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Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide

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Positive Relationships between Association Strength and Phenotypic Similarity Characterize the Assembly of Mixed-Species Bird Flocks Worldwide

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ABSTRACT: Competition theory predicts that local communities should consist of species that are more dissimilar than expected by chance. We find a strikingly different pattern in a multicontinent data set (55 presence-absence matrixes from 24 locations) on the composition of mixed-species bird flocks, which are important subunits of local bird communities the world over. By using null models and randomization tests followed by meta-analysis, we find the association strengths of species in flocks to be strongly related to similarity in body size and foraging behavior and higher for congeneric compared with noncongeneric species pairs. Given the local spatial scales of our individual analyses, differences in the habitat preferences of species are unlikely to have caused these association patterns; the patterns observed are most likely the outcome of species interactions. Extending group-living and social-information-use theory to a heterospecific context, we discuss potential behavioral mechanisms that lead to positive interactions among similar species in flocks, as well as ways in which competition costs are reduced. Our findings highlight the need to consider positive interactions along with competition when seeking to explain community assembly.

Introduction

Interspecific competition theory predicts that local communities, either through coevolution or species assortment, will consist of species that are more dissimilar than expected by chance (Dayan and Simberloff 2005). Numerous "assembly rules" (Diamond 1975) have been proposed on the basis of this prediction (Gotelli and Graves 1996; Weiher and Keddy 1999), and empirical support has been found in many cases, although not unequivocally

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(reviews in Gotelli and McCabe 2002; Webb et al. 2002; Cavender-Bares et al. 2009; Weiher et al. 2011). Expectations based on this prediction are currently expressed in terms of trait dispersion (Webb et al. 2002; Cavender-Bares et al. 2009; Pausas and Verdú 2010). Local communities structured by competition are expected to be phenotypically overdispersed (i.e., consisting of species morphologically or ecologically less similar than expected by chance; but see Mayfield and Levine 2010). At regional spatial scales, as habitat heterogeneity increases, the spatial sorting of species on the basis of habitat or environmental requirements (habitat or abiotic filtering) is likely to result in communities that are phenotypically clumped (i.e., consisting of species that are morphologically or ecologically more similar than expected by chance).

Recent work (Cavender-Bares et al. 2009; Pausas and Verdú 2010) has highlighted the need for community-assembly research to move beyond the competition–habitat filtering dichotomy and consider other processes, in particular, positive interactions (sensu Bertness and Callaway 1994). Although the role of positive interactions in communities has long been recognized (e.g., Bertness and Callaway 1994; Bruno et al. 2003), these interactions are rarely included in our conceptual understanding of communities (but see Gross 2008) or in tests of community assembly (Gross 2008). Similar to competition, positive interactions operate mainly at local spatial scales and can result in local community patterns that are similar or opposite to those produced by competition (Cavender-Bares et al. 2009; Pausas and Verdú 2010). Positive interactions between phenotypically similar species, as observed in cases of social information exchange (Seppänen et al. 2007), Müllerian mimicry rings in butterflies (Elias et al. 2008), and plant species that share pollinators (Sargent and Ackerly 2008), can result in phenotypic clumping. On the other hand, facilitation between dissimilar species, such as that observed between nurse-plant species and seedlings (Valiente-Banuet and Verdú 2007) and between fly-catching and gleaning bird species in mixed-species flocks (e.g., Satischandra et al. 2007), can lead to a whole-community pattern that is indistinguishable from that produced by competition. Therefore, local community assembly must be investigated and interpreted with the use of frameworks that account for both competition and positive interactions rather than just the former, as is currently the trend (Elias et al. 2008; Cavender-Bares et al. 2009; Pausas and Verdú 2010).

In this study we used an approach (following Sfenthourakis et al. 2006) that accounts for both negative and positive interactions, to investigate the assembly of terrestrial mixed-species bird flocks (hereafter, "flocks"). Flocks are roving groups of individuals of two or more species that form in response to foraging or antipredatory needs (Greenberg 2000). Flocks form important subunits of bird communities the world over and are gaining attention as useful models with which to investigate patterns and processes in communities in general (Goodale et al. 2010; Knowlton and Graham 2011). Flocks present an ideal system with which to investigate species interactions because, given the local spatial scale, the likelihood of habitat filtering is negligible and the patterns observed are, therefore, most likely the outcome of species interactions. Species interactions at the flock scale can potentially influence patterns at higher organizational levels (Seppänen et al. 2007; Goodale et al. 2010). Flocks are expected to be strongly competitively structured because they usually consist of members of the same foraging guild associating in close spatial proximity (Graves and Gotelli 1993; Gómez et al. 2010). Moreover, flocking propensity is generally higher in seasons when resources are scarce (e.g., Develey and Peres 2000) and when bird densities are enhanced through an influx of migrants (especially in tropical areas); both of these factors increase the likelihood of competition. Therefore, studies so far that have examined flock assembly have done so entirely in the context of competition (Graves and Gotelli 1993; Gómez et al. 2010). On the other hand, behavioral studies have documented positive interactions in flocks in terms of the use of heterospecific social information (Goodale and Kotagama 2005), copying of foraging behavior (Krebs 1973), and direct benefits such as feeding on prey flushed by other species' movements (e.g., Satischandra et al. 2007). Such benefits could in turn lead to higher survival rates for flock participants (Jullien and Clobert 2000). A high prevalence of pairwise positive associations in flocks has also been documented in numerous studies (e.g., Latta and Wunderle 1996a; King and Rappole 2001; Péron and Crochet 2009).

