



ORIGINAL ARTICLE

# From clustering to overdispersion: a north to south gradient in the patterns of phylogenetic structure in North American hummingbird assemblages

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## Abstract

Hummingbirds are a highly specialized bird group whose species assemblages may show differential patterns of phylogenetic and phenotypic diversification, largely driven by ecological and geographical factors, as well as by mutualistic interactions with plants. Here, based on a molecular phylogenetic tree of hummingbirds and 11 morphological traits, we estimated phylogenetic and phenotypic structure at the scale of biogeographic (Nearctic, Transitional, and Neotropical) and 105 ecoregions across North America. Since some species are migratory, we discriminated between breeding and winter species assemblages and performed a paired t test to determine if there are significant differences in the assemblages' structure between regions and seasons. We also performed linear models (LM) to determine the relationship of phylogenetic and phenotypic structure patterns with species richness, phylogenetic diversity, and proportion of species in clades with high diversification rates. Phylogenetic and phenotypic structure results ranged from clustered in Nearctic and some Transition ecoregions, to random in Transition and most Neotropical ecoregions, to overdispersion in two Neotropical ecoregions. Winter assemblages showed significant shifts in phylogenetic or phenotypic structure from resident assemblages in Transition and Neotropical ecoregions but showed a significant shift in phenotypic structure in Nearctic ecoregions. LMs showed that species richness and phylogenetic diversity presented negative and positive relationships with phylogenetic and phenotypic structure measures in both seasons. Our results suggest that the assembly process of North American hummingbird communities has been influenced by filtering, competition, and mutualism processes largely determined by the species pool available at different biogeographic regions.

**Keywords** Assembly process · Habitat filtering · Interspecific competition · Migratory behavior · Nectarivores · Trochilidae

## Introduction

The phylogenetic structure of species assemblages is the result of a highly complex process influenced by factors including lineage history, geographic and climatic conditions, biotic interactions, and historical contingency (Emerson & Gillespie, 2008; Cavender-Bares et al., 2009; Fukami, 2015; Segar et al., 2020). These factors may act individually, additively, or interactively over different spatial and temporal scales. For an example, interspecific interactions like competition operate at local scales and over relatively short periods, while climatic conditions may operate at regional scales over long time periods. Each of these factors (or combinations of factors) can lead to overdispersed, clustered, or random patterns in the phylogenetic and phenotypic structure of natural communities (Cavender-Bares et al., 2009; Pontarp & Petchey, 2016;

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Cadotte & Tucker, 2017); put another way, the same or highly similar assembly patterns can be the product of different factors. It is therefore necessary to evaluate phylogenetic and phenotypic data together to better discriminate between the significance of the factors involved in the evolution of natural communities (Cavender-Bares et al., 2009; Emerson & Gillespie, 2008; Webb et al., 2002).

Clustering patterns refer to the coexistence of species that are phylogenetically closely related or, phenotypically similar to each other (Cadotte & Tucker, 2017; Webb et al., 2002). Habitat filtering and adaptive radiations have been described as the main factors that generate clustering patterns (Cadotte & Tucker, 2017; Emerson & Gillespie, 2008). In habitat filtering, restrictions imposed by environmental conditions may generate differential presence of particular traits in local assemblages with respect to the regional species pool (Cadotte & Tucker, 2017). In adaptive radiations, niche availability may promote rapid divergence of an ancestral taxon into several derived ecologically specialized species (Schluter, 2000). Interspecific interactions can also generate clustering patterns, competition may allow a given phenotype to exclude similar phenotypes due to differences in competitive ability (Mayfield & Levine, 2010), while mutualism may favor the establishment and success of certain species in a community (Martorell & Freckleton, 2014). Due to tight interactions between plants and pollinators such as hummingbirds, mutualism is a common process between these two groups, in which plants provide the necessary resources for the successful establishment of different hummingbird species, and pollination services maintain and promote plant diversification (Abrahamczyk et al., 2017; Bergamo et al., 2018).

In opposition to clustering, overdispersion occurs when coexisting species tend to be either phylogenetically distant or phenotypically dissimilar (Cavender-Bares et al., 2009; Webb et al., 2002). Phylogenetic and phenotypic overdispersion may occur when competitive interactions are linked to ecologically relevant traits that are highly evolutionarily conserved. Competitive interactions may result in either competitive exclusion (phylogenetic overdispersion) or character displacement (phenotypic overdispersion), both of which release competitive stress (Brown & Wilson, 1956; Webb et al., 2002; Emerson & Gillespie, 2008; Cavender-Bares et al., 2009; Bassar et al., 2017; Lara et al., 2011). If ecological traits are labile or convergent, habitat filtering may generate overdispersion due to the selection of traits scattered across the phylogeny (Cavender-Bares et al., 2009; Emerson & Gillespie, 2008; Webb et al., 2002). Given that the same factors may lead to contrasting patterns depending on trait evolution, it is necessary to include trait evolution for a proper interpretation of phylogenetic and phenotypic community structure patterns (Emerson & Gillespie, 2008;

Losos, 2008; Revell et al., 2008; Cavender-Bares et al., 2009).

The evolution of traits may imprint patterns able to be measured across the phylogeny through the estimation of the phylogenetic signal (Losos, 2008; Revell et al., 2008), which is a statistical measure of trait dependence among species due to their phylogenetic relationship (Revell et al., 2008). This measure may suggest if a trait is either conserved, convergent or shows a Brownian motion evolution pattern across the phylogeny (Losos, 2008; Pagel, 1999; Revell et al., 2008). Phylogenetic signal may be sensitive to changes in trait evolution and extinction rates across time (Aristide & Morlon, 2019; Revell et al., 2008); the combination of trait phylogenetic signal with other community structure measurements (Mayfield & Levine, 2010) provides information about the significance of a given trait in the evolution of natural communities (Webb et al., 2002).

