Measurement of species associations in mixed-species bird flocks across environmental and human disturbance gradients

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Abstract. In a changing world, it is important to understand how species interactions, such as those among species in mixed-species animal groups, are impacted by human activity. New techniques for measuring associations, in particular social networks and null simulations, have been applied to mixed-species group analyses. Unanswered questions include: (1) How do these methods compare to each other and to the traditional frequency table approach? (2) How similar are associations for the same pair of species in different habitats, such those with different disturbance histories or at different altitudes? (3) What traits of species influence these association strengths? Using data from an intensive study of mixed-species bird flocks in Sri Lanka, we used Mantel tests to compare associations calculated through three methods: the phi coefficient, social networks, and null simulations. Results from the three methods varied ($0.53 < r < 0.75$), but converged when out-of-flock data were added to the phi coefficient and social network methods ($0.75 < r < 0.94$). Correlations between the associations in different habitats were uniformly low (all <0.50) across all methods. These results, when combined with the fact that only a small percentage of the associations were statistically significant (9–14%, depending on the method used), suggest that on average, birds may not have strong preferences for other species in flocks. The trait analysis, conducted using the Multiple Regression Quadratic Assignment Procedure found that species that are more similar to each other in their body mass and diet had higher association strengths. This result was similar to what has been found before in global meta-analyses; however, contrary to earlier reports, in this study association strength increased with increasing phylogenetic distance. The strength of these results decreased when non-statistically significant species associations were included in these analyses or out-of-flock data were excluded, again emphasizing that the method of calculating species associations can influence conclusions. Nevertheless, it is clear that species associations in avian mixed-species groups are not greatly consistent across natural or anthropogenic gradients, although they are influenced to a certain extent by similarities in species traits, especially for species that show statistically significant associations.

Key words: birds; community ecology; disturbance; South Asia; species interactions.

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INTRODUCTION

Interactions among species are critical to community assembly (Gotelli and McCabe 2002) and alter ecosystem function and services (Croll et al. 2005, Potts et al. 2010); hence, measuring species associations has been a key objective for ecology (Dice 1945, Gotelli 2000). Species associations are often used to study the clustering of species along environmental gradients (Peres-Neto 2004, Azeria et al. 2012). However, species associations can also arise when species prefer to interact with each other, and can be used to probe what traits influence these preferences, and whether there are general patterns of organization in species interaction networks (Bascompte and Jordano 2007).

Mixed-species animal groups represent one non-trophic type of species interaction networks that can be understood through species associations. These moving groups can be found infrequently among invertebrates, commonly among specific types of mammals and in shoaling fish, and frequently among birds, especially those of forested habitats (Goodale et al. 2017). Measures of species associations have been used to infer the relative contribution of competition and facilitation on the structure of groups (Graves and Gotelli 1993), the decisions animals make in joining or leaving associations (Farine et al. 2014*a*, *b*), and the presence of key nuclear species that are important for the formation or cohesion of groups (Moynihan 1962, Hutto 1994, Srinivasan et al. 2010, Sridhar et al. 2013, Farine et al. 2015). A global meta-analysis found that species more similar to each other in body size and diet were more likely to associate, and further that congeneric species were more likely to be associated than non-congeners (Sridhar et al. 2012, however, the influence of phylogeny on flocks appears to be complex, Péron 2017).

An important gap in knowledge about species associations is how similar they are in different environmental conditions or in different land-uses of varying disturbance intensity. One pattern that has been noticed in plant communities is that non-random associations, both positive and negative, grow stronger over ecological succession as the communities get more mature (Soro et al. 1999, Larsen and Ormerod 2014). A second pattern is that positive associations between plants become stronger in stressful environments due to increased facilitation and reduced competition (He et al. 2013). However, investigations of species associations across environmental gradients are particularly rare in animal mixed-species groups (but see Mokross et al. 2014). The question is of more than theoretical importance: For example, one management plan to conserve flock systems is to protect nuclear species (Mammides et al. 2015), but such a strategy is only applicable generally if the nuclear species are present and maintain their role consistently across different gradients. However, a previous study on mixed-species bird flocks has reported that species roles can change depending on many factors, including habitat and what other species are present (Gram 1998).

Traditionally, measurements of species associations in mixed-species animals groups used tables of co-occurrence in groups and associated chi-square statistics to determine the significance of these interactions (Bell 1983, Hutto 1994). One central weakness of this approach for determining whether species prefer to associate together in mixed-species groups was pointed out by Hutto (1994) when he remarked that positive associations could simply arise if a study site included heterogeneous landscapes and species had similar habitat preferences. Another weakness of this approach includes the differing abundances of species (both inside and outside of groups) that can confound the analysis. Very common species might be recorded as members of the group due to random movements that happen to be in the direction of the group, but actually show no preference to associate together; in contrast, non-associations between rare species may result because species are simply absent and not because they avoid each other.

