ORIGINAL PAPER

Disentangling abiotic and biotic mechanisms behind the formation of heterospecific Nearctic-Neotropical shorebird flocks

Cesar Cestari[1,2] · **Cristina da Silva Gonçalves[2]** · **Celine de Melo[1]**

Abstract

Defense, vigilance, and optimal foraging are frequently related to the formation of flocks in birds. Few studies concerning long-distance migrant shorebirds analyzed whether phylogeny and ecological similarities of species are associated with the formation of heterospecific flocks. Here, we explore (1) the niche conservatism theory, (2) the competition-relatedness hypothesis, and (3) the niche construction hypothesis to explain the formation of wintering Nearctic-Neotropical heterospecific shorebird flocks in the southeastern coast of Brazil. In the first, closely-related species keep their ecological traits over time. In the last two hypotheses, ecological dissimilar and distant-related species may coexist due to strong biotic interactions. Our results discard the influence of relatedness between species and/or phylogenetic filtering signals that could act in the formation of heterospecific flocks. Co-participation of species in flocks is explained by similarities in body weight and tarsus length, which invokes the niche construction hypothesis. Probably, some similar-sized and niche-constructing species are relocating in space and changing the environment that they experience to optimize individual capacity to flee from predators. From an ecological perspective, numerous phenotypically similar species with redundant roles could lead to greater resilience of the community under anthropogenic disturbances. From an evolutionary perspective, different species with similar phenotypes may diminish costs of activity matching and augment individual fitness.

Keywords Behavior · Biodiversity · Competition · Coast · Ecological niche · Facilitation

✉ Cesar Cestari
cesar_cestari@yahoo.com.br

[1] Instituto de Biologia, Universidade Federal de Uberlândia (UFU), Campus Umuarama – Bloco 2D. Avenida Pará, 1720, Uberlândia, MG CEP 1720, Brazil

[2] Departamento de Zoologia, Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), 24-A, 1515. CEP, Rio Claro, SP 13506-900, Brazil

Introduction

The understanding of niche-related traits among species is often a key to interpret biotic and abiotic mechanisms behind community assemblies (Darwin 1859; Hutchinson 1957; Holt and Gaines 1992; Che et al. 2019). The niche conservatism theory predicts that species keep their fundamental niches and related ecological traits over time (Harvey and Pagel 1991; Peterson et al. 1999), thereby abiotic filtering effects may assemble species with similar morphological/physiological functional traits (Webb et al. 2002; Wiens and Graham 2005; Wiens et al. 2010). If these assumptions are supported for closely-related species, then phylogenetic diversity adequately estimates the functional diversity of an assemblage (Wiens et al. 2010; Swenson 2014). By contrast, according to Darwin's competition-relatedness hypothesis (Darwin 1859), strong biotic interactions (e.g. competition) inherent from realized niches of species may cause phylogenetic over-dispersion and dissimilar species may coexist (Cahill et al. 2008; Mayfield and Levine 2010; Che et al. 2019).

Species may also assemble in flocks because of the relocation of individuals with recipient traits that promote benefits in living together, evidence of niche construction, and facilitation (Odling-Smee et al. 2003; Harrison and Whitehouse 2011; Sridhar et al. 2012; Goodale et al. 2020). The niche construction concept has been usually employed for ecosystem engineer species, such as beavers, earthworms or ants, which modify their physical environment and turn natural regime to the benefit of future and adapted generations of species (Folgarait 1998; Wright et al. 2002; Hastings et al. 2007). More recently, ecologists have pointed that the systematic presence of species with recipient traits (e.g., body size, plumage color, foraging behavior) may influence interactions with other species and drive coevolutionary events, thus leading to niche construction by relocation or movements between areas (Odling-Smee et al. 2003; Laland and Boogert 2008; Harrison and Whitehouse 2011). As consequences of a decision to associate with other species, an individual may create social conditions that benefit individual fitness such as optimization of antipredator defense strategies or facilitation access to resources. Therefore, the simple presence of individuals over time influence biotic mechanisms that shape their ecology and behavior as well as other interacting species (Laland and Boogert 2008; Harrison and Whitehouse 2011). In this sense, the evolution of recipient traits that mediate biotic interactions depends upon the frequency of association between species over generations (Laland and Sterelny 2006).

A flock is characterized by a group of individuals that exhibit cohesion and then social interaction among its members (Nichols 1931; Powell 1974). The Nearctic-Neotropical shorebirds are obligated migrants that flee from inhospitable winter conditions in their breeding grounds often forming heterospecific flocks (or mixed-species flocks) in southern regions (Burger et al. 1977; Newton 2012; Cestari et al. 2020). Flocking individuals forage and rest in stopover and staging sites along their migratory routes from North to South wintering areas in the Americas (Morrison 1984; Skagen 2006). Therefore, species co-adaptation derived by their relocation and interactions in flocks during thousands of years of migration using the same flyways probably also help to explain why they form heterospecific flocks.

Some biotic mechanisms derived from behavioral interactions between individuals, e.g., individual safety and feeding maximization because of collective caution and decreased intraspecific competition are pointed as main reasons of shorebird species to form heterospecific flocks (Recher and Recher 1969; Metcalfe 1989; Beauchamp 2012; Cestari et al. 2020). Nevertheless, abiotic filtering effects also may assemble species with similar

morphological/physiological functional traits and the discovery of phylogenetic signals in these traits is a key to understanding patterns of species aggregation (Mayfield and Levine 2010). Here, we analyzed abiotic and biotic mechanisms directing co-participation of Nearctic-Neotropical shorebird species in heterospecific flocks in a coastal wintering region of beaches in southeastern Brazil. We hypothesized that phylogeny should indicate that relatedness among species may act in the formation of heterospecific flocks thus corroborating with the phylogenetic niche conservatism theory. If so, we also expect that some traits (e.g., weight, lengths of the bill and tarsus) linked to the fundamental niche of species should present phylogenetic signals and explain the formation of flocks. In the absence of relatedness and/or phylogenetic signal, we expect that the competition-relatedness and/or niche-construction hypotheses should be corroborated and all or some of the above traits in consonance with negative and/or positive biotic interactions between species are acting in the formation of heterospecific flocks.