Recent benchmark tests have shown that it is not straightforward to infer relative importance of competition and positive interactions from whole-community metrics of trait dispersion (Ulrich and Gotelli 2012). Therefore, we used a species pairwise approach to investigate flock assembly (Cavender-Bares et al. 2004; Sfenthourakis et al. 2006). By using null models and randomization tests (Gotelli and Graves 1996), we first examined the relationship between association strength and phenotypic similarity of species pairs in flocks. Our measures of phenotypic similarity included body size, foraging behavior, and whether species pairs were congeneric or not. A positive relationship between association strength and phenotypic similarity is indicative of positive interactions between similar species. A negative relationship, however, can indicate either competition between similar species or positive interactions between dissimilar species. Therefore, we also counted the numbers of significant positive and negative

pairwise associations in each flock matrix, which allowed us to infer whether competition or positive interactions might be more important in causing the relationship. Flocks from different parts of the world vary in species composition but are remarkably similar in guild composition and structure; the use of data sets from studies performed in multiple continents allowed us to search for general patterns across species assemblages with different evolutionary histories (Goodale et al. 2010).

Methods

Data Matrixes

We compiled data from 24 studies that recorded the occurrences of species in mixed-species flocks (table 1). Our analysis was restricted to roving flocks of insectivores in terrestrial habitats, which are presumably based on social interactions. We excluded other mixed groups such as those composed of frugivores or army-ant followers, which are aggregations of animals at clumped resources (Greenberg 2000). We surveyed a flock bibliography ($N = 342$; Goodale and Sridhar 2010) to identify studies that had data that met our requirements ($N = 73$, including multiple studies based on the same data). If a study's data had been published, we extracted them directly ($N = 6$); otherwise, we contacted authors to request their unpublished data. Authors of 18 studies responded and agreed to share data. The locations of the 24 studies we ultimately included in our analysis spanned four continents and two island groups (table 1). One or more of the authors of this article were involved in data collection for all of these studies except those by Davis (1946) and Croxall (1976). None of the original studies aimed at examining questions related to community assembly; therefore, data are unlikely to be biased in a particular direction with respect to the hypotheses tested here.

Data were represented as presence-absence matrixes. In each matrix, rows represented species, columns represented flocks, and cell entries indicated presence (1) or absence (0) of a species in a particular flock. For each study, data from different habitats, elevational zones, or noncontiguous patches or from zones with different levels of human perturbation were represented in different matrixes. The result was a total of 55 data matrixes across 24 study sites (available in Dryad: http://dx.doi.org/10.5061/dryad.th198). We did this to minimize the chance that species occurrence in flocks would be influenced by broad habitat preferences (e.g., Péron and Crochet 2009). However, in sites where flocks are known to be vertically stratified (Munn 1985; Srinivasan et al. 2010), we pooled flocks from different strata (understory and canopy) together in the same matrix. This was done because species are known

to join flocks in more than one stratum and flocks from different strata also often forage jointly; moreover, it is possible that vertical stratification of flocks is in itself an outcome of species interactions, which is the main focus of our study.

Given that sampling was restricted to a single season in all cases except one, association patterns are not influenced by seasonal differences in species occurrences. In the data set for Coahuila (Mexico), sampling was mostly performed during the nonbreeding season but briefly extended into the early breeding season. Our overall results remained qualitatively unchanged when this data set was excluded from analysis. A species was included in a matrix only if it had participated in at least one flock in the area circumscribed by that matrix. Our full data set included 803 bird species representing more than 8% of all known bird species. We also recorded latitude, longitude, biogeographical zone (Ethiopian, Nearctic, Neotropical, Oriental, or Palearctic), and occurrence of human habitat perturbation (present or absent) for each data matrix.

Null Models and Randomization Algorithm

We used a null model implemented through the computer program EcoSim (Gotelli and Entsminger 2001) to randomize each data matrix. The use of the null model approach allowed us to control for differences in species' flocking tendencies and quantify species association in comparison to what is expected by chance. Currently, the null model of choice in community ecology is one that retains both row and column totals (Fayle and Manica 2010). In the context of flocks, however, retaining column totals might be biologically unrealistic. Flocks in a data matrix are only a sample; if sampling is repeated, we are almost certain to get a different set of flock richness values. We therefore used a null model that retained species' occurrences in flocks (row totals) as in the observed flock matrix but treated column totals as probabilities. Pairwise species-association strength values calculated by using the two null models were strongly correlated in all data matrixes ($P < .001$ for all 55 data matrixes; see the appendix, available online, for a detailed discussion of null model choice). For each data matrix, 5,000 null matrixes were created.

Calculation of Association Strength

Using the EcoSim accessory software cooc (Sfenthourakis et al. 2006), we counted the number of flocks in which each species pair co-occurred in a real-data matrix and in each of the corresponding 5,000 null matrixes. We then calculated an index of association strength (Srinivasan et al. 2010) for each species pair, as follows:

Table 1: Relationships between association strength and phenotypic similarity and relative proportions of unusual positive (+) and negative (−) pairs in the mixed-species-flock data sets used in this study

