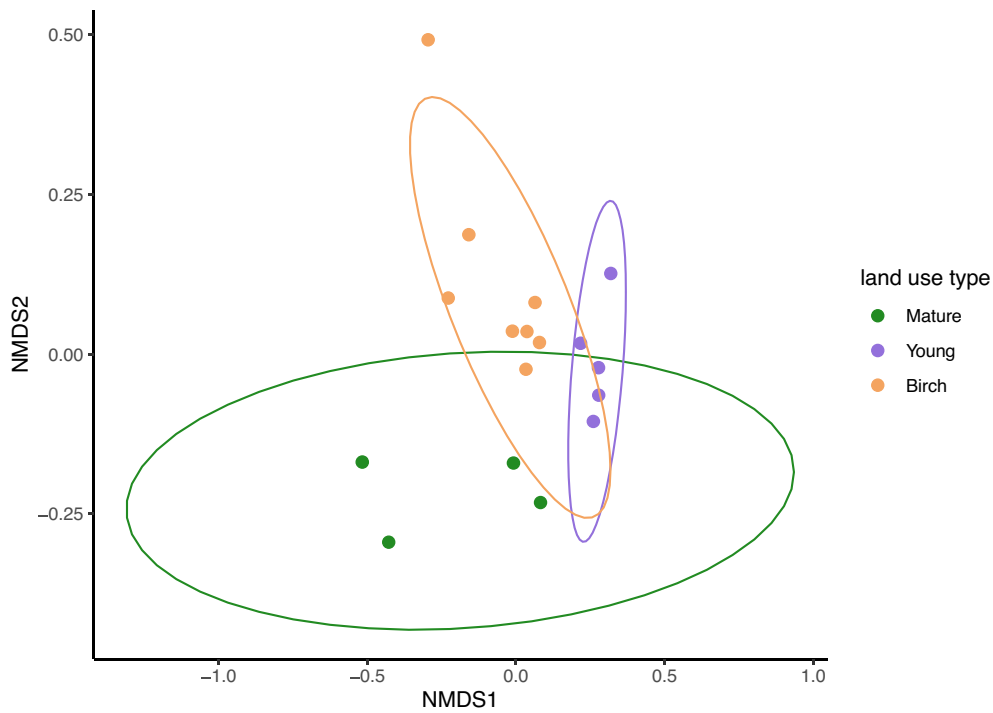

Fig. 4. NMDS plot demonstrating the difference in flocking species composition among land-use types (stress = 0.10). The points represent the 17 different transects.

statistical significance (Dunn's test, p = 0.08), permutation tests revealed that this difference, even if statistically significant, was due to random factors rather than social preferences (Table A4 in Appendix).

4. Discussion

Although species composition of flocks differed across land-use types, birch plantations preserved the interactions among flock participants. Specifically, both birch plantations and young forests lost flocking species with large bodies, low dispersal ability, and a fruit-eating diet. They also had lower rarefied species richness than mature forests. Despite these deficiencies, birch plantations had similar flock size and species richness per flock to mature forests. Also, birch plantations offered equal support to invertivores as both natural forests. More importantly, social network metrics measuring interactions among flock participants were similar across land-use types, suggesting that
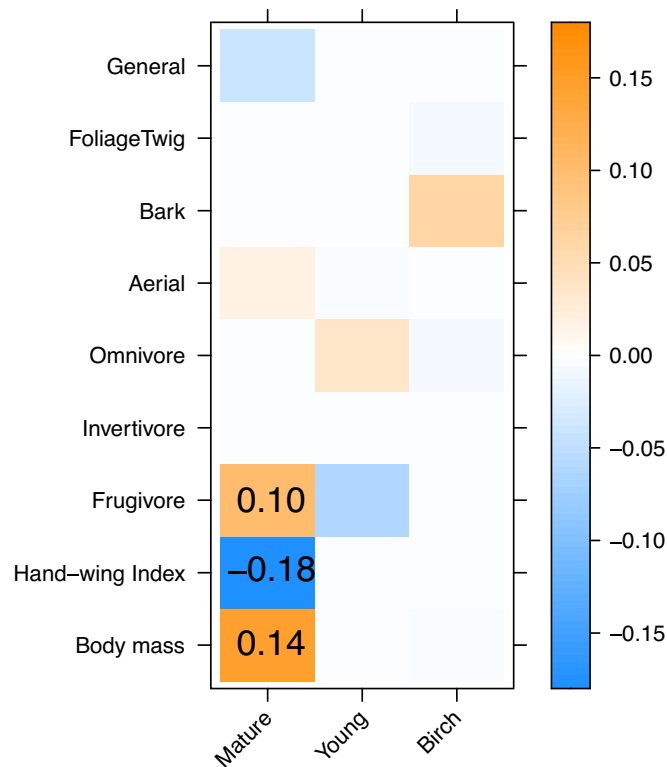
Fig. 5. Trait-environment interaction plot demonstrating the association between functional traits and land-use types. Orange and blue represent positive and negative correlations, respectively. Darker coloration indicates stronger correlation. Coefficients with absolute values greater than or equal to 0.10 are shown in black. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