Material and methods

Study area

We conducted the study in a nearly 9 km of beaches in southeastern Brazil (24°13′28.9″ S and 46°51′20.2″ W to 24°16′23.4″ S and 46°55′52.1″ W). Beaches are next to residential properties and native *restinga* vegetation. They were uniformly flat with 87 ± 9 m width during low tide and presented compact, moist sand at the largest portion where the tide reaches, and soft, dry sand at a small extent out of reach of the tide (approximately 10 m) (Cestari et al. 2020). Climate is Af type (rainy tropical climate) with an average annual temperature of 21 ℃, rainfall above 2000 mm/year, and relative humidity over 70% (Köppen 1948). From November (local late spring) to April (early autumn), Nearctic-Neotropical migratory shorebirds use the region as a stopover area during the southward and northward movements, respectively. The American Golden Plover (*Pluvialis dominica*), Red Knot (*Calidris canutus*), Ruddy Turnstone (*Arenaria interpres*), Sanderling (*Calidris alba*), Semipalmated Plover (*Charadrius semipalmatus*), and White-Rumped Sandpiper (*Calidris fuscicollis*) have long been recorded in sympatry in intraspecific and/or heterospecific flocks in wintering coastal habitats in the North and South American Hemispheres (Vooren and Chiaradia 1990; Hubbard and Dugan 2003; Barbieri 2007; Burger et al. 2007; Cestari 2015). Among these species, the Semipalmated Plover (*C. semipalmatus*) is one of the few plovers whose numbers are stable in the Americas probably due to its ecological and behavioral versatility (Morrison et al. 2006; Cestari 2009; BirdLife International 2016).

Sampling design

The Nearctic-Neotropical migratory birds were opportunistically recorded participating of heterospecific flocks during their north-southward (post-breeding) migration, from November to February of 2005–2006 (15 non-consecutive days), November to February of 2009–2013 (40 non-consecutive days), and in January 2019 (5 non-consecutive days), totaling 60 days of bird surveys in 21 months. We defined flock as a group of individuals distanced up to 5 m from each other that exhibit cohesive unidirectional movements

in flight (Powell 1974; Cestari 2015). Flocks were registered during the morning (8:00 to 11:00 h) or late afternoon (16:00 to 18:00 h) by one observer that used a bicycle and tried to maintain 10 km/h average speed to move along 9 km of beach stretches. When a feeding or resting shorebird flock was encountered, the observer briefly (no more than 2 min) annotated the species richness and the number of individuals per species. As shorebirds frequently use the stopover area for short periods (2–3 days) during southward and northward migrations (CC, pers. obs., monitoring banded shorebirds in the area), we adopted a minimum interval of three days between samplings; intervals with an absence of bird samplings lasted from 3 to 11 days. All the above procedures minimized the likelihood of sampling the same flocks. It was impossible to record data blind because our study involved focal animals in the field.

Phylogenetic trees of Nearctic-Neotropical migrants participating in heterospecific flocks were obtained from the phylogeny of the world's bird species website https://birdtree.org (Jetz et al. 2012). Although this phylogeny was not built using genetic data for all species, this is an online source that represents the most comprehensive phylogenetic data for modern birds (Sebastián-González and Green 2017; Che et al. 2019). We sub-sampled 2,000 trees "Ericsson All Species: a set of 10,000 trees with 9993 OUT each" and calculated the maximum clade credibility (MCC) tree using the phangorn R package. MCC tree uses Bayesian phylogenetic inference that produces the most likely phylogenetic tree considering the 2000 sub-sampled trees. Then we used the ape R package to extract the phylogenetic variance–covariance matrix (VCV) from the MCC tree assuming the Brownian Motion Model. In VCV, off-diagonal values estimate the expected covariance in the trait values between species that participated in heterospecific flocks. High off-diagonal values mean that pairs of species are closely related (Swenson 2014). We also created a matrix with co-participation frequency between pairs of species in heterospecific flocks. Co-participation frequencies between pairs of species were corrected for the relative abundance of the species that participated in flocks in the area during the period of study. The relative abundance of a given species was calculated considering its number of individuals divided by the total number of individuals of all species that participated in heterospecific flocks. This procedure was taken to avoid bias concerning species with different population sizes in further analyses. For example, a common species 'A' with 0.79 relative abundance in the area that interacted five times with a rare species 'B' with 0.06 relative abundance had $5 \times 0.79 \times 0.06 = 0.24$ co-participation frequency. Co-participation frequencies were correlated to the VCV pairwise species values to know if co-participation is related to their relatedness.

We selected three non-correlated functional traits (body weight, bill and tarsus lengths) that must represent the niche dimensions of shorebird species. The average weights of species were compiled from Dunning-Jr. (2008). The average bill lengths and average tarsus lengths of species were compiled from Schultz-Neto et al. (2008) and Jukema et al. (2015). We used Blomberg's K (applying the Brownian Motion Model) to discern if these traits (jointly or separately) explain the structure of the MCC tree, thus indicating phylogenetic signal subordinated by abiotic effects. We followed Swenson (2014) in considering the phylogenetic signal as the degree to which similarity in trait values between species can be predicted upon their relatedness. Also, differences in trait values (i.e., weight, bill length, and tarsus length) between co-participating species were related to the matrix of co-participation between pairs of species to know their recipient effects on the formation of heterospecific flocks (see data analyses).

We also used the species strength concept to identify a general overview of the dependency of shorebird species in heterospecific flocks, following Bascompte et al. (2006). The

strength of species values (SPV) is the sum of the dependencies of all species for a species. Dependence is considered to be the frequency of co-participation of a species 'A' with a species 'B' divided by the frequency of co-participation of species 'A' with all the species that form heterospecific flocks. Comparative of SPV means that a species (with the highest SPV) may exert strong momentary dependency on other species in the flock community (Cestari et al. 2020). Co-participation frequencies between pairs of species were corrected by the relative abundance of the species that participated in flocks.

Data analyses

The Mantel test was used to identify a relation between VCV values and frequency of co-participation between species in heterospecific flocks. Considering a non-phylogenetic perspective, the Generalized Linear Model (using quasipoisson distribution) was used to find the best model that explain the relation between modular differences in traits between pairs of co-participating species (i.e., weight, bill length, and tarsus length) and their frequency of co-participation in flocks. Previous statistics indicated that traits were not correlated ($P > 0.05$). A positive tendency in GLM analysis indicates that the formation of flocks is influenced by a difference in the ecological niche of species. A negative tendency indicates similarity in the ecological niche of species and/or niche construction with facilitation. The Principal Components Analysis (PCA) graphic was used to improve visualization on how the species were related to a potential pattern generated by their traits. We used the vegan R and the complementary RT4Bio R packages to conduct these analyses.