Location, type of forest	Flocks	Species	Body size	Standardized effect size Foraging guild	Standardized effect size Congeneric guild	Unusual pairs +	Unusual pairs −	Reference
Brazil:								
Teresopolis								Davis 1946
Secondary rain forest	8	10	.78	−.23[a]	NA	1	0	
Canada:								
Saskatchewan								Hobson and Van Wilgenburg 2006
Budworm-infested mature conifer forest	6	5	−.64	NA	NA	0	0	
Uninfested mature deciduous forest	13	7	−.56	−.56[b]	NA	0	0	
Uninfested young deciduous forest	14	11	.38	−.65[b]	.10[b]	0	0	
Budworm-infested mature mixed forest	25	14	−1.25	−.47[a]	−.60[b]	3	2	
Uninfested mature mixed forest	44	20	1.19	−.52[a]	.77[b]	4	3	
Budworm-infested old mixed forest	57	19	−.11	−.55[a]	−.46[a]	3	6	
Uninfested old mixed forest	17	13	.08	−.56[a]	−.55[a]	0	2	
Uninfested young mixed forest	8	10	.80	.72[a]	−.71[a]	0	1	
Congo:								
Salonga National Park								Péron and Crochet 2009
Lowland rain forest—edge	19	21	**2.60**	.86[a]	2.79[a]	5	0	
Lowland rain forest—interior	31	19	**2.28**	6.07[a]	−.56[a]	5	1	
Ecuador:								
Guandera Biological Reserve								Rodewald and Rodewald 2003
Primary cloud forest	32	21	**2.05**	.19[a]	−.48[a]	10	2	
Secondary cloud forest	18	19	1.54	3.53[a]	2.58[a]	9	4	
Machalilla National Park								Knowlton and Graham 2011
Low-disturbance arid scrub	112	28	1.99	−.61[a]	NA	24	22	
Moderate-disturbance arid scrub	110	22	−.05	**2.65**[a]	NA	24	9	
Low-disturbance tropical dry forest	97	43	**3.41**	.01[b]	1.42[b]	47	48	
Moderate-disturbance tropical dry forest	115	33	**4.25**	−.69[a]	−.56[a]	46	17	
Hawaii:								
Hakalau Wildlife Refuge								Hart and Freed 2003
Old-growth forest	28	8	−1.15	−.67[a]	−.31[a]	1	0	
India:								
Anaimalai Hills								Sridhar and Sankar 2008
Montane evergreen forest	28	22	.54	−.38[a]	.38[b]	1	3	
Midelevation evergreen forest	28	22	.48	−.53[b]	.36[a]	11	3	
Midelevation evergreen forest	38	29	**4.60**	1.35[a]	1.57[a]	18	12	
Lowland evergreen forest	30	44	**2.72**	3.55[a]	7.26[a]	21	7	
Anshi								Sridhar and Shanker, unpublished data[c]
Lowland evergreen forest	188	43	**2.63**	−.04[a]	−.68[a]	117	31	
Arunachal Pradesh								Srinivasan et al. 2010
Lowland evergreen forest	95	43	**11.29**	10.40[a]	8.32[a]	72	58	
Gujarat								Trivedi 2006
Deciduous forest	29	15	**2.03**	−.72[a]	−.12[b]	3	9	
Deciduous forest	32	20	**2.85**	−.67[a]	−.18[b]	3	5	
Parambikulam								Robin and Davidar 2002
Moist deciduous forest	117	41	**3.62**	3.85[a]	−.34[b]	30	16	
Teak plantation	88	37	**7.71**	1.64[a]	−.70[b]	49	25	

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Table 1 (*Continued*)

Location, type of forest	Flocks	Species	Body size	Standardized effect size		Unusual pairs		Reference
				Foraging guild	Congeneric guild	+	−	
Malaysia:								Lee et al. 2005
Fraser's Hill								
Submontane forest—edge	23	23	.19	.06[a]	−.09[a]	7	1	
Submontane forest—interior	23	23	.39	**15.38**[a]	**7.27**[a]	7	13	
Submontane forest—urban	30	19	−1.20	1.67[a]	**7.05**[a]	11	5	
Semengo								Croxall 1976
Coastal forest	14	15	**-2.10**	−.41[b]	**4.53**[b]	4	6	
Lowland rain forest	6	13	**2.03**	−.64[a]	NA	0	1	
Mexico:								
Coahuila								Canales-Delgadillo 2008
Grassland	64	17	.92	.17[a]	−.36[b]	3	3	
El Cielo Biosphere Reserve								Gram 1998
Humid oak-pine forest	9	11	−.74	−.33[a]	−.21[b]	1	0	
Dry pine-oak forest	43	25	**6.52**	**3.26**[a]	1.57[a]	32	1	
Tropical semideciduous forest	23	16	1.33	.04[b]	.24[a]	2	0	
Cloud forest	15	18	−.44	−.19[b]	.72[a]	3	5	
Jalisco								Hutto 1994
Lowland deciduous forest	57	20	1.86	.18[b]	−.25[b]	26	4	
Western Mexico								Hutto 1987
Boreal forest	5	14	−.67	−.60[b]	−.57[a]	0	0	
Deciduous forest	7	5	−.18	NA	−.69[a]	0	0	
Evergreen forest	10	9	1.53	NA	.22[a]	0	0	
Oak forest	4	9	1.34	−.62[b]	−.93[b]	0	0	
Pine-oak forest	11	32	−.51	.07[b]	−.70[a]	8	7	
Peru:								
Cocha Cashu								Munn 1985
Mature floodplain forest	32	78	−.07	**37.28**[a]	**6.53**[a]	564	399	
Sri Lanka:								
Knuckles Range								Nizam et al. 2007
Lowland evergreen forest	26	33	.37	−.17[a]	−.71[a]	9	3	
Midelevation evergreen forest	27	28	**2.13**	**3.66**[a]	−.53[a]	4	3	
Montane forest	38	21	−1.35	**3.06**[a]	−.71[b]	6	9	
Sinharaja								Kotagama and Goodale 2004
Rain forest	152	39	**2.53**	−.34[a]	.75[a]	48	18	
South Africa:								
Nylsvley Nature Reserve								Thomson and Ferguson 2007
Acacia woodland	47	22	1.63	1.80[a]	.43[b]	4	3	
Mixed woodland	88	30	.86	**5.05**[a]	**4.40**[a]	15	9	
Taiwan:								
Fushan Experimental Forest								Chen and Hsieh 2002
Subtropical wet forest	126	23	**4.26**	**11.10**[a]	**4.78**[a]	24	12	
Thailand:								
Khao Yai National Park								Nimnuan et al. 2004
Mature evergreen forest	75	41	**12.33**	**30.77**[a]	**3.48**[a]	108	64	
U.S. Virgin Islands (St. John and St. Thomas)								Ewert and Askins 1991 and unpublished data[d]
Subtropical moist forest	33	9	−.35	−.25[b]	−.27[b]	1	1	
Subtropical moist forest	6	3	−.64	NA	NA	0	0	

