RESEARCH ARTICLE

Do similar foragers flock together? Nonbreeding foraging behavior and its impact on mixed-species flocking associations in a subtropical region

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ABSTRACT

Mixed-species flocks are ubiquitous in forest bird communities, yet the extent to which positive (facilitative) or negative (competitive) interactions structure these assemblages has been a subject of debate. Here, we describe the fine-scale foraging ecology and use network analysis to quantify mixed-species flocking interactions of an insectivorous bird community in hardwood forests of north-central Florida. Our goal was to determine if similarly foraging species are more (facilitation hypothesis) or less (competition hypothesis) likely to associate in flocks, and if foraging ecology can explain intraspecific abundance patterns within flocks. We quantified attack maneuvers, foraging substrate, and foraging microhabitat of all 17 common insectivorous species in these forests and characterized the composition of 92 flocks encountered. Flocking was important in our community; 14 of 17 species joined more than 5% of flocks, and 10 species had flocking propensities of over 0.80. Our results supported both hypothesized mechanisms structuring flock composition. Species had distinct, well-defined foraging niches during the nonbreeding season, but foraging niche overlap among flocking species was greater than expected by chance. Consistent with the facilitation hypothesis, we found that similarly foraging species were significantly more likely to associate in flocks, a result driven by lower association strengths in large-bodied woodpeckers. We found no evidence of assortment by foraging behavior, however, likely because foraging behavior and substrate use showed strong niche partitioning at the fine scale within our community. Intraspecific abundance patterns were significantly linked to foraging substrate use, with live leaf use correlated with high within-flock abundance and relative abundance at study sites. Species that specialized on comparatively less abundant substrates (tree trunks, epiphytes, dead leaves) joined flocks as singletons, showed lower relative abundance, and may exhibit nonbreeding territoriality. Our results highlight the importance of foraging substrate use and mixed-species flocks in structuring the nonbreeding ecology of migratory birds.

Keywords: foraging behavior, foraging substrate use, intraspecific abundance, mixed-species flock, niche partitioning, nonbreeding ecology

¿Los que forrajean de modo similar se agrupan en bandadas? Comportamiento de forrajeo no reproductivo y su impacto en las asociaciones de bandadas de especies mixtas en una región subtropical

RESUMEN

Las bandadas de especies mixtas son muy conspicuas en las comunidades de aves de bosque; sin embargo, hasta qué punto las interacciones positivas (facilitación) o negativas (competencia) estructuran estos ensambles ha sido tema de debate. Aquí describimos la ecología de forrajeo de escala fina y usamos análisis de redes para cuantificar las interacciones de las bandadas de especies mixtas de una comunidad de aves insectívoras en bosques de maderas duras del centro norte de Florida. Nuestro objetivo fue determinar si las especies que forrajean de modo similar son más (hipótesis de facilitación) o menos (hipótesis de competencia) propensas a asociarse en bandadas, y si la ecología de forrajeo puede explicar los patrones de abundancia intraespecífica dentro de la bandada. Cuantificamos las maniobras de ataque, el sustrato de forrajeo y el micro-hábitat de forrajeo de las 17 especies insectívoras comunes de estos bosques y caracterizamos la composición de las 92 bandadas encontradas. La agrupación en bandadas fue muy importante en nuestra comunidad; 14 de las 17 especies se unieron a más del 5% de las bandadas, y 10 especies tuvieron una propensión a agruparse en bandadas de más de 0.80. Nuestros resultados apoyan los dos mecanismos que hipotetizamos que estructuran la composición de las bandadas. Las especies tuvieron nichos de forrajeo bien definidos durante la estación no reproductiva, pero la superposición del nicho de forrajeo entre las especies de las bandadas fue mayor que lo esperado por azar. De modo consistente con la hipótesis de facilitación, encontramos que las especies que forrajean de modo similar tuvieron una probabilidad significativamente mayor de asociarse en bandadas, un resultado que estuvo condicionado por las asociaciones más débiles de los pájaros carpinteros de cuerpo grande. No encontramos evidencia de una separación por comportamiento de forrajeo, probablemente debido a que el comportamiento de forrajeo y el

uso del substrato mostraron una fuerte partición del nicho a escala fina dentro de nuestra comunidad. Los patrones de abundancia intraespecífica estuvieron significativamente vinculados al uso del sustrato de forrajeo, con el uso de hojas vivas correlacionado con la alta abundancia dentro de la bandada y la abundancia relativa en los sitios de estudio. Las especies que se especializaron en los substratos comparativamente menos abundantes (troncos de árboles, epífitas, hojas muertas) se incorporaron a las bandadas como individuos solteros, mostraron una menor abundancia relativa y pueden exhibir territorialidad no reproductiva. Nuestros resultados destacan la importancia del uso del substrato de forrajeo y de las bandadas de especies mixtas en estructurar la ecología no reproductiva de las aves migratorias.

Palabras clave: abundancia intraespecífica, bandada de especies mixtas, comportamiento de forrajeo, ecología no reproductiva, partición del nicho, uso del substrato de forrajeo

INTRODUCTION

The relative importance of positive (facilitation, mutualism) and negative (competition) species interactions in community assembly remains one of the central issues in community ecology (Stachowicz 2001, Bulleri et al. 2016). In birds, community structure has often been studied in mixed-species flocks, which are defined as groups of 2 or more species that move and forage together (Morse 1970), because the species that flock together form a "community module" (Holt and Hochberg 2001) of strongly interacting species. In these associations, specific "nuclear" species lead the flock and contribute to its cohesion while other "attendant" species follow them. Such foraging flocks create a novel selection environment dominated by facilitative interactions (Harrison and Whitehouse 2011), in which species increase their foraging efficiency through reduced antipredator vigilance (Sridhar et al. 2009). Sentinel species that are better at detecting predators can also supply social information about predators to other flock participants in the form of alarm calls (Goodale et al. 2010). Participation in foraging flocks can therefore increase the fitness and survival of flock-following species (Dolby and Grubb 1998, Srinivasan 2019). However, foraging flocks also consist of long-term associations of large numbers of insectivorous species, with 60–70% of species in temperate bird communities participating (Goodale et al. 2017, Zou et al. 2018). Because these are foraging associations, we would therefore expect that competition avoidance should also play a structuring role. In spite of their ubiquity in forest bird communities (Goodale et al. 2015, Zou et al. 2018), however, there has been limited empirical research on the extent to which species that share foraging microhabitats, substrates, and maneuvers can coexist in flocks (but see Graves and Gotelli 1993, Colorado and Rodewald 2015).

Many authors have hypothesized that foraging competition is a structuring force that prevents similarly foraging species from co-occurring in flocks. Indeed, species can exclude competitors through aggressive chases in mixed flocks (e.g., Morse 1970, Muñoz and Colorado 2012), which could make joining a flock with a competitor impossible. In many temperate flocks there are social hierarchies in which larger, socially dominant species displace subdominant species and force them to shift their foraging niche (Jablonski and Lee 2002). In such cases, subordinate species may avoid flocking with similarly foraging social dominants. Similarly, flocking species can outcompete similarly foraging species through exploitation competition of a specialized foraging niche (Alatalo et al. 1987). Unsurprisingly, many flocking systems have been described in which extensive foraging niche partitioning by participants occurs (Alatalo 1982, Eguchi et al. 1993, Jablonski and Lee 1999, Matthysen et al. 2008), as well as "checkerboard" co-occurrence patterns where similarly foraging species pairs do not co-occur in flocks (Graves and Gotelli 1993, Colorado and Rodewald 2015).