We used the Blomberg's K metric associated with a randomization test to simulate a random trait database on the phylogeny and to generate null distribution from which a p-value can be calculated. Values of K greater than one indicate more phylogenetic signal than expected from Brownian Motion Model, whereas values less than one indicate less than expected (Blomberg et al. 2003; Swenson 2014). This combined analysis reveals if the selected traits (weight, bill length, and leg length) of species in flocks have a phylogenetic signal. We used phylosig function in the phytools R package for this analysis.

Analyses were performed in R Statistical software v 3.5.1. Significance was accepted at $P \leq 0.05$.

Results

The Semipalmated Plover (*C. semipalmatus*, 970 individuals), Sanderling (*C. alba*, 107 individuals), White-Rumped Sandpiper (*C. fuscicollis*, 74 individuals), Ruddy Turnstone (*A. interpres*, 55 individuals), Red Knot (*C. canutus*, 13 individuals), American Golden Plover (*P. dominica*, 2 individuals), and Lesser Yellowlegs (*Tringa flavipes*, 1 individual) were the species recorded in heterospecific flocks, in descending order of abundance. The Semipalmated Plover showed the highest SPV value (5.27) and participated in flocks with all other Nearctic-Neotropical shorebird species (Fig. 1). Co-participation between pairs of species ($n = 13$) were not related to their relatedness (Mantel test, $r = 0.02$, $P = 0.31$) (Fig. 2). Also, weight, bill length, and tarsus length did not explain the structure of MCC tree together (Blomberg's $k = 0.84$, $P = 0.15$) or separately (weight: Blomberg's $k = 0.59$, $P = 0.43$; bill length: Blomberg's $k = 0.87$, $P = 0.14$; tarsus length: Blomberg's $k = 0.84$, $P = 0.15$).
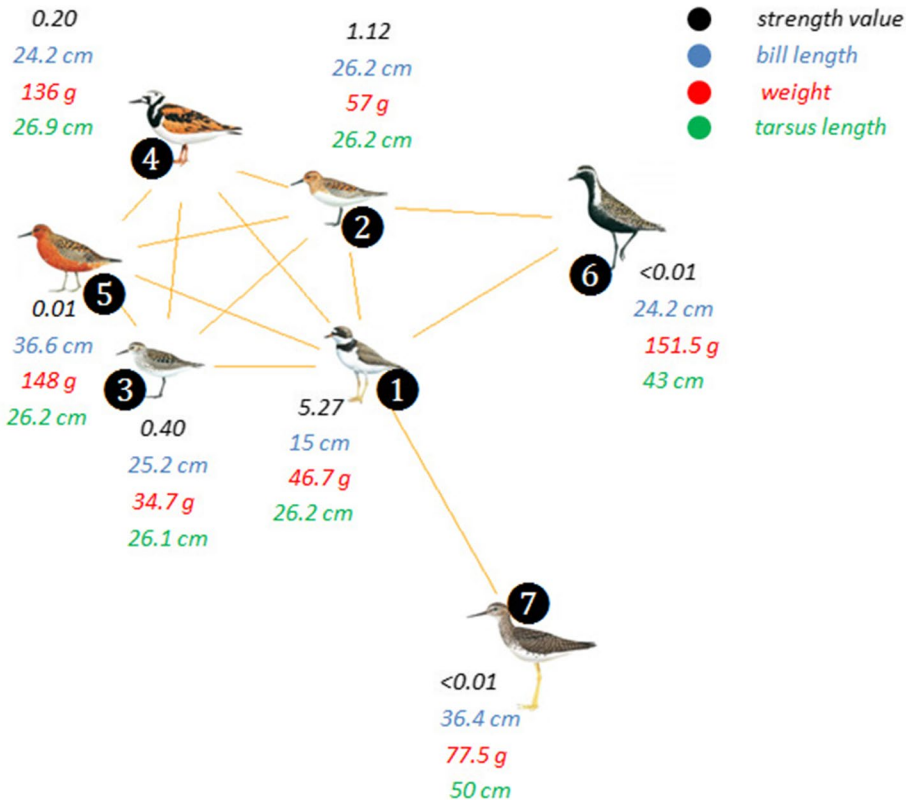
Fig. 1 Nearctic-Neotropical shorebird species that formed flocks.1: Semipalmated Plover (*C. semipalmatus*); 2: Sanderling (*C. alba*); 3: White-Rumped Sandpiper (*C. fuscicollis*); 4: Ruddy Turnstone (*A. interpres*); 5: Red Knot (*C. canutus*); 6: American Golden Plover (*P. dominica*); 7: Lesser Yellowlegs (*T. flavipes*). Values in black show species strength (high values indicate a strong dependency of one species on other species in the flock community). Values in blue, red, and green show the bill length, weight, and tarsus length of the species, respectively. Bird sizes are in approximate scale. Illustration of bird species reproduced by permission of Lynx Edicions

Considering a non-phylogenetic perspective, GLM analysis showed that modular differences in weight and tarsus length of interacting species (co-participation = Weight differences + Tarsus length differences) explain 40.74% and 31.58% their frequency of co-participation in flocks, respectively (Table 1). In other words, co-participation between shorebird species tended to decrease as differences in weight and tarsus length increase (Fig. 3), therefore evidencing that similarities of these traits explain co-participation and formation of heterospecific flocks. The first two axes from PCA explained 85.7% of data variation (PC1 = 61.8% and PC2 = 23.9%) considering the weight, tarsus, and bill traits (Fig. 4).

