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Published in:
Basic and Applied Ecology

DOI:
[10.1016/j.baae.2017.08.008](https://doi.org/10.1016/j.baae.2017.08.008)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2017

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Malpica, A., Covarrubias, S., Villegas-Patraca, R., & Herrera-Alsina, L. (2017). Ecomorphological structure of avian communities changes upon arrival of wintering species. *Basic and Applied Ecology*, 24, 60-67. <https://doi.org/10.1016/j.baae.2017.08.008>

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Ecomorphological structure of avian communities changes upon arrival of wintering species

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Received 27 November 2016; accepted 28 August 2017
Available online 5 September 2017

Abstract

Community composition reflects evolutionary and ecological processes such as diversification and species assortment. Communities are generally considered to be saturated, which means that the number of species is maximized and that regulatory mechanisms, such as interspecific competition, prevent the addition of new species. In the tropics, however, species numbers of local bird assemblages double up each winter after the arrival of migratory species, which suggests that a rearrangement of niches occurs. Here ecological space is defined by morphological traits that reflect the ecological position of species, to describe changes in the structure of local communities. We found that the average morphological distance between species was reduced, and the volume (the total extent of trait space) was expanded with the arrival of migrants, indicating that newcomers occupy the periphery and the interior of the available ecological space. Furthermore, with greater morphological differences between resident species, higher numbers of migratory species can take advantage of free space and potentially exploit unused resources due to their intermediate morphology. We highlight the differences in the attributes of resident versus migratory species that may allow both to be accommodated in the morphological space, and we suggest coexistence theory as a possible explanation for the co-occurrence of similar species.

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Keywords: Packing; Migration; Assemblages; Niche; Morphological analysis

Introduction

The arrival of migratory species increases complexity on both regional and local scales. For instance, mixed-species

flocks have been well studied in terms of species composition, internal structure, social relationships and competitive interactions within and between species and their consequences on the demography and community structure (Graves & Gotelli, 1993; Greenberg, 2000; Gómez, Bravo, Brumfield, Tello, & Cadena, 2010; Sridhar et al., 2012; Lees & Gilroy, 2014; Colorado & Rodewald, 2015). However, few studies have addressed how migratory species could be integrated into

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sedentary species niches in terms of their morphological space during migration (Herrera, 1978).

In their winter territories, migratory species compete for resources with other migrants as well as resident species, even more so as the abundance of food resources is lowest at this point in the annual cycle (Moreau, 1972; Greenberg, 1995). However, resources seem sufficient to allow the coexistence of both migrants and residents. Past studies have suggested that niches in tropical sedentary bird communities are tightly organized, so that there is no space available for new species (MacArthur, 1972; Diamond, 1975; Rabøl, 1993); however, this does not account for migration, which significantly increases the number of species in resident communities. Herrera (1978) hypothesized that migratory species may not be completely integrated into tropical communities but only added when the amount of resources permits the survival of additional populations. In contrast, more recent studies have proposed that migratory species are an integral part of tropical bird communities despite their temporary absence (Cox, 1985; Leisler, 1992; Jones, 1998). From an evolutionary point of view, understanding non-breeding interactions between migrants and residents is crucial to the theory of the evolution of migration (Pérez-Tris & Tellería, 2002; Winger, Barker, & Ree, 2014). Each year, billions of terrestrial birds in North America participate in one of the most important long-distance migrations to winter north of the equator in Mexico, the occidental Indies, or northern Central America (Faaborg et al., 2010). Rappole et al. (1983), defined Neotropical migrants (332 species in total) as the species with populations breeding north of the Tropic of Cancer and wintering south of it. Migratory species spend the winter season in a vast area which extends from Mexico south to Panama, including the Caribbean Islands and parts of South America (Newton, 2008). In the Neotropical region, the presence of migratory species in local avifaunas declines southwards (Slud, 1976).

Ecological requirements and life history traits are assumed to determine the size and shape of organisms (Wainwright & Reilly, 1994), thus the distribution of species within a morphological space (i.e., an ecological space defined by morphological traits) has been used to approximate ecological relationships (Ricklefs, 2012). Under this reasoning, the position occupied by a given species and its distance to others, provide valuable information to infer ecological processes. For instance, different combinations of beak sizes and wing lengths can define a complete variety of ways to exploit resources. If the annual addition of migrants to the assemblages of resident birds modifies the ecological relationships among species, it might be reflected in a new arrangement and distribution of species in ecological space, which could be studied through a morphological approach. So, in terms of morphological space, what happens when new species are added to communities? When the number of species increases, local communities may change in two basic directions (Ricklefs & Miles, 1994). Packing the new species within the niche occupied by the original species