An alternative to the competition hypothesis is that foraging similarly to flockmates is a prerequisite to joining a mixed-species flock (Sridhar et al. 2012). Birds that join flocks are not random subsets of the local community: a global meta-analysis showed that flocks are dominated by insectivorous canopy foragers (Sridhar et al. 2009). In some systems, multiple flock types coexist within the same habitat, and the flocking community is partitioned into subsets based on common aspects of foraging ecology, such as body size (Bell 1983, King and Rappole 2008, Mammides et al. 2018) and foraging height stratum (Munn 1985, Zou et al. 2011, Srinivasan et al. 2012). Flocking species are also more likely to join a nuclear species with similar body size and foraging ecology (Latta and Wunderle 1996, Mammides et al. 2015). One of the costs imposed on flocking birds is the necessity of moving and foraging at a rate that allows them to keep up with the flock, or "activity matching" (Hutto 1988, Sridhar and Guttal 2017). However, similarities in foraging ecology allow birds to join without having to extensively modify their foraging behavior—a non-trivial cost (Latta and Wunderle 1996, Darrah and Smith 2013). The social information acquired from flockmates is also most relevant to ecologically similar species that share predators and prey items (Goodale et al. 2010).

How then, can we reconcile these seemingly contradictory interpretations of flock assembly rules? In this paper, we hypothesize that both positive and negative species interactions influence flock assembly and argue that these hypotheses should be tested using fine-scale foraging data that include both broad characterization of foraging strata and diets and specific data on foraging substrates and tactics (e.g., Martínez and Robinson 2016). Nonbreeding

foraging behavior broadly influences the space use and social behavior of many birds (Salewski et al. 2002, Greenberg and Salewski 2005). Only when foraging data are collected at the finer scale, however, can we identify important differences in foraging microhabitat, substrate, and attack maneuver that are critical to a species' niche. Many studies that have looked at species co-occurrences in flocks do not quantify or account for foraging overlap (King and Rappole 2008, Péron and Crochet 2009). Where fine-scale foraging has been measured, many studies have concluded that negative interactions are an important structuring force (e.g., Alatalo et al. 1987, Jablonski and Lee 2002), whereas studies showcasing positive interactions have used a coarser scale of phenotypic similarity, such as body size or foraging guild (Sridhar et al. 2012). We hypothesize that foraging similarity constrains flock assembly at a coarse scale, whereas competition-driven resource partitioning at the fine scale, especially substrate use, dictates abundance and co-occurrence patterns within the flocking community.

In this paper, we use a combination of network analysis and fine-scale foraging data to test these hypotheses in a subtropical nonbreeding community. We quantified the foraging behavior, flocking propensities, and network structure of flocking interactions of all insectivorous birds in a winter bird community in northern Florida and determined if (1) species that occurred together in flocks differed in their foraging niches, (2) their foraging niche overlap was greater or less than expected by chance, (3) foraging similarity correlated with associations within mixed-species foraging flocks, and (4) similarly foraging species were positively or negatively assorted in our flocking system. We lastly (5) looked at intraspecific abundance patterns in flocks and at our study sites to see if they were correlated with foraging behavior. If the foraging competition hypothesis is correct, then we would expect that association strength within the flock would be negatively correlated with foraging similarity and we would see checkerboard assembly patterns of co-occurrence. Where significant intraspecific foraging competition occurs, we would furthermore expect species to join flocks in small numbers and exclude conspecifics. If, alternatively, the foraging similarity hypothesis is correct, then we would expect that association strength between species pairs should be positively associated with foraging similarity, and that foraging behavior of flock-joining species should be more similar than expected by chance.

METHODS

Study System
All fieldwork was conducted on wildlands in the vicinity of Gainesville, Florida, USA, in the north-central portion of the Florida peninsula. Study sites included San Felasco

Hammock Preserve State Park (29.7191°N, 82.4531°W), Paynes Prairie State Park (29.5588°N, 82.3261°W), Split Rock Conservation Area (29.6331°N, 82.4103°W), and Newnan's Lake Conservation Area (29.6784°N, 82.2331°W). To standardize the habitat types sampled, we selected only field sites in broadleaf forest, which has the most species-rich winter bird community (Engstrom 1993). This upland hardwood forest grows near lakes and spring-fed steams; the closed canopy of the forest is structurally diverse and dominated by an assemblage of deciduous and evergreen trees (Florida Natural Areas Inventory 2010). Common tree species at our study sites are American sweetgum (*Liquidambar styraciflua*), spruce pine (*Pinus glabra*), Southern magnolia (*Magnolia grandiflora*), swamp chestnut oak (*Quercus michauxii*), diamondleaf oak (*Q. laurifolia*), bluff oak (*Q. austrina*), pignut hickory (*Carya glabra*), and sugarberry (*Celtis laevigata*). Understory trees include American holly (*Ilex opaca*), eastern hophornbeam (*Ostrya virginiana*), southern sugar maple (*Acer floridanum*), and flowering dogwood (*Cornus florida*).

Florida is home to a diverse nonbreeding bird community, primarily composed of short- and long-distance migrants (Sibley 2014). In hardwood forest, the Tufted Titmouse (*Baeolophus bicolor*) is an abundant, year-round resident that acts as a sentinel species for other forest passerines (Gaddis 1980, Sieving et al. 2004). This species, along with Carolina Chickadee (*Poecile carolinensis*), also acts as a nuclear species for mixed-species foraging flocks (Farley et al. 2008, Contreras and Sieving 2011) that form around small family groups of 2–5 individuals that hold stable winter territories (Brawn and Samson 1983). These speciose subtropical foraging flocks are joined by many small forest passerines that follow titmouse groups and forage with them (Gaddis 1983, Farley et al. 2008).

Characterizing Foraging Behavior
We gathered foraging data on wild birds from December 2014 to February 2015 (winter 1) and from November 2015 to January 2016 (winter 2). A single observer (H.H.J.) performed the observations with 10x binoculars. The observer walked trails or transects through hardwood habitat and recorded the foraging behavior of all birds encountered. We observed only individuals that were actively foraging, and did not sample individuals that were resting, preening, or engaged in aggressive behavior. To maximize independence of the foraging data, we did not resample trails or transects during the same winter sampling period. We performed focal individual sampling, where a single individual was observed until it was lost from sight; the observation period varied from a few seconds up to several minutes. When we encountered a mixed-species flock, we only sampled the foraging behavior of a single individual of

each species within the flock to avoid repeated sampling of individuals.

We recorded each foraging maneuver as the sample unit ("attack maneuver" following Remsen and Robinson 1990), along with 4 associated microhabitat variables for each maneuver observed: height from ground (vertical position), distance from trunk (horizontal position), foliage density, and substrate. Foraging data were recorded using a voice recorder in the field and later transcribed into a spreadsheet. We classified foraging maneuvers and substrates according to the Remsen and Robinson typology (1990), recording the substrate from which the prey item was captured. Distance from trunk was binned into 3 categories (near-trunk, medium, and far from trunk), and we estimated height above ground to the nearest meter with the help of a laser rangefinder (Raider 600 Digital Laser Rangefinder, Redfield, Beaverton, Oregon, USA). Foliage density in an estimated 1-m radius sphere around the focal individual was estimated on a 0 to 5 scale after Remsen and Robinson (1990) based on the percentage of light passing through the surrounding vegetation. A zero on this scale indicates no vegetation whereas a 5 represents dense vegetation. To simplify the number of attack maneuver categories, we amalgamated all reach and hang type maneuvers into one category before calculating proportions of use for all substrates, microhabitats, and attack maneuvers for each species.