birch plantations and natural forests provided equal support to the flocking behavior itself. Our study demonstrates the conservation potential of birch in preserving interactions in flocks and the irreplaceability of mature forests because of their distinctive species composition. Below, we discuss our results and propose directions for future studies.

4.1. Largely similar flock size and species richness per flock across land-use types

The overall similar flock size and species richness per flock indicated that birch plantations maintained the basic structure of flocks. However, because sympatric Asian birds often form different types of flocks (Srinivasan et al., 2012; Zou et al., 2011), birch plantations may have supported some flock types but not others (see next section). Our results differed from findings of a previous study in southern India and Sri Lanka (Goodale et al., 2014), which found that flocks in agricultural fields and buffer zones have fewer individuals and species, respectively, than flocks in forest reserves. However, our results echoed those of another study in southwestern China, which found little difference in these two measures across a reserve-buffer-agriculture gradient (Zhou et al., 2019). As no species in our study were on the IUCN Red List (2022), flock participants in this region may be particularly resilient to disturbance.

Young forests had significantly lower species richness per flock than mature forests. This result differed from that of a previous study in Taiwan, which found that "mega-flocks" with more individuals and species are more likely to occur in early-successional pine woodlands than forests of later successional stages (Liao et al., 2022). The authors attributed this finding to the lower canopy height in the pine woodlands. These low-stature habitats have a reduced canopy-to-understory distance, which allows canopy flocks to interact with understory flocks.

While we observed understory and canopy species flocking together in young forests, canopy species there seemed to be less abundant. This decline could be related to the underdeveloped canopy layers in most of our young forests, which reduced the foraging microhabitats available for canopy birds. Some canopy species that became less abundant in young forests were White-bellied Erpornis (*Erpornis zantholeuca*), four minivet species in the genus *Pericrocotus*, two species of nuthatches (*Sitta frontalis & S. nagaensis*), and White-browed Shrike-Babbler (*Pteruthius aeralatus*). The reduced abundance of these canopy species may have contributed to the overall lower species richness per flock in young forests.

Additionally, similar to Goodale et al. (2009), flock size positively correlated with species richness (Fig. A1 in Appendix). More importantly, the rate at which flock size increased in response to increasing species richness was high, which indicated a higher average number of individuals per flock. This pattern likely resulted from the gregariousness of many flock participants in Asia (Goodale et al., 2015). In contrast, flocking species in other regions normally consist of single individuals, pairs, or small family groups (Jones et al., 2020; Munn and Terborgh, 1979), leading to a lower average number of individuals per flock.