Note: Only species that occurred in at least three flocks in a matrix were included in the analyses. Significant standardized effect size values are indicated in bold.

[a] Higher average association strength observed within guild compared with across guilds.

[b] Higher average association strength observed across guilds compared with within guild.

[c] Field methods used in this study were the same as those used in the study by Sridhar and Sankar (2008).

[d] Field methods used to collect these unpublished data were the same as those used in the published study by Ewert and Askins (1991).

$$\text{association strength} = \frac{O - \mu}{\sigma},$$

where O is the number of co-occurrences in the real-data matrix, μ is the average number of co-occurrences across 5,000 null matrixes, and σ is the standard deviation of the number of co-occurrences across the 5,000 null matrixes. Our measure of association strength is a dimensionless value that can theoretically range from negative to positive infinity. Negative values indicate avoidance between species, positive values indicate association, and zero indicates no interaction.

We also counted the number of "unusually negative" and "unusually positive" species pairs (Sfenthourakis et al. 2006) in each matrix. Unusually negative and unusually positive pairs were those whose observed number of co-occurrences lay in the lower (<5%) and higher tail (>95%), respectively, of the frequency distribution of expected co-occurrences.

Association strengths and the number of unusual pairs were calculated only for species that occurred in at least three flocks in the data matrix. Species-association patterns inferred from only one or two occurrences in flocks might not be robust and may obscure the overall pattern. Rare species in flocks also often tend to be accidental (sensu Farley 2008) participants, that is, those that become caught up in a flock's movement and are not actually participating in the flock. To examine whether the exclusion of rare species affected our results, we also performed analyses that included all of the species that occurred in the data sets we examined. The results of these analyses were qualitatively similar whether all species or only those species with greater than three occurrences were included.

Measurement of Phenotypic Similarity

Our phenotypic measures included body size and foraging guild. Body-size similarity of species is thought to be a good surrogate for overlap in resource use. (Wilson 1975). Body-size ratios of species pairs have previously been related to intensity of competition (Leyequién et al. 2006). [q3] Competition is also expected to be strong between species that use food resources in a similar manner (Fox 1987). Both body size and foraging guild have been used extensively in null-model tests of community assembly (Gotelli and Graves 1996; Weiher and Keddy 1999). Body-size similarity of a species pair was calculated as the ratio of the natural logarithms of the body masses of the two species, with the heavier species always being in the denominator (Leyequién et al. 2007). All body-mass values were obtained from Dunning (2008).

Given that most species in mixed-species flocks are insectivorous, we did not use diet categories for foraging

guild; instead, we designated guilds on the basis of foraging behavior (following Remsen and Robinson 1990). As far as was possible, species were assigned to foraging guilds on the basis of field observations; otherwise, information was obtained from appropriate field guides. In all cases, species were assigned to their most frequently used guild. Species that could not be clearly assigned to a guild (~4% of species) were excluded from the foraging guild–level analysis. The guild designations we used varied between study sites, but in each case we consistently tried to achieve as fine a classification as was possible by using the available data. Species pairs were then classified as being from the same or different foraging guilds.

A third measure of phenotypic similarity we used was to determine whether species belonged to the same genus or different genera. This was done on the basis of the assumption that ecologically relevant species traits are phylogenetically conserved. Members of the same genus are often similar in morphology and resource use and show higher levels of aggression toward each other compared with species from different genera (Peiman and Robinson 2010); for this reason, past tests of competition often focused on congeneric pairs (Graves and Gotelli 1993; Sfenthourakis et al. 2006). However, a recent study has shown that species traits, including those relevant for mixed-species flocks, can be evolutionarily labile (Gómez et al. 2010). Therefore, we first examined the levels of similarity among the congeneric species in our data set. The congeneric pairs in our data set were generally similar in body size and foraging guild; in 95% of the congeneric pairs we examined, both members belonged to the same foraging guild, compared with 24% of noncongeneric pairs; body-size ratio (mean ± SD) was 0.91 ± 0.07 for congeneric pairs, compared with 0.76 ± 0.16 for noncongeneric pairs. Therefore, to a large extent the congeneric guild represents a combination of our other two measures and provides a clear demarcation of phenotypic similarity.