Surveys of Mixed Flocks and Paired Point Counts

From November 2018 to January 2019 (winter 3), we conducted surveys to determine the composition of mixed-species foraging flocks in the same habitat type and study areas as those used for the foraging data. One or more observers familiar with the local avifauna walked trails or transects through suitable habitat until a flock was encountered, at which point the flock was followed for a minimum of 10 min to characterize the composition and the abundance of all participating species. We defined a flock as 2 or more species moving in the same direction and foraging within 10 m of each other over the course of the survey, as is standard in the flocking literature (Morse 1970). Bird species were identified by sight (using 10x binoculars) and sound; inter-observer bias was minimized by having multiple observers present for each survey. Either H.H.J. or M.J.W. was present for all surveys, and they each have over a decade of experience identifying the birds at our study sites. To calculate the flocking propensity of species in our community, we paired 50-m radius point counts with each of our flock surveys, following the methodology of Farley et al. (2008). After characterizing the flock composition, we waited until the flock had moved at least 100 m away before conducting a 10-min, 50-m fixed-radius point count at the last point at which the flock was observed. This allowed us to account for species that joined the flock

temporarily before dropping out as the flock moved on, as well as species that do not join foraging flocks. We recorded all species seen or heard, excluding fly-overs; we feel that the point count method was appropriate because many species that do not join mixed-species flocks in our system either exhibit nonbreeding territoriality defended by song (e.g., Hermit Thrush, Brown et al. 2000) or join large, conspicuous single-species flocks (e.g., American Goldfinch [*Spinus tristis*]; Farley et al. 2008). To calculate a flocking propensity, or percentage of time spent in mixed flocks during the survey period, we divided the total number of individuals observed in a flock by all individuals observed.

Cluster, Principal Coordinates, and Niche Overlap Analysis of Foraging Behavior

All statistical analyses were performed in R 3.5.1. To classify species in our nonbreeding bird community into foraging guilds, we calculated proportions of use of each substrate (12 categories), attack maneuver (15 categories), distance category from trunk (3 categories), and foliage density score (5 categories) for all insectivorous bird species with observations of more than 5 unique individuals, assuming no double-counting of individuals (n = 17 species). We created a dissimilarity matrix using the Gower dissimilarity index, which is appropriate for our proportion data (Gower 1971), and the *daisy* function in the *cluster* package (Maechler 2008). We used polythetic agglomerative hierarchical clustering using an average-linkage (UPGMA) fusion strategy (Sokal and Michener 1958) to create a dendrogram using the *hclust* function in the *stats* package. We selected the fusion strategy with the highest cophenetic correlation coefficient, after comparing this value for multiple agglomerative and divisive hierarchical clustering methods (Supplementary Material Table 3). The average-linkage fusion strategy is considered the most robust linkage method because it produces the least amount of distortion of the original data when creating the dendrogram (Romesburg 2004). We defined foraging guilds as clusters of species with a dissimilarity between them that was greater than the mean pairwise dissimilarity between all species (Holmes et al. 1979).

In order to quantify niche overlap in our community, we calculated the average pairwise Pianka's niche overlap (Pianka 1973) for all species that commonly join mixed-species flocks (n = 14 species) on the proportion of use of 4 categories of foraging data: foraging substrate, attack maneuver, foliage density at the site of attack, and distance from trunk. This metric is bounded between zero and one, with zero indicating no overlap and one indicating complete overlap between all species pairs. In order to determine if niche overlap was greater or less than expected by chance with our observed data, we compared

the observed statistic with 1,000 Monte Carlo null model permutations of the species by resource category matrix. While sequential foraging data are non-independent, these null models compare the observed statistic to expected test statistics generated from permutations of the original (non-independent) data generated according to a null hypothesis. Therefore, there are no assumptions made about the distribution or independence of the empirical data. We used the *RA3* randomization algorithm from the *EcoSimR* package (Gotelli et al. 2015), which retains the overall number of resource categories used and zero states for each species while shuffling the proportion of use values between resource categories. This is considered a conservative null model that retains the niche breadth of each species; we obtained similar results with other algorithms, and when including non-flocking species in the analysis. Analyses were run using the *niche_null_model* function of the *EcoSimR* package. In order to calculate a standardized effect size (SES), we divided the difference between the observed value and the mean of the simulated values by the standard deviation of the simulated niche overlap values.

Lastly, we quantified various aspects of foraging behavior for the network analyses by ordinating the proportion of use of our 4 categorical variables using principal coordinates analysis (PCoA; Gower 2015). One principal coordinate axis was selected to quantify each of the 4 categorical foraging variables. Additional methods and PCoA results are provided in Supplementary Material S2.

Creation of Social Networks and Network Analyses

To characterize the flocking interactions of our winter bird community we assembled a social network (Farine and Whitehead 2015). Because species move and forage in close proximity in mixed-species flocks, we consider 2 species observed in the same flock to be interacting ecologically (the "gambit of the group" approach; Franks et al. 2010). We therefore defined an interaction between species as a co-occurrence of the species in a flock. We used a presence–absence, flock-by-species matrix to calculate a network using the *get_network* function of the *asnipe* package (Farine 2013). Only species observed in more than 5% of all flocks ($n = 14$) were included in analyses; other species did not join flocks or represent rare, vagrant species overwintering outside of their normal nonbreeding range. Because detectability of birds in flocks is high, and associations were likely rarely missed, we used the simple ratio index (SRI), an undirected, weighted measure of association, to calculate an association index for each species pair in the flocking network (Farine and Whitehead 2015). We then used a linear model to quantify the relationship between the SRI and the Gower dissimilarity in foraging behavior (calculated for the cluster analysis) for each species pair. Because network data and sequential

foraging observations are inherently non-independent, we tested for statistical significance using permutation-based null models (Farine 2017). We do not believe this non-independence biased the results because we obtained similar results with a subset of foraging data taking only the second foraging observation of each sequence (detailed in Supplementary Material S2). We compared the slope coefficient of the linear model of the observed data to the slopes of 1,000 linear models in which the SRI values were randomly permuted to generate a *P*-value.

To look for patterns of interspecific assort in the foraging flocks, we calculated assortativity coefficients (Farine 2014) for our weighted network of flocking interactions. This coefficient indicates the extent to which nodes (species) with similar attribute values differ either negatively or positively from random in their association (SRI). We calculated the assortativity coefficients of 6 different quantitative aspects of foraging behavior: body mass, foraging height, distance from trunk, foliage density, foraging substrate, and foraging maneuver. The foraging height measure was the average of observed values for each species, whereas the other foraging values were obtained from the relevant PCoA analysis (see Supplementary Material S2). We obtained body mass values from Sibley (2014). We calculated assortativity coefficients on the network using the *assortment.continuous* function of the *assortnet* package (Farine 2014), and did not threshold the network prior to analysis. We tested for significance by using the *network_permutation* function in *asnipe* to generate null networks where species were swapped between flocks while maintaining a constant species flocking propensity (Farine, 2017). We did not control for the spatiotemporal distribution of species in the null networks because all flocking species were present at all sites, and all sampling sites were in the same habitat type.

Statistical Modeling of Intraspecific Flock Abundance

We modeled the influence of foraging ecology on intraspecific flock abundance using linear models. We used the average intraspecific abundance of a species in foraging flocks ($n = 14$ species) as the response variable, and 6 predictor variables including body mass of each species as well as 5 measures of foraging behavior derived from our PCoA analysis: average foraging height, distance from trunk, foraging substrate, foraging maneuver, and foliage density at the foraging microsite. We ran single-predictor models for all 6 variables and selected a best model by evaluating all possible subsets of the full model using the Akaike Information Criterion (AIC) to identify the most parsimonious model (Burnham and Anderson 2002). Models were evaluated using the AIC value modified for small sample sizes (AIC_c) using the *model.sel* function of the *MuMIn* package (Barton 2016). We evaluated the significance of each predictor

variable using *P*-values and assessed model goodness-of-fit using r^2 values derived from each linear model.

