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# Persistent species relationships characterize migrating bird communities across stopover sites and seasons

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**Global migrations of diverse animal species often converge along the same routes, bringing together seasonal assemblages of animals that may compete, prey on each other, and share information or pathogens. These interspecific interactions, when energetic demands are high and the time to complete journeys is short, may influence survival, migratory success, stopover ecology, and migratory routes. Numerous accounts suggest that interspecific co-migrations are globally distributed in aerial, aquatic, and terrestrial systems, although the study of migration to date has rarely investigated species interactions among migrating animals. Here, we test the hypothesis that migrating animals are communities engaged in networks of ecological interactions. We leverage over half a million records of 50 bird species from five bird banding sites collected over 8 to 23 y to test for species associations using social network analyses. We find strong support for persistent species relationships across sites and between spring and fall migration. These relationships may be ecologically meaningful: They are often stronger among phylogenetically related species with similar foraging behaviors and nonbreeding ranges even after accounting for the nonsocial contributions to associations, including overlap in migration timing and habitat use. While interspecific interactions could result in costly competition or beneficial information exchange, we find that relationships are largely positive, suggesting limited competitive exclusion at the scale of a banding station during migratory stopovers. Our findings support an understanding of animal migrations that consist of networked communities rather than random assemblages of independently migrating species, encouraging future studies of the nature and consequences of co-migrant interactions.**

migration | community ecology | species interactions | social network analysis | bird banding

## Significance

Seasonal migrations of many species often converge in space and time, providing opportunities for interspecific interactions that, although rarely studied, may influence migratory routes, timing, and success. Here, we test the hypothesis that co-migrating birds are engaged in a consistent network of interspecific associations across stopover sites. We apply social network analysis to over half a million bird banding records collected from five sites across northeastern North America, finding that species co-occurrence is influenced by species relationships that are generally positive, persist across sites and seasons, and are partly explained by phylogeny, foraging behavior, and nonbreeding ranges. Our results demonstrate that interspecific relationships can help shape the en route ecology of migrating animals.

Migration is a global spectacle, with mass movements of animals often converging in space and time, their journeys shaped by similar geographic and seasonal forces (1–3). These co-migrations bring together seasonal assemblages of diverse animal species, often in high densities, where they may compete (4), prey on each other (5), share parasites and information (6, 7), and facilitate each other's movement (8). Interactions among co-migrating species are expected to affect survival and infection risk, influence migrants' stopover ecology, and shape migratory routes and movements, with mostly unexplored implications for populations (3). A recent global literature review found that while multispecies migrations are common across taxonomic groups, interactions among co-migrating animals are rarely studied (3). This may in part be because migratory phases of the annual cycle remain poorly studied for many species (9) and because of inherent challenges in tracking and detecting encounters among animals moving great distances. Given the prevalence of co-migrations and the potential impact of interactions among migrating species, we place migrating animals in a community context, testing the null hypothesis that co-migrants are random assemblages of species with co-occurrence incidentally resulting from each species' independent patterns of migration phenology (10) and habitat selection (11). Alternatively, networks of ecological interactions may be fundamentally characteristic of migration seasons, indicated by nonrandom and persistent interspecific relationships.

We apply a community ecology lens to the seasonal migrations of birds, a stunning example of co-migration. Avian migrations are often characterized by hundreds of species co-occurring in high densities during two alternating phases of flight and stopover along their migration routes (12, 13), providing opportunities for species interactions during both the aerial and terrestrial phases. Even though nocturnally migrating landbirds have generally been thought to be solitary migrants (14–16), their sheer numbers and our expanding knowledge of their in-flight vocalizations (17–19) suggest the potential for relevant in-flight interactions. Pencil-beam tracking radar suggests songbirds sometimes

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fly in loose flocks (20) that can be interspecific (21). Many bird species produce flight calls that are hypothesized to facilitate navigation, maintain groups, and trigger migratory restlessness in conspecifics (17). Both conspecific and heterospecific song can influence habitat selection among birds transitioning from flight to stopover (6), where birds can co-occur in high densities. Stopovers account for the majority of the time and energy expenditure of the entire migration season (22, 23), and stopover habitat can impact refueling rate and migratory timing (24). Thus interspecific interactions among co-migrants that improve or limit a bird's ability to rest, refuel, and recover between flight bouts—critical functions of stopover (25)—have the potential to be both common and intense for co-migrants with extreme energetic demands and time constraints traveling in high densities through unfamiliar landscapes (26). Negative interactions like competition and territoriality (27) can impair migratory success by limiting access to resources (28, 29) and reducing the refueling rate (30–33). On the other hand, participation in mixed-species groups can reduce predation risk and improve foraging efficiency (34), and social information—both conspecific and heterospecific—shared between migrating birds may assist navigation (35), habitat selection (6, 36), and predator avoidance (37). Conspecifics are expected to provide the most relevant information about threats and resources, and in some cases, conspecific relationships are more important than environmental features in influencing habitat selection (38). But heterospecifics can also be a valuable source of information: Typically, the majority of other observable individuals in a given community are heterospecifics, making heterospecific information readily available (39), and related species sharing similar trophic niches can provide relevant information with less risk of competition for the same limited resources (36).

Here, we test the hypothesis that migrating birds are engaged in a migrating community, using an operational definition of a community: interacting species that co-occur in space and time (40, 41). Ecologists typically constrain community analyses within spatial and temporal bounds, traditionally anchoring a community to a particular location across time (42). Spatial boundaries are extended for "metacommunities," multiple, connected communities (42) among which migrating animals transport nutrients, energy, and diseases (43–45). In conceptualizing a migrating community, however, we define the spatial and temporal boundaries of the community by the co-occurrence of interacting species as they move along the migration route. In the present study, we focus on migrating communities while they are at stopover sites, but the concept is inclusive of the full migratory period: stopovers, flights, and the transition between the two.

