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Mixed-species bird flocks re-assemble interspecific associations across an elevational gradient

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Understanding how non-trophic social systems respond to environmental gradients is still a challenge in animal ecology, particularly in comparing changes in species composition to changes in interspecific interactions. Here, we combined long-term monitoring of mixed-species bird flocks, data on participating species' evolutionary history and traits, to test how elevation affected community assemblages and interspecific interactions in flock social networks. Elevation primarily affected flocks through reassembling interspecific associations rather than modifying community assemblages. Specifically, flock networks at higher elevations (compared to low elevations) had stronger interspecific associations (larger average weighted degree), network connectivity (enhanced network density) and fewer subnetworks. A phylogenetic and functional perspective revealed that associations between similar species weakened, whereas connections between dissimilar and/or random species were unchanged or strengthened with elevation. Likewise, network assortativity for the traits of vertical stratum and breeding period declined with elevation. The overall pattern is a change from modular networks in the lowlands, where species join flocks with other species that have matching traits, to a more open, random system at high elevations. Collectively, this rewiring of interspecific networks across elevational gradients imparts network stability and resiliency and makes mixed-species flocks less sensitive to local extinctions caused by harsh environments.

1. Introduction

Understanding how communities respond to environmental change is one of the essential aims of ecology [1,2]. Three non-exclusive mechanisms can summarize these responses, including the alteration of community assemblages (i.e. taxa, functional or phylogenetic composition), changes in species interaction frequencies, and coevolutionary processes and patterns [3–5]. Community–environment interactions generate diverse communities, and play a key role in maintaining biodiversity and ecosystem functioning [6,7]. Fortunately, the development of network theory provides a flexible framework to study community assemblages and species interactions simultaneously [8,9], especially when applied across environmental gradients [3]. Ecological networks consist of nodes connected by edges, where nodes represent the interacting species and edges represent the strength of the interactions among species [9]. However,
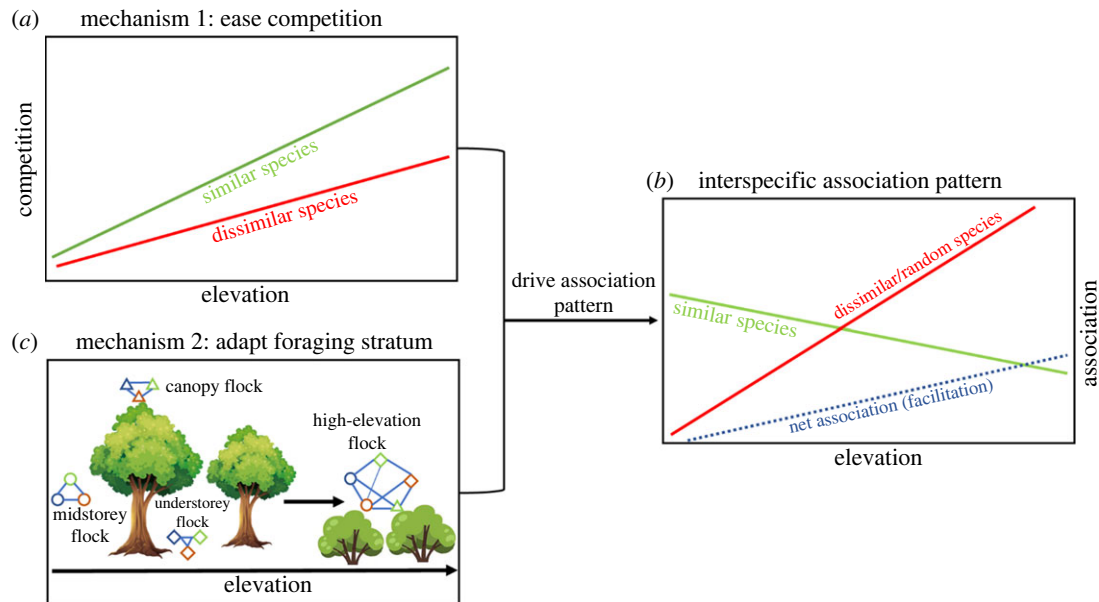
Figure 1. Conceptual illustration of potential changes in the association patterns among mixed-species flocks (MSFs) of birds across an elevational gradient. We assume that increasing elevation generates stress for birds (i.e. harsher physical environments and reduction of resources). In order to buffer environmental stress, facilitative interactions within MSFs can be increased, but this will also increase competition, specifically among similar species that use similar niches (*a*). This mechanism results in a decrease in associations of similar species, but increases in association among dissimilar and/or random species, and an overall increase in net associations (*b*). However, another mechanism that could alter MSF structure is changes in vegetation structure. With increasing elevation, the reduction of vertical vegetation complexity cannot support different flock types; lowland flocks are characterized by separate flock types in which birds chose to flock with other species on the same vertical strata, but montane flocks are less modular, with most species join together one flock system (*c*). In (*c*), the same shape symbols indicate similar species, colours indicate different species. (Online version in colour.)

studies of ecological networks have historically focused on trophic or bipartite interaction networks, such as food webs and mutualistic networks [10–12], with non-trophic associations receiving less attention [13]. The social interactions among species in mixed-species animal groups represent a good example of such non-trophic interaction networks. Over the past decade, network analyses have emerged as an important tool to understand mixed-species group organization and structure [3,9,14], including diverse taxa, such as mammals [15] and birds [16].

Mixed-species bird flocks (MSFs), in particular, represent a model system for studying animal networks and community assembly across ecological gradients [13]. MSFs are defined as 'groups of two or more species that move and forage together' [17], and are found throughout the world, in the non-breeding seasons in temperate regions and in tropical regions throughout the year [18]. MSFs are thought to increase predator avoidance and foraging efficiency [19,20], and to create a novel selection environment structured by interspecific facilitative interactions [21]. Although several studies have now investigated MSF network changes across anthropogenic disturbance gradients [22–27], less research has studied the response of MSFs to natural gradients such as elevation (but see [16,28,29]).