RESULTS

Observations of Foraging Behavior
Over 2 winters of observations, we observed 1,242 foraging maneuvers of 327 foraging individuals belonging to 25 species. Of these, 17 species had more than 5 independent observations of foraging individuals (summarized in Table 1; full foraging data in Supplementary Material Tables 4–6). The number of foraging observations was not biased by average foraging height of a species (linear model, $F = 0.09$, df = 1 and 13, $P = 0.77$) or average microsite foliage density (linear model, $F = 0.19$, df = 1 and 13, $P = 0.67$), suggesting that foraging observations were not biased towards more easily detectable species. Generally, winter foraging behavior was specialized, with only 2 pairs of species not having unique combinations of the main attack maneuver, main substrate used, and main distance from trunk at which they forage (Table 1).

Flock and Point Count Surveys
Over 15 days of sampling in the mesic hardwood habitat, we recorded 2,368 individuals belonging to 45 bird species across both flock and point count surveys (see Table 2; Supplementary Material Table 1 for the full species list). We observed 39 species in 91 point count surveys and 22 species (49% of the winter bird community) in 92 mixed-species flock surveys for which we completely characterized the flock composition. Of these, 14 species were regular flock participants, observed in 4 or more flocks (e.g., greater than 5% of all flock compositions; Figure 1A and Table 2); the other 9 flocking species represented infrequent flockers and rare species outside of their normal winter range (e.g., Northern Parula [*Parula Americana*], American Redstart [*Setophaga ruticilla*]). Mixed-species flocks were large and speciose for a subtropical flocking system with a mean of 8.7 species and 15.7 individuals, although flock size and species richness were variable across flocks (range: 3–12 species, 4–36 individuals). Among the commonly flocking species, we observed high flocking propensities in the hardwood forest habitat, with 10 species having over 80% of detections in mixed-species flocks (Table 2). Relative abundances and intraspecific abundance in the flock were variable. Some species (e.g., Ruby-crowned Kinglet [*Regulus calendula*], Blue-gray Gnatcatcher [*Polioptila caerulea*], and Pine Warbler [*Setophaga pinus*]) had high relative abundances and intraspecific abundance within flocks whereas others had lower intraspecific abundance and joined flocks singly (e.g., Blue-headed Vireo [*Vireo solitarius*], Yellow-throated Warbler [*Setophaga dominica*], and Orange-crowned Warbler [*Leiothlypis celata*]; Table 2, Figure 2D).

TABLE 1. Summarized foraging data. Data shown are from species with more than 5 unique individuals observed (*n* = 17 species). Species codes correspond to 4-letter alpha codes (see Supplementary Material Table 1 for full species names). Sample sizes represent the number of independent individuals observed foraging and the total number of observed foraging maneuvers, respectively. Foraging height was estimated to the nearest meter for each foraging maneuver with the help of a rangefinder. Distance from tree trunk was binned into 3 categories (near to trunk, medium, and far from trunk) by dividing the branch on which a focal individual was perched into thirds. Foliage density is calculated based on percentage of light penetrating the foliage on a 0 to 5 scale in a 1-m diameter sphere around the focal individual. Substrates and attack maneuvers were categorized following Remsen and Robinson (1990). Most frequent substrates and maneuvers were those observed at the highest frequency across all foraging observations

Species	N total individuals	N all maneuvers	Mean foraging height	Mean foliage density	Most freq. substrate	Most freq. maneuver	Most freq. distance
BAWW	25	163	10.78	1.29	Trunk	Glean	Near
BGGN	27	102	12.55	2.28	Live leaf	Glean	Far
BHVI	22	42	11.23	1.50	Branch	Glean	Medium/Near
CACH	13	42	12.18	2.46	Branch	Glean	Far
CAWR	6	18	4.17	2.61	Dead leaf	Probe	Near
DOWO	12	61	16.05	1.18	Trunk	Hammer	Near
EAPH	13	32	9.63	1.55	Branch	Sally	Far
ETTI	17	56	11.11	2.60	Branch	Glean/Probe	Far
MYWA	19	71	9.92	2.26	Branch	Glean	Near
NOCA	13	47	4.28	1.53	Ground	Reach-down	Far
OCWA	12	63	9.65	2.27	Dead leaf	Probe	Far
PIWA	19	72	14.58	2.03	Epiphyte	Probe	Far
RBWO	24	100	14.61	1.42	Trunk	Probe	Near
RCKI	39	159	8.32	2.48	Live leaf	Glean	Far
WEVI	11	27	7.91	2.74	Live leaf	Glean	Far
YBSA	7	37	15.83	0.81	Trunk	Hammer	Near
YTWA	18	69	15.22	2.29	Dead leaf	Probe	Far

TABLE 2. Flocking propensities and relative abundances of common flocking species. Only commonly flocking species that were observed in more than 4 (5%) flocks (*n* = 14) are presented (see Supplementary Material Table 1 for a full list of species). Species names are given as 4-letter alpha codes (see Supplementary Material Table 1 for full species names). Total detections = total number of individuals detected in surveys of mixed-species flocks and paired 10-min point counts. Relative abundance = average number of individuals detected per day of sampling across survey types. Percentage flocks = percentage of all mixed-species flocks surveyed (*n* = 92) of which a species was attending. Flocking propensity = proportion of total detections for a species in mixed species flocks. Avg. and SD individuals/flock = the mean and standard deviation of intraspecific abundance of a species in mixed-species foraging flocks, when it was present