Relation between Association Strength and Phenotypic Similarity

We first examined the relationship between association strength and phenotypic similarity for each data matrix separately. Following the approach of Cavender-Bares et al. (2004), a matrix of pairwise association strengths was related to a matrix of pairwise phenotypic similarity values. Given the nonnormality of data and the nonindependence of species pairs, we performed randomization equivalents of standard parametric tests, using EcoSim (Gotelli and Entsminger 2001). The null hypotheses for randomization tests are subtly different from those for standard parametric tests. Randomization tests examine whether the test statistic is greater than what would be obtained from ran-

domized samples of the same data, whereas parametric methods compare the statistic against a reference distribution. We used randomized Pearson's correlations to examine the relationship between body-size ratios and association strength for species pairs. In the case of foraging and congeneric guilds, randomized ANOVAs were used to compare the average association strengths of species from the same guild and species from different guilds. A total of 1,000 simulations were performed for each test with each data matrix. To make the results comparable across matrixes of different sample sizes, we calculated a standardized effect size (SES; Gotelli and McCabe 2002) for each test result, as follows:

$$SES = \frac{\text{observed test statistic} - \text{average of simulated test statistics}}{\text{SD of simulated test statistics}}.$$

The test statistics were the product-moment correlation coefficient r in the case of randomized Pearson's correlation and the F-ratio in the case of randomized ANOVA. Theoretically, SES values can range from negative to positive infinity, but the interpretation of the sign ($+$ or $-$) varies between the tests. For randomized Pearson's correlations, the sign of an SES value indicates the direction of the relationship, whereas in the case of randomized ANOVA it indicates whether the difference between the two groups is greater than ($+$) or less than ($-$) that expected by chance.

Meta-Analysis

We first examined the influence of site characteristics (latitude, longitude, biogeographical zone, and occurrence of human perturbation) on SES values. Then we examined the overall pattern across data matrixes by computing cumulative SES values (Gotelli and McCabe 2002). In the case of the body-size test (randomized Pearson's correlation), we directly calculated the cumulative SES as the average of matrix SES values. In the case of foraging and congeneric guild tests (randomized ANOVA), we modified the original SES values as follows: first, we made all SES values positive by adding a constant such that the smallest SES value was 0. Next, we assigned negative signs to SES values for data matrixes in which the average association strength of pairs of species from different guilds was greater than that of pairs of species from the same guild. The SES values of data matrixes that showed the opposite pattern were retained as positive. We then calculated cumulative SES as the average of the modified SES values. Using one-sample t-tests, we tested the null hypothesis that the cumulative effect size across all data matrixes is 0 (Gotelli and McCabe 2002). Values significantly greater than 0 indicated a positive relationship between association strength and the phenotypic similarity of species in

flocks. Matrixes from the same study site likely share many bird species and therefore do not contain independent data points; as such, we also performed t-tests with cumulative SES recalculated across study sites instead of across individual data matrixes.

Results

Relationship between Association Strength and Phenotypic Similarity

Overall, we found strong positive relationships between association strength and phenotypic similarity (table 1; fig. 1). In the case of body size, significant positive correlations between association strength and body-size ratio were detected in 19 of the 55 data matrixes, whereas significant negative correlation was detected in only one matrix (table 1). Cumulative SES was significantly greater than 0 when averaged across matrixes (one-sample t-test, $P < .0001$; fig. 1A) or study sites (one-sample t-test, $P < .005$), indicating an overall positive relationship between association strength and body-size similarity. In the case of foraging guilds, in 14 matrixes the average association strength was significantly higher for species from the same foraging guild compared with for species from different foraging guilds; the reverse pattern was not observed in any matrix (table 1). Cumulative SES for the foraging-guild test was significantly greater than 0 when averaged across matrixes (one-sample t-test, $P < .005$; fig. 1B) or study sites (one-sample t-test, $P < .05$), indicating a higher association strength within the same foraging guild overall. In the congeneric test, a significantly higher average association strength was observed for congenerics compared with for noncongenerics in 10 matrixes, whereas only one matrix revealed the opposite pattern (table 1). The cumulative SES value for the congeneric test was significantly greater than 0 when averaged across matrixes (one-sample t-test, $P < .005$; fig. 1B) or study sites (one-sample t-test, $P < .05$), indicating a higher association strength between congenerics overall. In all cases latitude, longitude, biogeographical zone, and occurrence of human perturbation did not significantly explain the patterns observed ($P > .05$ with both randomized ANOVA for categorical variables and randomized Pearson's correlation for continuous variables).