Elevational gradients offer many characteristics that make them suitable for uncovering the underlying causes of spatial variation in species diversity [30]. The simultaneous changes in climatic conditions (i.e. temperature, water) and vegetation (i.e. influence food, habitat) driven by elevational change [31–33], generate varied environments. High elevations may also represent stressful environments. Several factors may produce environmental stress for birds at high elevations, and these factors likely work simultaneously [31]. Low temperature and limited water availability at high elevations might directly

restrict bird survival through physiological constraints [32]. Indirect effects may work through changing vegetation, such as a reduction of vegetative diversity, productivity and canopy height, which could influence food availability and shelter [31,34,35]. Interactions with other species can also shape birds' response to elevation [36]. As the benefits gained by joining a MSF will vary among species and will depend upon habitat context and MSF composition [24,25], these environmental changes with increasing elevation have the potential to restructure MSF networks.

How might MSF networks change across elevational gradients? Generally, studies have provided evidence that with increasing environmental stresses (i.e. when resources are scarce and/or predation risk is high), MSF participation becomes increasingly important for providing foraging and anti-predation benefits [17,37–39], which is in line with the idea that facilitation is more common at higher stress environments [7]. Also, studies have found that MSF behaviour can play a role in buffering environmental stress [24,40]. Hence, it is predicted that MSFs should strengthen overall interspecific facilitation with increasing environmental stress [13], generating more complex networks with more intense interactions at stressful environments like at high elevations, although how competition, especially among similar species, is reduced under such conditions requires further study (figure 1*a*). Apart from measuring the total number of interactions and their strength, one can also investigate what kind of interactions are found in MSFs. For example, one can study whether MSF structure is modular, with certain groups of species interacting together and forming MSF subtypes [16,24]. Further, of all the possible interactions that could occur in MSFs, we would like to understand which specific relationships are found, how similarities among species influence these relationships, and how these factors, too, change across the elevational gradient.

Similarities among species are important modulators of the benefits to the relationships in MSFs [41]. Similarities can strengthen relationships because by joining others with similar foraging microhabitats and speed, termed 'activity matching', birds of multiple species can forage together without extensively modifying their foraging behaviour [42–45]. At the same time, similarities could impose costs, because more similar species compete for the same niches and/or resources [46,47]. Previous studies suggested that niche partitioning by MSF participants and 'checkerboard' co-occurrence patterns between closely related species might ease competition [13,48–50]. Others have emphasized how bird species can be similar in some aspects like diet and body size, but maintain differences in others, like foraging technique, to avoid competition [43].

The idea that competition is lower in stressful conditions leads to a hypothesis that similar species might have less strong associations in MSFs at high elevations (figure 1b), either because of inability to coexist for species that would compete strongly were they in the same MSF, or because stress reduces species' population densities. At the same time, however, the same pattern (dissimilarity of species at high elevations) could be produced by a different mechanism: at low elevations where there are high canopy heights, birds may be able to match their activity with other species of the same vertical stratum (figure 1c), which would not be possible in the smaller high-elevation forest. To distinguish between these two mechanisms, we would want to know whether species have dissimilar associations at high elevations, which would reduce competition, or if high-elevation associations were simply random.

In this study, we combined long-term monitoring of MSFs in the Nanling Mountains in southern China with data on the evolutionary history and traits of MSF participants, to investigate how community assemblages and interspecific associations in MSF networks change along an elevational gradient. We tested whether species pairs with different phylogenetic and functional distances shifted their connections, and which functional traits drive the shifts in species interaction patterns along the elevational gradient. Our previous work in Nanling Mountains, comparing flocking and non-flocking species, demonstrated that the assemblage of flocking birds had consistent diversity and community membership, and showed few trait-environment associations along an elevational gradient, in comparison to an assemblage of non-flocking birds that changed dramatically across the gradient [40]. Thus, we hypothesized that: (i) elevational stress would primarily affect MSFs' networks through reassembling interspecific associations rather than modifying the diversity and composition of the flocking assemblages; (ii) harsh environments would increase the average strength of interspecific associations in MSF networks at high elevations; (iii) competition and/or adaption to a smaller canopy height would cause associations to shift from being between similar species at low elevations to being between random or dissimilar species at high elevations.

2. Material and methods

(a) Study site
This study was conducted in the Nanling National Nature Reserve (NNNR, 112°30′–113°04′ E, 24°37′–24°57′N) in southern China, an important biodiversity ecoregion in China. NNNR has a subtropical monsoon climate and annual precipitation ranges from 1570 to 1800 mm, with the wet season extending from March to August. The average annual temperature is 17.4°C, and the mean monthly temperature ranges from 9°C (January) to 29°C (July). The highest point is 1902 m.a.s.l.

Our survey was conducted along the south slope of NNNR, in the central part of the Nanling Mountains. The forest has been relatively undisturbed since the National Nature Reserve was established in 1994. We established 16 transects ranging in elevation from 347 to 1775 m.a.s.l. (electronic supplementary material, figure S1 and table S1). In addition to bird surveys, ten 10 m × 10 m vegetation plots were established 200 m apart on each transect to understand the change in vegetation structure with elevation (see electronic supplementary material, Methods and Results).