| Species	Total detections	Relative abundance	Percentage flocks	Flocking propensity	Avg. individuals/ flock	SD individuals/ flock
BAWW	114	7.60	88.04	0.939	1.32	0.50
BGGN	249	16.60	81.52	0.928	3.08	2.61
BHVI	106	7.07	91.30	0.858	1.08	0.28
CACH	144	9.60	66.30	0.833	1.97	0.31
DOWO	75	5.00	51.09	0.907	1.45	0.50
MYWA	67	4.47	19.57	0.597	2.22	1.86
OCWA	61	4.07	59.78	0.951	1.05	0.23
PIWA	139	9.27	58.70	0.964	2.48	1.67
RBWO	79	5.27	29.35	0.418	1.22	0.42
RCKI	301	20.07	97.83	0.774	2.59	1.09
TUTI	199	13.27	92.39	0.960	2.25	0.58
WEVI	42	2.80	38.04	0.857	1.03	0.17
YBSA	39	2.60	6.52	0.154	1.00	0.00
YTWA	70	4.67	73.91	0.971	1.00	0.00
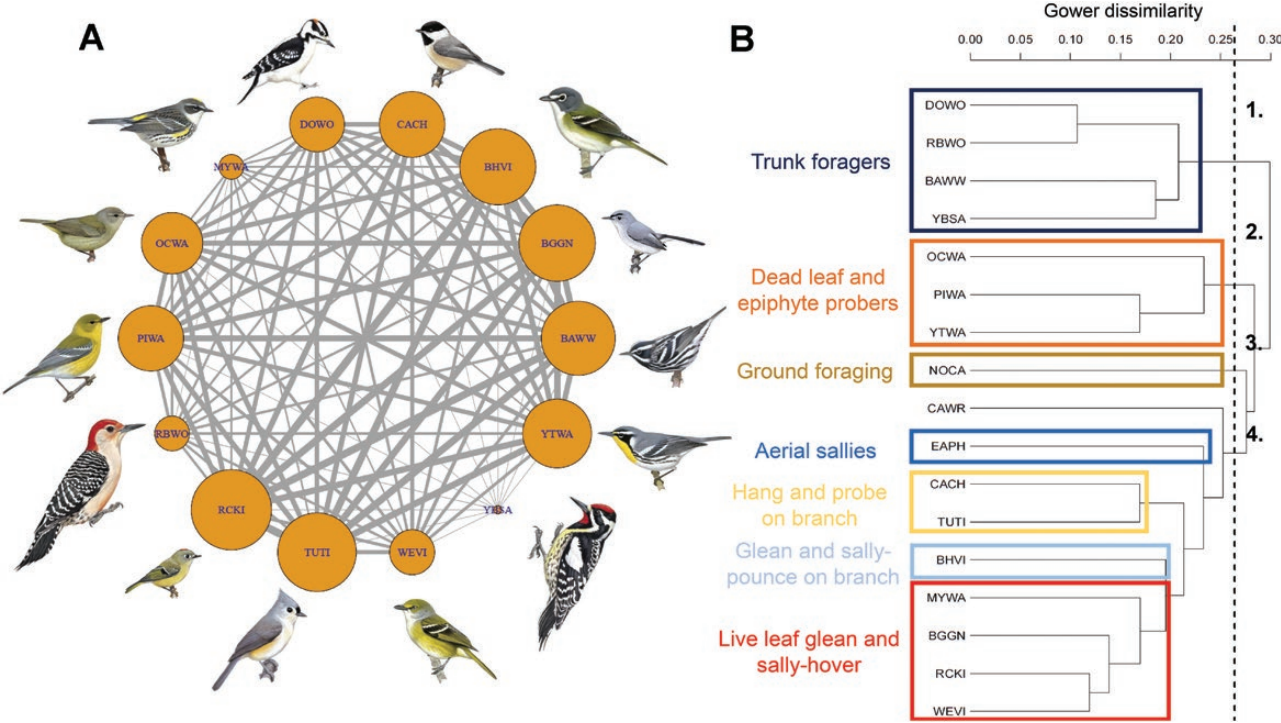
FIGURE 1. Foraging ecology and mixed-species flocking interactions of a nonbreeding insectivorous bird community. Species names use alpha codes (see Supplementary Material Table 1 for full species names). (**A**) Social network of species associations in mixed-species foraging flocks (*n* = 92 flocks) in hardwood hammocks. Node width indicates weighted degree (strength), while edge width indicates strength of association (degree of co-occurrence) of 2 species within flocks (SRI). Species shown (*n* = 14) were observed in 5% or more of all flock compositions. Illustrations reproduced by permission of Lynx Edicions. (**B**) Dendrogram showing foraging guilds as identified by agglomerative cluster analysis. Four distinct foraging guilds are denoted by numbers; the dashed line represents the mean dissimilarity between all species pairs. Colored boxes highlight foraging guilds and subgroupings within while the text describes foraging maneuvers and substrates associated with each (see Table 1; a full description of foraging guilds is available in Supplementary Material S2).
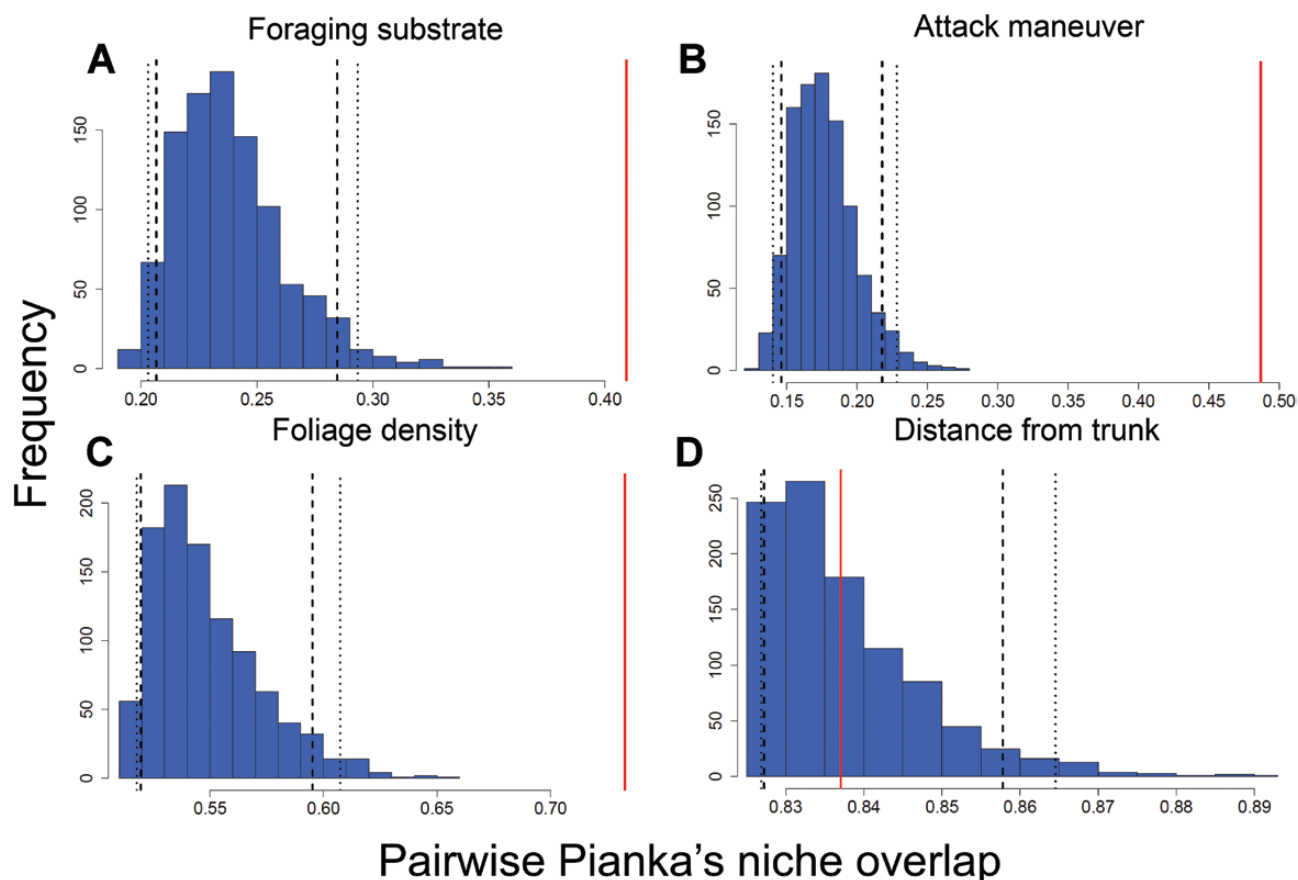
FIGURE 2. Pairwise Pianka's niche overlap values for 4 aspects of foraging ecology. The vertical red line represents the observed value of the mean pairwise Pianka's niche overlap for all commonly flocking species (n = 14 species), while the histogram displays 1,000 expected values generated using a null model that assumes random resource use of each species while maintaining a constant niche breadth. Dotted lines correspond to the upper and lower 95% confidence intervals for a 1-tailed (inner) and 2-tailed (outer) permutation test. We found significantly higher niche overlap than expected by chance of (**A**) foraging substrate use, (**B**) foraging attack maneuver, and (**C**) foliage density at the foraging microsite, while distance from trunk of the foraging microsite (**D**) did not differ from the null expectation.