Hummingbird evolution and their distributional patterns have been highly influenced by several factors operating at different scales, such as biogeographic history, past and current ecological conditions, and biotic interactions (Altshuler, 2006; Graham et al., 2012; McGuire et al., 2014; Weinstein et al., 2017; Martín Gonzalez et al., 2015; Maruyama et al., 2018; Rodríguez-Flores et al., 2019). Hummingbirds are distributed in almost all terrestrial environments from Alaska to Patagonia, and have established highly important mutualistic interactions with plants (Rodríguez-Flores et al., 2019; Stein, 1992; Temeles et al., 2009), such as pollination (Martín-Gonzalez et al. 2015; Maruyama et al., 2018; Rodríguez-Flores et al., 2019). Despite the relatively highly conserved morphology in hummingbirds, coexisting taxa form complex species assemblages (Brown & Bower, 1985; Ornelas et al., 2002; Lara et al., 2011; Abrahamczyk & Kessler, 2015; Rodríguez-Flores & Arizmendi, 2016; Bribiesca et al., 2019). These assemblages may be arranged by niche partitioning through different foraging strategies and competitive interactions between different species, generating distinctive phenotypic, and phylogenetic patterns at local and regional scales (Feinsinger & Colwell, 1978; Ornelas et al., 2002; Lara et al., 2011; Martín & Ghalambor, 2014; Martín Gonzalez et al., 2015; Rodríguez-Flores & Arizmendi, 2016; Wolowski et al., 2017). In addition, the evolution of short- and long-distance seasonal migration in some North American hummingbird species has been described as a strategy of competitive ecological release, both for intra- and interspecific competition (Licona-Vera & Ornelas, 2017; Magrach et al., 2020; Weinstein et al., 2017). Long-distance migratory species present changes in niche occupation across the latitudinal gradient. In wintering grounds, migratory taxa show a highly overlapped niche with resident species, therefore likely adopting a generalist strategy. In their breeding regions, these species presumably turn to a specialist strategy due to both the abundance of resources and a very low hummingbird species number (Magrach et al., 2020).

Here, we analyzed the phenotypic and phylogenetic structure of hummingbird assemblages across North American biogeographic regions and ecoregions to assess the relative significance of habitat filtering and interspecific competition in community assembly. Several factors make North American hummingbird assemblages particularly suitable for addressing this question. Nearctic and Neotropical biogeographic regions overlap in Mexico and Central America, resulting in highly diverse communities where different biogeographic histories converge, likely to contain different phylogenetic structure patterns. Secondly, there is a north-to-south gradient of increase in both species' diversity and phylogenetic diversity, which suggests a gradient of phylogenetic structure ranging from clustering to overdispersion. Finally, migrant and resident species form mixed assemblages in Neotropical and the southernmost Nearctic ecoregions during the winter, potentially shifting the phylogenetic structure of resident communities. If inter-specific competition and habitat filtering have played significant roles in the assembly process of hummingbird communities at different regions across North America, we expect that: (1) phylogenetic and phenotypic structure values will gradually shift from an overdispersed pattern in Neotropical ecoregions to a clustered pattern toward the Nearctics; (2) migration will not affect phylogenetic and phenotypic structuring patterns in Neotropical and Transitional ecoregions because migratory species will have a generalist foraging strategy while wintering to avoid competition with closely related resident species; and (3) proportion of species in high diversification rates clades, and phylogenetic diversity, will all show a positive (interspecific competition) or negative (habitat filtering) relationship with phylogenetic and phenotypic structure values, depending of which factor is predominant across ecoregions.

## Material and methods

### Species composition

To calculate the phenotypic and phylogenetic structure of hummingbirds across North America (here defined as continental Mexico, USA, and Canada), we used level II ecoregions. The scale of these climatic and geological units reflects the distribution of natural communities at a subcontinental scale, appropriate for our study. Ecoregions level II were chosen because, comparatively, level I ecoregions are too coarse a scale for some of the patterns we were interested in (Bailey, 2004; Olson et al., 2001), while level III ecoregions are appropriate for local monitoring and decision-making studies (Omernik & Griffith, 2014). We grouped the ecoregions into three biogeographic regions (Morrone et al., 2017): (1) Nearctic, (2) Transitional, and (3) Neotropical.

We established hummingbird species composition for each ecoregion using distributional range maps in Nature Serve (BirdLife International & NatureServe, 2014) and CONABIO (available at <http://www.conabio.gob.mx/informacion/gis>). We overlapped the species' range maps with the ecoregions map using ArcGis 10.1 (ESRI, 2012). These data were used to build the presence/absence matrix used for all subsequent analyses. Given that some hummingbird species in the Bees clade show long-distance seasonal migration (Licona-Vera & Ornelas, 2017), we ran all analysis considering two different datasets: a) breeding species assemblages, which included resident species and migratory species in their breeding ranges, and b) winter species assemblages, including resident species and migrant species in their wintering ranges. Since our analyses focused on continental North America, we excluded the island endemic *Cyananthus forficatus* from all analyses.

### Phylogenetic and phenotypic data

We based our phylogenetic analyses on a molecular phylogenetic tree for hummingbirds reconstructed using mitochondrial and nuclear DNA markers (6461 nucleotides) that was previously published (McGuire et al., 2014), and kindly provided by J. McGuire. The original phylogenetic tree recovered nine clades, which we pruned to include only North American species. Some species distributed in our study region (i.e., *Lophornis brachylophus*, *L. helenae*, *Doricha enicura*, *Calothorax pulcher*, *Selasphorus ellioti*, *Cyananthus auriceps*, and *Pampa curvipennis*) were not included in the original phylogeny. We therefore estimated their corresponding branch lengths attaching each of these species to its closest relative available in the phylogenetic tree using the *bind.tip* function in phytools (Revell, 2012) for R (R Development Core Team, 2017); following Banks, 1990; Monroe et al., 1995; Licona-Vera & Ornelas, 2017; Stiles et al., 2017).