(b) Mixed-species flocks survey
Bird surveys were conducted from 2012 to 2020, in each of the four seasons (generally in April, July, September and January), with sampling evenly distributed across the transects and years. We used both fixed line-transects and point counts, with each transect being 2.5 km long and at a relatively constant elevation, placed along existing forest trails, and being composed of 10 point count locations. Transects were 50 m wide and were walked by two observers in approximately 3 h. Point counts had a radius of 25 m and were conducted for 10 min, counting all birds seen and heard. The bird survey was initiated on windless and rainless days at sunrise and terminated before 10.30. An MSF was defined as 'a roving group of individuals from at least two species, moving in concert and behaving cohesively while foraging,' usually staying within 25 m of each other for at least 5 min [19]. When an MSF was visually detected on transects or at point locations, we recorded the number of species and individuals participating in it, for a maximum time of 15 min.

Data from point count and transect surveys were combined across seasons in the subsequent analysis. In general, seasonal variation in southern Chinese bird flock systems is low [51–53], although flocks can get smaller in the breeding season, presumably because birds are nesting [54]. In this study, breeding season (i.e. spring and summer) flocks tended to be smaller, but there were few significant differences in the size or encounter rate of flocks between seasons at most elevations (electronic supplementary material, figure S2), and no significant differences in the composition of flocks (as judged by PerManova, see statistics section, electronic supplementary material, table S2).

(c) Phylogenetic tree and traits of flocking species
We used the data from the global phylogenetic tree of birds from BirdTree (http://birdtree.org) to make a phylogenetic tree of all the flocking species for each transect [55]. We then sampled 5000 pseudo posterior distributions, and performed Bayesian reconstruction of the maximum clade credibility tree using mean node heights in TreeAnnonator v.1.8.2 of the BEAST package. This estimated the phylogenetic relationships and divergence times simultaneously. Branch lengths on the phylogenetic tree were expressed as an approximate relative divergence time, as estimated by the PATHd8 algorithm (in mya). Support values were derived from 1000 bootstrap replicates. We used the resulting tree for all subsequent phylogenetic and functional analyses (electronic supplementary material, figure S3).

We selected 13 bird species traits that are functionally related to the niches that influence bird life history, habitat selection, resource use and dispersal ability (specifically including foraging, breeding and morphology measurements, electronic supplementary material, table S3). Most of the values for the seven morphological traits were obtained from the measurement of individuals captured by mist-netting in the Nanling Mountains. A few

Table 1. Summary of the three network-level metrics used in the study, how they are defined and what qualities of the networks they represent.

network-level metric	abbreviation	definition	network quality that the metric represents
weighted degree	WD	the sum of the simple ratio index (SRI) for each node	association strength
network density	DEN	the realized proportion of all possible associations. DEN = normalized degree (ND), when using simple ratio index to construct network	connectivity
network modularity	MOD	measures how divided the network is into particular subnetworks	the degree to which the flock is compartmentalized

missing values for the morphological traits were measured on museum specimens (Institute of Zoology, Guangdong Academy of Sciences) collected at nearby sites [56]. Mean trait values were calculated from these individual samples to represent species trait values. The other six traits related to breeding and foraging, including breeding period, clutch size, nest height, dietary guild, habitat specificity and vertical stratum, were obtained from Wang *et al.* [57].

To assess the phylogenetic signal for different traits, we used the Blomberg's K statistic to measure continuous traits, and a generalized least-squares approach for discrete traits [58]. Phylogenetic signal for each trait was considered to be significant if the observed variance of independent contrasts was lower than the variance of at least 95% of the randomly generated trait distributions. These approaches evaluate if traits on a phylogeny are overdispersed, independent, consistent with a model of Brownian motion or conserved. If empirical patterns are consistent with a model of Brownian motion or conserved, traits contain a phylogenetic signal and phylogenetic patterns can be interpreted with regard to those traits. We used the function 'phylosignal' R package 'picante' [59] to compute phylogenetical signals for 11 continuous traits, and the function 'phylo.signal.disc' developed by Enrico Rezende for two categorical functional traits (dietary guild and vertical stratum) [60] in the R statistical environment. In this study, most functional traits exhibited weak phylogenetic signals (except for dietary guild, nest height and dispersal ability, electronic supplementary material, table S3), which implies that most of the traits were phylogenetically independent.

(d) Data analysis

(i) Community assemblage metrics for mixed-species bird flocks

Species richness was calculated for each elevation (i.e. the total number of species seen in all MSFs at that elevation). We also measured Faith's phylogenetic diversity (PD, the sum of the total phylogenetic branch length) by the package 'picante' [59], and functional diversity (functional dispersion, FD), which quantifies the mean distance of individual species to the centroid of all species in the community. Functional dispersion was measured with the dbFD function in the FD package [61].

The significance of relationships between elevation and species richness, phylogenetic and functional diversity, as well as MSF size (number of species and number of individuals), were tested by generalized linear models (GLMs) with Gaussian errors distribution. Non-metric multidimensional scaling (NMDS) was conducted to compare the composition of flocking species for each elevation, and permutational analysis of variance (PerManova), and pairwise a posteriori PerManova analyses with Bonferroni corrections, were calculated to measure whether elevations differed in their NMDS scores [16], including between breeding and non-breeding seasons (see electronic supplementary material, table S2). NMDS was conducted using the 'vegan' package [62].

(ii) Network-level metrics for mixed-species bird flocks

To best represent the elevational gradient and have a dataset that was appropriate for conducting network analysis, we analysed only transects in the central mountain complex and those without strong anthropogenic disturbance. As a result, we used 11 transects (from 500 to 1650 m, electronic supplementary material, figure S1 and table S1) in these analyses. In addition, some species are not MSF participants, but will occasionally appear accidentally in MSFs. Hence, we removed species that only occurred once in the overall sample of MSFs from all transects.