Niche Overlap and Hierarchical Clustering of Foraging Behavior

In accordance with the facilitation hypothesis, we found that 3 of 4 aspects of foraging ecology studied had a greater niche overlap than expected by chance alone (Figure 2). As predicted by the competition hypothesis, the use of foraging substrates showed low overlap (mean Pianka's niche overlap = 0.41), indicating niche partitioning by substrate; however, overlap of substrate use was larger than expected in a null hypothesis scenario (SES = 7.06, $P < 0.001$; Figure 2A). The niche overlap values for foraging attack maneuver (mean Pianka's niche overlap = 0.49, SES = 13.82, $P < 0.001$; Figure 2B) and foliage density at the site of attack (mean Pianka's niche overlap = 0.73, SES = 7.85, $P < 0.001$; Figure 2C) were also much greater than predicted by our null models. We also found a high niche overlap value for the distance from the trunk of the foraging microhabitat, although this value was no different from a null

expectation of random microhabitat use (mean Pianka's niche overlap = 0.84, SES = −0.06, $P = 0.59$; Figure 2D). Our cluster analysis identified 4 nonbreeding foraging guilds with distinctive foraging behavior and foraging substrates (Figure 1B; see Table 1 and Supplementary Material Tables 4–6); the fourth foraging guild contained numerous subgroupings, which are further divided by attack maneuver use. The clustering algorithm accurately captured the structure of the original data (cophenetic correlation coefficient = 0.78). A full description of the foraging behavior associated with each foraging guild is provided in Supplementary Material S2.

Network Analyses and Linear Models

We found a significant negative relationship between the strength of association of 2 species and their foraging dissimilarity (linear model; slope = −1.04, adjusted r^2 = 0.06, $P = 0.01$), supporting the predictions of the facilitation

hypothesis (Figure 3A). However, there was substantial variability in the strength of association (SRI) values and the linear model had a low r-squared value. The trend was driven in part by the lower strength of association values for the large-bodied woodpecker species relative to the smaller Parulid, Vireonid, and Parid species (linear model; slope = −0.08, adjusted r^2 = 0.37, P = 0.01; Figure 3B). Our flocking network also showed significant negative assortativity by foraging height (assortment coefficient = −0.07, P = 0.02; Table 3), which suggests that species showed a slight tendency to preferentially associate with heterospecifics that forage in different height bands. We also found a non-significant negative assortativity by foraging substrate (assortment coefficient = −0.08, P = 0.06). However, assortment coefficient values were near zero for all 6 variables measured, and 5 out of 6 assortment coefficient values did not significantly differ from random (Table 3), suggesting that species associate near-randomly with respect to foraging ecology and do not exhibit checkerboard distributions within flocks.

Using our information-theoretic approach, we found that foraging substrate use was the best predictor variable for intraspecific flock abundance patterns (linear model; Akaike weight [w_i] = 0.89, r^2 = 0.47, P = 0.004; Table 4), as predicted by the competition hypothesis. Greater intraspecific abundance within flocks was associated with increasingly negative values on the substrate-use PCoA axis, which is correlated with increased use of live leaves and air as a foraging substrate (Figure 3C). This model was the only significant model of the 6 tested and had a ∆AIC$_c$ of greater than 2 over all other models (Table 4), indicating that it is significantly better at explaining intraspecific
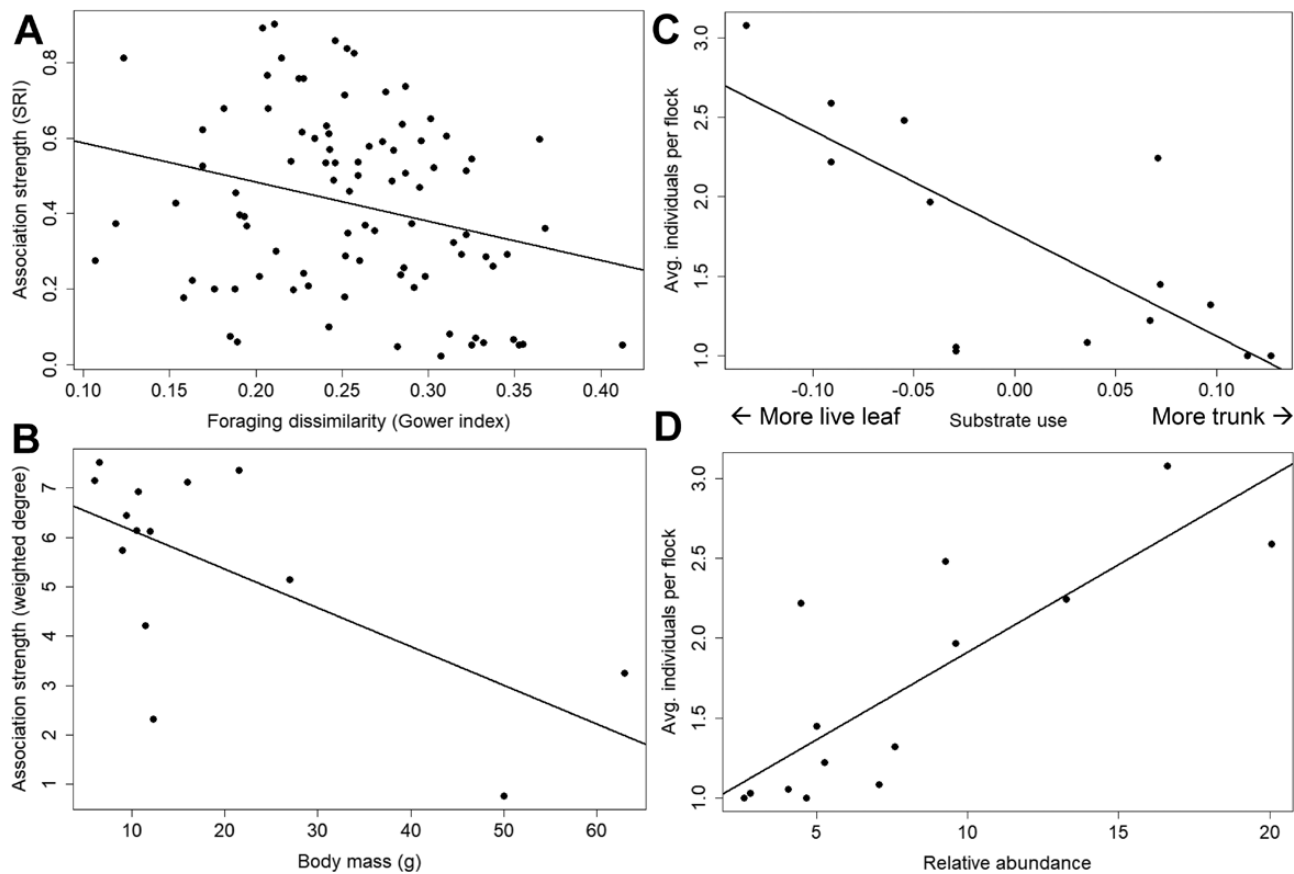

FIGURE 3. Effects of nonbreeding foraging ecology on mixed species flocking behavior. (**A**) Species that forage more similarly had significantly higher association rates in mixed-species foraging flocks (linear model; slope = −1.04, r^2 = 0.06, P = 0.01). The simple ratio index is a weighted measure of association based on co-occurrences in foraging flocks. Foraging dissimilarity was calculated from proportions of substrate, maneuver, and microhabitat use derived from foraging observations (see Methods). Only regularly flocking species observed in 4 or more flocks (5% of all observations) were included in the analysis. (**B**) This trend was driven in part by lower association rates of large-bodied woodpeckers (linear model; slope = −0.08, r^2 = 0.37, P = 0.01). Weighted degree is the sum of all weighted edges connected to a node (species) in the flocking network (see Figure 1B). Body mass values are from Sibley (2014). (**C**) Foraging substrate use significantly predicted intraspecific flock abundance (linear model; slope = −6.00, r^2 = 0.47, P = 0.004). (**D**) Intraspecific abundance within the flock was significantly correlated with relative abundance of a flocking species (n = 14 species) at our field sites (linear model; slope = 0.11, r^2 = 0.64, P < 0.001).

flock abundance (Burnham and Anderson, 2002). Species that were more abundant in flocks also had a higher local abundance at our study sites, and the 2 were significantly positively correlated (linear model; slope = 0.11, r^2 = 0.64, P < 0.001; Figure 3D and Table 2).