Discussion

Although shorebirds have diverged relatively recently (Baker et al. 2007; Prum et al. 2015), our results discarded the influence of relatedness between Nearctic-Neotropical shorebird species and/or that phylogenetic filtering signals could be acting in the formation
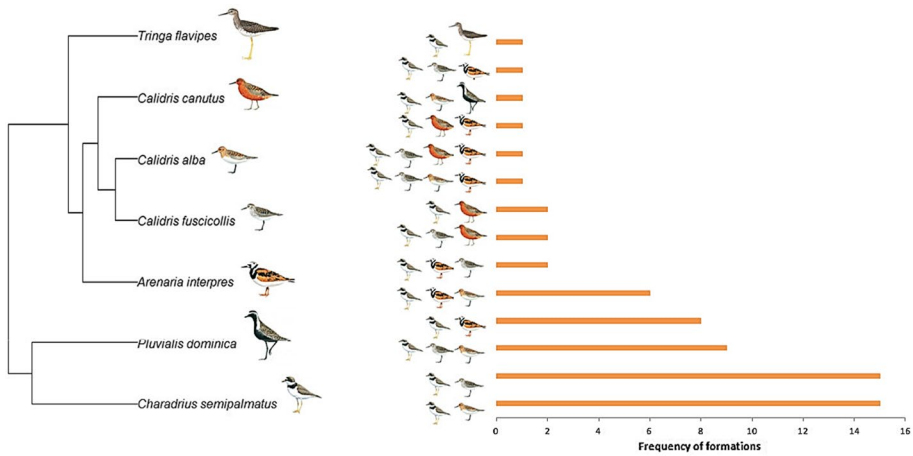
Fig. 2 On the left: Maximum Clade Credibility phylogenetic tree of shorebird species. On the right: formation and frequency of co-participation between species in flocks in southeastern Brazil. Bird sizes are in approximate scale. Illustration of bird species reproduced by permission of Lynx Edicions

Table 1 Best model results (GLM) on the effects of the traits difference between pairs of species on their co-participation in flocks

Co-participation						
Parameter	Estimate ($\pm$ SE)	z	Dev	df	Res. Dev	$P(>$ Chi)
Intercept	0.60 ± 0.37	1.63			13.22	
Wd	-0.02 ± 0.01	-1.77	1.85	11	7.83	0.003*
Td	-0.57 ± 0.42	-1.34	1.02	10	3.66	0.006*

Wd Weight difference, *Td* Tarsus difference

of heterospecific flocks. Our significant results showing similarity of weight and tarsus lengths between co-participative shorebird species open a discussion about the influence of biotic mechanisms on the attractiveness of individuals in heterospecific flocks. All the studied species are obligated long-distance migrants that can overlap a broad geographic range (Morrison 1984; Newton 2012). They have been participating in flocks in wintering habitats (Vooren and Chiaradia 1990; Hubbard and Dugan 2003; Barbieri 2007; Burger et al. 2007; Newton 2012; Cestari 2015), which increases their familiarity through the occurrence of interactions for generations. Here, we argue that the similarity of traits in some species of Nearctic-Neotropical shorebirds is linked to mutual benefits when they associate in heterospecific flocks, thus indicating for the first time a constructive effect for this group of birds (Laland and Sterelny 2006; Krebs 2009; Harrison and Whitehouse 2011).

The function of flocks determines the nature and extends of interaction between participants (Harrison and Whitehouse 2011; Sridhar and Shanker 2014). If certain traits are required to persist in a specific environment, then an assemblage may be comprised of phylogenetically overdispersed species sharing these traits and augmenting supplementary/complementary benefits at costs of low competition (Sebastián-González and Green 2017; Goodale et al. 2020). Our results showed that the similarity in weight and tarsus lengths of species may favor the formation of heterospecific flocks, and there is a tendency of shorebirds flocking with similar-sized species composed mainly by lighter, and smaller
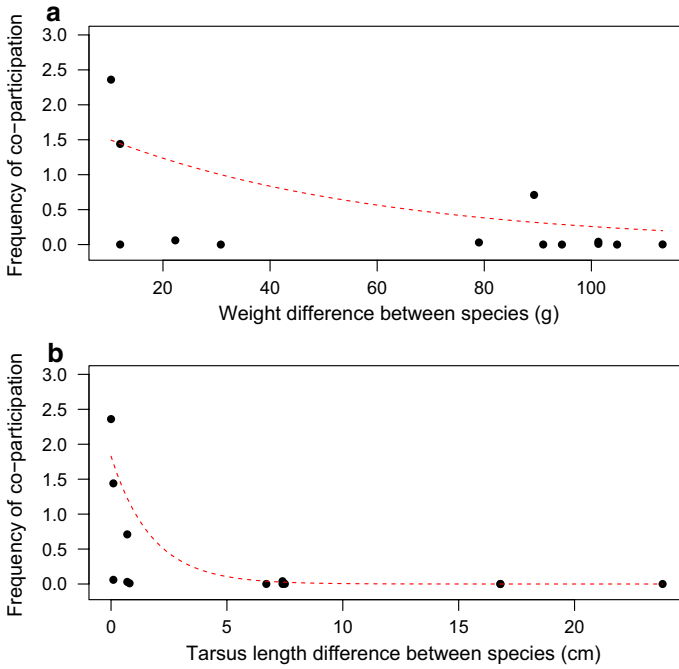
Fig. 3 Relation between frequency of co-participation of shorebird species: their difference in weight (**a**), and their difference in tarsus length (**b**). Species similar in weight and tarsus length tend to associate each other. Bird sizes are in approximate scale
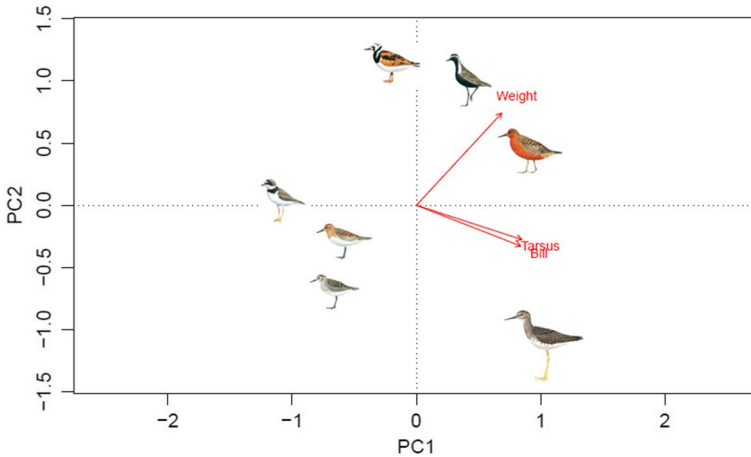