To test our hypothesis, we applied social network analysis to long-term bird banding records, a massive, standardized, and underutilized dataset (46). We analyzed over half a million bird banding records of migrating passerines and near-passerines collected over 8 to 23 y at five bird observatories and research stations across eastern North America (Fig. 1*A*). Social network analyses enable rigorous hypothesis testing of large, observational datasets and facilitate differentiating the contributions of random spatiotemporal co-occurrence and nonrandom species relationships (38, 47, 48). Within a stopover site, we inferred species "associations" from instances when multiple birds were captured in the same mist net (12 m) during the same 20 to 45 min interval (49). Species associations reflect the probability two species are captured together. These associations can be shaped by nonsocial, "structural" predictors that happen to bring two individuals in close proximity to each other, like a species' abundance, habitat use, and migration phenology (Fig. 1*B*). Thus a key challenge is disentangling social relationships that are the focus of our research question from nonsocial factors that incidentally influence species associations. We use an analytical approach proposed by ref. 50, calculating a more relevant

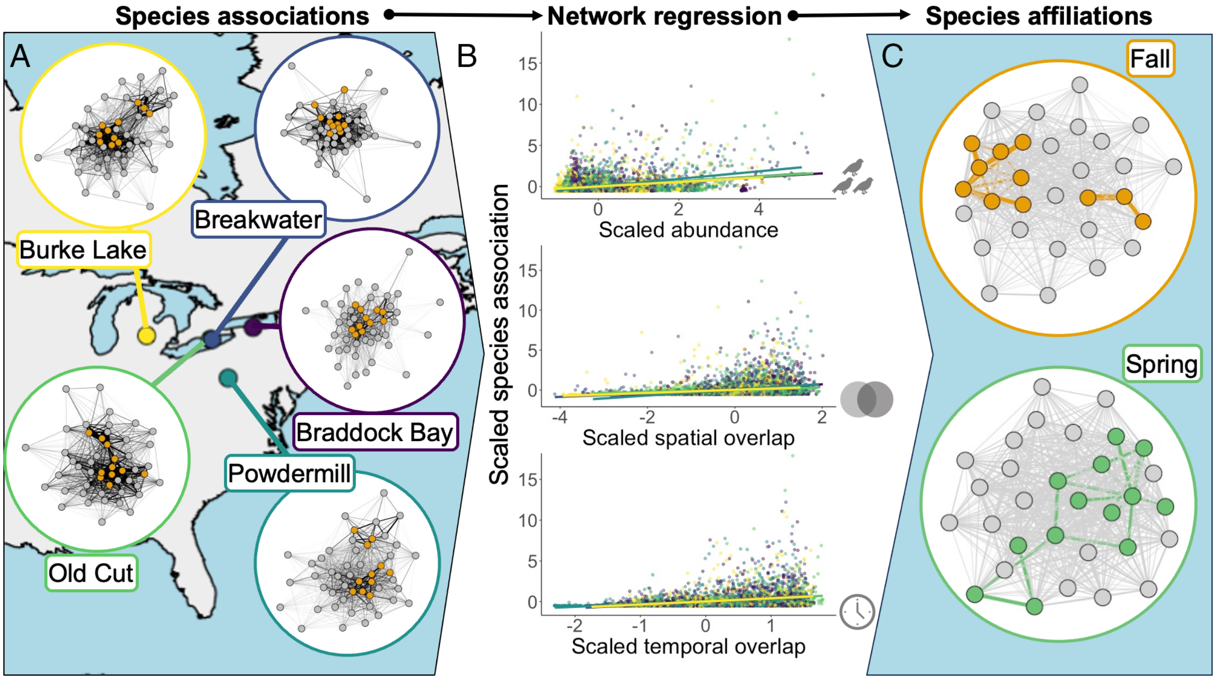

**Fig. 1.** Data analysis workflow for over 500,000 bird banding records collected during spring and fall across 8 to 23 y and five sites in eastern North America. (*A*) We first constructed spring and fall social networks of species associations for the top 50 most abundant species at each site (only fall networks shown). Orange network nodes in (*A*) represent the species involved in relationships with strong affiliation indices during fall migration. (*B*) Next, we used network regression to relate the abundance, spatial overlap, and temporal overlap of each species pair to their species association. This analytical technique is called MRQAP. The data points are site specific, and their colors correspond with the colors of the circles on the map (*A*). Standardized residuals from these regression analyses are species affiliation indices (48). (*C*) We end up with a network of species affiliation indices, here averaged across sites in fall (orange) and spring (green). Colored nodes and edges in (*C*) denote strong species affiliation indices (>2 or < -2), all of which were positive.

metric at the pairwise species level—the "affiliation index" (50) (Table 1 and Fig. 1 *B* and *C*). Affiliation indices represent the variation in association strength after accounting for variation in nonsocial factors (in this case, a species pair's abundance and overlap in migration timing and space use) and thus more likely reflect social behavior (50–53). Positive affiliation indices (i.e., species captured together much more often than expected) describe preferred relationships, and negative affiliation indices (i.e., species captured together much less often than expected) describe avoided relationships (50, 51, 54). We tested for a generalizable community structure among co-migrating birds by predicting that 1) species associations have a social component and are not solely determined by incidental spatial and temporal co-occurrence, 2) species affiliation indices are consistent across space (multiple sites) and time (between spring and fall migration) and 3) species affiliation indices represent ecologically meaningful relationships, reflected by phylogenetic relatedness, similarity in foraging behaviors, and/or similarity in breeding and nonbreeding latitudes. A lack of support for the null hypothesis would demonstrate that interspecific relationships, long recognized as shaping communities during stationary phases of the annual cycle, including breeding bird communities (40), are also key to understanding species coexistence during fast-moving animal migrations.