4.2. Higher rarefied species richness in mature forests

The higher rarefied species richness in mature forests likely resulted from their complex vegetation structure, which included gigantic trees, uneven canopies, vine tangles, tree ferns, bamboos, snags, and fall nurse logs. Because more complex vegetation structure creates diverse microhabitats for different species, habitats with higher structural complexity typically have higher species richness (Ferger et al., 2014; Sam et al., 2019). One example to illustrate this point is the bamboo-specializing flock consisting of the White-hooded Babbler (*Gampsorhynchus rufulus*), one or two species of scimitar-babblers in the genus *Pomatorhinus*, and the Rufous-headed (*Psittiparus bakeri*) and occasionally Pale-billed parrotbills (*Chleuasicus atrosuperciliaris*). All these species are strongly associated with bamboo habitats. Because bamboos were only found in mature forests in our study area, this type of flock only occurred in mature forests.

Contrary to mature forests, young forests and birch plantations had much simpler vegetation structure. Therefore, they failed to create diverse microhabitats utilized by different species. Additionally, birch plantations offered a limited variety of food resources (mostly invertebrates) and were thereby unable to support bird communities with diverse dietary requirements (see next section). This result concurred with that of a previous flock study in southern China, which found a reduced rarefied flocking species richness in Masson Pine (*Pinus massoniana*) plantations than natural broadleaf forests (Zhang et al., 2013). Similar to our interpretation, the authors also attributed this result to the reduced microhabitat diversity in Masson Pine plantations.

4.3. Trait-driven differences in flock composition

The differences in flock composition across land-use types were likely related to their different habitat quality and food availability. In terms of habitat quality, mature forests provided large and contiguous tracts of undisturbed habitats, which attracted large-bodied birds that have a higher area requirement (Pe'er et al., 2014) and poor dispersers that require unfragmented habitat (Habel et al., 2019). In contrast, the reduced vegetation complexity and overall smaller size of birch plantations could not sustain these birds. Similar to our findings, large-bodied birds also disappeared in plantations of Mangium (*Acacia mangium*) in Malaysian Borneo (Styring et al., 2011). Apart from habitat quality, differences in food availability also led to differences in flock composition. While mature and young forests provided birds with alternative food resources such as fruit and nectar, birch plantation provided mostly invertebrates such as caterpillars. Therefore, birch
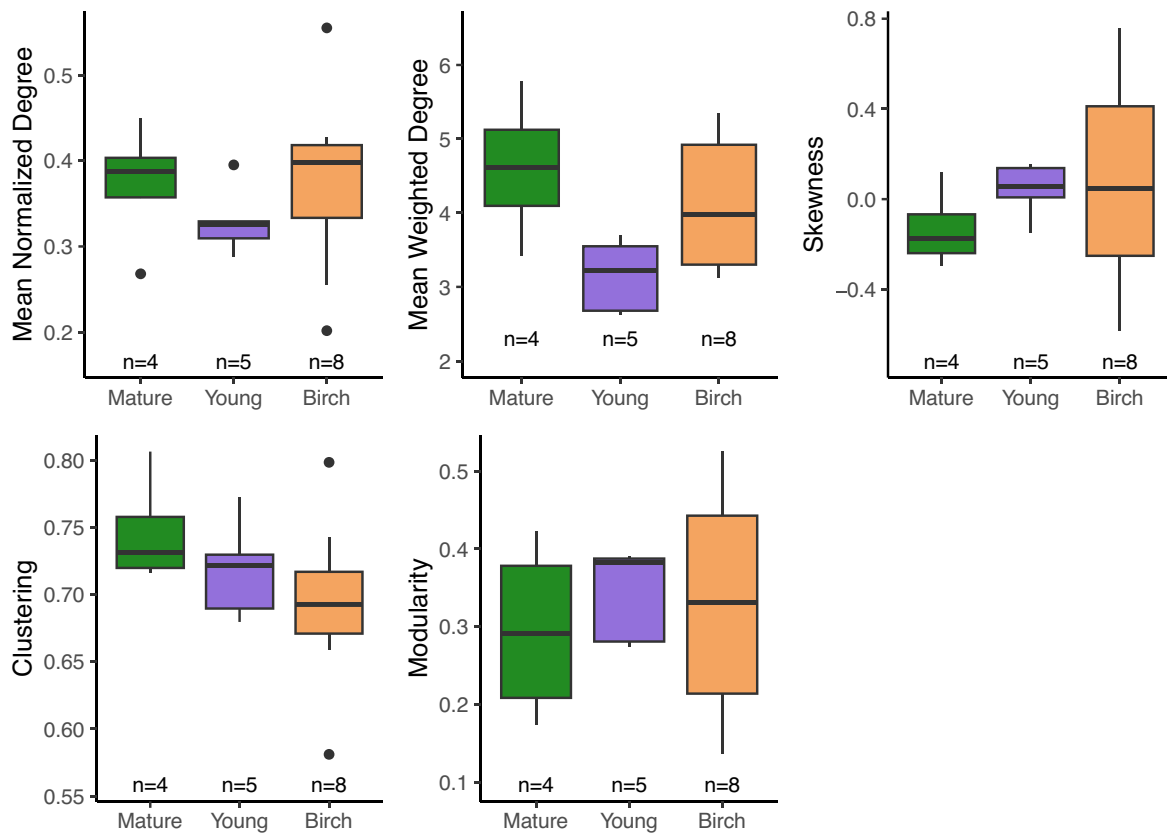
Fig. 6. Boxplots comparing five social network metrics among land-use types. These metrics are mean normalized degree, mean weighted degree, skewness, clustering coefficients, and modularity.