Two new methods of analyzing species associations have been applied to mixed-species groups recently that address some of the weaknesses of traditional approaches. First, network analyses, which have been used widely to investigate monospecific animal groups (Whitehead 2008), have been used in the mixed-species group context to determine which species are nuclear or central within the whole community (Sridhar et al. 2013), or even to map the position of certain individual birds (Farine and Milburn 2013). The earliest implementation of these techniques did

not include data from individuals outside of groups (Farine and Milburn 2013, Sridhar et al. 2013, Mokross et al. 2014), although the most recent papers have incorporated this kind of data (Farine et al. 2015, Borah et al. 2018). Second, a simulation procedure (hereafter referred to as "null simulations") has been proposed to measure which species are nuclear by comparing the observed co-occurrences to those generated randomly when species availability (i.e., the total abundance of a species in the community, including individuals outside of groups) is taken into account (Srinivasan et al. 2010). No study has, however, yet compared the results of these two methods or compared them to the traditional frequency table approach.

In this project, we had three questions: First the methodological question—How do the social networks and the null simulations methods compare to each other and to frequency tables (specifically, the phi coefficient; Yule 1912)? Second, the broad ecological question—How similar are species associations in mixed-species groups across habitat gradients? In other words, is the strength of the association of a pair of species in one habitat informative about the strength of the association of that same pair in another habitat? Third, the more specific ecological question—What traits of birds shape the strength of the associations among the species pairs in our region?

To address these questions, we use a large dataset on the composition of mixed-species bird flocks, as well as the density of birds (including outside-of-flock data) in three types of land-uses (forest, buffer, and agriculture) and across different altitudes in Sri Lanka (specifically comparing among low, middle, and high altitudes, Goodale et al. 2014, Mammides et al. 2015). At any one transect, we only use information from relatively homogenous habitats, thus making it unlikely that habitat affinities are driving the species associations, the problem pointed out by Hutto (1994) and discussed above. Our modeling approach followed three steps: First (step A), we used data only from flocks in the calculation of the phi coefficient and social networks, as has been traditionally used in the analysis of avian mixed-species flocks (e.g., Hutto 1994); second (step B), we added out-of-flock data to the phi coefficient and social network methods by considering any solitary bird or monospecific group

to also be a flock (the null simulation already had this out-of-flock data); third (step C), we limited the analysis to only statistically significant species associations, judging significance for the phi coefficient and social networks through permutation tests (Farine 2017b), and using the null simulation's own method, as described by Srinivasan et al. (2010).

We had the following hypotheses: First, in comparing the three methods of measuring species associations, we expected the phi coefficient and social network methods to be more similar to each other than to the null simulations, but for the results of the three methods to converge once the out-of-flock data were entered into the first two methods in step B; second, for the comparisons of associations in different habitats, we hypothesized that the correlations between associations in extreme habitats (forest and agriculture, high and low altitudes) would be lower because species associations are dependent to some extent on environmental conditions, and in these comparisons, the environments are most different. Furthermore, species are more likely to be consistently present and abundant in similar habitats than very different ones, and this also influences their associations with other species and the power to detect them. We also hypothesized that comparisons across the anthropogenic disturbance gradient would be in general higher than those along the altitudinal gradient, because in Sri Lanka, there are two different flock systems, one in the lowlands and one in the montane regions, whereas the change along the anthropogenic gradient is less, with flocks in disturbed areas including a nested subset of the species in forest flocks (Mammides et al. 2015). Third, for the traits important to association strength, we hypothesized that they would follow the results of the global analysis (Sridhar et al. 2012), with stronger associations among species of similar size and diet, and also among more closely related species.

METHODS

Study area and data collection

We collected data in four areas of southwestern Sri Lanka, where the vegetation is moist evergreen rainforest (Gunatilleke and Gunatilleke 1990). Parts of this region have been converted to

timber plantations, such as plantations of *Eucalyptus* sp. in montane areas and *Pinus caribaea* in lowland and mid-altitudes. Between December 2006 and January 2009, we sampled 41 transects (24 2-km and 17 1-km) that were distributed across two gradients: altitude, from 90 to 2180 m, and in three land-use categories—relatively undisturbed forests inside reserves, buffer zones (timber plantations or degraded forest) near the reserves' boundaries, and agricultural lands (Table 1). Each transect was mapped as to the specific land-uses encountered on it, with the following habitat categories: I-a, primary forest; I-b, primary forest with some minor disturbance from villagers; I-c, selectively logged forest, regenerated more than 20 yr since logging (there has been a logging moratorium in reserves in the area since the late 1980s); II-a, heavily disturbed forest by villagers (firewood or understory crop); II-b, completely cut and regenerated forest more than 20 yr old; III-c, eucalyptus timber plantation; III-d, pine timber plantation; IV-a, tea; IV-b, home garden; IV-c, other agriculture; V-a abandoned farmland in shrub stage.