We assumed that any species that occurred in an MSF was associating with all species present in that MSF [24,25]. Based on species co-occurrences in each MSF, we measured association strength using the simple ratio index (SRI) [9]. SRI was calculated as follows:

$$\text{SRI} = \frac{AB}{AB + A + B},$$

where AB is the number of times both species A and B were present, A is the number of times only species A was present and B is the number of times only species B was present. We used the SRI to construct weighted networks for MSFs for each of the 11 transects.

We calculated three network-level metrics to describe network association characteristics (weighted degree, WD), connectivity (network density, DEN) and compartmentalization (network modularity, MOD) for each network from each transect (elevation) (table 1) [16,22,24,25]. WD was calculated as the sum of the SRI for each node (species), indicating the association strength of a species with other flocking species. DEN represents the realized proportion of all possible associations. DEN is equivalent to normalized degree (ND), when using SRI to construct networks. Specifically, degree represents the number of co-occurrences (i.e. network edges) between each node in the network. We normalized each species' degree by dividing it by the total number of possible connections (i.e. the total number of species $n - 1$) to obtain DEN in this study. High average DEN indicates a network with high connectivity. MOD measures how divided the network is into particular subnetworks, quantifying the fraction of connections that fall into given groups minus the expected fraction if links were distributed at random [16]. Higher MOD values indicate that more MSF subtypes exist. Network construction and metric estimation were conducted by the 'igraph' package [63].

(iii) Null models for mixed-species bird flock networks

To examine if our observational networks were likely caused by social interactions and not random associations among flocking species, we constructed null models by permutating raw observational data for MSFs [64]. We first randomized raw MSF data and generated random species by MSF matrices ($n = 9999$), constraining the null models to match the original data in species richness per MSF and species incidence. The randomized

matrices were used to establish weighted networks at each transect, and we also calculated the same three network-level metrics for the permuted data, comparing them with our observational network-level metrics, and considering the observed value to be a significant departure if fewer than 2.5% of the 9999 random values were greater than the observed value, or if more than 97.5% of the random values were greater than the observed value [16]. Network permutation was conducted with the 'asnipe' package [65].

(iv) Network beta diversity

As another measure of how MSF networks responded to elevational change, we measured network beta diversity between networks at adjacent elevations using the 'betalink' package [66]. Total network dissimilarity (β_{WN}) can be partitioned into two components: dissimilarity contributed by the differences in species composition (β_{ST}), or by the dissimilarity in interactions among shared species (β_{OS}). Lennon's dissimilarity metric (β_{SIM}) was selected in this analysis [67], because this metric focuses more on compositional turnover than on species richness, and is less sensitive to richness differences that resulted from sampling biases. Also, a previous study found that β_{SIM} performed better than other metrics when testing for differences across environmental gradients [68]. However, β_{ST} is strongly constrained by the values of β_S (the species composition dissimilarity), which was calculated as

$$\beta_S = \frac{\min(b, c)}{a + \min(b, c)},$$

where a is the total number of species that occur in both networks; b is the total number of species that occur in the neighbouring network but not in the focal one and c refers to the total number of species that occur in the focal network but not in the neighbouring one.

(v) Estimating the relationship between species similarity and frequency of co-occurrence

The phylogenetic and functional distances (dissimilarity) for each pair of flocking species was calculated for each transect. Based on the phylogenetic tree of flocking species for the transect, the pairwise phylogenetic distance was measured through cophenetic distances. Functional distances for all species traits were estimated with a dissimilarity matrix using the Gower dissimilarity index in the 'cluster' package [43]. Trait dissimilarities between species pairs are presented in electronic supplementary material, figure S4. Although phylogenetic signals for most of traits were weak (electronic supplementary material, table S3), phylogenetic and functional distance for species pairs were moderately positively correlated (Pearson's correlation, $r = 0.29$, $p < 0.001$). We then fitted a GLM with Gaussian error distribution to test the effects of elevation, pairwise functional or phylogenetic distance (done in two separate models), and their interactions on the frequency of co-occurrence (the number of times the two species were found together in MSFs) among species:

$$\text{Frequency of co-occurrence} = \beta 0 + \beta_1 \text{distance} + \beta_2 \text{elevation}$$
$$+ \beta_3 \text{distance : elevation}.$$

To test the differences of regression slopes from different elevations, we used an analysis of covariance (ANCOVA), with frequency of co-occurrence as the dependent variable, species phylogenetic or functional distances as covariates and elevation as a grouping factor. A significant elevation × covariate interaction would indicate that the slope of the distance–frequency of co-occurrence relationship differs among elevations. We then extracted the regression slopes at each transect and looked at

their relationships to elevation using GLMs with Gaussian error distributions, for both functional and phylogenetic distance.

(vi) Assortment of traits in mixed-species bird flock networks

To test which functional traits are the main drivers in the relationship between species functional distance and association, we evaluated network assortativity by calculating the assortativity coefficient (r) for each weighted network and trait [69]. The assortativity coefficient measures whether associations are typically between functionally similar or dissimilar species [70], and ranges from −1 (disassortment) to 1 (assortment), with $r = 0$ referring to a random association. We randomly re-allocated the trait value across the nodes in the network 9999 times and calculated the assortativity coefficient for each permutated network to test significance. The p-value is equivalent to the proportion of assortativity coefficients that were larger than the observed coefficient [71].

3. Results

We recorded 185 available MSFs along our 11 transects. A total of 6527 individuals of 32 species were recorded in MSFs. Each MSF contained between two and eight species (mean 3.13 ± 1.54 s.d.). The number of MSFs included in each network ranged from 10 to 27 (16.82 ± 5.67 s.d.; electronic supplementary material, figure S5). Combining all MSFs observed on each transect to build a network for each elevation, the number of species in each network ranged from nine to 20 (mean 14.91 ± 3.05 s.d.), and the total number of individuals ranged from 361 to 1426 (mean 593.36 ± 310.52 s.d.). Network structure was visualized by constructing a network figure for each transect (electronic supplementary material, figure S5).