Relative Proportions of Unusual Positive and Negative Associations

When summed across all data matrixes, unusual positive associations outnumbered unusual negative associations (1,369 vs. 834, respectively; table 1). Of the 302 pairs of congenerics in all of the data sets, unusual positive asso-
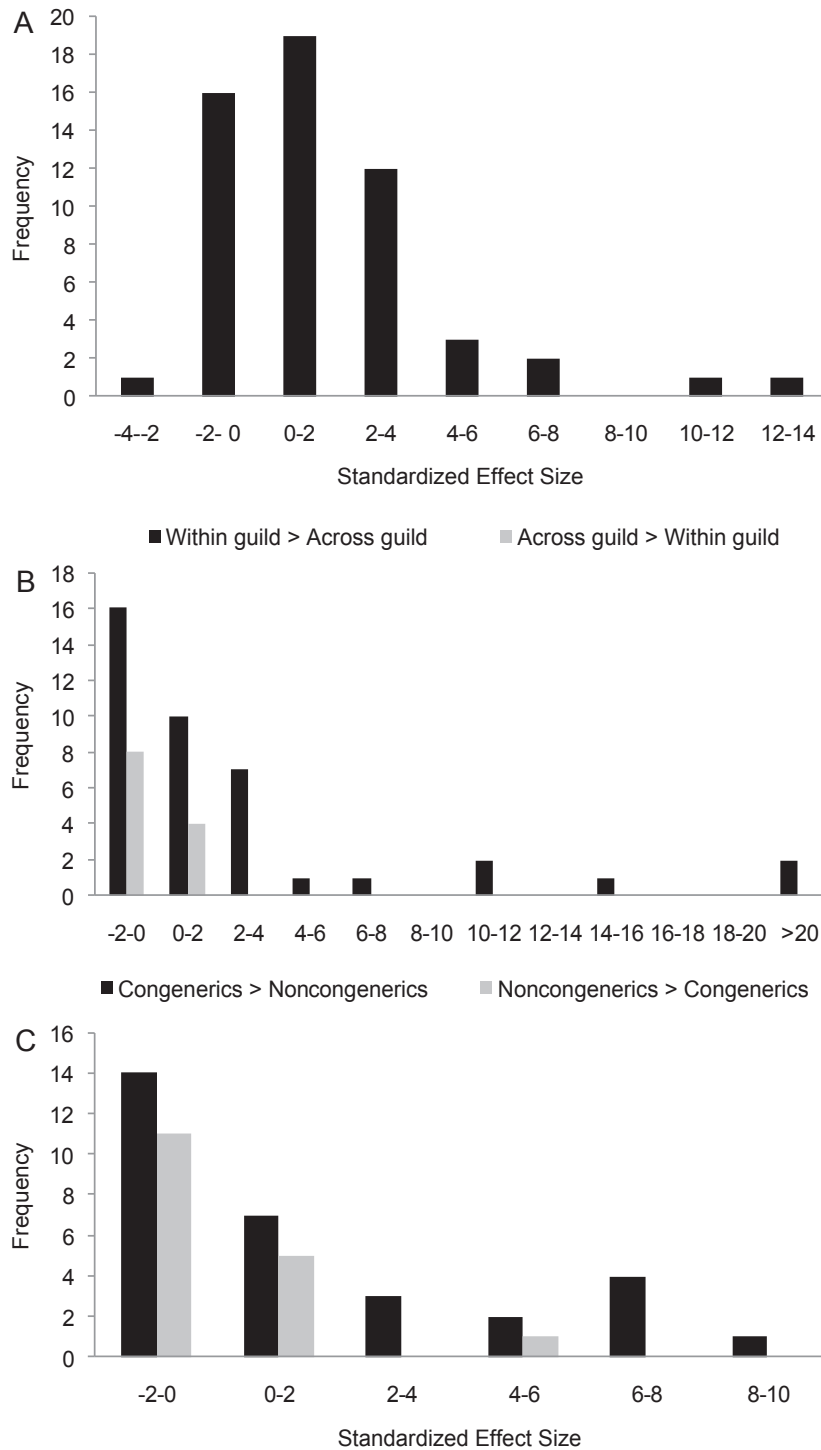
Figure 1: Histograms for standardized effect sizes (SESs) of the relationship between association strength and phenotypic similarity of species in mixed-species bird flocks. *A*, SES scores for randomized Pearson's correlation tests of the relationship between association strength and body-size similarity. *B*, SES scores for randomized ANOVAs where the average association strengths of species pairs within the same foraging guild are compared with those of species pairs across foraging guilds. *C*, SES scores for randomized ANOVAs comparing the average association strengths of congeneric pairs with those of noncongeneric pairs. In *A*, the sign (positive or negative) of the SES value indicates the direction of the relationship; in *B* and *C*, the sign indicates the magnitude of the difference: positive SES values indicate that the difference between the groups was greater than that expected by chance, whereas negative values indicate the opposite.

ciations were observed in 52, whereas unusual negative associations were detected in only 14. Unusual positive associations were predominant even at the individual data-matrix level: the number of unusual positive associations was greater than that of unusual negative associations for 33 matrixes, whereas the opposite was true for 12 matrixes and 10 matrixes revealed equal numbers of unusual positive and unusual negative associations (table 1).

Discussion

Because of interspecific competition, biological communities at local spatial scales are expected to consist of dissimilar species (Dayan and Simberloff 2005). However, the opposite pattern is observed in mixed-species bird flocks, which are important subunits of bird communities the world over (Goodale et al. 2010). Across 55 data sets from multiple continents, the association strength of species in flocks was positively correlated with phenotypic similarity. Even at the congeneric level, where competition is expected to be the strongest (Graves and Gotelli 1993), we found strong evidence of positive association. These results clearly indicate a pattern of assembly contrary to that generally predicted for communities at local scales. However, it is important to note that our analysis was based entirely on proxies for resource use (body size, foraging guild, and congenerics). It is possible that species co-occurring in flocks diverged in other resource use–related traits that we did not measure. Direct measures of resource overlap of flock participants are likely to provide a stronger test of these patterns.