For this study, we wanted to use samples of mixed-species flocks that were all made within relatively homogeneous habitats, so that species associations were not largely affected by habitat preferences. Habitats I-a and I-b were combined together, as they were similar in vegetation, as were habitats II-a and II-b. We then used data from any transect/habitat combination that had at least four flock records (n = 30 transect/habitat combinations). The resulting data were uneven in the number of flocks, with more records in forests than buffer and agriculture, and with the most records at high altitudes (see Table 1). This was due to flock density being higher inside forests and especially low in agriculture, as well as being higher at the montane altitudes. Further, mid-altitude and lowland transects in disturbed areas (buffer, agriculture) were highly heterogeneous in the habitats represented on them, limiting the number of flocks in homogeneous patches.

Transects were placed on pre-existing, relatively straight paths or roads, with a minimum distance of 250 m between transects. Any one transect was visited on average seven times over one year. Like most mixed-species flock studies, we assume that if flocks are seen on separate days, they are independent of each other, since birds at least had the opportunity to re-associate with other birds in that morning. Transects were relatively straight and so we were able to be fairly confident that flocks were not resampled. Occasionally, we collected data on flock composition while walking back along the transect, but only in areas at least 500 m from where a flock had been seen that day.

During the surveys, observers recorded all birds seen or heard along the transect and the distance from the transect. They also recorded whether the birds were part of a mixed-species flock, which was defined as at least two species moving in the same direction (Goodale et al. 2009). When a flock was seen, its composition was recorded, along with the distance of the closest individual to the transect. Each flock was

Table 1. Sampling for the project covered all altitudes and three levels of land-use intensity.

Land-use type	High	Middle	Low
Forest			
Transects	7 transects	4 transects	4 transects
Transect/habitat	8 transect/habitat	4 transect/habitat	4 transect/habitat
Flocks	61 flocks	43 flocks	29 flocks
Buffer			
Transects	5 transects	8 transects	4 transects
Transect/habitat	6 transect/habitat	4 transect/habitat	1 transect/habitat
Flocks	47 flocks	17 flocks	7 flocks
Agriculture			
Transects	3 transects	3 transects	3 transects
Transect/habitat	2 transect/habitat	1 transect/habitat	0 transect/habitat
Flocks	9 flocks	8 flocks	0 flocks

Notes: However, mixed-species flock records were unevenly distributed, with more records at high altitude and forest transects. The numbers below show how many transects, transect/habitat combinations, and flocks were recorded in each case.

observed for at least 5 min and a maximum of 15 min.

Calculation of species associations

We calculated the association strength between each flocking pair using three methods: (1) the phi coefficient, (2) social networks, and (3) null simulations. The first method, the phi coefficient, has the longest history (Yule 1912) and is based on the conventional 2 × 2 presence/absence tables. It is calculated as follows (Jackson et al. 1989):

$$\text{Phi coefficient} = \frac{ad - bc}{[(a+b)(a+c)(b+d)(c+d)]^{1/2}}$$

where a is the number of times both species A and species B were present, b is the number of times only species A was present, c is the number of times only species B was present, and d is the number of times neither species A nor species B were present. The phi coefficient ranges from -1 to 1; the larger the number, the stronger the relationship is considered to be. To calculate the coefficient we modified the sp.pair function in the spaa package in R (Zhang 2013).

The second method, also based on species co-occurrences, is related to social networks, which are being increasingly used in community ecology studies (Farine and Whitehead 2015) to assess species importance (e.g., using a centrality measure) and connectedness between species (Whitehead 2008, Sridhar et al. 2013), and to measure species associations (Farine 2013). For the purposes of this study, we measured association strength using the simple ratio index (SRI), as described in Farine and Whitehead (2015). Simple ratio index is calculated as follows:

$$\text{SRI} = \frac{x}{x + y_{AB} + y_A + y_B}$$

where x is the number of times both species A and B were present, y_{AB} is the number of times species A and B were present but not together, y_A is the number of times only species A was present, and y_B is the number of times only species B was present. Note that in our analysis, we did not include a measurement of y_{AB}, as we were only using a flock by species matrix (please see Farine 2017a for details on the method). Simple ratio index ranges from 0 to 1; the larger the value, the stronger the association is considered to be. We

calculated SRI using the get_network function in the asnipe package in R (Farine 2013, 2017a).

In the third method, null simulations, we measured association strength by comparing the observed co-occurrences of flocking species to those expected if species joined flocks randomly based only on their total abundance (Srinivasan et al. 2010). Rather than using raw abundances, we used estimates of density after taking into account detectability with DISTANCE software (Thomas et al. 2010). For a detailed description of the detectability analysis, see Sreekar et al. (2015). For each species, densities of individuals (per ha) were converted into number of groups, by dividing the density adjusted number of individuals by the average group size of that species outside of flocks, because some species join flocks as a group (Srinivasan et al. 2010). These density adjusted data were used to simulate as many null flocks as recorded in the field ($n = 221$). Each simulated flock had as many species as the corresponding observed flock. We repeated the process 999 times to obtain the mean and standard deviation of the simulated co-occurrences for each observed pair. We then used the following formula, from Srinivasan et al. (2010), to calculate association strength:

$$\text{Association Strength} = \frac{O - \mu}{\sigma}$$

where O is the observed co-occurrence, μ is the mean number of simulated null co-occurrences, and σ is the standard deviation of simulated null co-occurrences. Associations calculated by this method result in both negative and positive values that can be beyond the -1 to 1 range of the phi coefficient.