To summarize the flock system, the most dominant family detected in MSFs was Timaliidae, the babblers; Old World warblers (Sylviidae), bulbuls (Pycnonotidae), minivets (Campephagidae) and tits (Paridae) were also common in MSFs. Huet's fulvetta (*Alcippe morrisonia hueti*) was considered to be the nuclear species in most MSFs, since it was the most frequently detected and abundant species. Most commonly, MSFs were observed in the understorey; however, we also observed a few MSFs of warblers, bulbuls, minivets and tits foraging in the midstorey or canopy, especially at the lower elevations. There were also some regular MSF subtypes, including MSFs that only consisted of the greater necklaced laughingthrush and the lesser necklaced laughingthrush, and MSFs that included strong associations between Huet's fulvetta and the rufous-capped babbler (*Stachyris ruficeps*). These different subtypes were found at all elevations (electronic supplementary material, figure S5).

As to the vegetation, changes in elevation were associated with a change in forest structure. With increasing elevation, forest types change from subtropical evergreen broadleaved forests to montane elfin forests. Tree density increased with elevation; species diversity, and mean diameter at breast height decreased (electronic supplementary material, figure S6a–c). Tree height was also negatively correlated to elevation ($r = -0.41$, $p = 0.01$).

(a) Bird community assemblages and network-level metrics across the elevational gradient

We first examined how community assemblages of flocking species along each transect changed with elevation. Overall,
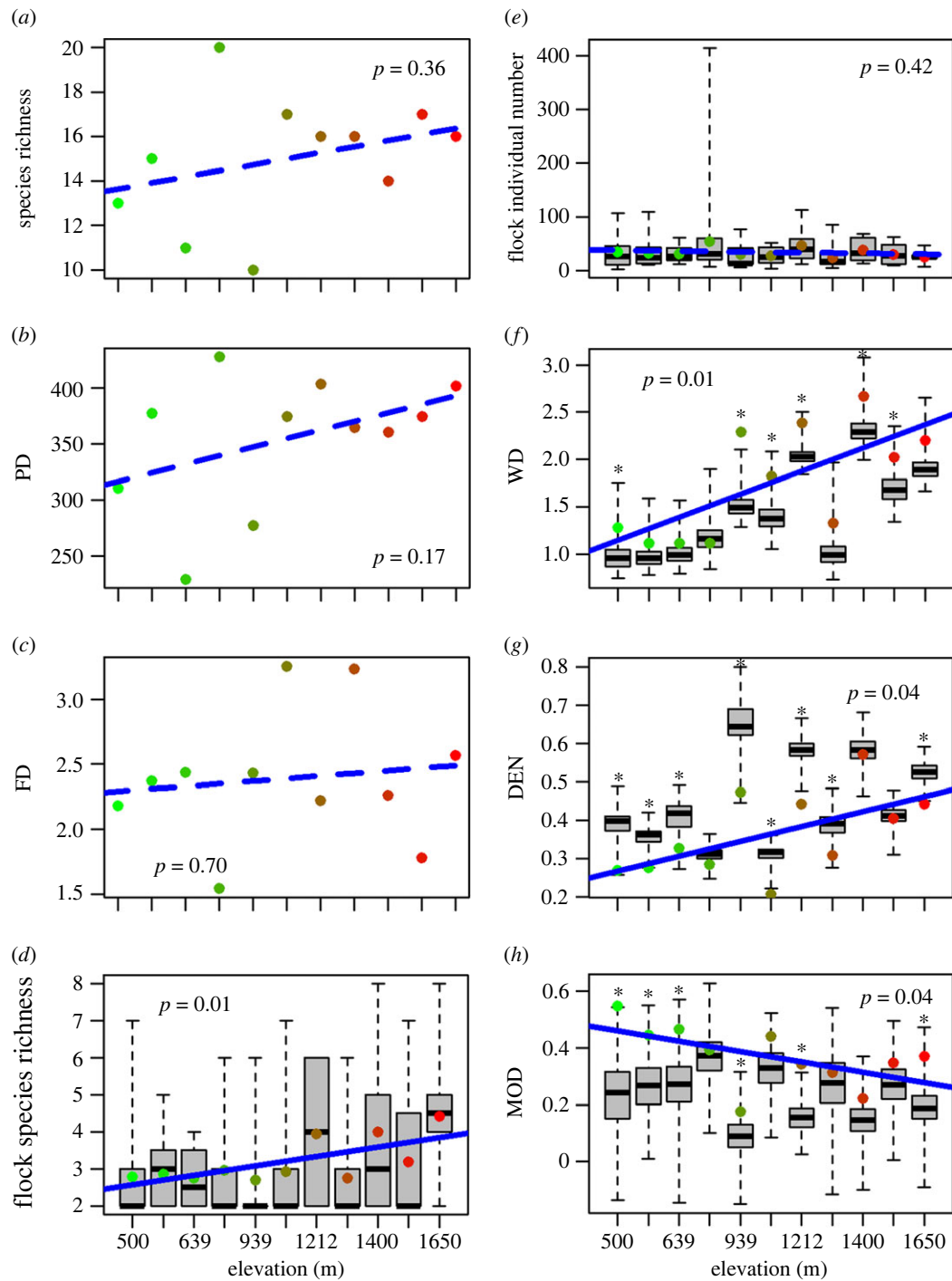
Figure 2. The comparison between community assemblage metrics of flocking species (*a–c*), flock size (*d,e*) and network-level metrics (*f–h*) along an elevational gradient. The community assemblage metrics (calculated for an elevation) include total species richness of all flocks, Faith's phylogenetic diversity (PD), functional diversity (FD, functional dispersion). Flock size is shown as number of species and number of individuals. Network-level metrics are weighted degree (WD), network density (DEN) and modularity (MOD). The boxplots for flock size (*d,e*) represent median ± standard deviation. The boxplots in the network-level metrics (*f–h*) represent median ± standard deviation of values obtained for 9999 randomized assemblages at each elevation. The asterisks above the boxes indicate that the observed values are significant departures from 9999 values generated randomly (*p* < 0.05). Transects at different elevations, from low to high, are presented by colours ranging from green to red (points). Generalized linear models with Gaussian errors were used for significance tests of regressions (blue lines), solid and dotted lines indicate significant and insignificant relationships with elevation, respectively. (Online version in colour.)