Although the overall pattern revealed by our analysis indicated positive associations between similar species, we highlight a couple of caveats. First, substantial variation in the results was observed among data matrixes, including a few that showed relationships that were opposite to the general pattern (table 1). Although we found that site characteristics were not significantly associated with assembly patterns, this observation might in part be due to the low power of these tests. It is likely that a focused study designed to explicitly examine geographical differences might reveal otherwise. For example, although we found no significant effect of latitude, there were noticeable differences between data matrixes for temperate and tropical study locations. In contrast to our overall pattern, the former did not show strong relationships between association strength and phenotypic similarity (table 1). Flock formation and flocking propensities of species are known to differ between sites that vary in resource dispersion and predation pressure (e.g., Thiollay 1999); this could, in turn, influence the relative importance of facilitative and competitive interactions in flock assembly. In this context, given that the majority of our data came from tropical sites (table 1), our findings are more readily extrapolated to tropical bird communities than bird communities in general. The second caveat is that because in our analysis we dealt with only presence-absence matrixes, our findings present a simplified view of flock assembly. Taking into consideration species abundance would likely provide a more nuanced picture of assembly patterns (Graves and Gotelli 2003). ^{q4}

Comparisons with Other Flock Assembly Studies

Graves and Gotelli (1993) found a higher-than-expected number of mutually exclusive distributions among congenerics in Peruvian rain forest–understory flocks, a result they interpreted as indicative of competition at the congeneric level. In our study, on the other hand, we found the average association strength of congeneric pairs to be positive overall and higher than that of noncongeneric pairs (table 1). In fact, we found three times as many significant positive associations as negative associations among congenerics overall. Graves and Gotelli's (1993) data were included in our analysis, but as part of a larger data matrix that included both canopy and understory flocks from the Peruvian study site (Munn 1985). Nevertheless, to compare our results, we analyzed separately the subset of flocks included in Graves and Gotelli's (1993) data set, using our methods. On the basis of our association-strength index, we found no evidence for strong competition between congenerics across all congeneric pairs (average association strength $\pm$ SD, -0.07 ± 1.3). We found equal numbers of positive and negative associations even among significantly associated congeneric pairs. Moreover, a recent reanalysis of Graves and Gotelli's (1993) data set that used all species and included all levels of associations found these flocks to be phylogenetically clumped (Gómez et al. 2010). These contrasting results highlight the importance of using all pairwise associations rather than only extremely negative ones when investigating community assembly (Graves and Gotelli 1993). Interestingly, Gómez et al. (2010) interpreted their results only in terms of the absence of competition and did not discuss the possibility that positive associations contributed to this pattern. However, a higher prevalence of positive compared with negative associations in flocks, in contrast to in communities in general (Sfenthourakis et al. 2006; Gotelli and Ulrich 2010), has been documented in numerous earlier studies (e.g., Latta and Wunderle 1996*a*; King and Rappole 2001; Péron and Crochet 2009, and references therein). Our results validate this pattern across multiple continents and species assemblages by using a standard measure, and they further demonstrate that positive associations in general do exist between similar species.

Mechanisms of Flock Assembly

Habitat Filtering or Positive Interactions? Positive associations between similar species are generally interpreted as being caused by habitat filtering, that is, spatial sorting of species on the basis of habitat or environmental requirements (Cavender-Bares et al. 2009). Habitat filtering is primarily influential at large spatial scales where environments are sufficiently heterogeneous to allow such sorting to occur (Webb et al. 2002; Cavender-Bares et al. 2009; Pausas and Verdú 2010). In our study, each matrix included only those flocks from a single well-defined habitat. Species associations within each matrix are therefore unlikely to have been caused by broad-scale habitat filtering. Given the spatial proximity and interaction potential of flock members (Graves and Gotelli 1993) and the behavioral evidence for positive interactions in flocks (e.g., Krebs 1973; Goodale and Kotagama 2005; Satischandra et al. 2007), we believe that many of these associations likely reflect direct interactions between species. Nevertheless, it is possible that fine-scale microhabitat selection, which we did not measure in our study, might also play a role in producing some of the species-association patterns reported here (Graves and Gotelli 1993).

Positive Interactions between Similar Species. Species might choose to associate in flocks with similar species for different reasons. Recent conceptual work (Seppänen et al. 2007) predicted that social information, which is an important benefit of flock participation (Goodale et al. 2010), is often most profitably obtained from ecologically similar heterospecifics. Support for this proposition has been found in contexts in which flock members usually obtain social information, namely, location of food (e.g. Krebs 1973) and threat of predation (Fallow et al. 2011). Alternately, associating with similar species might be a way for species to obtain group-living benefits, which are normally linked to single-species groups, without suffering the concomitant costs of intraspecific competition (Buskirk 1976; Beauchamp 2002; Péron and Crochet 2009); this pattern is extensively documented in fish schools (Krause and Ruxton 2002). Finally, irrespective of the nature of the benefit, associating with phenotypically similar rather than dissimilar species is likely to minimize the costs of behavioral adjustments that must be made in order to match activity with other flock participants (e.g., Hutto 1988; King and Rappole 2001). However, there is one important exception to the general pattern of association between similar species: One characteristic feature of flocks, especially in tropical areas, is the association of sallying bird species with actively foraging bird species. In these associations, the former can catch prey flushed out by the latter (e.g., Satischandra et al. 2007). Actively foraging species are also known to benefit from these associations, because sallying species act as sentinels and warn the active foragers of the presence of predators (Goodale and Kotagama 2005; Satischandra et al. 2007). Consistent with these findings, we found that sallying species associated more strongly with species from other foraging guilds than with species from their own guilds (results not presented here); however, because sallying species formed a small proportion of the assemblage at all study sites, this association remains hidden within the overall pattern of phenotypic clumping.