For all three methods, we converted the total species abundance (i.e., inside and outside the flocks) to presence/absence data and used that to identify the transects at which both species of each pair were found. We calculated each pair's association strength by pooling together the data from those transects only. In this way, we excluded from our analysis any lack of co-occurrences that were due to species absences.

Species traits

To assess the effects of species traits on association strength, we used the literature to collect data on body mass and diet. The data on body

mass were extracted from Dunning (2008). For each species pair, we calculated the absolute difference in grams between the associated species. The higher the number, the more dissimilar the species were in terms of body mass. The data on diet were collected from Rasmussen and Anderton (2012) and supplemented with information from the BirdForum (http://www.birdforum.net) when necessary. Each species was classified into one of the following three feeding guilds: insectivores, omnivores, and frugivores. If the species pair had the same diet, then the pair was assigned 0; if the diet of the two species was different, then the pair was assigned 1.

In addition to body mass and diet, we calculated the phylogenetic distance between each pair using the phylogenetic trees described by Jetz et al. (2012) and the dist.phyl function in the ape package (Paradis et al. 2004) in R (R Core Team 2017). We downloaded 1000 trees from www.birdtree.org (Hackett all species; 10,000 trees with 9993 OTUs each) and calculated the phylogenetic distance between species in each pair. We then averaged those values to obtain an overall estimate for each pair. Smaller distances indicated closer phylogenetic relationship between species.

Statistical analysis

Correlations between the three measures of association strength.—To assess how the three methods compared to one another, we used the Mantel test (Mantel 1967), which is suitable for measuring correlations between matrices comprised of non-independent observations (Croft et al. 2011), as in our data where the same species are recorded in multiple pairs. To run the test, we used the mantel function in the vegan package (Oksanen et al. 2017). Each time, we ran 999 node permutations, using the Pearson's coefficient as the preferred correlation method. We considered results statistically significant if the *P*-value was lower than 0.05. We used the same significance level for all the analyses in the study.

Correlations between habitats in association strength.—Using the Mantel test, we measured how consistent associations are in different habitats, by comparing association strength calculated at one altitude or land-use type to the association strength at other altitudes or land-use types. For each altitude and land-use type, we

first pooled together the flocks of the transects belonging to that habitat. We then calculated the association strength for each pair using the flocks in the transect in which both species were found. We did this analysis separately for the three methods (phi coefficient, social networks, and null simulations).

Factors affecting association strength.—To assess the effect of the species traits on the association strength, we used the Multiple Regression Quadratic Assignment Procedure (MRQAP) with Double-Semi-Partialing (Dekker et al. 2007, Farine 2017a). Multiple Regression Quadratic Assignment Procedure is a multiple regression method, which allows for the response and the explanatory variables to take the form of matrices. Like the Mantel test, MRQAP is appropriate for cases in which observations (e.g., species pairs) are not independent from each other (e.g., the same species could be in more than one pair). We ran the regressions, separately for the three association measures, using the mrqap.dsp function in the asnipe package (Farine 2017a). Each time, we ran 99 node permutations. Explanatory variables included difference in body mass, similarity in diet, and phylogenetic distance.

Description of the analytical procedure.—We ran the above three analyses following three analytical steps: In step A, we measured the associations in the case of the phi coefficient and the social networks using only the in-flock-data (i.e., in the same way the two methods have been traditionally applied in avian mixed-species flocks studies). In this step, the null simulation approach was the only method that included the out-of-flock data. In step B, we added to the phi coefficient and the social networks the out-flock-data, by considering each single species and monospecific group as a flock on their own, increasing the number of flocks from 221 to 5920. In step C, we measured the associations as in step B, but this time we excluded from the subsequent analyses all associations that were not statistically significant. For the phi coefficient and the social networks, we measured statistical significance by comparing the observed associations to those calculated from 999 permuted null models (randomized flocks). We generated the null models using the permatswap function (and the quasiswap method) in the vegan package (Oksanen et al. 2017). These null models were generated for each

transect separately, so that impossible combinations of species (ones that were found on different transects of the same treatment) would not occur. An association was considered statistically significant if the observed value was either smaller than the 0.025 quantile or larger than the 0.975 quantile of the values obtained from the null models (Farine 2017*b*). Similarly, for the third method, the null simulations, we considered an association significant if the observed number of co-occurrences was smaller than the 0.025 quantile or larger than the 0.975 quantile of the number of co-occurrences obtained from the simulated flocks (Srinivasan et al. 2010). For the correlations in association strength between habitats, in step C we had very few associations that were statistically significant in both habitats (*n* ranged from 1 to 53). Consequently, we were unable to run the Mantel test on these sample sizes, and therefore, we excluded this analytical step from this particular analysis.