community assemblages did not significantly change (*p* > 0.05) in species richness, phylogenetic or functional diversity with increasing elevation (figure 2*a–c*). The number of species per MSF did increase with elevation, but the mean number of individuals did not (figure 2*d,e*). NMDS indicated no significant changes in species composition among transects at different elevations: the results of the PerManova test were non-significant (*p* = 0.59), and

the correlation between the first axis of NMDS and elevation was not significant (Pearson moments correlation, *R* = −0.05, *p* = 0.53, electronic supplementary material, figure S7). Furthermore, the results of pairwise a posteriori PerManova analyses also showed no significant differences among elevations in the composition of their communities, after Bonferroni corrections (*p* > 0.05 in all cases, electronic supplementary material, table S4).
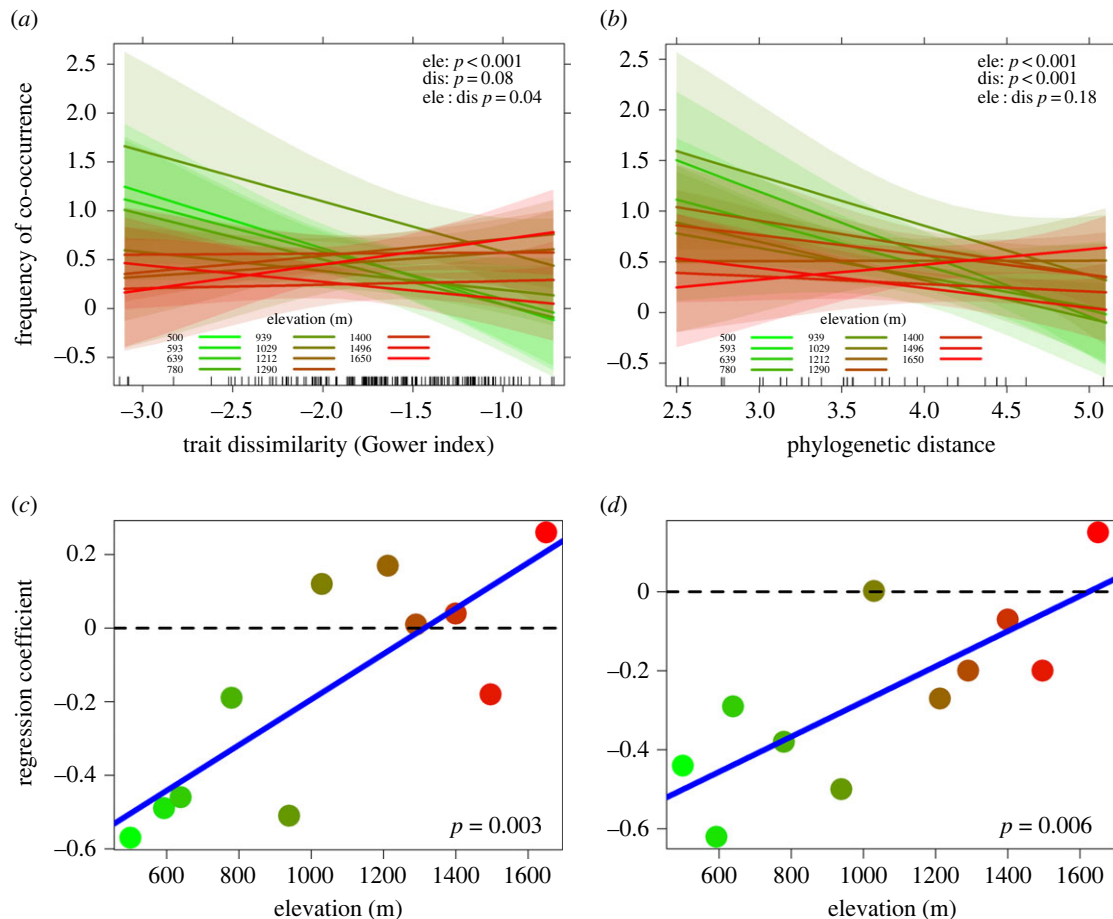
Figure 3. Results of regression models for testing the relationships between pairwise species association strength (frequency of co-occurrence) and trait dissimilarity (a) or phylogenetic distance (b) along an elevational gradient. Transects at different elevations, from low to high, are presented by colours from green to red. The significance of differences between regression slopes was tested by ANCOVA. Data were logarithmically transformed before fitting models. The coefficient for each regression (distance–elevation) for each elevation is presented in the bottom panel ((c) for trait dissimilarity and (d) for phylogenetic distance), and generalized linear models with Gaussian errors were used to test the significance of the relationship between those coefficients and elevation. (Online version in colour.)

However, network metrics significantly changed along the elevational gradient (figure 2). Specifically, the network WD significantly increased with increasing elevation (figure 2f). Network DEN also was larger at higher elevations (figure 2g). In addition, network MOD decreased (figure 2h). In all these cases, our observational network-level metrics differed from null expectations, and the observed value was a significant departure from the 9999 random values ($p < 0.05$) for most transects (see values marked with asterisks in figure 2f–h). These results indicate that social interactions among flocking species changed with elevation, and that the patterns were not produced by random species associations, such as changes in species presence and absence in MSFs in particular habitats (or elevations).