plantations mostly supported invertivorous birds. This result is not surprising because species in the genus *Betula* are known to attract invertebrates, which then attract invertivorous birds (Holmes and Robinson, 1981; Patterson, 1993). Specifically, invertebrates (e.g., caterpillars) are drawn to the soft leaves on which they can easily chew. Also, the peeling bark texture provides them with hiding space, which likely explains birch's additional support for bark-foraging birds. Similar to birch, teak and albizia (*Albizia falcataria*) plantations also provide birds with few alternative food sources other than invertebrates, therefore supporting mostly invertivorous birds (Beehler et al., 1987; Mitra and Sheldon, 1993).

4.4. Persistence of flocking behavior

The persistence of flocking behavior in birch plantations was likely tied to their support for invertivores. Compared to other dietary guilds, invertivores are most vulnerable to predation because their foraging behavior involves constant searching, which reduces the amount of time spent being vigilant. Therefore, to lower their predation risk, invertivores frequently join flocks to gain anti-predation benefits (Sridhar et al., 2009). Because birch plantations supported mostly invertivores, it was perhaps not surprising that flocking behavior persisted there. Additionally, the persistence of flocking behavior could be related to the persistence of nuclear species. These species are important to the formation of flocks and their loss will reduce flock participation from and foraging niche of other species (Martínez et al., 2018). In tropical and subtropical Asia, many fulvettas in the genus *Alcippe* are nuclear species in flocks (Chen and Hsieh, 2002; McClure, 1967; Zhang et al., 2013; Zhou et al., 2019). While these fulvetta-led flocks often decline or become absent in disturbed habitats (Zhang et al., 2013; Zhou et al., 2019), they were abundant in birch plantations.

Our results contrasted with most previous studies, which found altered interaction patterns among flock participants in disturbed

habitats (Borah et al., 2018; Mokross et al., 2014; Vásquez-Ávila et al., 2021; Zhou et al., 2019). However, our results agreed with those of a flock study in the Colombian Andes, which found little effect of fragmentation on the interaction patterns (Jones and Robinson, 2021). While authors of this study attributed their findings to the open-membership nature of Andean flocks, we believe it was the support from birch plantations to invertivores and nuclear species that sustained the flocking behavior in our system.