Results

Correlations between the three measures of association strength

When we used only in-flock data, and all associations (step A), we found strong correlations between social networks and phi coefficient ($r = 0.77$; *P*-value = 0.001), and between social networks and null simulations ($r = 0.69$; *P*-value = 0.001; Table 2). The phi coefficient was moderately correlated with null simulations ($r = 0.53$; *P*-value = 0.001). In Table 2, we show the 97.5% percentile of the permuted *r* values, which were much lower than the observed ones, indicating strong statistical significance.

Correlations between the methods increased when out-of-flock data were added to the phi coefficient and social network methods (step B). The phi coefficient and social network results were now very similar ($r = 0.94$; *P*-value = 0.001), and the other two correlations were higher than results from step A (Table 2). A small percentage of the total associations ($n = 1836$) were statistically significant: 14% for phi coefficient and social networks, and 9% for null simulations (we should note that this percentage was relatively consistent between methods and higher than the 2.5% expected when using an upper 97.5% percentile). When we compared methods by using only the associations that were statistically significant for

Table 2. Correlations between the three different methods of calculating species associations (phi coefficient, social networks, null simulations) in mixed-species flocks, and over the three-step analytical sequence.

Step	Methods compared	*n*	*r*	97.5%	*P*-value
A	Phi coefficient–social networks	1448	0.77	0.07	0.001
A	Phi coefficient–null simulations	1448	0.53	0.07	0.001
A	Null simulations–social networks	1836	0.69	0.09	0.001
B	Phi coefficient–social networks	1836	0.94	0.10	0.001
B	Phi coefficient–null simulations	1836	0.85	0.11	0.001
B	Null simulations–social networks	1836	0.75	0.10	0.001
C	Phi coefficient–social networks	266	0.94	0.54	0.001
C	Phi coefficient–null simulations	166	0.86	0.61	0.002
C	Null simulations–social networks	166	0.73	0.57	0.006

Notes: In step A, we included only in-flock data for the phi coefficient and the social networks, the traditional way of using these methods in mixed-species flock research. In step B, we added out-of-flock to these two methods. In step C, we excluded non-statistically significant associations for the methods compared each time. Also shown is the number of complete pairwise observations (*n*) and the 97.5% percentile of the permuted *r* values. A large difference between this value and the observed *r* indicates high significance; *P*-values calculated by the procedure for all but two tests were 0.001, which is the lowest possible *P*-value based on the number of node permutations.

both the two methods compared (step C), the results were very similar to those in step B, but the 97.5% percentile of the permuted *r* values were closer to the observed values, because of the smaller number of associations (Table 2).

Correlations between habitats in association strength

In general, the correlations of the associations between the different habitats were not strong, regardless of the method applied and regardless of whether only in-flock data were used (step A in Appendix S1: Table S1) or whether out-of-flock data were added (step B, Tables 3–5). In none of the 36 tests ran for these steps was $r > 0.50$ (step C was not ran because of small sample sizes, see *Methods*). For step B, there was not a consistent pattern for the extreme habitat combinations (i.e., forest vs. agriculture, high vs. low altitudes) to have lower correlations than the other

Table 3. Correlations in association strength at one altitude or land-use compared to associations at other altitudes or land-uses, when association strength was calculated using the phi coefficient method.

Altitude/land-use	Phi coefficient			
	n	r	97.5%	P-value
High-middle	1124	0.25	0.11	0.001
Middle-low	940	0.43	0.14	0.001
High-low	694	0.26	0.14	0.002
Forest-buffer	1309	0.39	0.10	0.001
Buffer-agriculture	769	0.24	0.14	0.001
Forest-agriculture	748	0.27	0.14	0.002

Notes: This table is the output of analytical step B: It includes out-of-flock data and all associations (for results of step A see Appendix S1: Table S1). Also shown is number of complete pairwise observations (n), the 97.5% percentile of the permuted r values, and the corresponding P-values (see interpretation in the caption of Table 2).

Table 5. Correlations in association strength at one altitude or land-use compared to associations at other altitudes or land-uses, when association strength was calculated using the null simulations method.

Altitude/land-use	Null simulations			
	n	r	97.5%	P-value
High-middle	1124	0.36	0.10	0.001
Middle-low	940	0.47	0.13	0.001
High-low	694	0.20	0.13	0.001
Forest-buffer	1309	0.39	0.10	0.001
Buffer-agriculture	769	0.24	0.11	0.001
Forest-agriculture	748	0.39	0.14	0.001

Notes: This table is the output of analytical step B: It includes out-of-flock data and all associations (for results of step A see Appendix S1: Table S1). Also shown is number of complete pairwise observations (n), the 97.5% percentile of the permuted r values, and the corresponding P-values (see interpretation in the caption of Table 2).

comparisons. Nor were correlations higher on the anthropogenic disturbance gradient than on the altitudinal gradient, as hypothesized.