Fig. 4 Shorebird species and their pattern of distribution according to body weight, tarsus length, and bill length in PCA analysis. Bird sizes are in approximate scale. Illustration of bird species reproduced by permission of Lynx Edicions

ones such as the Semipalmated Plover (*C. semipalmatus*), White-Rumped Sandpiper (*C. fuscicollis*), and Sanderling (*C. alba*) (Fig. 2). Positive interactions between phenotypically similar species have been pointed for several animal groups. Some examples are similarities on wing patterns in butterflies (Elias et al. 2008), color, body size, and shape in fish (Krause et al. 1996; Pereira et al. 2011), calls, color, and body size in forest birds (Ficken 2000; Beauchamp and Goodale 2011; Sridhar et al. 2012). Our findings on shorebird species corroborate the results of the latter study, which found a relation between the similarity of body size and the strength of species association in heterospecific flocks from forests of multiple continents, although it is not the rule for terrestrial birds (see Colorado and Rodewald 2014).

Studies evidenced that most birds may be less vulnerable to predators when they participated in flocks (Morse 1977; Caraco 1979; Elgard 1989; Beauchamp 2012) and specifically when flocking birds are small body-sized (Sainz-Borgo and Jaffe 2018). That is, smaller (and lighter) species have a high capacity to flee from predators. The greater the weight, the smaller the proportional power of pectoral muscles that supports flapping flight (Alexander 2004; Pough et al. 2013). In addition, similar sizes among members improve the coordinated response of individuals that diminishes vulnerability to predators (Beauchamp 2012; Sridhar et al. 2012). Therefore, if there are numerous species with a similar size in a flock, they can contribute to each other with supplementary benefits with minimum competition. This may be extremely important to highly moving or migrant species in which the participation in heterospecific flocks could also change the predation risk in unfavorable habitats (Laundré et al. 2010; Goodale et al. 2020).

In our study, the Semipalmated Plover (*C. semipalmatus*), White-Rumped Sandpiper (*C. fuscicollis*), and Sanderling (*C. alba*) are the smaller and commoner species presumably exerting the role of niche-constructing species in heterospecific flocks. In other words, in unfavorable occasions of predation risk, they may socially depend on each other to improve anti-predator strategies. When they move in space, they change the experienced environment via positive interactions and ecological feedbacks regulating environmental selective pressures (Laland and Sterelny 2006; Harrison and Whitehouse 2011; Cestari et al. 2020). In addition to supplementary benefits such as the high capacity to escape from predators and risk dilution, niche-constructing species may be reference or "information centre" of other complementary benefits for individuals in heterospecific flocks because of their different foraging tactics and capacity to find food (Odling-Smee et al. 2003; Goodale et al. 2020). For example, the Semipalmated Plover (*C. semipalmatus*) may be followed by other shorebirds because it reveals buried prey in sandy beaches using the foot-trembling technique (Cestari 2009). Other examples of interacting species of birds include the Black-browned Albatross (*Thalassarche melanophrys*), which is an expert in following fur seals and penguins that drive food (krill) to surface, and it may be followed by others tube-nosed seabirds (Harrison et al. 1991), or Snowy Egrets (*Egretta thula*) that exert an attractive force to others egrets and herons in foraging areas (Caldwell 1980)—when most waterbirds were together they increased their foraging success without competitive evidence. In our study, the smaller plovers and sandpipers find their prey more visually, and sanderlings frequently probed their longer bills in the moist sand; the red knots and turnstones may employ both foraging techniques. These different foraging strategies of species reduce interspecific competition (Burger et al. 1977; Davis and Smith 2001; Choi et al. 2017) and/or diminish predation risk once species vary in the time of vigilance (Metcalfe 1989; Beauchamp 2002). In addition, visual foragers may react faster than tactile foragers (Ye et al. 2017; Linley et al. 2019). All these characteristics probably influence dependency (higher SPV values, see Fig. 1) for the benefits of individuals in heterospecific flocks, mainly if we

consider that species may stop several times to rest and refuel at stopover sites along same migratory journeys (Morrison 1984; Skagen 2006; Alerstam 2011; Zhang et al. 2018).

Parallel to the constructive effects of species interactions and social information exchanges, the coexistence and interaction between species probably exists due to their niche differences, ecological flexibility, and phylogenetic over-dispersion (Darwin 1859; Silvertown et al. 2001; Webb et al. 2002; Mayfield and Levine 2010). Interspecific competition is uncommon in migratory shorebirds (Recher 1966; Metcalfe 1989); by moving continually from one foraging area to another, shorebirds may exploit heterogeneous habitats and feed numerous prey using distinct foraging techniques. Therefore, in addition to body size similarity which invokes niche construction, there are others morphological and behavioral differences among shorebirds that probably evolved to exploit environmental conditions and resources of food with reduced competition (Recher 1966; Burton 1974; Lifjeld 1984; van Gils et al. 2016; Haram et al. 2018). Although body size and foraging behavior are strongly correlated among intraspecifics, this is unlikely to occur among heterospecifics (Sridhar and Guttal 2018). Even in a highly competitive staging site dominated by few prey species in the northern Yellow Sea, shorebirds show plasticity on feeding different sizes of the same species of prey or have distinct feeding methods (Choi et al. 2017). In this sense, ecological flexibility of some species may be complementary to their role as niche-constructing and the formation of heterospecific flocks. For example, in our study, the Semipalmated Plover (*C. semipalmatus*) is a versatile forager that occupies a variety of wetland habitats in natural and urbanized regions (Baker 1977; Strauch and Abele 1979; Smith and Nol 2000; Cestari 2009) and exert strong dependency over other species.

Niche differences among shorebird species in flocks may also be evidenced by intraspecific competition more than interspecific competitors, i.e., a species will diminish potential competition with other species if it balances its own population in number (Chesson 2000; Cestari et al. 2020) and in space (Jensen 1987; Chesson 2000; Bijleveld et al. 2012) then promoting more diverse and less competitive flocks that may vary according to ecological and sociological conditions along migratory routes. Increased niche differences between similar species in heterospecific flocks were also noticed for tits (*Parus* spp.), in which each species used different spots when foraging (Alatalo et al. 1986). Over longer time periods, niches of species with similar traits may be diverging to avoid competition but this is not so intense that benefits are lost, such as predation reduction or food searching (Seppänen et al. 2007; Sridhar et al. 2012; Sridhar and Guttal 2018). Therefore, similarities in some traits can develop while niche differentiation related to other traits can be maintained over time (Goodale et al. 2020).