(b) Network beta diversity

We measured network beta diversity turnover between MSF networks at consecutive elevations, to compare the relative importance of species composition and interspecific interactions to dissimilarity. The results showed that species composition dissimilarity (β_S) was very low (0–0.36): β_S in eight out of 10 cases was lower than 0.3 (electronic supplementary material, table S5), indicating a very low dissimilarity between networks at consecutive elevations in their species composition. When β_S is so low, further partitioning β_{WN} into β_{ST} and β_O is not very meaningful [66].

(c) The relationship between frequency of co-occurrence and species-pair distances changed with elevation

When we combined all 13 traits (electronic supplementary material, table S3) and used a Gower index to estimate trait dissimilarity among species within species pairs (electronic supplementary material, figure S3), we found that the coefficients for the relationship between trait dissimilarity and the frequency of co-occurrence tended to change from negative to zero and/or positive with increasing elevation (figure 3a). These results suggest that functionally similar species pairs had decreased interspecific associations (as measured by co-occurrence) at high elevations compared to low elevations. The results of ANCOVA showed that the difference among regression slopes was significant ($p = 0.04$; figure 3a). A similar tendency was observed in the case of phylogenetic distances (figure 3b) in contrast to trait similarity. However, this pattern was not significant when tested by ANCOVA ($p = 0.18$). Extracted regression slopes for each transect significantly increased with elevation, changing from negative to zero and/or positive slopes for both functional and phylogenetic distance (figure 3c,d, $p = 0.003$ and 0.006, respectively).

(d) Network assortativity

Assortativity coefficients (r), indicating the relationship between association and functional similarity, were not
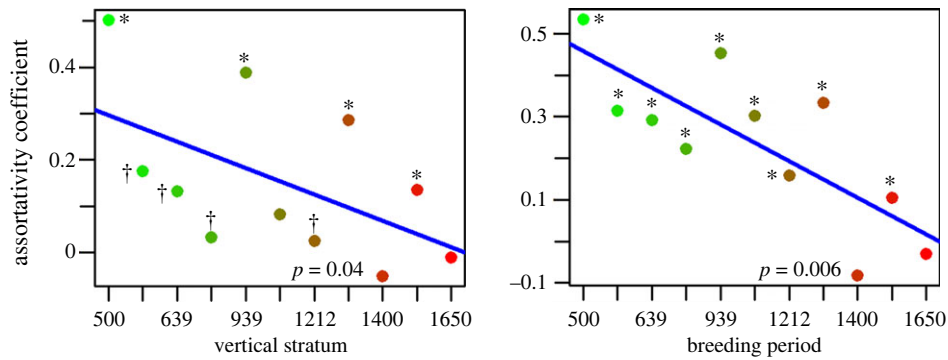
Figure 4. Examples of significant network assortativity coefficients (*r*) for traits along an elevational gradient. *r* ranges from −1 (disassortment) to 1 (assortment), with *r* = 0 representing a random association. The trait value was randomly re-allocated across the nodes in the network (9999 times) and *r* was calculated for each permutated network to test the significance. The *p*-value equals the proportion of assortativity coefficients that were larger than the observed coefficient. Significance (*p* < 0.05) and marginal significance (0.05 < *p* < 0.1) are marked by * and †, respectively. The *p*-values at the bottom of the panels show significance for the relationship between *r* and elevation (univariate linear regression). This figure only shows those traits for which relationships between elevation and assortativity were significant and *r* values at the majority of elevations were significantly different from random; all relationships are shown in electronic supplementary material, figure S8. (Online version in colour.)

significantly different from 9999 permutated networks for most of the traits and elevations (electronic supplementary material, figure S8). However, we observed that assortativity coefficients for tarsus length, breeding period and vertical stratum were significant or marginally significant at most elevations. When we focused on how assortativity coefficients of these three traits changed with elevation, we found that the assortativity coefficients of vertical stratum and breeding period significantly decreased with increasing elevation (figure 4, *p* = 0.04 and 0.006, respectively). That is, assortativity was high in the lowlands, denoting that birds chose to associate with species that were similar in these traits, but assortativity dropped close to zero at high elevations, showing there that the birds did not sort themselves by these traits more than would be expected randomly.

4. Discussion

In this study, we evaluated community assemblages and interspecific interactions of MSFs along an elevational gradient. Our results indicate that MSFs generated more complex networks at high elevations, rather than having altered species composition. However, this was not the only change in network structure across the elevational gradient: associations among similar species weakened with elevation, but connections among dissimilar and/or random species were unaffected or strengthened. Below, we argue that the weight of evidence, especially from the assortativity analysis, indicates that this change was due to assortment among similar species at lower elevations (figure 1*c*), especially those that inhabit the same vertical strata, rather than a direct avoidance of competition (figure 1*a*). Our comparative studies provide novel insights into the links between species associations and elevation, and also have wider relevance for management and conservation of animal species for which interspecific social systems are relevant.

(a) Elevation altered interspecific associations but not community assemblages of mixed-species bird flocks

Previous studies have found a pattern of decline in diversity with increasing elevation in the overall avifauna [32,33].

Whether the diversity and stability (species' persistence) of flocking assemblages can be maintained with increasing elevation, is still an open question, because it has been reported that flocking behaviour can buffer environmental stress [39,40]. Most of the work on this subject has paid attention to how anthropogenic disturbance affects the qualities of MSFs [51], such as in the number of individuals, species richness and encounter rate, with the general result that MSF structure decreases as the intensity of land degradation and fragmentation increase [22,25,52].