Factors affecting association strength

The adjusted R^2 values for step C of the analyses assessing the influence of species traits were consistently higher than the other two analytical steps (ranging between 0.13 and 0.24; compared to 0.01–0.07 for steps A and B), and all three methods (phi coefficient, social networks, and null simulations) showed similar results (see Appendix S1: Tables S2, S3 for results from the other two steps). The MRQAP results for the three

Table 4. Correlations in association strength at one altitude or land-use compared to associations at other altitudes or land-uses, when association strength was calculated using the social networks method.

Altitude/land-use	Social networks			
	n	r	97.5%	P-value
High-middle	1124	0.19	0.11	0.005
Middle-low	940	0.39	0.13	0.001
High-low	694	0.20	0.12	0.004
Forest-buffer	1309	0.31	0.10	0.001
Buffer-agriculture	769	0.18	0.12	0.008
Forest-agriculture	748	0.20	0.13	0.004

Notes: This table is the output of analytical step B: It includes out-of-flock data and all associations (for results of step A see Appendix S1: Table S1). Also shown is number of complete pairwise observations (n), the 97.5% percentile of the permuted r values, and the corresponding P-values (see interpretation in the caption of Table 2).

methods showed that the effect of all three explanatory variables on the species associations strength was statistically significant. For mass and diet, greater similarity was related to greater association strength (negative coefficients; Tables 6–8). However, greater phylogenetic distance was related to greater association strength (positive coefficient).

Discussion

We explored three questions in this project. The first question was whether the results of measuring species associations change when using different methods to calculate them. We hypothesized that traditional ways of applying the phi coefficient and social networks, using only in-flock data, would be different from null simulations that incorporated abundances into the models, but that the methods would converge when the out-of-flock data were added to the phi coefficient and the social networks. We found some support for this hypothesis, indicating that the inclusion of out-of-flock data changes the results of species association analyses. Our second question was about how similar associations were across habitats. We found that in general they were low, and neither hypothesis —that (1) extreme habitat comparisons would have lower correlations or (2) the disturbance gradient would have higher correlations than the altitudinal gradient—was supported. Our third question asked what traits of the bird species

Table 6. Regression coefficients showing the effect of each independent variable on the species association strength calculated using the phi coefficient method.

Variable	Phi coefficient ($R^2 = 0.19$, $n = 266$)			
	β	$P(\beta > =r)$	$P(\beta < =r)$	$P(|\beta| < =|r|)$
Intercept	0.0369	0.758	0.242	0.434
Mass (g)	−0.0007	0.000	1.000	0.000
Diet	−0.0624	0.000	1.000	0.000
Phylogenetic distance	0.0014	1.000	0.000	0.000

Notes: This table is the output of analytical step C: It includes out-of-flock data and excludes non-significant associations (for results of step A and step B, see Appendix S1: Tables S2, S3). For each model, the adjusted R^2 is also shown. "$P(\beta > =r)$" represents the probability of the regression coefficient (β) being equal or larger than the permuted value; "$P(\beta < =r)$" represents the probability of the regression coefficient being equal or less than the permuted value; "$P(|\beta| < =|r|)$" represents the probability that the absolute value of the regression coefficient (β) being equal or less than the absolute permuted value.

influence association strength. Here, similar to an earlier global meta-analysis (Sridhar et al. 2012), similarity in size and diet increased association strength, while contrary to that analysis, greater evolutionary relatedness decreased association strength.

Another important part of our results was that the percentage of all associations that were statistically significant was low (9–14%, depending on the method). It is important to understand why these associations were non-significant: Were they non-significant because of inadequate sample size or because the presence of one species did not influence the other? In general, we think that much of the lack of significance was not due

Table 7. Regression coefficients showing the effect of each independent variable on the species association strength calculated using the social networks method.

Variable	Social networks ($R^2 = 0.12$, $n = 266$)			
	β	$P(\beta > r)$	$P(\beta < =r)$	$P(|\beta| < =|r|)$
Intercept	0.0532	0.970	0.030	0.040
Mass (g)	−0.0003	0.000	1.000	0.000
Diet	−0.0335	0.020	0.980	0.030
Phylogenetic distance	0.0006	1.000	0.000	0.010

Notes: This table is the output of analytical step C: It includes out-of-flock data and excludes non-significant associations (for results of step A and step B, see Appendix S1: Tables S2, S3). For each model, the adjusted R^2 and each variable's probabilities are also shown (see interpretation in caption of Table 6).

Table 8. Regression coefficients showing the effect of each independent variable on the species association strength calculated using the null simulations method.