Niche construction through species relocation and interactions depends on the strengthening selection of recipient traits over generations, sometimes leading to new and unexpected evolutionary trajectories (Laland et al. 1999). In the present paper, we argue that weight and tarsus length similarities connect phylogenetically over-dispersed Nearctic-Neotropical species in heterospecific flocks, which make some similar, commoner, and ecologically flexible species as probable niche-constructing protagonists important to the formation of heterospecific flocks. Over this scenario, urbanization, habitat loss, and climate warming are currently impacts that affect the fitness and survival of shorebirds (Burton et al. 2006; Thomas et al. 2003; Cestari 2015; Rakhimberdiev et al. 2018). Therefore, we do not discard that these relatively recent impacts may also be acting as new selective forces to augment behavioral flexibility and morphological adjustments of long-distance migratory birds (van Gils et al. 2006; Zhang et al. 2019), which also may include reduction of body size (van Gils et al. 2016). From an ecological point of view, numerous similar species with redundant roles could lead to greater resilience of the community under

anthropogenic disturbances (Oliver et al. 2015; Goodale et al. 2020). From an evolutionary point of view, different species with similar phenotypes may diminish costs of activity matching and augment individual fitness (Sridhar and Guttal 2018). In the light of our results, we encourage field experiments that reinforce the body size as a trait related to the social linkage of species and formation of heterospecific flocks in long-distance migratory shorebirds. One realistic and simple test could be to use stuffed individuals with different body sizes to simulate the presence of species keeping up with its consequent social attraction of living individuals.

Compliance with Ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the development of this observational study were followed.

Informed consent The authors declare that they have consented with the ethical statements and development of this manuscript.

References

Alatalo RVL, Gustafsson L, Lundberg A (1986) Interspecific competition and niche changes in tits (*Parus* spp.): evaluation of non-experimental data. Am Nat 127:819–834

Alerstam T (2011) Optimal bird migration revisited. J Ornithol (Suppl 1):S5–S23

Alexander DE (2004) Nature's flyers: birds, insects, and the biomechanics of flight. Johns Hopkins University Press, Baltimore

Baker AJ, Pereira SL, Paton TA (2007) Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. Biol Lett 3:205–209. https://doi.org/10.1098/rsbl.2006.0606

Baker MC (1977) Shorebird food habits in the eastern Canadian Arctic. Condor 79:56–62

Barbieri E (2007) Seasonal abundance of shorebirds at Aracaju, Sergipe, Brazil. Wader Study Group Bull 113:40–46

Bascompte J, Jordano P, Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431–433. https://doi.org/10.1126/science.1123412

Beauchamp G (2002) Higher-level evolution of intraspecific flock-feeding birds. Behav Ecol Sociobiol 51:480–487. https://doi.org/10.1007/s00265-002-0461-7

Beauchamp G (2012) Flock size and density influence speed of escape waves in semipalmated sandpipers. Anim Behav 83:1125–1129. https://doi.org/10.1016/j.anbehav.2012.02.004

Beauchamp G, Goodale E (2011) Plumage mimicry in avian mixed-species flocks: more or less than meet the eye? Auk 128:487–496

Bijleveld AI, Folmer EO, Piersma T (2012) Experimental evidence for cryptic interference among socially foraging shorebirds. Behav Ecol 23:806–814. https://doi.org/10.1093/beheco/ars034

BirdLife International (2016) Charadrius semipalmatus. The IUCN Red List of Threatened Species 2016. https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22693764A93421037. Acessed 19Aug 2020

Blomberg SP, Garland T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Burger J, Marshall A, Howe D, Caldwell H, Chase J (1977) Effects of tide cycles on habitat selections and habitat partitioning by migrating shorebirds. Auk 94:743–758. https://doi.org/10.2307/4085271

Burger J, Carlucci SA, Jeitner CW, Niles L (2007) Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. J Coast Res 23:1159–1166

Burton NHK, Rehfisch MM, Clark NA, Dodd SG (2006) Impacts of sudden winter habitat loss on the body condition and survival of Redshank *Tringa totanus*. J Appl Ecol 43:464–473

Burton PJK (1974) Feeding and the feeding apparatus in waders: a study of anatomy and adaptations in the Charadrii. British Museum, Natural History, London

Cahill JF, Kembel SW, Lamb EG, Keddy P (2008) Does phylogenetic relatedness influence the strength of competition among vascular plants? Perspect Plant Ecol Evol Syst 10:41–50. https://doi.org/10.1016/j.ppees.2007.10.001

Caldwell GS (1980) Attraction to tropical mixed-species Heron flocks: proximate mechanisms and consequences. Behav Ecol Sociobiol 8:99–103

Caraco T (1979) Time budgeting and group size: a test of theory. Ecology 60:618–627. https://doi.org/10.2307/1936082

Cestari C (2009) Foot-trembling behavior in Semipalmated Plover *Charadrius semipalmatus* reveals prey on surface of Brazilian beaches. Biota Neotrop 9:299–301

Cestari C (2015) Coexistence between Nearctic-Neotropical migratory shorebirds and humans on urban beaches of the Southern Hemisphere: a current conservation challenge in developing countries. Urban Ecosyst 18:285–291. https://doi.org/10.1007/s11252-014-0399-3

Cestari C, Gonçalves CS, Melo C (2020) Keeping safe and fed: large heterospecific shorebird flocks to decrease intraspecific competition. J Avian Biol 51:1–8. https://doi.org/10.1111/jav.02316

Che X, Chen D, Zhang M, Quan Q, Møller AP, Zou F (2019) Seasonal dynamics of waterbird assembly mechanisms revealed by patterns in phylogenetic and functional diversity in a subtropical wetland. Biotropica 51:421–431. https://doi.org/10.1111/btp.12648

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Choi C, Battley PF, Potter MA, Ma Z, Melville DS, Sukkaeewmanee P (2017) How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. Auk 134:76–91. https://doi.org/10.1642/AUK-16-58.1