## Results

**Nonrandom Co-Occurrence.** For each site and season, we tested the differential effects of species' spatial overlap, temporal overlap, and relative abundance on their species association. As expected, we found that species associations were stronger among species pairs with greater overlap in stopover space use, greater temporal overlap in migration phenology, and when one or both species were more abundant (Table 2). Subsequent analyses use the standardized residuals from these network regressions, termed "affiliation indices," which represent species captured together more (positive residual and affiliation index) or less (negative residual and affiliation index) often than expected and therefore suggestive of social relationships.

We next tested the prediction that species associate beyond spatial and temporal co-occurrence by constructing null models with permutation tests (48). The first null model assumed that species associations are entirely random: An individual has an equal probability of being captured in any net during any part of the migration season. The second null model assumed that species associations are a function of shared habitat use, migration timing, and abundance alone, with spatially and temporally co-occurring species being otherwise randomly distributed throughout a stopover site. When comparing observed and permuted networks, the coefficient of variation (CV) of association strengths is an interpretable test statistic: A larger CV in the observed network indicates there are more positive and negative relationships than in a network of random associations (48), meaning that there is structure in the network not explained by the spatial and temporal patterns underlying species' captures. At every site during both spring and fall migration seasons, the CVs of the observed networks (*SI Appendix*, Figs. S1–S9) were consistently greater than the CVs of 1,000 null networks of completely randomized associations and 1,000 null networks that were randomized within a particular week and portion of the banding site (all $P$-values < 0.01). Significant differences between the observed and permuted networks suggest social relationships also influence whether individuals of different species are captured together. This result indicates that there are more preferred and/or avoided relationships in our observed networks than expected by spatial and temporal co-occurrence alone (48), demonstrating the additional influence of social relationships on species co-occurrence during stopover.

**Persistent Species Relationships.** To test whether species affiliation indices were consistent across space, we ranked the affiliation indices of each species pair within a site and compared ranks across sites (*SI Appendix*, Figs. S10–S18). Species affiliation indices were similarly ranked across all five sites in fall (Kendall's $W = 0.558$, $P = 0$) and all four sites in spring (Kendall's $W = 0.536$, $P = 0$) (*SI Appendix*, Fig. S19), meaning that, for instance, the strongest relationship at one site was among the strongest across all sites. Geographic distance between sites, which ranged from 13 to 742 km, did not explain differences between networks of affiliation indices in fall (Mantel $r = -0.176$; $P$-value = 0.583) or spring (Mantel $r = 0.029$; $P$-value = 0.417 (*SI Appendix*, Fig. S20), nor did differences in latitude between sites (fall: Mantel $r = -0.273$, $P$-value = 0.325 spring: Mantel $r = 0.943$, $P$-value = 0.083) or longitude (fall: Mantel $r = -0.176$, $P$-value = 0.583; spring: Mantel $r = 0.029$, $P$-value = 0.417).

We also tested whether the same species serve as social hubs across sites. Eigenvector centrality is a within-network measure of species connectedness that accounts for a species' connections as well as the connections of their associates such that species with high eigenvector centrality may serve as highly connected social hubs within their networks (31) (Table 1). It is important to note, however, that unlike affiliation indices, eigenvector centrality does not account for structural variables (i.e., abundance, migration phenology, habitat use). Species' eigenvector centrality was similarly ranked across all five sites in fall (Kendall's $W = 0.757$, $P = <0.0001$) and all four sites in spring (Kendall's $W = 0.707$,

**Table 1. Glossary of social network analysis terminology**

Glossary of terms

| Term | Definition |
|---|---|
| Species association | Fine-scale spatial and temporal co-occurrence of individuals of different species (48). We calculated associations as the proportion of times individuals of two species were captured together, out of the total number of times individuals of both species were captured, together or apart. |
| Species affiliation index | Variation in species associations that is not explained by variation in nonsocial, "structural" variables (48). Affiliation indices are calculated as the scaled residuals from a regression of species associations on structural predictor variables, which in this study were temporal and spatial overlap and abundance. Because affiliation indices essentially control for predictor variables, they more likely represent social (preferred and avoided) relationships. |
| Eigenvector centrality | An estimate of a species' role as an important "social hub" in its network (48). Eigenvector centrality is calculated taking into consideration the strength and number of the focal species' associations as well as the strength and number of its associates' associations. A species can have high eigenvector centrality by being strongly connected to many other species and/or by being connected to highly connected species. |

**Table 2. Across sites and seasons, pairs of species had stronger associations when they had greater temporal overlap, spatial overlap, and abundance during stopover**