Variable	Null simulations ($R^2 = 0.24$, $n = 173$)			
	β	$P(\beta > =r)$	$P(\beta < =r)$	$P(|\beta| < =|r|)$
Intercept	0.6381	0.687	0.313	0.586
Mass (g)	−0.0250	0.000	1.000	0.000
Diet	−1.2094	0.020	0.980	0.030
Phylogenetic distance	0.0301	1.000	0.000	0.000

Notes: This table is the output of analytical step C: It includes out-of-flock data and excludes non-significant associations (for results of step A and step B, see Appendix S1: Tables S2, S3). For each model, the adjusted R^2 and each variable's probabilities are also shown (see interpretation in caption of Table 6).

to a sample size issue. For example, Farine and Strandburg-Peshkin (2015) suggested that to accurately quantify the relationship between two species, each needs to be observed at least 20 times. Once we have added the out-of-flock data, depending on the method used, 73–74% of our non-significant associations had at least this number of observations. Therefore, it seems that the vast majority of associations among the species pairs in our dataset are non-significant because the two species do not influence each other's presence in flocks. This paints an overall picture of associations among flock members as weak, and a system without many rules about which species must (or cannot) associate together, often incorporating whatever species are found in the area.

Correlations between the three measures of association strength

Traditionally, most mixed-species flocks papers included species association tests based on in-flock data only (Bell 1983, Eguchi et al. 1993, Hutto 1994, Latta and Wunderle 1996, King and Rappole 2001, Péron and Crochet 2009). The initial work using social networks also included only in-flock data (Farine and Milburn 2013, Sridhar et al. 2013, Mokross et al. 2014). This was one area where Srinivasan et al. (2010)'s approach differed from previous work, in that they used abundance data (including out-of-flock data) to produce the simulated flocks. The most recent usage of networks has used out-of-flock data too (Farine et al. 2015, Borah et al. 2018). A concrete example of how abundance data can influence

flock composition is seen in how especially numerous species may be included in flock records although they may not have a strong affinity toward flocks or any species in them. As a flock moves like a wave through the forest, abundant territorially stable species may forage with them temporarily, or their random movement in the direction of the flock may mean that they are counted in the flock observation. Abundant species will consequently be over-represented in flock records.

When we included out-of-flock data into the calculation of the phi coefficient and social networks (going from step A to step B of the analysis), the results of these tests converged with those of the null simulations; results of the phi coefficient and social networks became very close indeed ($r = 0.94$). This is because the out-of-flock data were incorporated by counting solitary birds and monospecific groups as their own flocks, and the n changes from 221 flocks to 5920. Adding this large amount of non-interactive data (single species) made the correlations between methods stronger and the average strength of the associations closer to zero (for phi, they can be on both sides of zero, whereas for social networks, they are always positive). Thus, it must be clarified that the higher correlations in step B do not necessarily mean that the associations were measured more accurately. Going from step B to step C of this analysis did not change the results much, although the sample size was much reduced (Table 2). It seems that the agreement between the methods is similar for statistically significant and non-significant associations.

The take-home message from this analysis is that the inclusion of out-of-flock data into traditional frequency table analysis or social networks changes the results of those methods. From our project, we cannot argue that one approach is more accurate than another because we are just looking at the correlations between the methods, and we do not know in reality what the associations between species are. Nevertheless, Srinivasan et al. (2010)'s argument (also see Borah et al. 2018) that abundance should be incorporated into association analysis makes sense to us, as flocks are a subset of the avifauna as a whole —changes to the species pool available to flock will dictate what occurs in flocks over different environmental gradients (Sridhar and Sankar 2008). For these theoretical reasons therefore we urge inclusion of out-of-flock data. However, researchers should keep in mind that their results with out-of-flock data may not be directly comparable to results in previous studies that have not used this approach.

Correlations between habitats in association strength

In looking at the differences between analytical steps for the habitat consistency analysis, we can see large differences between the results of the phi coefficient for different steps of the analysis: Value are very low in step A (-0.05 to 0.12), and considerably higher in step B (0.24–0.43), where the values are more in-line with the other two methods (Tables 4, 5). The samples size is also much lower for the phi coefficient in step A (Appendix S1: Table S1). This is because when both species are present at a transect, but one of them is absent from the flocks of that transect, the phi coefficient cannot make a calculation because the denominator becomes zero. Adding out-of-flock data, in step B, always made the denominator positive and allowed for as many calculations as the other two methods.

We were not able to calculate step C for this habitat consistency analysis because of the small number of associations that were statistically significant within each habitat level. From the results of the third analysis (see *Factors affecting association strength*), significant associations seem to be influenced more by species traits, and it is thus possible that statistically significant associations in this analysis could be more consistent across habitats. Nevertheless, such significant associations make up only a minor proportion of all associations in the dataset; therefore, at the community level, it is fair to conclude that correlations between habitats were weak.

No patterns (e.g., extreme habitat combinations vs. other combinations, or one gradient being higher than the other) can be seen in the results of step B. To a degree, these results may be affected by some limitations of the dataset, leading to a lack of ability to see differences among habitats. Specifically, the dataset is unbalanced, with some levels of the gradients having fewer flocks (e.g., flocks in buffer, and especially agricultural habitats) and the two gradients being not independent of each other (lowland

forest had especially few buffer and agricultural flocks, see Table 1).