4.5. Discovery of a new flock type

Besides interpreting our main results, we highlight our discovery of a previously undescribed flock type. This novel association typically consisted of a group of Rusty-capped Fulvettas (*Schoeniparus dubius*) and one or more individuals of Bianchi's (*Phylloscopus valentini*) and/or Martens's warblers (*P. omeiensis*). These species appeared to form the beater-sallier relationship (Swynnerton, 1915). Specifically, as the fulvettas foraged in the understory, the warblers performed aerial maneuvers to take advantage of the extra food made available by the fulvettas' foraging movement. The fulvetta likely acted as a passive nuclear species (Moynihan, 1962), which is often joined by other species and is important to flock formation. This discovery contrasted with the previous view that the Rusty-capped Fulvetta rarely associates with other species (Collar and Robson, 2020). More importantly, while this fulvetta-warbler flock occurred in both young forests and birch plantations, it occurred most frequently in birch plantations where it seemed to have adapted especially well. The well-developed understory layers in birch plantations may have enabled this association.

4.6. Limitations and future directions

4.6.1. Landscape context
Future comparative studies of flocks across different land-use types

should consider the effects of surrounding landscapes. While our study used a buffer distance to separate the focal land-use types from others, flocks may be able to move across land-use types if their home ranges are large enough. On the landscape level, flock participants may be transient birds that only temporarily feed in the focal land-use type. If flocks prefer natural forests to birch plantations, loss of natural forests will reduce flocks in not only birch plantations but also the entire landscape (Mitra and Sheldon, 1993). Therefore, whether flocks visit birch plantations could depend on the availability of nearby natural forests.

To understand flocks' habitat use within a heterogeneous landscape, we suggest conducting flock follows as done in a previous study in the Brazilian Amazon (Mokross et al., 2018). When following flocks, researchers should record not only the total amount of time spent but also movement trajectories in each land-use type. These trajectories may reveal more details about flocks' habitat preference. For instance, slow movement and high turning angles may reflect flocks' strong association with a given habitat (Mokross et al., 2018). Given the steep terrain in our study system, which renders physically following flocks challenging, automated tracking systems will be useful for recording the movement patterns of flocks.

4.6.2. Other plantation forests

Besides birch, our study region has other commercial timber species including Teak and Chinese Fir. We did not consistently survey flocks in plantations of these species because we encountered very few structured flocks there. In particular, we found no flocks in most Chinese Fir plantations during our pilot season. Because these plantations support few bird species (Beehler et al., 1987; Sidhu et al., 2010; Williams, 2017), the scarcity of flocks we observed should be expected. Apart from Teak and Chinese Fir, Nepalese Alder is another timber species used in plantation forestry in southwestern China. While this species enhances soil properties and promotes forest succession (Xia et al., 2023), its support for biodiversity remains poorly known. Future research should systematically study birds and other groups of organisms in different plantations to better understand the conservation values of different timber species. Additionally, future research should consider the profitability of different timber species to local stakeholders. A sustainable afforestation plan will require comprehensive knowledge about not only the biological but also the economic values of these timber species.

5. Conclusion

We demonstrate that while birch plantations fail to support flock participants with large bodies, low dispersal ability, and a fruit-eating diet, they support invertivorous flocking species and preserve the flocking behavior itself. We recommend 1) emphasizing birch in plantation forestry in southern China because of its conservation value and 2) preserving mature forests embedded in agroforestry landscapes because of their unique flocking species communities. To prioritize birch over less biodiversity-friendly timber species, land management authorities should collaborate with local stakeholders to develop sustainable afforestation plans that advocate birch planting without compromising local economies. To protect mature forests, the authorities should not only organize education programs to raise awareness of biodiversity conservation, but also welcome researchers to continue studying the extraordinary biodiversity inside these forests.

CRediT authorship contribution statement

Wenyi Zhou: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Liping Zhou:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Miguel A. Acevedo:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Conceptualization. **Liyan Wang:** Resources, Conceptualization. **Changsheng Zuo:** Resources, Conceptualization. **Zhenghua Yang:** Resources, Conceptualization. **Yang Liu:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition, Conceptualization. **Scott K. Robinson:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110595.

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