DISCUSSION

Our results suggest that the interaction between competition and facilitation in structuring flocks is scale-dependent, and that both mechanisms are operating in our system. At the coarse scale, we found that the association strength of a species pair was significantly positively associated with their foraging similarity, in accordance with the facilitation hypothesis. Large-bodied woodpeckers had lower association strengths compared with small-bodied passerine species that joined flocks more frequently. We also found that flocking species had a greater foraging

TABLE 3. Weighted assortment coefficients from a network of associations from mixed-species flocks. Assortment coefficients were calculated for a weighted social network of 14 species observed in over 5% of mixed-species flocks. This value represents the degree to which species positively or negatively associate with species of similar foraging ecology or body mass. Positive and negative values indicate positive and negative assortment association within the network, while zero values indicate random assortment. Foraging variables were quantified using a PCoA ordination of proportions of substrate, maneuver, and microhabitat use from foraging observations. P-values are calculated by comparing observed values to 1,000 null networks generated by pre-network permutation of the flock by species matrix. Assortment coefficients significantly different from random are in bold

Variable	Assortment coefficient	P-value
Foraging height	**−0.068**	**0.024**
Body mass	−0.023	0.212
Distance from trunk	−0.075	0.141
Microhabitat foliage density	−0.081	0.377
Substrate use	−0.084	0.062
Foraging maneuver use	−0.083	0.488

niche overlap of substrates, attack maneuvers, and foliage density at foraging microsite than expected by chance, further support for the facilitation hypothesis. Our analysis of assortment patterns found no evidence of either negative checkerboard patterns or positive assortment by foraging ecology, and indeed most flocking species were present in most flocks, suggesting that composition was not influenced by the presence of other species. When examining foraging behavior at a fine scale, however, we found evidence of niche partitioning, particularly on the basis of foraging substrate. Flock-joining species had distinct foraging maneuvers and substrates (Table 1), clustered into distinct foraging guilds, and exhibited relatively low niche overlap of foraging substrate (~40%). We also found that intraspecific abundance in foraging flocks was best explained by foraging substrate use, with live leaf and aerial foragers having higher abundances in flocks and at our study sites.

Small-bodied Flocking Species Have Stronger Association Strengths
We found a significant positive association between the foraging similarity of a species pair and their co-occurrence in flocks, which was driven by the interactions of a core group of 8–9 small-bodied species that were present in most flocks (Table 2) and showed high association strengths (Figure 1A). This pattern has also been found globally (Sridhar et al. 2012), which suggests that positive species interactions may be important in structuring many flock systems, including our own, at a coarser scale such as body size or foraging stratum. However, we cannot preclude the possibility that scrounging behavior or kleptoparasitism of similarly foraging species may be driving this pattern. Most small-bodied flocking species showed stronger associations with more similarly foraging species (Figures 1A and 3B). The exceptions to this trend were several large-bodied species of woodpecker that joined fewer flocks and generally had a lower strengths of association relative to foliage and branch-gleaning insectivores (Figure 3B), which mirrored findings by Farley et al.

TABLE 4. Akaike Information Criterion (AIC) tables of linear models of effect of foraging ecology on within-flock abundance of insectivorous birds in winter. Single-variable models of 6 components of foraging ecology on 14 insectivorous bird species' intraspecific flock abundances (Table 2) were evaluated using the Akaike Information Criterion modified for small sample sizes (AIC_c). Foraging height is the mean of all foraging height variables for a species from foraging observations at our field sites. Foliage density, foraging maneuver, distance to trunk, and foraging substrate values were quantified using PCoA ordination (see Supplementary Material S2)

Model rank	Variable	df	log likelihood	ΔAIC_c [a]	w_i	Slope	r^2	P
1	Foraging substrate	3	−9.55	0.00	0.89	−6.00	0.47	0.004
2	Foliage density	3	−12.78	6.46	0.04	−1.59	0.17	0.082
3	Distance to trunk	3	−13.06	7.01	0.03	−1.58	0.13	0.109
4	Foraging maneuver	3	−13.38	7.65	0.02	−2.34	0.09	0.154
5	Body mass	3	−13.51	7.91	0.02	−0.02	0.07	0.177
6	Foraging height	3	−14.41	9.71	0.01	−0.04	0.00	0.562

[a] The lowest AIC_c value was 27.51.

(2008) and Morse (1970) of lower flocking propensities by woodpeckers. As in other systems, species are more likely to flock with heterospecifics of similar body size (Bell 1983, King and Rappole 2008, Mammides et al. 2018), suggesting there are costs to moving and foraging with different-sized species.

These similarities in foraging among species that associate in flocks may be driven by changes to movement behavior necessary to maintain flock coherence (e.g., the frequency of hops, flights, and attack maneuvers). To obtain many benefits from flocking, such as access to social information (Goodale et al. 2010), the "many eyes" effect of group vigilance (Lima 1995), or the confusion effect of mass flight (Landeau and Terborgh 1986), a species must move at the same rate as the flock. Indeed, the movements of flock-following species in our system closely track those of the sentinel species (Tufted Titmouse; Contreras and Sieving 2011). Species within mixed-species flocks, however, forage and move at different rates (H. H. Jones personal communication; Hutto 1988), so species must adjust their movement behavior while foraging to match the flock speed (Hutto 1988, Sridhar and Guttal 2017). This modification of movement behavior may be particularly costly for large-bodied species because mixed-species flocks are generally composed of small-bodied birds (Sainz-Borgo et al. 2018). The woodpecker species in our system are all relatively slow-moving while foraging and some specialize on spatially aggregated resources such as masting oaks and sap wells (e.g., Miller et al. 2019). Alternatively, large-bodied woodpeckers may be subject to reduced predation pressure, resulting in lower flocking propensities; relative predation risk of forest birds in our system is unknown.

Foraging Specialization Leads to Weak Interspecific Assortment Patterns

In contrast to the expectations of both the facilitation and competition hypotheses, we found that species show little assortativity, either positive or negative, with respect to foraging ecology (near-zero values for all 6 assortment coefficients that we calculated; Table 3). Species joined flocks irrespective of flock composition, and indeed most species were present in most flocks (median species richness = 9). This suggests an absence of mutually exclusive species pairs or checkerboard patterns that have been observed in some tropical flocking systems (Graves and Gotelli 1993, Colorado and Rodewald 2015), likely due to niche-partitioning of foraging within our community. Instead, we found that the foraging niches of flocking species overlapped more than expected by chance (Figure 2). Nevertheless, species were remarkably specialized on specific substrates and attack maneuvers (Table 1 and Figure 1B), exploited a wide variety of foraging substrates, and showed relatively low niche overlap of foraging

substrates. Our results match similar niche partitioning by diet in a winter community of migrants in the Caribbean (Sherry et al. 2016) and by foraging behavior in the Andes (Newell et al. 2014). Species in our subtropical system could specialize on dead leaves, epiphytes such as *Tillandsia* bromeliads, and live leaves of numerous evergreen tree species (*Magnolia*, *Quercus* spp.), foraging niches more characteristic of tropical forests (Thiollay 1988, Rosenburg 1990, Marra and Remsen 1997, Mansor et al. 2019). Breadth of available foraging substrates may therefore influence the degree of nonbreeding niche partitioning in bird communities and allow for more diverse flocks than those that occur in winter at more temperate latitudes (Zou et al. 2018).