The take-home message, however, is simple: The similarity of the associations across gradients was low, with no calculable correlation higher than 0.5. This means that the association strength of a pair of species in one habitat was not very informative about the association strength of that same pair in another habitat. In other words, supporting the earlier conclusion—based on the fact that most associations are not statistically significant—this is a fluid system, open to different species in different habitats.

One possible caveat in this conclusion of an open system is that not all species play equal roles in flocks. Most systems that have been described have certain nuclear species that appear to be particularly important to flock formation and cohesion (Moynihan 1962, Goodale and Beauchamp 2010). It could be that associations with nuclear species remain consistent while others do not, and that because such associations are a minority of all comparisons, total correlations remain low between habitats (similar to the argument about significant associations made above). However, we did not have the power to test such a hypothesis ourselves, because the nuclear-follower pairs make up a very small proportion of the total number of associations; there were only 125 species pairs that included a nuclear species, and depending on the method used, only 30–49 of those were statistically significant.

Factors affecting association strength

In this third analysis, there was an increase in model fit from step A and step B (shown in Appendix S1: Tables S2, S3) to step C (Tables 6–8), although we must acknowledge that even in step C, only 12–24% of the variation in the strength of the associations was explained. In step C, all three of the methods have the same results (this is not true for the results of step A, see Appendix S1: Table S2). Phylogeny was significant in the results of step C only, diet significant in the results of step B and C, and body size in the results of all three steps. These patterns support the idea that models that include out-of-flock data and exclude non-significant associations are probably best equipped to decipher ecological patterns, at least for species traits that underlie the associations.

The final results are consistent with the idea that mass and diet similarities increase associations, supporting the global meta-analysis (Sridhar et al. 2012) at a different, regional scale. There is now strong evidence that size, in particular, is an important determinant of mixed-species bird flocks. In several locations around the world, it has been observed that there may be multiple flock types in one area, with the size of the average bird seeming to play an important role in distinguishing the flock types (Bell 1983, King and Rappole 2001, Srinivasan et al. 2012), and Colorado and Rodewald (2015) showed clustering of body sizes at a regional scale such as our study. In earlier research on these flock systems, we also found size to be an important factor predicting associations between leading and following species (Mammides et al. 2015). Similarity in diet is probably a less important factor for mixed-species flocks, generally because most species are insectivorous (Goodale et al. 2017), but Sridhar et al. (2012)'s results and our results here imply that the presence of some omnivores and frugivores in a mixed flock might increase the chances of other such species joining.

Our study also found a relationship by which stronger associations were formed between species more dissimilar in their phylogenetic history (at least for step C). This result is contrary to that of Sridhar et al. (2012), who found closer associations between congenerics, and the results of Gómez et al. (2010) who found phylogenetic clustering within Amazonian flocks (see also Graves and Gotelli 1993, who found that some congeneric pairs always avoided each other in Amazonian flocks, although Sridhar et al. 2012 re-analyzed the data and argued that this result only applies to a few strongly negative species associations). However, the disparity between our result and earlier work could be explained by the recent findings of Péron (2017). Péron also found mixed-species flocks to be phylogenetically clustered overall—in five biogeographical regions—but this clustering was less apparent for flocks that were more stable (i.e., found in the same area over a period of days), suggesting that competitive interactions are important in stable flocks (Péron 2017). Flocks in Sri Lanka, especially in forest, are quite stable in this way, often moving in the same areas every day (E. Goodale and S. W. Kotagama, *personal observations*), perhaps driving our result.

Conclusions

We found that if species associations in mixed-species bird flocks are measured using the traditional frequency table approach, using in-flock data only, results will differ than if social networks (also with only in-flock data) or null simulations (following Srinivasan et al. 2010) are used. However, once out-of-flock data are added to the phi coefficient and social networks methods, the results of all three methods converge ($r \geq 0.75$). From a theoretical perspective it makes sense to incorporate out-of-flock data into flock analyses for the reasons explained above. Moreover, because using only significant associations should reduce noise, our recommendation is for analyses to include out-of-flock data and exclude non-significant associations. Indeed, our multiple regression models, that investigated how bird traits influence species associations, had highest fit when they followed these analytical steps. Having said this, while it makes sense to remove these weaker associations when trying to understand species traits that underlie co-occurrence, when exploring other questions non-significant, associations could be retained. For example, these non-significant associations (especially those with higher sample sizes) can improve our understanding of which species, and what proportion of species, do not interact in these communities.

When the three methods were then applied to look at how similar associations were across land-use and altitudinal gradients, all calculable correlations between habitat types were low ($r < 0.50$). Combined with the fact that only a minority of associations were significant (between 9% and 14%, depending on the method), this indicates that the bird flocks are fluid systems in which on average the identity of other species is not very important to decisions of whether to join or not. All three methods showed that in this region, species that were more similar to each other in body mass and diet tended to have stronger species associations, supporting earlier global analyses. However, contrary to earlier studies, species that were more related had weaker associations, a result that might indicate some competition in structuring the community, at least for the minority of species pairs that were significant.

Acknowledgments

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