We collected morphological data from specimens in the Colección Nacional de Aves at the Instituto de Biología-UNAM and the Museo de Zoología "Alfonso L. Herrera" at the Facultad de Ciencias-UNAM. We measured nine morphological traits that are likely to be related to foraging strategies, flying efficiency, and habitat use (see Wolf et al., 1972 for details; Feisinger & Colwell, 1978; Zeffer et al., 2003; Temeles et al., 2009; Claramunt et al., 2012; Graham et al., 2012; Jönsson et al., 2015): length of the exposed culmen; angle, length, width, and depth of the bill; tarsus length, wing chord, secondary length of the wing (distance from carpal joint to the tip of the first secondary feather), and length of central rectrices (Fig. S1). We measured the angle of the bill using the length of the bill (a straight line from the base to the tip of the bill) and the line resulting from bill deviation (Fig. S1B). We also estimated two composite morphological traits: bill curvature and hand-wing

index (HWI). Following Temeles et al. (2009), we calculated bill curvature using measurements from the bill angle and bill length with the formula:

$$K = \frac{1}{\frac{\frac{1}{2}C}{\sin(\text{radians } A)}}$$

where  $K$  is the curvature,  $C$  is the length from the base to the tip of the bill, and  $A$  is the angle of the bill. We calculated HWI as a measure of wing shape (Claramunt et al., 2012), using wing chord and secondary length of wing as follows:

$$HWI = 100 * \left( \frac{\text{wing chord} - \text{secondary length of wing}}{\text{wing chord}} \right)$$

In addition, we obtained the weight of each specimen from the specimen label. All morphological data are available from the first author upon request. We measured only mature male specimens to avoid variation in the morphological data due to sex- or age-associated differences (Rodríguez-Flores & Stiles, 2005; Temeles et al., 2009).

Considering the phylogenetic non-independence of our morphological dataset, we performed a phylogenetic principal component analysis (PCA; Revell, 2009) using the *phy.pca* function in phytools (Revell, 2012) for R (R Development Core Team, 2017). Phylogenetic PCA requires of a phenotypic trait matrix and a phylogenetic tree. Before analyses, we transformed raw morphological measurements using the natural logarithm. The first PCA axis (PC1) explained 60.87% of variance and was related to body size, the second axis (PC2) explained 10.99% and was related to bill curvature, and the third axis (PC3) explained 8.05% of the variance and was related to the wing shape. The cumulative variance explained by PC4–PC6 was 15.03% and was mainly related to bill size and the length of the central rectrices (Tables S1 and S2). Using phylogenetic PCA scores per species (PC1 to PC6), we calculated a Euclidean distance matrix, which was used for phenotypic structure analyses of hummingbird assemblages. We built a phylogenetic heatmap using *phylo.heatmap* function in phytools (Revell, 2012) for R (R Development Core Team, 2017) which allowed us to show the dispersion of each PC axis using the standard deviation (SD) for each species.

### Phylogenetic and phenotypic mean pairwise distance (mpd) and mean nearest taxon distance (mntd)

To estimate the phylogenetic and phenotypic structure of hummingbird assemblages in each ecoregion, we considered four metrics: phylogenetic MPD and MNTD, and phenotypic pMPD and pMNTD. MPD averages the pair-wise distances among all pairs of co-occurring taxa throughout the

phylogenetic tree, while MNTD considers the mean distance between pairs of co-occurring closely related taxa (Webb et al., 2002). Similarly, pMPD averages morphological distances between all pairs of co-occurring taxa, while pMNTD averages distances in morphological characters for pairs of taxa. Both phenotypic structure metrics are estimated using a Euclidean distances matrix (Kembel et al., 2010). We estimated the significance of phylogenetic and phenotypic structure measurements by calculating standardized effect sizes (SES), which compares the observed phylogenetic and phenotypic structure measurements to a null model (Kembel et al., 2010; Webb et al., 2002). Relevant null models were obtained from the randomization of the species assemblages' matrix by drawing species from the corresponding pool (pruned phylogenetic tree or Euclidean matrix) with equal probability using the phylogeny pool model with 100 iterations, as implemented in picante (Kembel et al., 2010) for R (R Development Core Team, 2017). Hereafter, MPD and MNTD refer to the standardized effect sizes of these parameters rather than the raw parameters. The values of MPD and MNTD indicate the three possible patterns: MPD and MNTD values  $< -1.96$  indicate clustering values;  $x > 1.96$  indicate overdispersion, and values between  $1.96 < x < 1$  indicate a random pattern (Vamosi et al., 2009; Webb et al., 2002). Given that some trends may be overlooked within the random patterns, we also considered nonsignificant trends of clustering ( $-1.96 < x < 0$ ) and overdispersion ( $0 < x < 1.96$ ; Vamosi et al., 2009).

Using the species presences/absence matrix, we calculated phylogenetic and phenotypic structure metrics for the breeding and wintering season separately at two different geographic scales: the Nearctic, Transitional, and Neotropical biogeographic regions (Fig. S2); and at the level II ecoregions. Given that phylogenetic and phenotypic structure analyses require the conformation of an appropriate species group to serve as a relevant pool for null model comparisons (see Webb et al., 2002; Kembel, 2009), we used the relevant species pools for each analysis: (1) the pruned phylogenetic tree for the phylogenetic pattern, and (2) the morphological Euclidean matrix for the phenotypic pattern (Table S3).