| Site | Season | Predictor | B | *p* |
|---|---|---|---|---|
| Braddock Bay Bird Observatory | Fall | Temporal overlap | 0.316 | <0.0001 |
| | | Spatial overlap | 0.324 | <0.0001 |
| | | Abundance | 0.356 | <0.0001 |
| | Spring | Temporal overlap | 0.388 | <0.0001 |
| | | Spatial overlap | 0.328 | <0.0001 |
| | | Abundance | 0.341 | <0.0001 |
| Burke Lake Banding Station | Fall | Temporal overlap | 0.387 | <0.0001 |
| | | Spatial overlap | 0.218 | <0.0001 |
| | | Abundance | 0.307 | <0.0001 |
| Breakwater (Long Point Bird Observatory) | Fall | Temporal overlap | 0.163 | 0.008 |
| | | Spatial overlap | 0.284 | <0.0001 |
| | | Abundance | 0.402 | <0.0001 |
| | Spring | Temporal overlap | 0.347 | <0.0001 |
| | | Spatial overlap | 0.174 | <0.0001 |
| | | Abundance | 0.350 | <0.0001 |
| Old Cut (Long Point Bird Observatory) | Fall | Temporal overlap | 0.433 | <0.0001 |
| | | Spatial overlap | 0.120 | 0.001 |
| | | Abundance | 0.374 | <0.0001 |
| | Spring | Temporal overlap | 0.447 | <0.0001 |
| | | Spatial overlap | 0.124 | <0.0001 |
| | | Abundance | 0.335 | <0.0001 |
| Powdermill Avian Research Center | Fall | Temporal overlap | 0.384 | <0.0001 |
| | | Spatial overlap | 0.075 | 0.238 |
| | | Abundance | 0.308 | <0.0001 |
| | Spring | Temporal overlap | 0.311 | <0.0001 |
| | | Spatial overlap | 0.155 | 0.018 |
| | | Abundance | 0.281 | <0.0001 |

Results are from a network regression, testing the differential effects of matrices of each predictor variable on a matrix of species associations. All matrices were scaled, so effect sizes can be compared. Standardized residuals from these analyses are the "affiliation index" for each species pair.

$P < 0.0001$) (*SI Appendix*, Fig. S19). Species with eigenvector centralities ranked within the top 10 at all sites in the fall included Magnolia Warbler (*Setophaga magnolia*), American Redstart (*Setophaga ruticilla*), Red-eyed Vireo (*Vireo olivaceus*), Nashville Warbler (*Leiothlypis ruficapilla*), and Chestnut-sided Warbler (*Setophaga pensylvanica*), and in the spring included Magnolia Warbler, American Redstart, Common Yellowthroat (*Geothlypis trichas*), Chestnut-sided Warbler, and Gray Catbird (*Dumetella carolinensis*).

To test for the consistency of affiliation indices between seasons, we first averaged each species pair's affiliation index across sites. These average species affiliation indices were significantly correlated between seasons (Mantel Test, $r = 0.687$, $P = 0.001$) and were ranked consistently between seasons (Kendall's $W = 0.783$, $P = 0$).

**Ecologically Meaningful Relationships.** To understand the potential ecological relevance of species affiliation indices, we tested whether the affiliation indices of species pairs related to four predictor variables: their phylogenetic distance, similarities in foraging behavior, and similarities in the latitudes of their stationary nonbreeding and breeding ranges (statistics summarized in *SI Appendix*, Tables S3–S5). In models that included all four predictor variables, either phylogenetic distance or foraging behavior significantly predicted species affiliation indices across all sites and seasons, except for one site in the spring (*SI Appendix*, Table S3). Phylogeny and foraging behavior are closely related to each other. For instance, all the focal species who forage with a flycatching behavior belong to the family Tyrannidae, and the majority of focal species in the Parulidae family are foliage gleaners. In subsequent models that included either phylogenetic distance or foraging behavior, phylogeny and behavior remained significant predictors of species affiliation indices at most sites and during both seasons (*SI Appendix*, Tables S4 and S5). That is, species were more likely to have strong, positive affiliation indices when they were closely related to each other and had the same foraging behavior.

In models that controlled for both phylogenetic distance and foraging behavior, we found that species with similar nonbreeding range latitudes often had larger, more positive affiliation indices during both spring and fall migration (*SI Appendix*, Table S3). Similarity in breeding range latitudes only related to affiliation indices at one site during one season (*SI Appendix*, Table S3).

In evaluating pairwise relationships with affiliation indices, we used a cutoff of 2, with affiliation indices >2 representing strong preferred relationships and affiliation indices <−2 representing strong avoided relationships (51, 54). For pairwise relationships, we found positive affiliation indices were much more common than negative affiliation indices (*SI Appendix*, Figs. S10–S18 and Table S2). At each site during each season, there were an average of 35 species pairs with significant, positive affiliation indices (34.89 ± 10.51, mean ± SD), whereas there was a single species pair with a significant negative affiliation (*SI Appendix*, Figs. S10–S18 and Table S2). When considering affiliations indices averaged across sites for each season, there were 13 species pairs with significantly large positive affiliation indices in spring, 11 species pairs with significantly large positive affiliation indices in fall, and no species pairs with significantly large negative affiliation indices in either season (Fig. 2). The affiliation index for Chestnut-sided Warbler (*S. pensylvanica*)—Magnolia Warbler (*S. magnolia*) was ranked in the top 12 at all sites during spring. The affiliation index for American Redstart (*S. ruticilla*)—Magnolia Warbler was ranked in the top 10 at all sites during fall (*SI Appendix*, Figs. S10–S18 and Table S2).

## Discussion

Taken together, our results support the hypothesis that migrating birds in eastern North America constitute a migrating community. We find 1) evidence for nonrandom associations among migrating birds, supporting the role of interspecific relationships in structuring species' spatial and temporal co-occurrence, and 2) that these relationships are remarkably consistent across space and between migration seasons. We additionally show that species are often more likely to associate with closely related species with similar foraging behaviors and nonbreeding range latitudes, even after accounting for species abundance and overlap in migration timing and habitat use, meaning that these relationships could result in interactions that impact refueling and stopover behavior of species sharing similar trophic niches (55). Finally, we find positive affiliation indices are much more prevalent than negative affiliation indices, suggesting that interspecific competitive exclusion is not common within migrating communities at the scale of a banding station.