Colorado GJ, Rodewald AD (2014) Assembly patterns of mixed-species avian flocks in the Andes. J Anim Ecol 84:386–395. https://doi.org/10.1111/1365-2656.12300

Darwin C (1859) On the origin of species. Harvard University Press, Cambridge

Davis CA, Smith LM (2001) Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the Southern Great Plains. Auk 118:484–495. https://doi.org/10.1093/auk/118.2.484

Dunning JB Jr (2008) CRC handbook of avian body masses. CRC Press, Boca Raton

Elgard MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol Rev 64:13–23. https://doi.org/10.1111/j.1469-185X.1989.tb00636.x

Elias M, Gompert Z, Jiggins C, Willmott K (2008) Mutualistic interactions drive ecological niche divergence in a diverse butterfly community PLoS Biol 6:e300. https://doi.org/10.1371/journal.pbio.0060300

Ficken MS (2000) Call similarities among mixed species flock associates. Southwes Nat 45:154–158

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers Conserv 7:1221–1244

Goodale E, Sridhar H, Sieving KE, Bangal P, Colorado ZGJ, Farine DR, Heymann EW, Jones HH, Krams I, Martínez AE, Montaño-Centellas F, Muñoz J, Srinvasan U, Theo A, Shanker K (2020) Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. Biol Rev. https://doi.org/10.1111/brv.12591

Haram LE, Kinney KA, Sotka EE, Byers JE (2018) Mixed effects of an introduced ecosystem engineer on the foraging behavior and habitat selection of predators. Ecology 99:2751–2762. https://doi.org/10.1002/ecy.2495

Harrison NM, Whitehouse MJ (2011) Mixed-species flocks: an example of niche construction? Anim Behav 81:675–682. https://doi.org/10.1016/j.anbehav.2011.01.013

Harrison NM, Whitehouse MJ, Heinemann D, Prince PA, Hunt-Jr GL,Veit RR (1991) Observations of multi-species seabird flocks around South Georgia. Auk 108:801e810.https://www.jstor.org/stable/4088309

Harvey PH, Pagel MR (1991) The comparative method in evolutionary biology. Oxford University Press, USA

Hasting A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG (2007) Ecosystem engineering in space and time. Ecol Lett 10:153–164. https://doi.org/10.1111/j.1461-0248.2006.00997.x

Holt RD, Gaines MS (1992) Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evol Ecol 6:433–447. https://doi.org/10.1007/BF02270702

Hubbard DM, Dugan JE (2003) Shorebird use of an exposed sandy beach in southern California. Estuar Coast Shelf S 588:41–54

Hutchinson GE (1957) A treatise on Limnology. Wiley, New York

Jensen AL (1987) Simple models for exploitative and interference competition. Ecol Modell 35:113–121. https://doi.org/10.1016/0304-3800(87)90093-7

Jetz W, Thomas G, Joy J, Hartmann K, Mooers A (2012) The global diversity of birds in space and time. Nature 491:444. https://doi.org/10.1038/nature11631

Jukema J, Dunning Jr JB, Vlas P, Brierley L, Brooks P (2015) Morphological variation in spring migrant and wintering American Golden-Plovers *Pluvialis dominica*. Wader Study 122:128–134. https://doi.org/10.18194/ws.00015

Köppen W (1948) Climatologia: con un estudio de los climas de la tierra. Fondo de Cultura Econômica, Mexico

Krause J, Godin JGJ, Brown D (1996) Size-assortiveness in multiple species shoals. J Fish Biol 49:221–225

Krebs CJ (2009) Ecology. Pearson Education, Harlow

Laland KN, Boogert NJ (2008) Niche construction, co-evolution and biodiversity. Ecol Econ 69:731–736

Laland KN, Odling-Smee FJ, Feldman MW (1999) Evolutionary consequences of niche construction and their implications for ecology. PNAS 96:10242–10247. https://doi.org/10.1073/pnas.96.18.10242

Laland KN, Sterelny K (2006) Seven reasons (not) to neglect niche construction. Evolution 60:1751–1762. https://doi.org/10.1554/05-570.1

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: ecological implication of being afraid. Open Ecol J 3:1–7

Lifjeld JT (1984) Prey selection in relation to body size and bill length of five species of waders feeding in the same habitat. Ornis Scand 15:217–226. https://doi.org/10.2307/3675930

Linley GD, Guay P, Weston MA (2019) Are disturbance separation distances derived from single species applicable to mixed-species shorebird flocks. Wildlife Res 46:719–723. https://doi.org/10.1071/WR18198

Mayfield MM, Levine JL (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecol Lett 13:1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

Metcalfe NB (1989) Flocking preferences in relation to vigilance benefits and aggression costs in mixed-species shorebird flocks. Oikos 56:91–98. https://doi.org/10.2307/3566091

Metcalfe NB, Furness RW (1986) Aggression in shorebirds in relation to flock density and composition. Ibis 129:553–563. https://doi.org/10.1111/j.1474-919X.1987.tb08243.x

Morrison RIG (1984) Migration systems of some new world shorebirds. In: Burger J, Olla BL (eds) Shorebirds: migration and foraging behavior. Plenum Press, New York, pp 125–202

Morrison RIG, McCaferry BJ, Gill RE, Skagen SK, Jones SL, Page SW, Gratto-Trevor CL, Andres BA (2006) Population estimates of North American shorebirds. Wader Study Group Bull 11:67–85

Morse DH (1977) Feeding behavior and predator avoidance in heterospecific groups. Bioscience 27:332–339. https://doi.org/10.2307/1297632

Newton I (2012) Obligate and facultative migration in birds: ecological aspects. J Ornithol 153:S171–S180. https://doi.org/10.1007/s10336-011-0765-3

Nichols JT (1931) Notes on the flocking of shore birds. Auk 48:181–185. https://doi.org/10.2307/4076784

Odling-Smee FJ, Laland KN, Feldman MW (2003) Niche construction. Princeton University Press, New Jersey

Oliver TH, Heard MS, Isaac NJB, Roy DB, Procter D, Eigenbrod F, Freckleton R, Hector A, Orme DL, Petchey OL, Proenca V, Raffaelli D, Suttle KB, Mace GM, Martin-Lopez B, Woodcock BA, Bullock JM (2015) Biodiversity and resilience of ecosystem functions. Trends in Ecol Evol 30:673–684