We used DAMOCLES (Pigot & Etienne, 2015) for R (R Development Core Team, 2017) to test for phylogenetic and phenotypic structure patterns. DAMOCLES generates dynamic null models based on colonization, local extinction, and speciation processes. We built dynamic null models by drawing species from the corresponding pool (the pruned phylogenetic tree or the Euclidean matrix) with unequal probabilities and 100 iterations. Since DAMOCLES yields negative MPD and MNTD structure measurements, we multiplied results by -1, which allowed us to compare these with values derived from Picante (Kembel et al., 2010). Due to a low species richness in several ecoregional assemblages, we built null models using equal probabilities to draw species



from the species pool, which are as equally efficient as random draw models (Pigot & Etienne, 2015). We obtained the mean and standard deviations from 100 iterations of each of these null models using Picante (Kembel et al., 2010) for R (R Development Core Team, 2017).

It has been suggested that a more accurate phylogenetic structure process may be inferred by coupling phenotypic and phylogenetic structure information, as well as by estimating trait phylogenetic signal (Cadotte & Tucker, 2017). Using of all these results allows for a better inference of processes implicated in the phylogenetic structuring of community assemblages (Kraft et al., 2007). We therefore estimated the phylogenetic signal of each selected morphological trait using Pagel's  $\lambda$  (Pagel, 1999), which measures the statistical dependence of trait values among species given their phylogenetic relationship (Revell et al., 2008). Values of  $\lambda$  tending to 0 indicate lability or convergence of the traits, while significant values closer/equal to 1 indicate that trait evolution conforms to Brownian motion (Freckleton et al., 2002; Symonds & Blomberg, 2014). Phylogenetic signal analyses were calculated using the *phylosig* function in phytools (Revell, 2012) for R (R Development Core Team, 2017).

## Data analysis

To determine whether the arrival of migratory species into wintering grounds shifts the phylogenetic and phenotypic structuring patterns across biogeographic regions, we performed a paired t test (Dytham, 2011) of the ecoregions' structure scores between the breeding and winter seasons. Since both measures were calculated from pairwise comparisons, ecoregions inhabited by less than two species were discarded from this test.

Since interspecific competition cannot be measured at the biogeographic or ecoregion scales, we used three variables (species richness, phylogenetic diversity, and proportion of species in high-diversification rate clades) to indirectly measure the relative influence of interspecific competition and habitat filtering in the structuring patterns of hummingbird assemblages. However, although both interspecific competition and habitat filtering may generate similar values for species richness, phylogenetic and phenotypic structure values would be different depending on the main assembly process and the evolution of the traits (Aristide & Morlon, 2019). We performed linear regression models (LM; Crawley, 2007) for each phylogenetic structure measure within each season. For each season, we evaluated the influence of 1) hummingbird species richness, 2) phylogenetic diversity (measured following Faith, 1992), and 3) the proportion of species in high-diversification rate clades (Emeralds, Mountain Gems, and Bees clades; McGuire et al., 2014). The proportion

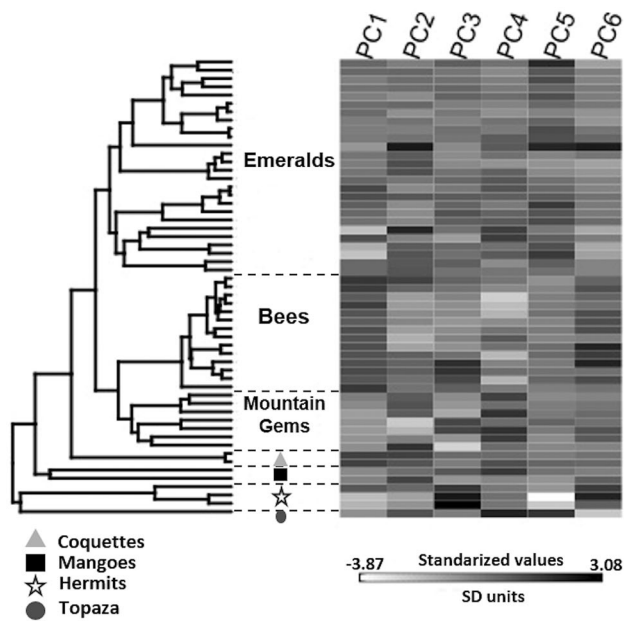
of species in high-diversification rate clades allowed us to indirectly measure the age of the different assemblages, as the Emerald, Bee, and Mountain Gem clades are the youngest in the hummingbird phylogeny (McGuire et al., 2014). Therefore, hummingbird communities mainly composed of species from any of these three clades would indicate that the assemblage is younger than assemblages composed by species from other clades. On the other hand, the relationship between phylogenetic diversity and MPD, MNTD, pMPD, pMNTD may be influenced by the phylogenetic signal. When a trait is conserved, competition may promote communities with species not closely related; and phylogenetic diversity and phylogenetic structuring measures tend to increase together. In the case of traits convergent evolution, phylogenetic diversity and structuring measures would not be different (Webb et al., 2002; Emerson & Gillespie, 2008; see Kembel et al., 2010).

We compared among LMs including all possible combinations of the three explanatory variables (species richness, phylogenetic diversity, and proportion of species in high-diversification rate clades), including the intercept-only null model (Burnham et al., 2001). We obtained 32 LMs per phylogenetic structure measure in each ecoregion, for a total of 256 models in total. We used the corrected Akaike information criterion (AICc) to choose the best supported models. We also calculated  $\Delta AIC$  ( $< 2.00$ ) and the weight of the model as part of model evaluation (Johnson & Omland, 2004). We performed model selection using *MuMIn* (Barton, 2018), as implemented in R (R Development Core Team, 2017).