(“species-packing” mechanism), where the morphological distance between species should decrease while the volume (i.e., defined by total space occupied by species) remains constant. On the other hand, the niche volume might increase to accommodate the new species (“volume-increasing” mechanism), while the mean morphological distance either decreases (volume-increasing, packing limited) or remains constant (volume-increasing, packing prevented). Based on results from vertebrate assemblages, the volume-increasing mechanism is empirically the most common process in communities (Ricklefs & Schluter, 1993; Ricklefs & Miles, 1994). Moreno et al. (2006) found that in ensembles of frugivorous bats, the volume-increasing mechanism with a limited species packing occurs. They explained that these ensembles may be experiencing ecological processes that ultimately determine their species richness and structure.

Here, we study the extent to which morphological similarity within sedentary assemblages explains the capacity to receive migratory species. Focusing on three passerine families in two ecoregions of Mexico, we also research how communities are re-arranged once the migratory component is present. We expect that the integration of migratory species into sedentary assemblages follows the volume-increasing mechanism. Specifically, our goals are: (1) to test whether the morphological space (i.e. morphological distance and volume) occupied by resident passerine birds is modified when migratory species are added to each community and (2) to establish the relationship between the morphological space occupied by resident species and its capacity to receive migrants.

Material and methods

Ecoregions

We focused on two ecoregions in Mexico: the Central Mexico Mountains region and the Central Pacific Plains region (hereafter mountain and pacific region respectively). Both are located in the central-western part of the country at similar latitudes (Fig. 1; see Appendix A: Table 1 in Supplementary material). These areas boast a great biological diversity due to geological and ecological complexity (Sarukhán et al., 2009). The Central Mexico Mountains principally comprises the Trans-Mexican Volcanic-Belt where temperate climate fosters woodland vegetation such as pine–oak and cloud forest. In stark contrast, the pacific region is located in the Balsas Basin along the Pacific coast where tropical forest, shrub land and riparian vegetation are dominant (Berlanga et al., 2008). The high contrast of these regions will shed insight into the relative importance of environment for the intensity of biological interactions.

We compiled a list of avian species of local communities for each region: 28 for the mountain region and 10 for the pacific region. For our analysis, we considered species from the families *Tyrannidae*, *Vireonidae* and *Parulidae* (see

Fig. 1. Two important ecoregions in Mexico: mountain (green) and pacific (yellow) regions. Dots show the location of communities studied. As to locality codes, refer to Appendix A, Table 1 in Supplementary material. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Appendix A: Table 2 in Supplementary material), which are mainly frugivores–insectivores that occupy similar niches and generally occur in mixed flocks (Howell & Webb, 1995). Morphological measurements of the species were obtained mainly from the literature (Howell & Webb, 1995; Pyle, 1997, Table S2; Guallar, S., Santana, E., Contreras, S., Verdugo, H., & Gallés, 2009). For those species for which no information was available, specimens were measured in scientific collections (1–10 individuals per species; Colección Nacional de Aves, Instituto de Biología, Universidad Nacional Autónoma de México and the Colección de Aves, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo).

Morphological analysis

The analysis relies on the position of each species in an n -dimensional morphological hyperspace (Ricklefs & Travis, 1980). We used the average of six morphological traits for

each species: total length, wing chord (the distance from carpal joint to the tip of the longest primary), tarsus (from the inner bend of the tibiotarsal articulation to the base on the toes), exposed culmen (from the tip of the upper mandible to the base of the skull), tail length (from the base of the tail to the tip of the longest rectrix), and live weight (g). Total length was calculated as the total body length minus the lengths of the culmen and tail. For birds in the collections, we used the weight reported in the accompanying information for each specimen. To reduce redundancy in our variables and, given the natural differences in magnitude among the variables, we standardized them in order to make a fair contribution of each one to the analysis (Ricklefs & Travis, 1980).