There has been less research on the changes in MSFs along natural environmental gradients [16]. Our results showed that increasing elevation did not considerably alter the overall assemblages of the flocking community (figure 2*a–c*) and flock size (figure 2*d,e*), and species composition was generally stable as elevation increased (electronic supplementary material, table S5 and figure S7). However, interspecific associations among MSF members were affected, because their network WD and DEN were significantly raised, whereas MOD was reduced (figure 2*f–h*). These changes in network parameters overall describe stronger average interspecific associations and a more cohesive, less divided network at higher elevations. This result is important because cohesive networks can impart stability to the community, and has high resiliency to species loss and environmental change [72,73].

Our results are similar in some ways to those of Montaño-Centellas [16], who found networks of MSFs were more connected and cohesive at higher elevations. However, Montaño-Centellas showed that the composition of the flocking assemblages was also significantly altered with increasing elevation, resulting from the loss of rare species and their interactions [74,75]. We suggest that the range of elevation might be responsible for these differences in results among studies. The substantially higher elevation (1350–3500 m) of the study of Montaño-Centellas [16] might produce a more stressful environment by imposing extreme energetic constraints [76], which could restrict the survival of many bird species by physiological constraints [32]. This might explain why both flocking assemblages and interspecific associations responded to elevational change simultaneously in the study of Montaño-Centellas [16].

(b) Reduction of vegetation complexity reduces interactions among similar species

Different not mutually exclusive mechanisms might alter the structure of MSF networks along an elevational gradient, and underlie a general increase in the intensity of associations at higher elevations. Specifically, mean temperature and barometric pressure decrease with increasing elevation, so low temperatures could impose an important trade-off between increased starvation and predation risks [77,78], attracting more species and individuals to join MSFs to gain increased vigilance and foraging benefits. Another mechanism could be more directly related to food resources. Productivity, and in particular insects and fruits, often decline with increasing elevation [79,80], and so MSF participation could become more important in providing foraging benefits.

Why did interspecific associations change from being mostly among similar species at low elevations to dissimilar and/or random species pairs at high elevations (figure 3)? The decline in vertical vegetation complexity might be a key factor that drove these interspecific association changes. At low elevations with complex vertical vegetation, species have the ability to 'activity match', joining MSFs with other species that travel in the same vertical strata and speed [43,45]. This could explain why MSFs had distinct composition between canopy and understory subtypes [29]. However, as elevation increases, the vertical height of the trees decreases strongly, and all species may interact together. This idea is supported by the fact that the MSFs became less modular at increasing elevations (figure 2), indicating that higher elevation MSFs were 'open-membership' systems that were less structured than their lowland counterparts [16]. Further, species richness of flocks increased (figure 2d), as one would expect if multiple MSF types at lower elevations dissolved into a single MSF system.

The network assortativity analysis provided further evidence about which traits reduced the co-occurrence of functionally similar species at higher elevations. Intriguingly, we found that the assortativity coefficient of vertical stratum and breeding period significantly decreased with elevation (figure 4). The fact that vertical stratum was significant in this analysis supports the arguments made above that birds are assorting into vertically segregated subgroups at low elevations, and that organization at higher elevations was random. As for breeding period, in our system there is a lull in MSF frequency at the beginning of the breeding season (April, May and June): birds may be able to find MSFs that matched their seasonality in the lowlands, but have fewer options at higher elevations, again with the idea that all species joined together at high elevations in one MSF type.

Two findings suggest that the mechanism of reduced matching of vertical strata at low elevations is a more likely explanation of our results than species directly avoiding competition at high elevations. First, low elevations show a very strong frequency of co-occurrence among similar species and avoidance of dissimilar species; but at high elevations there is not a strong co-occurrence of similar associates, as the avoidance of competition hypothesis would predict. Second, trait assortativity for vertical strata and breeding period is close to zero at high elevations. This implies that the birds are randomly assorting related to these traits, rather the specifically finding partners that are dissimilar

from themselves. Nevertheless, although the mechanism of our results may be related to vertical strata, the competition implications are still there: birds at high elevations are interacting with less similar species and that should result in less competition.

These general patterns can be illustrated by looking at the associations among particular species pairs. The nuclear species *Alcippe morrisonia* occupied a central position in MSFs at most elevations, and the associations between it and *Stachyris ruficeps* played a key role in the formation and maintenance of the MSFs, as these species were connected in all networks (electronic supplementary material, figure S5). But relationships among other species increased with elevation. For example, at high elevations, some connections between relatively dissimilar species occurred or strengthened, such as *Alcippe morrisonia–Parus spilonotus*, *Stachyris ruficeps–Parus spilonotus*, *Phylloscopus goodsoni–Parus spilonotus* and *Phylloscopus goodsoni–Pericrocotus solaris*. Species like *Pericrocotus solaris* are typical of the canopy, and *Parus spilonotus* of the midstorey. So as the forest structure gets simpler at high elevations, understorey, midstorey and canopy species may mix together more freely.

5. Conclusion

Our study supports the findings of the pioneering work of Montaño-Centellas [16] in showing that at higher elevations there are more intense and complex MSF networks. In addition, our functional and phylogenetic analyses allow us to see which interactions change altitudinally, with interactions between similar species declining and interactions between more dissimilar species getting relatively more frequent. We argue that these changes are driven by birds joining MSFs that share their vertical stratum at lower elevations, compared to a more open-membership system at high elevations, but this argument is based on observational data that cannot be used to infer causation. Further work, particularly focused on MSF composition and vertical strata would be fruitful. As to the implications of this work, the ability of associations to re-assemble has been considered as an important feature that could stabilize mutualistic networks against extinction cascades [81]. In MSF networks, this ability might also confer robustness to the network and make MSFs less sensitive to local extinctions in harsh environments [16].

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