## Results

### Morphological and phylogenetic data

We compiled a list of 58 species for hummingbirds in North America (based on Gill et al., 2021; Table S3). Our pruned phylogenetic tree included 55 hummingbird species, and we measured a total of 803 specimens from 55 hummingbird species (Table S3; Figs. S2 and S4). Morphological data showed that phylogenetically closely related species are highly similar to each other (Fig. 1). The Bees and Coquettes clades included species with small body-sizes and showed similar positive SD values. Species in the Emeralds clade varied in body-size (negative and positive values of SD; Fig. 1), while the Mountain Gems clade included larger body-sized (negative SD values) species. On the other hand, the SD of the shape and size of the bill (PC2, PC4, PC5, PC6), and the wing shape (PC3) showed high variation within hummingbird clades.



**Fig. 1** Phylogenetic heatmap of the pruned phylogenetic tree (see Methods) based on McGuire et al. (2014) for North American hummingbird species and the matrix of the PC from phylogenetic PCA scores. Colors indicate standard deviation (SD) values for each PC axis by species

## Phylogenetic and phenotypic structure patterns across North America

Phylogenetic and phenotypic structure measures of the Neotropical and Transitional biogeographic regions showed a random structure across North America in both seasons (Table 1). Contrast values for MPD and pMPD in the Nearctic region showed a clustered pattern in both seasons. At the ecoregional scale, we obtained 105 hummingbird assemblages which can be generally grouped into the three biogeographic regions (Fig. 2). In general, phylogenetic MPD and MNTD for the wintering and breeding seasons showed mostly clustered pattern in western Nearctic ecoregions (Fig. 2); and random patterns in ecoregions from the southern Nearctics, Transitional, and the Mexican and northern Central American

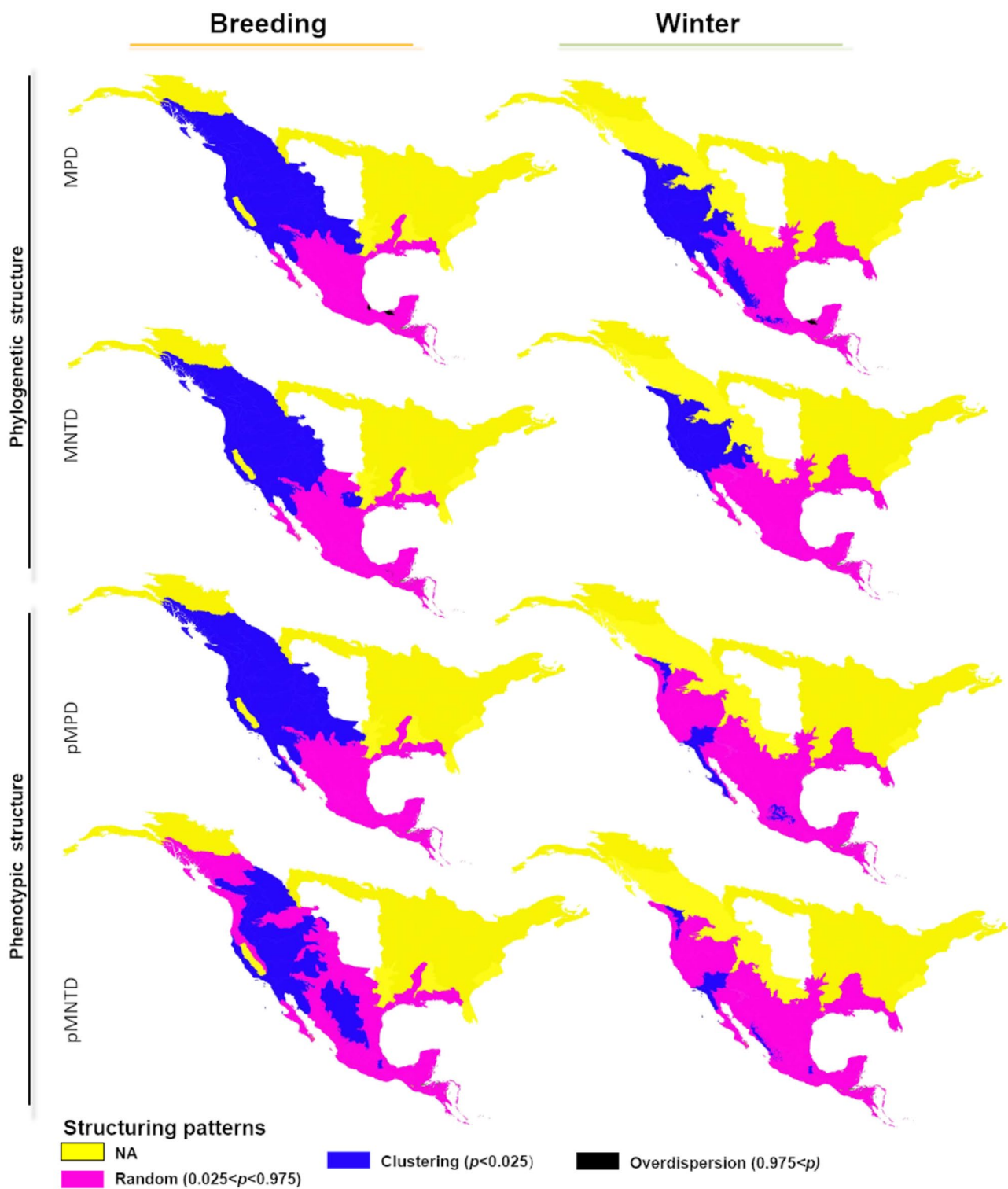
Neotropics ecoregions. There was an overdispersed pattern in MPD values in ecoregions in the southern Gulf of Mexico (Pantanos de Centla and Veracruz Dry Forest ecoregions; Tables S4 and S5). The wintering and breeding assemblages differed in MPD pattern in Balsas Dry Forests in the Neotropics and for the Sierra Madre Occidental pine forest in the Transitional biogeographic region (Fig. 2). The clustered pattern in the breeding season was maintained during the winter in some of the western Nearctic ecoregions (Fig. 2; Table S4).