We assembled a dataset with morphological variables that contained 92 species, 45 of them being migratory and 47 being sedentary. The mountain dataset included 44 migratory and 47 resident species whereas the pacific dataset had 38 and 39 species, respectively. We described the morpholog-

Fig. 2. Distribution of species in the morphological space for (A) Mountain and (B) Pacific regions. Only the first three axes (PC1, PC2, and PC3) are shown. The distribution of migratory (blue) and sedentary (green) species inside this space tells how tight ecological relationships are. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ical space occupied by each local assemblage in each region through a principal components analysis (PCA) (Morrison, 1967; Pielou, 1969) based on a covariance matrix. The distribution of species within the morphological space can be described in several ways, however the presence of both gaps and outliers in the hypervolume might mislead inferences. To prevent this, we calculated the mean Euclidean distance between pairs of species and the multidimensional Kernel density estimated hypervolume, a robust method that handles these issues (Blonder, Lamanna, Violle, & Enquist, 2014). This morphological space characterization was performed for each community in each region. Because we were interested in describing the occupation of the morphological space by migratory species, the above-mentioned calculations were first performed for resident species (Res) followed by the set containing both migratory and resident species (Mig + Res). Then, we applied a *t*-test (paired version) to determine if there were significant differences in Euclidean distance and Kernel density when adding the migratory component to each region. Data normality was tested with a Shapiro–Wilk test prior to the analysis. To analyze the relationship between the structure of the morphological space of the resident species and its capacity to receive migratory species, we tested for correlations (Pearson or Spearman depending on the normality of variables) using the morphological Euclidean and Kernel density values and the number of migratory birds recorded for each site. All of the analyses were performed in R 3.1.2 (“R Development Core Team,” 2010) using the “hypervolume” library (Blonder, 2015).

Results

We kept the first four principal components that collectively explained 85.11% of the total variation for the mountain region and 85.63% for the pacific region (Table 1). For both regions, migratory species settle both on the periphery and at the core of the morphological space (Fig. 2A and B).

When migratory species were added to the mountain region, the interspecific distance between species of the community decreased significantly ($V = 390$, $P < 0.0001$) (Fig. 3A), while in the case of the volume, we found a significant increase when migratory species were added to this community ($t = 18.0466$, $df = 27$, $P < 0.0001$) (Fig. 3C). Conversely the paired tests in the pacific region indicate that interspecific distance did not decrease with the inclusion of migrants ($t = -0.2358$, $df = 9$, $P = 0.8189$) (Fig. 3B), but the volume did ($t = -24.731$, $df = 9$, $P < 0.0001$) (Fig. 3D).

We found a positive and significant correlation between the morphological distance among resident species and the number of migratory species in the mountain region ($r = 0.51376$, $S = 1776.694$, $P = 0.005$). We failed to detect this relationship in the pacific dataset ($r = 0.1147$, $t = 0.3267$, $P = 0.7523$). The relationship between the Kernel density volume occupied by resident mountain species and their capacity to receive migratory species was positive and significant ($r = 0.7954$, $t = 6.6934$, $P < 0.0001$). Similarly for the pacific region, the relationship was also positive and significant ($r = 0.65300$, $t = 2.4387$, $P = 0.0406$). That is, the greater the volume of the

Table 1. Factor loadings for the first four principal components used to morphologically characterize the winter community of passerine (migratory and resident) in (A) the mountain and (B) the pacific regions.

(A) Mountain region

Measurement	PC1	PC2	PC3	PC4
Wing Chord	−0.421451	0.3880494	−0.1041708	0.094941
Tarsus	−0.314051	−0.8756135	0.0519246	−0.219197
Exposed culmen	−0.426761	−0.1357744	−0.1344055	0.787834
Body weight	−0.457165	0.0650591	0.0384977	0.000633
Tail length	−0.414244	0.1476436	−0.5954424	−0.518181
Total length	−0.401280	0.1955823	0.7825303	−0.231824
% variance	44.10	17.59	12.94	10.47
Cumulative	44.10	61.69	74.64	85.11

(B) Pacific region

Measurement	PC1	PC2	PC3	PC4
Wing chord	−0.415892	−0.395112	0.101452	−0.803428
Tarsus	−0.313375	0.891331	0.045584	−0.236482
Exposed culmen	−0.440355	0.066419	−0.070891	0.069253
Body weight	−0.455805	−0.061816	−0.034727	0.229365
Tail length	−0.405249	−0.144722	0.687329	0.418955
Total length	−0.403646	−0.142254	−0.713425	0.256224
% variance	45.06	17.61	14.03	8.92
Cumulative	45.06	62.678	76.71	85.63

resident communities, the higher the number of incoming migratory species.

Discussion

Morphological space shifts during winter

We found that an important shift in the species' configuration takes place when migratory species arrive to local communities. Similar to previous studies (Ricklefs & Schluter, 1993; Ricklefs & Miles, 1994; Moreno, Arita & Solis 2006), we found that volume-increasing was the way by which species were sorted into assemblages in both habitats. For communities within the mountain region the distance between species significantly decreased while volume increased, so a limited species packing occurs (similar to Moreno, Arita & Solis 2006), by which new species settle “outside” of the original community space and migratory species closely aggregate between them. In contrast, in the pacific region, the distance between species was not modified which means that species keep a certain distance among themselves.