We find that although species abundance, spatial overlap, and temporal overlap all significantly predict species associations, they still do not fully explain interspecific associations during migration. At all sites and during both seasons, the observed social networks significantly differed from randomized null models in which the capture of multiple birds was only determined by spatial and temporal co-occurrence, with no social component. The presence of nonrandom species associations means that migrating birds may indeed be part of a migrating community, not just a random assemblage of species with similar migration timing, distributing themselves within a stopover habitat according to their own particular habitat preferences. This key finding indicates that species relationships contribute to habitat selection during migration, not just during stationary phases of the annual cycle (38, 56, 57). That is, individuals of a given species are not randomly distributed throughout their preferred habitat type, but instead, the preferred or avoided social relationships they have with other species also influence which particular 12 m net and ~30 min interval they are captured in.

We tested the persistence of species relationships across multiple sites within the same flyway, finding remarkable consistency of species relationships. The rankings of species affiliation indices (i.e., the strength of species pair associations after accounting for their abundance and spatial and temporal overlap) were statistically significantly consistent across sites and between seasons. The species pairs with the largest affiliation indices at one site were among the pairs with the largest affiliation indices across all sites, and the species pairs with average affiliation indices ranked first and third during spring migration (American Redstart—Magnolia Warbler and Ruby-crowned Kinglet (*Regulus calendula*)—White-throated Sparrow (*Zonotrichia albicollis*) were also ranked first and third during fall migration. The persistence of species affiliation indices across space and between seasons is noteworthy. These relationships persist despite geographic differences among sites that could relate to proximity to breeding grounds or the presence of nonfocal species whose range includes some, but not all, sites. These relationships also persist despite large seasonal differences in bird migration: Spring migration often involves more time pressure to arrive early to breeding grounds (58), and fall migration includes the addition of an entire generation of first-time migrants, just hatched over the summer (59). The persistence of species relationships across space and time points to their ecological importance. We encourage investigations of species relationships across broader geographic scales than we were able to include in this study. Species associations may differ across larger latitudinal gradients as the migration season progresses, and the inclusion of data from breeding and nonbreeding ranges

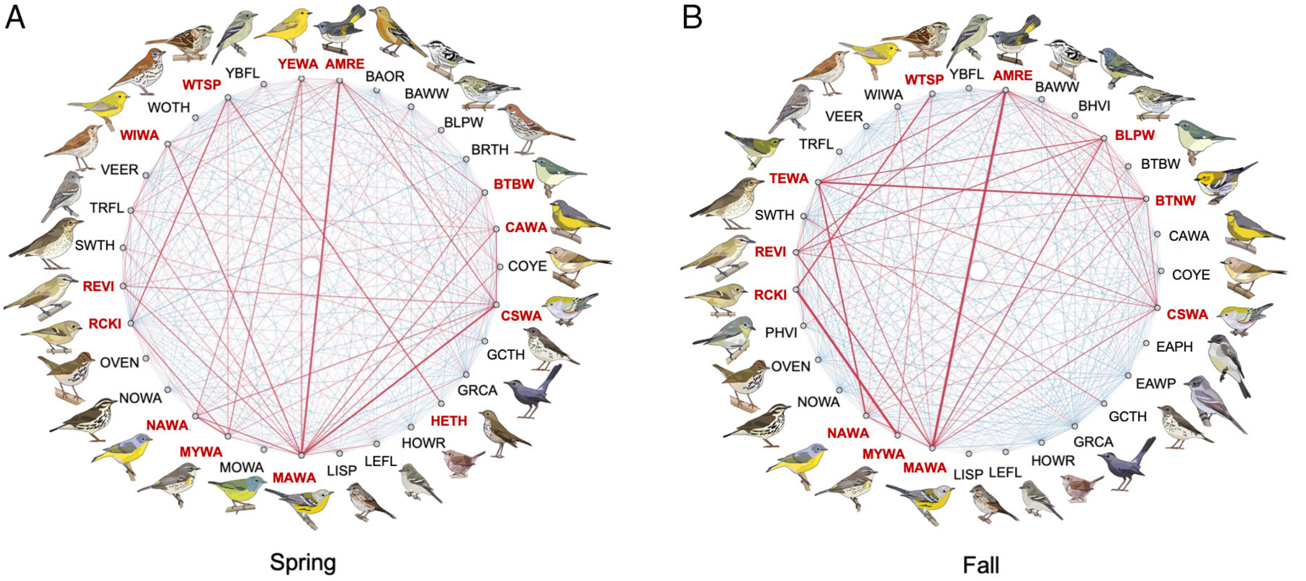

**Fig. 2.** Co-migrating bird species are highly connected; the strongest affiliation indices are positive, suggesting attracted relationships; and affiliation indices are generally consistent between seasons. (*A*) and (*B*) show networks of affiliation indices among abundant species, averaged across sites during spring (n = 4 sites) and fall migration (n = 5), respectively. Here, affiliation indices represent the strength of association between two species, controlling for spatial and temporal co-occurrence and species abundance. Species are in alphabetical order clockwise (see *SI Appendix*, Table S1 for four-letter species abbreviations). The width of the lines connecting species reflects the size of the affiliation index, with positive affiliation indices in red and negative affiliation indices in blue. The labels of species that are part of pairs with large affiliation indices are shown in bold red text. The species included in each network are the set of species that are among the top 50 most abundant species at each site during each season (n = 31 in both seasons). Bird illustrations by Emily Underwood.

could reveal the full-annual cycle of species interactions. Inclusion of data from sites with greater geographic and environmental variation could identify whether species affiliation indices and interactions during migration are unique to the migratory phase or persist throughout other phases of the annual cycle. Such analysis could estimate the full spatial and temporal extent of these migrating communities by identifying when species relationships form and disband, as well as explore the effects of migratory species on the resident species with which they temporarily co-occur (60). Intriguingly, we found that species with similar nonbreeding range latitudes often had stronger, more positive affiliation indices in both spring and fall. This result demonstrates that interspecific relationships during migration could be influenced by relationships outside of the migration season or by similarities in migration distances and destinations (18). We do not find an overall effect of breeding latitude similarity, but because the sites included in this study are generally northern, the species we investigated necessarily have relatively similar northern breeding latitudes.