Costs of Competition. Given that flocks present a setting in which competition appears to be unavoidable, similar species are expected to mutually exclude each other through interspecific territoriality (Graves and Gotelli 1993). Our findings raise the question of how phenotypically similar species reduce or avoid competition in flocks. One possibility is that the participation of similar species in the same flock is temporally separated. However, this is unlikely to have occurred in our analysis because in most of the studies we included, flocks were observed only long enough to obtain snapshots of composition. Therefore, species recorded as being part of the same flock were almost certainly present at the same time.

Another route to reduced competition between similar species in the same flock is increased niche divergence. Several studies have shown that similar species show greater niche separation when foraging together in flocks than when foraging alone (e.g., Alatalo et al. 1986; Latta and Wunderle 1996*b*). Thus, species might be willing to pay the cost of narrowed resource use in order to obtain the benefits of flock association. Alternately, foraging in flocks might facilitate access to resources that are not available otherwise. For example, studies have shown that species can extend their vertical (e.g., Herrera 1979; Satischandra et al. 2007) and horizontal (Powell 1989) foraging ranges by joining flocks. Such increases in foraging range potentially provide access to new resources, which might in turn relax competition.

Our results do not altogether preclude the possibility of competition between similar species. Although we focused only on interactions among the pool of flock participants, competition might have already resulted in certain species being excluded from flocks altogether (Narcissus effect; Colwell and Winkler 1984). Even among flock participants, there might be a threshold level of species similarity above which competition leads to mutual exclusion. For example, Graves and Gotelli (1993) showed that of three *Xiphorhynchus* woodcreeper species found in a Peruvian rain forest, the two similarly sized species never occurred together in the same flocks but each co-occurred with the larger species independently. There might be other such examples in our data sets that remain undetected due to

the coarse scale of our analysis. Direct measurements of species-resource use and overlap will provide a more nuanced understanding of this relationship.

Incorporating Facilitation between Similar Species into Community Ecology

Until recently, community assembly was examined largely through the lenses of competition and habitat filtering (e.g., Webb et al. 2002; Cavender-Bares et al. 2009; Pausas and Verdú 2010). Recent conceptual work has highlighted the need to also consider positive interactions between species when interpreting community patterns (Bertness and Callaway 1994; Bruno et al. 2003); however, these studies considered only positive interactions between dissimilar species (e.g., nurse plant–seedling interactions: Valiente-Banuet and Verdú 2007). Our study provides an important extension to this idea by describing assembly patterns that most likely are an outcome of facilitation between similar species. Our findings and those of earlier conceptual work together make it clear that there are no simple inferences to be drawn from looking at community-level patterns, because the same pattern can be observed with different mechanisms. Phenotypic overdispersion can be the result of competition between similar species or facilitation between dissimilar species. Phenotypic clumping can reflect abiotic filtering, facilitation between similar species (as our study has shown), or competition between dissimilar species (Mayfield and Levine 2010). Moreover, even an overall random community pattern can be produced as a result of equal proportions of two opposing interactions. Therefore, we advocate more circumspection in interpreting overall community patterns and the use of species pairwise approaches and mechanistic understanding of interactions, wherever possible, in future community-assembly research (see also Ulrich and Gotelli 2012).

More fundamentally, our findings question the general stereotyping of ecologically similar species as competitors. Although there has been strong theoretical support for the expectation that similar species compete and as such avoid each other (Dayan and Simberloff 2005), our study describes the exact opposite pattern. This is not surprising when one considers that similar species are similar not only in the resources they compete for but also in other aspects of their ecologies, such as the identities of their predators, pathogens, pollinators, and seed dispersers (Seppänen et al 2007; Beltrán et al. 2012). As a result, if association is beneficial in any of these contexts (e.g., social information about predators: Seppänen et al 2007; joint attraction of pollinators: Sargent and Ackerly 2008), it is likely that these benefits are more profitably obtained with similar rather than dissimilar species (Seppänen et al 2007). Therefore, we believe that a more general and re-

alistic characterization of interactions between similar species is as a dynamic trade-off between the costs of competition and the benefits of facilitation. In most cases, associational benefits presumably do not play a role and therefore, the net interaction is negative (and the stereotype is accurate). However, under conditions where heterospecific association is important, the nature of the interaction will depend on how these costs and benefits trade off. Over longer time periods, the trade-off between facilitation and competition is also likely to play itself out in terms of niche evolution and divergence (Bruno et al. 2003): niches of phenotypically similar species may diverge sufficiently to avoid competition, but not so much that the benefits of association are lost (Seppänen et al 2007).

The critical question asks how general these patterns are. To our knowledge, flocks are only the third documented example, after plant species that share pollinators (Sargent and Ackerly 2008) and Müllerian mimicry rings in butterflies (Elias et al. 2008), of a system that shows phenotypic clumping as a result of facilitative interactions. However, given the numerous taxa and contexts in which positive interactions and heterospecific associations occur (Seppänen et al. 2007; Goodale et al. 2010), this pattern may be more prevalent than is currently known. For example, in plants, associations between similar species are likely among those that share mycorrhizal networks, pathogens, and seed dispersers (Beltrán et al. 2012). In fact, we believe that viewing facilitation as a continuum will provide useful insights. In cases where intraspecific competition is not strong, positive interactions are expected between conspecifics (McIntire and Fajardo 2011). In cases where strong intraspecific competition prevents association between conspecifics, species might instead choose to associate with similar heterospecifics (Buskirk 1976; Beauchamp 2002; Péron and Crochet 2009). As the costs of interspecific competition increase, association is likely to be observed between more and more dissimilar species. When viewed in this fashion, association based on similarity might be a much more common phenomenon than is currently believed.

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