Our results suggest three important ideas: first, migratory species, whose morphology differs from residents, join the assemblages and potentially exploit resources that are not normally used. Although migratory movements on the global scale are related to food surpluses in reproductive territories (Somveille, Rodrigues, & Manica, 2015), we suggest that those normally unused resources in non-reproductive areas

are sufficiently attractive to migratory species. Therefore, a combination of weather, adequate return distance to breeding grounds (Somveille et al., 2015), and the availability of unexploited resources facilitate the settlement of migratory species. Second, resident assemblages are capable of hosting a larger number of species than they do for at least half of the year. Resident species within communities are not placed at the minimal permissible distance in the morphological space. A direct implication of this observation is the need to elaborate more conservative hypotheses in studies that use ecological distance as a proxy for the intensity of ecological interactions because the distance between any two species may be not the minimum necessary to allow coexistence. We argue that communities have evolved in such a way that the niches of migratory species, which are absent for six months of the year, remain unoccupied and available until their return. Third, morphological diversity is related to ecological opportunity, which allows new species to join local communities (at least for the mountain region), so communities with more available resource space will be more prone to receiving new species.

Ecoregions are driven by different processes

Based on our results, the bird assemblages in the two regions are structured differently. Biological interactions play an important role in community structure in the pacific region because morphological/ecological similarity limits the establishment of new species. For the mountain region, on the other

Fig. 3. Mean ($\pm$ SE) Euclidean distance (A and B) and Kernel density volumes (C and D) showing how the morphological structure of local communities changes with the arrival of migratory birds. Identical letters indicate non-significance.

hand, the morphological distance between species is reduced suggesting that biological interactions are less tight, and there may be some flexibility in the environment to allow species with similar morphologies to successfully coexist.

Different methods to assess the relative contribution of environment and biological interactions on community structure have been used by ecologists, for example phylogenetic relatedness can be useful for inferring assembly mechanisms (Webb, Ackerly, McPeck, & Donoghue, 2002; Swenson, Enquist, Thompson, & Zimmerman, 2007; Emerson & Gillespie, 2008; Cavender-Bares, Kozak, Fine, & Kembel, 2009). We argue that our methodological approach may be more adequate for determining the relative importance of structuring processes because it makes no assumption about the phylogenetic conservatism of important ecological traits. For instance, a dissociation between ecological traits and phylogenetic relatedness has been shown for avian clades (Böhning-Gaese & Oberrath, 1999). Our results are consistent with those reported by Graham et al. (2009), who found that biological interactions play a key role in structuring communities in tropical lowlands. In contrast, in montane areas, where environmental conditions are particularly harsh, traits that allow adaptation are filtered regardless of the negative effects of ecological similarity (i.e., only species with similar morphologies are capable of settling).

Potential shifts in broad-scale biological phenomena due to climate change such as bird migration, has encouraged ecologists to question how avian communities will be affected in such scenarios. Species geographic boundaries might be shifted and this poses a problem of an abnormally fast species

accumulation and turnover in some regions, for instance, a rearrangement in community composition is expected in the presence of a variation in global temperature (Lemoine, Schaefer, & Böhning-Gaese, 2007). Whether recipient communities are able to cope with an increase in species, remains as an intriguing question that we consider could be tackled by combining a large-scale predictive methodology similar to Lemoine et al. (2007) and a local ecological approach like ours.

The relatively recent conceptual framework of coexistence theory (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012) may explain the existence of communities where species are placed close to each other in niche space (or complement other explanations). In this light, self-regulating intraspecific processes are capable to limit populations more than interactions among species; for example, density-dependent mechanisms could regulate population growth rates. Long-term coexistence can be possible in those cases where differences in fitness among competitors play an important role so that even a weak stabilizing action may allow the co-occurrence of species (Adler, HilleRisLambers, & Levine, 2007). However, one of the crucial times in a species' life history is the raising of offspring, and for resident species, it takes place in the absence of migratory birds, lowering the competitive pressure.

Conflicts of interest

None declared.

Author contributions

AM, SC, and LHA conceived of the idea and designed and conducted analysis. AM, SC, RVP, and LHA wrote and approved the manuscript.

Acknowledgements

We thank Escalante Pliego (Colección Nacional de Aves, Instituto de Biología, Universidad Nacional Autónoma de México) and Javier Salgado (Colección de Aves, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2017.08.008>.

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