To provide ecological context to the species we identified with persistent affiliation indices, we tested whether species affiliation indices related to species' phylogenetic relatedness and the similarity of their foraging behavior in addition to the latitude of their breeding and nonbreeding ranges. We found that species that are closely related and have the same foraging behaviors often have larger, more positive affiliation indices, further supporting the potential for these relationships to result in meaningful interspecific interactions. Competition may be more intense or social information more beneficial between related species with similar foraging niches. We notably only found support for one significant negative affiliation index (avoided relationship) at one site, whereas there were many significant positive affiliation indices (preferred relationships), suggesting that interactions among related species with similar foraging behaviors do not result in competitive exclusion during migration (55), at least within the spatial scale of a banding station. Importantly, even though we do not find evidence for species altering their space use to avoid competitors, species could still be engaging in competitive interactions and experiencing reduced refueling rates (30–33). Furthermore, studies conducted at broader spatial scales may find competitive interactions do influence stopover habitat use (28, 61): In our study, one species avoiding another at the landscape scale would simply result in low capture numbers and undetectable competitive exclusion within the banding site. The numerous positive affiliation indices we identify indicate that heterospecific relationships are common and could be beneficial during migration. Many Neotropical insectivorous migrants participate—and even play a central role—in mixed-species foraging flocks within their nonbreeding ranges (62), and social information can outweigh competitive exclusion in unfamiliar habitats (63, 64). Heterospecific attraction—whereby one species is more likely to select habitat given the presence of another species—has been described between migrant and resident birds (36). In an unfamiliar environment, heterospecifics can provide reliable cues about habitat quality that inform much quicker decisions about habitat selection than an individual can make based on its own direct sampling of the landscape (36). Heterospecific information from species of a similar trophic level is likely especially valuable: These species might use similar resources and be avoiding similar predators while not posing as direct a competitive cost as conspecifics (39). It will be valuable for future studies to more closely examine the balance between interspecific social information sharing and competition in the field, especially in the context of brief stopovers, where migrating birds must rapidly refuel in unfamiliar habitats (65).

In this paper, we account for the nonsocial factors that influence species associations to focus on social relationships. However, these nonsocial factors may also influence and be influenced by community dynamics (66) in ways worthy of further investigation. For instance, we found that temporal overlap always significantly predicted species associations, but notably, patterns of temporal overlap may change as animals of diverse taxa shift their migration phenology in response to climate change (67–69). Marked variation in the degree and sometimes even direction of species' phenological shifts (68) could break down relationships between species that historically migrated together or create opportunities for new interactions between species that now have similar phenology (70). Conversely, important social relationships may influence the flexibility of a species' phenological response, facilitating or hampering phenological shifts in order to maintain consistent migration cohorts. In these ways, processes affecting one population have the potential to reverberate throughout an entire migrating community, and viewing co-migrating animals as an interconnected network may influence the ways that we study and conserve animal migration.

This work represents the tip of an iceberg of potential research on the community ecology of migration (71), toward an understanding of entire migration systems (72). Perhaps foremost is the need to identify the types and impacts of species interactions occurring during migration. Unlike this study, experimental fieldwork could explore how these species interact, and how species interactions impact migration timing or success. Future studies could evaluate species interactions at different spatial and temporal scales. For instance, studies that incorporate behavioral observations could identify the nature of species associations at temporal scales smaller than 20 to 45 min and even characterize leader–follower dynamics among mixed-species flocks (73). Additionally, raptors, songbirds, bats, and insects can all co-occur during migration (74) and future work in this system could address predator–prey and host–parasite interactions across more taxa. Finally, recent research is revealing that vocalizations produced during migratory flight could aid the navigation of both conspecifics and heterospecifics: Flight calls are often more similar between species with overlapping migration timing and similar breeding latitudes (18); species with similar flight calls tend to fly in close proximity to each other (22); and in urban centers, the social influence of flight calls on navigation may contribute to the much higher rates of building collisions for species that produce flight calls (23). Our study focuses solely on the terrestrial phases of bird migration, but future work could investigate whether the relationships we observed at stopover persist during nocturnal flight, or whether different processes shape aerial and terrestrial co-migrant interactions.

The lens of community ecology has been focused on communities anchored to a particular location across time (42) and this work highlights the need for an explicit integration of movement ecology to understand the processes underlying species associations through both space and time (75–77). The concept of "metacommunities"—multiple, connected communities (42)—expanded the scale of community ecology's focus and sparked a new understanding of migrating animals as "mobile links" (43) transporting nutrients, energy, and diseases among components of a metacommunity (44, 45). Under this framework, however, communities are still essentially fixed in space. From the perspective of a single location through time, communities of migrating animals appear to be highly dynamic, with periodic pulses of migrants passing through a particular location (45). By untethering this perspective from a particular location to follow a community throughout migration, we may find consistent and persistent species interactions through time, as we have in the present study. Indeed, migration is a paradoxical strategy of maintaining stability through movement, with animals maintaining climatic niches by moving through seasonal environments (78, 79).