Phenotypic structure patterns showed some similarities with the phylogenetic patterns above (Fig. 2). During the breeding season, pMPD showed a clustered pattern in western Nearctic ecoregions (USA, Canada, northern Baja California, and the Sonora desert); there were random patterns in some western and southern Nearctic ecoregions and most of the Transitional and Neotropical ecoregions (Table S4). In the winter season, the pMPD of most of the ecoregions recovered as clustered shifted to random structure patterns. In the case of pMNTD during the breeding season, the western Nearctic ecoregions (Columbia Plateau, Northwestern Pacific Coast, California Coast, and the Chihuahua Desert) showed a clustered pattern; we found no patterns of phenotypic overdispersion. During the winter season, almost all ecoregions that had clustered patterns during the breeding season shifted to random patterns, while the Sonora-Sinaloa Transitional Subtropical Dry Forest ecoregion shifted from a random to clustered phenotypic pattern (Table S5).

Boxplots by biogeographic region showed that Nearctic ecoregions had a nonsignificant trend toward clustering (negative values) in both the phylogenetic and phenotypic structure (Fig. 3). For Transitional ecoregions, MPD and MNTD showed positive and negative values, suggesting overdispersion and clustering tendencies; however, pMPD showed a trend toward more positive values while pMNTD showed mainly negative values. Neotropical ecoregions showed both positive and negative values for all MPD, MNTD, pMPD, suggesting clustering, but pMNTD suggested overdispersion for both breeding and wintering communities. Paired t test results (Table 2) and boxplots (Fig. 3) indicated that migratory species significantly shifted their phylogenetic patterns among seasons, except MNTD in the

**Table 1** Phylogenetic (MPD and MNTD) and phenotypic (pMPD and pMNTD) structure values of hummingbird assemblages at biogeographic regions (Neotropical, Transitional, and Nearctic) estimated using the *bootstrap* function in *DAMOCLES* (Pigot & Etienne, 2015)

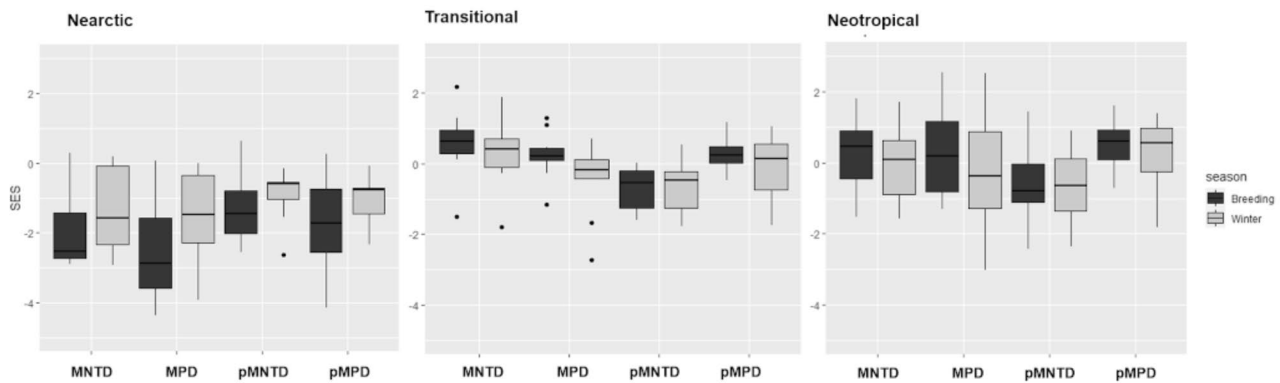
|              | MPD                |                    | MNTD              |                   | pMPD               |                   | pMNTD             |                   |
|--------------|--------------------|--------------------|-------------------|-------------------|--------------------|-------------------|-------------------|-------------------|
|              | breeding           | winter             | breeding          | winter            | breeding           | winter            | breeding          | winter            |
| Neotropical  | 0.3464<br>random   | 0.1084<br>random   | -0.5225<br>random | 1.0923<br>random  | -1.7355<br>random  | -1.681<br>random  | -1.1377<br>random | -1.1045<br>random |
| Transitional | 0.8809<br>random   | 0.9835<br>random   | 0.6432<br>random  | 0.6216<br>random  | 0.2692<br>random   | 0.3890<br>random  | 0.5932<br>random  | 0.6666<br>random  |
| Nearctic     | -3.0621<br>cluster | -2.2942<br>cluster | -1.5287<br>random | -1.2610<br>random | -2.9740<br>cluster | -2.408<br>cluster | -1.3493<br>random | -0.8975<br>random |



**Fig. 2** Geographic patterns of phylogenetic and phenotypic MPDs and MNTDs across North America according to seasons considered (breeding and winter)

Nearctics. The phenotypic structure (pMPD and pMNTD) shifted at Nearctic ecoregions, but not in Transitional and Neotropical ecoregions.

Values of  $\lambda$  for body size (PC1) and wing shape (PC3) suggested that the evolution of these traits is conserved, while bill curvature (PC2) is a convergent trait, showing



**Fig. 3** Boxplots of MPD, MNTD, pMPD, and pMNTD between breeding and winter seasons by biogeographic region

a nonsignificant  $\lambda$  value different from 0 (Table 3). Traits related to bill size (PC4 and PC6) showed  $\lambda$  values that suggest convergence;  $\lambda$  values of the length of rectrices (PC5) suggest that this trait is conserved.