Our observational data do not allow us to determine whether interspecific competition is currently occurring in our system or what mechanism is driving niche partitioning. One possible mechanism is that specialization on specific substrates could lead to exploitation competition in which species better adapted to exploiting specific microhabitats will exploit food resources at those sites more efficiently than competitors (Alatalo et al. 1987). In many insectivorous birds, foraging substrate and behavior are tied to ecomorphological adaptations of the bill (Carrascal et al. 1990, Corbin 2008), leg (Moreno and Carrascal 1993), and eye (Moore et al. 2013), which could increase foraging success in specific microhabitats through more efficient detection, capture, and handling of prey items. On the other hand, foraging in many temperate flocking systems is subject to interspecific dominance hierarchies in which subordinate species are aggressively excluded from certain substrates and therefore forced to shift their foraging behavior in the presence of socially dominant flockmates (e.g., Alatalo 1981, Hogstad 1989, Jablonski and Lee 2002). Morse (1970) found that Parids in Louisiana winter flocks were socially dominant over other flock members and frequently supplanted them from foraging locations. Given that we found higher overlap in substrate use than expected by chance, however, it is also possible that species are converging in their foraging niche in order to minimize the costs of activity matching while foraging in the flock (see above).

Nonbreeding foraging niche partitioning may be more pronounced in systems where most species join mixed-species flocks. Flocking has been considered a form of niche construction (Harrison and Whitehouse 2011) because the presence of this behavior can change the selection pressures acting upon forest birds. The presence of social information about predators can make certain foraging microhabitats safer and therefore exploitable (Darrah and Smith 2013, Martínez et al. 2018). Species that forage by probing within dead leaves and in other substrates that occlude vision and limit vigilance might therefore more safely

be able to exploit these resources within a flock. Secondly, many species in our system may exclude conspecifics from flocks (see below) such that only a single individual of the species is encountered per flock (Table 2). Because titmouse flocks occupy large territories in winter (Brawn and Samson 1983), the aggressive exclusion of conspecifics from a flock could reduce the density of such species on the landscape to one per flocking territory (Powell 1989). This in turn allows for exploitation of more specialized and therefore less numerous resources, and the reduced competition from lower densities may also help explain the greater than average niche overlap in foraging microhabitat we observed in our flocking community.

Foraging Substrate Use Determines Intraspecific Abundance Patterns Within Flocks

As expected by the competition hypothesis, we found that intraspecific abundance within flocks varied among species and was strongly correlated with increasing use of live leaf and air as a foraging substrate (Figure 3C). We interpret this as 2 different overwintering strategies based on the abundance of the main foraging substrate. In the first case, species specialize on using relatively uncommon substrates and/or prey items such as dead leaves, epiphytes, or large-bodied prey, which could limit their nonbreeding densities, whereas in the second, the relatively common nature of live leaves as a foraging substrate permits higher nonbreeding densities (Figure 3D). Suhonen et al. (1992) similarly found that the intraspecific abundance of bird species in a boreal mixed-species flocking system was correlated with the arthropod abundance in their foraging microhabitat. While we measured foraging microhabitat use and not prey abundance, nonbreeding migrants that were specialized in their foraging substrate use have been found to be specialized in prey choice as well (Strong 2000). Nonbreeding densities of migratory insectivores have been strongly linked to arthropod abundance (Johnson and Sherry 2001, Johnson et al. 2005), yet the extent to which foraging substrate specialization influences this dynamic has not been previously described.

All species that occurred as singletons in flocks also had low relative abundances at our study sites (Figure 2D). We suggest that the mechanism explaining this trend may be nonbreeding territoriality and aggressive exclusion of conspecifics while the flock is in the nonbreeding territory, as observed in nonbreeding migrants in Central America (Rappole and Warner 1980). We frequently observed that species encountered singly in flocks called or sang repeatedly while in the flock (the authors' personal observations), particularly Blue-headed Vireo, Yellow-throated Warbler, Orange-crowned Warbler, and Black-and-white Warbler (*Mniotilta varia*). The above species all occurred at low densities, were strongly specialized by

prey type or substrate choice, and have anecdotally been reported to exhibit nonbreeding territoriality (Morton 1980, Morton and James 2014). Low densities have also been reported for other substrate-specialized migrants during the nonbreeding season such as the Golden-winged Warbler (*Vermivora chrysoptera*; Chandler et al. 2016). For such species, joining mixed-species flocks may therefore be a strategy to benefit from membership in a social group while mitigating the costs of intraspecific competition. Playback experiments to test for nonbreeding territoriality could help increase our understanding of these systems.

Shifts in Foraging Substrates Between the Breeding and Nonbreeding Season

We observed qualitative shifts in substrate use for a small number of migratory species between the breeding and nonbreeding season. Ruby-crowned Kinglets largely foraged on live leaves on the outer branches of trees and shrubs in our system in contrast to the breeding foraging ecology, where it is largely a conifer specialist (Franzreb 1984). These results corroborate findings from Louisiana forests (Remsen et al. 1989), although Western nonbreeding populations in Colorado and New Mexico (Austin and Smith 1972, Laurenzi et al. 1982) still forage primarily on conifers. As reported in Louisiana (Remsen et al. 1989), we found that Orange-crowned Warblers were dead-leaf specialists, using this substrate for roughly 75% of foraging observations (Supplementary Material Table 4). Detailed descriptions of foraging behavior on its breeding grounds are scarce, but it primarily gleans insect prey from live leaves (Curson et al. 1994). This species is also known to exploit other resources such as live leaves and flowers (Rosenburg et al. 1991) in other parts of its nonbreeding range.

Both Pine and Yellow-throated warblers also exploited novel foraging substrates in the form of epiphytic bromeliads (*Tillandsia* spp.), which are unavailable to northern populations. Northern populations of the Yellow-throated Warbler exploit bark crevices of sycamore trees (Gabbe et al. 2002) or probe in clusters of pine needles, cypress leaves, or pine cones (Ficken et al. 1968, Gabbe et al. 2002). Nonbreeding populations in our study system frequently exploited epiphytic plants in addition to those substrates (Supplementary Material Table 4). Pine Warblers also exploited epiphytes that are unavailable to them on northern breeding grounds (Ficken et al. 1968) while also continuing to use many substrates available year-round, including the bark and large limbs of trees. These 2 species use novel foraging substrates in addition to their breeding range foraging substrates, in contrast to Orange-crowned Warblers, which switched foraging substrates completely. Thus, nonbreeding migrants in our system shifted foraging substrate use to wholly or partially

use subtropical substrates not available on their breeding grounds.

Mixed Flocks are Central to Nonbreeding Ecology of Migrants

We found high flocking propensity values in our community, with 10 out of 14 flocking species being encountered in flocks over 80% of the time (Table 2). We obtained similar ratios to Farley et al. (2008), and similarly high values are also reported for other flock-following migratory species in Central and South America (Latta and Wunderle 1996, Pomara et al. 2007, Colorado et al. 2012). Such data should be interpreted with caution, however, as they represent "naïve" estimates that do not account for differences in detectability between individuals in and out of flocks (i.e. occupancy modeling; MacKenzie et al. 2002). Furthermore, flocking propensities for nonbreeding migrants may differ between habitat types (Post 1978, Pomara et al. 2007), such that propensities may be higher or lower in scrub or secondary forest sites for some species. That said, the weight of evidence suggests that foraging flocks may play a central role in structuring the social and foraging ecology of nonbreeding species in forest habitats. Future studies should look to understand how foraging ecology interacts with flocking behavior to determine nonbreeding densities, as low-density species may require intact flocking systems, specialized substrates, and larger areas of habitat during the nonbreeding season.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

(http://ufdc.ufl.edu/IR00010727/00001) are archived at the University of Florida Institutional Repository.

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