Here, we provide another example of consistency inherent in the dynamic process of migration—persistent en route species relationships that could extend across continents. Future theoretical and experimental work could explore how the spatial transience but temporal consistency of migrating species' associations affects community dynamics (45). For instance, perhaps the fact that migrating animals move through unfamiliar landscapes but with familiar cohorts of species promotes social information sharing over competitive exclusion (64). We encourage future integrations of movement and community ecology to advance our understanding of animal migrations and community dynamics.

## Materials and Methods

**Banding Stations.** We used long-term banding datasets from Braddock Bay Bird Observatory (43.324, −77.717), Long Point Bird Observatory's banding stations at Old Cut (42.584, −80.398) and Breakwater (42.561, −80.284), Powdermill Avian Research Center (40.164, −79.268), and Michigan State Bird Observatory's Burke Lake Banding sSation (42.812, −84.383). Data are from spring and fall migration at Braddock Bay Bird Observatory (34 nets; 1999 to 2022), Old Cut (14 nets, 2002 to 2022), Breakwater (13 nets; 2002 to 2022), and Powdermill Avian Research Center (79 nets; 2009 to 2022), and from fall only at Burke Lake Banding Station (27 nets; 2014 to 2022). As all these sites are in North America, we use "spring" and "fall" here and throughout the paper to refer to the Northern Hemisphere's spring and fall seasons.

At all sites, mist nets were opened 15 to 30 min before sunrise and kept open for 5 to 6 h. Nets were checked every 20 to 30 min (Old Cut, Breakwater, and Braddock Bay Bird Observatory), 40 min (Powdermill Avian Research Center), or 45 min (Burke Lake Banding Station). Birds recaptured within the same day were not recorded in the banding data for Old Cut, Breakwater, or Powdermill Avian Research Center; birds recaptured within 3 h of initial release were not recorded in the banding data at Burke Lake Banding Station; birds recaptured within 2 h of the previous capture were not recording in the banding data at the Braddock Bay Bird Observatory.

**Data Filtering.** We started with a total of 689,404 band records. For each site, we defined each migration season as the interval of dates with consistent bird captures across all years, aligning with the start and end of each station's migration banding protocols. Spring migration is 90 to 160 d since January 1 for Old Cut and Breakwater, 73 to 153 for Powdermill Avian Research Center, and 105 to 158 for Braddock Bay Bird Observatory. Fall migration is 213 to 318 d since January 1 for Old Cut and Breakwater, 218 to 303 for Burke Lake Banding Station, 221 to 317 for Powdermill Avian Research Center, and 227 to 303 for Braddock Bay Bird Observatory. Birds captured outside of these migration seasons were excluded from analyses. We excluded from analyses any species that occur year-round at any of the banding stations, as determined by range maps (80). We were left with a total of 520,754 records of banded migratory birds during migration seasons.

**Species Associations.** Network analyses were performed with the asnipe (81) and igraph (82) packages in RStudio (Version 2022.07.1).

We constructed weighted networks for each site using group-by-individual (GBI) matrices. The GBI matrices consisted of a column for the number of individuals of each species captured in every "group" (i.e., a specific net and its net run time). While traditional GBI matrix values are 0 or 1, ours included values greater than 1 for instances in which multiple individuals of the same species were captured in the same net at the same time. We then used a modification of the asnipe package's get_network function to create an adjacency matrix consisting of the Simple Ratio Index of each species pair. The SRI is a weighted measure describing the proportion of the time that two species are associated (48) and is used as the edge weight in social networks. Here, for each species pair,

$$\mathrm{SRI} = \frac{x}{x + y_A + y_B},$$

where $x$ is the number of times Species A and Species B were captured together, $y_A$ is the number of times only Species A was captured, and $y_B$ is the number of times only Species B was captured. We modified the function so that, in instances where multiple individuals of the same species were captured together, that translated into A*B pairwise associations, with A being the number of individuals of Species A and B being the number of individuals of Species B captured together.

**Permutation Test.** To determine whether observed associations differed from random, we conducted a permutation test (83, 84), using a modification of asnipe's network_permutation function. Under this procedure, two species are randomly selected from two separate groups and swapped. "Group" here refers to the group of birds captured in the same mist net during the same net run. This design ensures that the number of groups and the number of species in each group match the original dataset. Because only 29% of groups contained multiple species, and swaps between groups with single species do not affect the network in any way, we required the permutation test to include in each swap at least one group that contained more than one species capture. We ran 10,000 permutations with 10 "flips" each time, with the resulting network representing a null hypothesis of random associations. We compared the coefficient of variation of the observed network (i.e., the SD of edge weights divided by the average edge weight) and each of the permuted, null networks. The *P*-value is calculated as the number of times the random networks' CVs were greater than the observed CV, divided by the number of permutations (48). In all instances, 10,000 permutations were enough for the *P*-values to stabilize. A significantly greater observed CV than the CVs of random networks indicates that the observed network contains more preferred/avoided relationships than expected.

Preferred/avoided relationships may arise from social forces but can also result from spatial and temporal factors structuring species associations. For example, a weak association could result from negative social interactions or could simply reflect the fact that two species migrate through the site during different periods of the season. Therefore, we next conducted permutation tests that controlled for overlap in migration timing and habitat use for each species pair (84). We accomplished this by restricting species swaps to only occur between individuals captured during the same week and within the same group of nets. We defined net groups by overlaying a grid of 60 m × 60 m squares over a map of the net locations, adjusting its position to minimize the number of grids containing only one net, and grouping nets with others occurring in the same 3,600 $\mathrm{m}^2$ area. We chose this area because it allowed for the creation of multiple net groups across banding sites of differing areas. Permutation test CVs and *P*-values were calculated as described above. Here, significant *P*-values indicate that species' preferred/avoided relationships are not simply due to similarities/differences in habitat use or migration phenology, but may indeed have a social component.