LMs showed that species richness was negatively related to both phylogenetic and phenotypic MPD and MNTD values in both seasons (Table 4). For the breeding season, the best models explaining MPD, pMPD, and pMNTD included significant effects for species richness and phylogenetic diversity (Table 5). However, MNTD was better explained by species richness, phylogenetic diversity, and proportion of species in high-diversification rate clades. In general, the best models indicated that phylogenetic and phenotypic structuring measures were negatively related to species richness, and positively related to phylogenetic diversity (Table 5).

**Table 2** Paired *t* tests between breeding and winter season for MPD, MNTD, pMPD, and pMNTD at the ecoregions level

|                                | <i>t</i> value | <i>p</i> value | <i>df</i> |
|--------------------------------|----------------|----------------|-----------|
| <b>Nearctic ecoregions</b>     |                |                |           |
| MPD                            | -3.267         | 0.0027*        | 29        |
| MNTD                           | -1.296         | 0.2051         | 29        |
| pMPD                           | -2.199         | 0.0359*        | 29        |
| pMNTD                          | -2.769         | 0.0097*        | 29        |
| <b>Transitional ecoregions</b> |                |                |           |
| MPD                            | 3.741          | 0.0046*        | 9         |
| MNTD                           | 6.164          | 0.0001*        | 9         |
| pMPD                           | 2.070          | 0.0683         | 9         |
| pMNTD                          | -0.075         | 0.9417         | 9         |
| <b>Neotropical ecoregions</b>  |                |                |           |
| MPD                            | 2.627          | 0.0170*        | 18        |
| MNTD                           | 2.124          | 0.0477*        | 18        |
| pMPD                           | 2.067          | 0.0533         | 18        |
| pMNTD                          | -0.112         | 0.9117         | 18        |

\*significant values

For the winter season, the best-supported models MPD included species richness, phylogenetic diversity, and the proportion of species in high-diversification rate clades, while MNTD included species richness and phylogenetic diversity (Table 4). For pMPD, the best model included only the proportion of species in high-diversification rate clades, while for pMNTD, in addition to species richness and phylogenetic diversity, proportion of species in high-diversification rate clades has a strong positive effect (Table 5).

## Discussion

Our analyses suggest that present-day North American hummingbird communities have been structured by historical and ecological processes that have shaped their morphological characters. Our results showed that the different phylogenetic and phenotypic structure patterns detected in hummingbird assemblages may be explained, in part, by the lability of traits such as bill size and shape, as well as of conserved traits such as body size and wing shape. Both the Pagel  $\lambda$  values of the traits and the SD of PC1 (Fig. 1) suggested that body size is a conserved trait in North American hummingbirds, except for the Emeralds, which showed high variability. Bill curvature (PC2) and bill size (PC4 and PC6) are apparently labile traits, for which both extreme positive and extreme SD negative values were observed across our pruned phylogeny. Variation in these traits may be the result of character displacement processes allowing for resources

**Table 3** Quantification of the phylogenetic signal using Pagel's  $\lambda$  values for each selected morphological trait

| Trait | $\lambda$ value | <i>p</i> value |
|-------|-----------------|----------------|
| PC1   | 0.991           | <0.001*        |
| PC2   | 0.741           | 0.051          |
| PC3   | 0.961           | <0.001*        |
| PC4   | 0.584           | 0.001*         |
| PC5   | 0.951           | <0.001*        |
| PC6   | 0.806           | <0.001*        |

\*significant values



**Table 4** AICc scores of best performing linear models ( $\Delta AIC < 2.00$ ). SR = species richness, PD = phylogenetic diversity, Prop = Proportion of species in high-diversification rate clades

| Model                  | Coefficient estimated |        |       | AICc   | $\Delta$ AICc | Weight |
|------------------------|-----------------------|--------|-------|--------|---------------|--------|
|                        | SR                    | Prop   | PD    |        |               |        |
| Breeding               |                       |        |       |        |               |        |
| MPD ~ SR + PD          | -0.713                |        | 0.081 | 100.5  | 0.00          | 0.545  |
| MPD ~ SR + Prop + PD   | -0.760                | 1.319  | 0.087 | 100.8  | 0.36          | 0.454  |
| MNTD ~ SR + Prop + PD  | -0.478                | 1.415  | 0.061 | 69.6   | 0.00          | 0.643  |
| MNTD ~ SR + PD         | -0.427                |        | 0.061 | 70.8   | 1.18          | 0.356  |
| pMPD ~ SR + PD         | -0.380                |        | 0.045 | 154.85 | 0.00          | 0.749  |
| pMNTD ~ SR + PD        | -0.223                |        | 0.026 | 154.14 | 0.00          | 0.378  |
| Winter                 |                       |        |       |        |               |        |
| MPD ~ SR + Prop + PD   | -0.490                | -1.474 | 0.062 | 113.40 | 0.00          | 0.658  |
| MNTD ~ SR + PD         | -0.3770               |        | 0.057 | 106.84 | 0.00          | 0.783  |
| pMPD ~ SR + Prop + PD  | -0.188                | 0.026  | 0.026 | 136.15 | 0.00          | 0.448  |
| pMPD ~ Prop            |                       | 6.849  |       | 137.91 | 1.75          | 0.186  |
| pMNTD ~ SR + Prop + PD | -0.248                | 2.996  | 0.034 | 118.88 | 0.00          | 0.682  |

partition and species co-occurrence, thus reducing inter-specific competition (Bassar et al., 2017; López-Segoviano et al., 2018; Martín González et al., 2018). Interestingly, Emeralds showed a wide range of SD values, indicating variation in bill curvature and size ranging from long, curved bills like in *Campylopterus hemileucurus* to short, straight bills, as in *Abeillia abeillei*. This contrasts with previous findings in which Emerald species have been considered

generalist species with mostly straight bills (Rodríguez-Flores et al., 2019). Thus, our findings underline the need to quantitatively assess potentially ecologically relevant characters in specialized groups.