Pereira PHC, Feitosa JLL, Ferreira BP (2011) Mixed-species schooling behavior and protective mimicry involving coral reef fish from the genus *Haemolon* (Haemulidae). Neotrop Ichthyol 9:741–746

Péron G (2017) Multicontinental community phylogenetics of avian mixed-species flocks reveal the role of the stability of associations and of kleptoparasitism. Ecography 40:1267–1273

Peterson AT, Soberon J, Sanchez-Carnero V (1999) Conservatism of ecological niches in evolutionary time. Science 285:1265–1267. https://doi.org/10.1126/science.285.5431.1265

Pough FH, Janis CM, Heiser JB (2013) Vertebrate life. Pearson Education, Boston

Powell GVN (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. Anim Behav 22:501–505. https://doi.org/10.1016/S0003-3472(74)80049-7

Prum RO, Berv JS, Dornburg A, Field DJ, Towsend JP, Lemmon EM, Lemmon AR (2015) A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526:569–573. https://doi.org/10.1038/nature15697

Rakhimberdiev E, Duijns S, Karagicheva J, Camphuysen CJ, Castricum VRS, Dekinga A, Dekker R, Gavrilov A, ten Horn J, Jukema J, Saveliev A, Soloviev M, Tibbitts TL, van Gils JA, Piersma T (2018) Fuelling condition at staging sites can mitigate warming effects in a migratory bird. Nat Commun 9:4263. https://doi.org/10.1038/s41467-018-06673-5

Recher HF (1966) Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407. https://doi.org/10.2307/1932979

Recher HF, Recher JA (1969) Some aspects of the ecology of migrant shorebirds. II Agression Wilson Bull 81:140–154

Sainz-Borgo C, Jaffe K (2018) On the adaptive characteristics of bird flocks: small birds form mixed flocks. Ornitol Neotrop 29:289–296

Schulz-Neto A, Serrano IL, Efe MA (2008) Mudas a parâmetros biométrico de aves migratórias no norte do Brasil. Ornithologia 3:21–33

Sebastián-González E, Green AJ (2017) Phylogenetic relatedness of co-occurring waterbird communities: a test of Darwin's competition-relatedness hypothesis. J Avian Biol 48:1372–1382. https://doi.org/10.1111/jav.01295

Seppänen JT, Forsman JT, Mönkkönen M, Thomson RL (2007) Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88:1622–1633

Silvertown J, Dodd M, Gowing DJG (2001) Phylogeny and the niche structure of meadow plant communities. J Ecol 89:428–435. https://doi.org/10.1046/j.1365-2745.2001.00553.x

Skagen SK (2006) Migration stopovers and the conservation of the arctic-breeding Calidriidae sandpipers. Auk 123:313–322. https://doi.org/10.1590/S1984-46702009005000013

Smith AC, Nol E (2000) Winter foraging behavior and prey selection of the Semipalmated Plover on coastal Venezuela. Wilson Bull 112:467–472

Sridhar H, Guttal V (2018) Friendship across species borders: factors that facilitate and constrain heterospecific sociality. Philos T R Soc B 373:20170014

Sridhar H, Shanker K (2014) Using intra-flock association patterns to understand why birds participate in mixed-species foraging flocks in terrestrial habitats. Behav Ecol Sociobiol 88:185–196. https://doi.org/10.1007/s00265-013-1633-3

Sridhar H, Srinivasan U, Askins RA, Canales-Delgadillo JC, Chen CC, Ewert DN, Gale GA, Goodale R, Gram WK, Hart PJ, Hobson KA, Hutto RL, Kotagama SW, Knowlton JL, Lee TM, Munn CA, Nimnuan S, Nizam BZ, Péron G, Robin VV, Rodewald AD, Rodewald PG, Thomson RL, Trivedi P, van Wilgenburg SL, Shanker K (2012) Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. Am Nat 180:777–790

Strauch JG Jr, Abele LG (1979) Feeding ecology of three species of plovers wintering on the bay of Panamá, Central America. In: Pitelka A (ed) Shorebirds in marine environments. Cooper Ornithological Society, Lawrense, pp 217–230

Swenson NG (2014) Functional and phylogenetic ecology in R. Springer, New York

Thomas K, Kvitek RG, Bretz C (2003) Effects of human activity on the foraging behavior of the sanderlings *Calidris alba*. Biol Conserv 109:67–71

van Gils JA, Lisovski S, Lok T, Meissner W, Ozarowska A, Fouw J, Rakhimberdiev E, Soloviev MY, Piersma T, Klaassen M (2016) Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. Science 352:819–821. https://doi.org/10.1126/science.aad6351

van Gils JA, Piersma T, Dekinga A, Battley PF (2006) Modelling phenotypic flexibility: An optimality analysis of gizzard size in Red Knots (*Calidris canutus*). Ardea 94:409–420

Vooren CM, Chiaradia A (1990) Seasonal abundance and behavior of coastal birds on Cassino beach, Brazil. Ornitol Neotrop 1:9–24

Webb C, Ackerly D, McPeek M, Donoghue M (2002) Phylogenies and community ecology. Annu Rev Ecol System 33:475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes J, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecol Lett 13:1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Ann Rev Ecol Evol S 36:519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increase species richness at the landscape scale. Oecologia 132:96–101

Ye Y, Jiang Y, Hu C, Liu Y, Qing B, Wang C, Fernández-Juricic E, Ding C (2017) What makes a tactile forage join mixed-species flocks? A case study with the endangered Crested Ibis (*Nipponia Nippon*). Auk 136:421–431. https://doi.org/10.1642/AUK-16-191.1

Zhang S, Ma Z, Choi C, Peng H, Bai Q, Liu W, Melville DS, He P, Chan Y, van Gils JA, Piersma T (2018) Persistent use of a shorebird staging site in the Yellow Sea despite severe declines in food resources implies a lack of alternatives. Bird Conserv Int 28:534–548. https://doi.org/10.1017/S0959270917000430

Zhang S, Ma Z, Choi C, Peng H, Melville DS, Zhao T, Bai Q, Liu W, Chan Y, van Gils JA, Piersma T (2019) Morphological and digestive adjustments buffer performance: How staging shorebirds cope with severe food declines. Ecol Evol 9:3868–3878. https://doi.org/10.1002/ece3.5013

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.