**Species Affiliation Indices.** A key challenge in animal social network analysis is separating social reasons why animals may associate with each other from structural predictors like spatial and temporal factors that happen to bring two animals in close proximity to each other. One approach, proposed by Whitehead and James (50), is to calculate "Generalized Affiliation Indices." In practice, affiliation indices are calculated as the standardized residuals from a regression analysis where the dependent variable is an association metric (here, the SRI) and the independent variables are nonsocial, "structural" predictors, like home range overlap. The regression analysis used in this case is a powerful tool specialized for analyzing relational data that are organized in matrices, called Multiple Regression Quadratic Assignment Procedure (MRQAP; (47, 85)). MRQAP notably assesses the differential effects of multiple independent matrices on a dependent matrix (85, 86). For each site and season, we used MRQAP with double semi-partialling (85), using the mrqap.dsp function in R package asnipe, to relate a matrix of species associations to matrices of the temporal overlap, spatial overlap, and combined abundance of each species pair (defined below). Each matrix was scaled for direct comparison of effect sizes. Residuals from this analysis represent variation in association strength that is not explained by the predictor variables–temporal overlap, spatial overlap, or species abundance–and therefore the affiliation indices for each species pair are more likely to represent the social, rather than structural, reasons why two species are captured together. We scaled the residuals so they had a mean of 0 and SD of 1. Large affiliation indices ($>2$) represent strongly preferred relationships and affiliation indices $<-2$ represent strongly avoided relationships (51, 54). Affiliation indices have been calculated and used in this way throughout recent literature, most commonly in studies of marine animals (e.g., refs. 51–54).

**Network Regression Covariates.** The strength of species associations is influenced by the degree of spatial and temporal overlap between two migrating species, as well as their overall abundance. We calculated these values in order to control for them in network regression models.

***Spatial overlap.*** Using the R packages sf and adehabitatHR (87, 88), we calculated 95% Kernel Density Estimates (KDE) of each species' space use within each site based on the number of captures in nets of known location. 90% KDEs were used for Old Cut and Breakwater because these sites had many fewer nets. We calculated the volume of intersection between the home range densities of all possible species pairs for each site and season.

***Temporal overlap.*** We created density plots of captures over the course of a migration season for each species and then calculated the area of overlap between all possible species pairs for each site and season.

***Combined abundance.*** We calculated the proportion of total captures contributed to by all possible species pairs for each site and season. For instance, if a hypothetical site had 100 total captures, including the capture of 1 American Redstart, 1 Blackburnian Warbler, and 10 Canada Warblers, the combined abundance of American Redstarts and Blackburnian Warblers is 0.02, and that of American Redstarts and Canada Warblers is 0.11.

**Across-Site Comparisons.** To determine consistency of species relationships across stopover sites, we tested whether the ranks of species affiliation indices remained consistent across sites for each season, as in ref. 89. Each species pair was assigned a rank based on their affiliation indices, and we calculated the Kendall's coefficient of concordance ($W$) of ranks across sites for spring and fall. Similar to (89), we generated 1,000 permutations of the observed data, randomizing the ranked order at each site, and recalculating $W$ each time. We calculated the probability that the observed $W$ could come from the distribution of randomized $W$'s to determine the $P$-value.

We tested whether the geographic distance between sites influenced the similarity of their social networks. We limited our analysis to species that were among the top 50 most abundant species at all sites ($n = 31$ in spring and fall). We calculated an Euclidean distance matrix using the vegdist function from the R package vegan (90), comparing the matrices of species affiliation indices among sites. We used the distm function from the R package geosphere (91) to calculate the great circle distance ("distHaversine") between each pair of sites. We performed a Mantel test to test whether the geographic distance between sites correlated with the Euclidean distance matrix of species affiliation indices in spring and fall.

**Between-Season Comparisons.** To determine the consistency of species relationships between seasons, we tested whether the ranks of average species affiliation indices remained consistent between seasons. For spring and fall, we averaged the species affiliation indices across all sites. Burke Lake Banding Station was excluded from this analysis because they lack spring data. Each average species affiliation index was assigned a rank, and the consistency and statistical significance of the ranks were calculated as above.

**Assortative Affiliations.** We tested whether species affiliation indices were related to their phylogenetic distance and similarities in foraging behavior, nonbreeding range, and breeding range. To calculate pairwise phylogenetic distances, we first constructed a consensus tree from 1,000 randomly sampled trees from birdtree.org (92) based on the Hackett backbone (93). We used ape functions "chronos" and "multi2di" to convert the consensus tree into a chronogram and to resolve any multichotomies (94). We used ape function "cophenetic" to calculate pairwise phylogenetic distances. Foraging behaviors and habitat categories were broadly defined according to (95) (see *SI Appendix*, Table S1 for all category assignments). Range categories were determined using eBird abundance maps. For nonbreeding ranges, we classified species predominantly wintering north of 25°N as "North," species predominantly wintering between 25°N and 10°N as "Central," and species predominantly wintering south of 10°N as "South." For breeding ranges, species primarily breeding north of all five banding stations were "North," and species with breeding ranges including or south of the banding stations were "South."

For each site and season, we ran MRQAP with double semi-partialling, testing the relationship between a matrix of species affiliation indices and a matrix of phylogenetic distances for each species pair and similarity matrices for each other category (family, foraging behavior, habitat type, nonbreeding range, and breeding range) for each species pair.

**Data, Materials, and Software Availability.** Original data have been deposited in Persistent Species Relationships Characterize Migrating Bird Communities Across Stopover Sites and Seasons (10.5061/dryad.3xsj3txqp) (96).

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