Hummingbird assemblage structure at the biogeographic scale showed that most of the Transitional and Neotropical ecoregions presented a random structure, which may be due to either the masking of local phylogenetic structure patterns given the large geographic scale (Table 1; Swenson et al., 2006), or to the diversity of other biotic groups with similar ecologies not included in studies focused on single taxonomic groups (Wilcox et al., 2018). The Nearctic biogeographic region, however, showed clustered patterns in MPD and pMPD: only some small body-sized species in the Bees clade range into higher latitudes (Table 1; Figs. 1–2). Values for MNTD and pMNTD showed a random pattern (Figs. S3–S4), which together with clustered patterns for MPD and pMPD, indicate that some closely related species did not range to northern regions (e.g., *S. sasin* and *S. platycercus*), and that co-occurring species show slightly morphological differences (e.g., differences in the SD of PC2 to PC6 between *S. rufus* and *S. calliope*; Figs. 1 and S4). Another important factor that may influence our assemblage structure results at the biogeographic scale is the distributional range and seasonal availability of flowering plants. The high species richness of flowering plants in the Neotropics has likely favored a high number of specialized hummingbird-flower interactions (Martín González et al., 2015), while at high latitudes in North America, drastic seasonal temperature changes may have favored generalist species, as in Bees, which show a mainly generalist morphology.

In comparison, at the ecoregional level, the smaller geographic scale, which has higher resolution in terms of habitat heterogeneity and climatic conditions, showed more detailed patterns. Nearctic ecoregions showed that clustered

**Table 5** Estimated coefficient and p values of the best-supported linear models. SR = species richness, PD = phylogenetic diversity, Prop = proportion of species in high diversification rates clades

| Model                  | Coefficient estimated |                  |                   |
|------------------------|-----------------------|------------------|-------------------|
|                        | SR                    | Prop             | PD                |
|                        | p value               | p value          | p value           |
| <b>Breeding</b>        |                       |                  |                   |
| MPD ~ SR + PD          | -0.713<br>< 0.001*    |                  | 0.081<br>< 0.001* |
| MNTD ~ SR + Prop + PD  | -0.478<br>< 0.001*    | 1.415<br>0.069   | 0.061<br>< 0.001* |
| pMPD ~ SR + PD         | -0.38<br>< 0.001*     |                  | 0.045<br>< 0.001* |
| pMNTD ~ SR + PD        | -0.223<br>< 0.001     |                  | 0.026<br>< 0.001  |
| <b>Winter</b>          |                       |                  |                   |
| MPD ~ SR + Prop + PD   | -0.49<br>< 0.001*     | -1.474<br>0.4126 | 0.062<br>< 0.001* |
| MNTD ~ SR + PD         | -0.29<br>< 0.001*     |                  | 0.057<br>< 0.001* |
| pMPD ~ SR + Prop + PD  | -0.188<br>0.0154*     | 0.026<br>0.2694  | 0.026<br>0.014*   |
| pMNTD ~ SR + Prop + PD | -0.248<br>< 0.001*    | 2.996<br>0.1193  | 0.034<br>< 0.001* |

patterns for MPD, MNTD, and pMPD (Tables 1 and S4; Fig. 2), predominate at northwestern ecoregions, while pMNTD showed both random and clustered patterns for several ecoregions. Clustering patterns in both the phylogenetic and phenotypic structure in these ecoregions may be explained by habitat filtering (see Webb et al., 2002, Mayfield & Levine, 2010). This is exemplified by species in the Bees clade, which have similar body size and bill curvature, the extreme climatic conditions in northernmost Temperate Forests and western deserts may have favored the assembly of closely related and phenotypically similar species, generating clustering in both phylogenetic and phenotypic structure patterns (Figs. 1 and S3). Similar phylogenetic patterns have been found in high-elevation Andean hummingbirds, where only a few clades have been able to diversify (García-Moreno et al., 1999; Graham et al., 2009; McGuire et al., 2014). On the other hand, pMNTD in northwestern Nearctic ecoregions (Fig. 2) showed phenotypic random patterns, suggesting that species in these assemblages (e.g., *Selasphorus rufus*, *S. calliope*, and *Archilochus alexandri*) are similar in body size (PC1), bill curvature (PC2), and wing shape (PC3; Figs. 1 and S4), but not in bill size (PC4-PC6), therefore suggesting that, in addition to habitat filtering, ecological differentiation via character displacement has probably reduced interspecific competition (Mayfield & Levine, 2010). Furthermore, due to their mutualistic interactions, plant species may have facilitated the colonization of northernmost regions by species in the Bees clade, likely due, in part, to the generalist habits of these species (Rodríguez-Flores et al., 2019). Most Nearctic desert ecoregions showed phylogenetic (MPD and MNTD) and phenotypic (pMPD and pMNTD) clustered patterns, which may be due to habitat filtering promoted by the extreme environmental conditions, which some species of the Bees clade are able to manage. However, the Chihuahuan and Baja California deserts showed random phylogenetic and phenotypic patterns (pMPD), but a clustered pattern in pMNTD (Table S4). This might be due to the regular presence of species from the Mountain Gems (e.g., *Eugenes fulgens*) or the Emeralds (e.g., *Cynanthus latirostris*) which have medium to large body sizes (Figs. 1 and S4), which may be the result of the availability of floral resources and of the proximity of these ecoregions to environmentally different ecoregions such as the Sierra Madre Oriental and the Sierra Madre Occidental (St-Louis et al., 2009).

Phylogenetic and phenotypic metrics in Transitional ecoregions showed values closer to zero (random pattern; Fig. 3). MPD, MNTD, and pMPD scores ranged from positive (i.e., overdispersion) to negative (i.e., clustered) values, but pMNTD values tended to be only negative (i.e., toward a clustered pattern; Figs. 2–3). This combination of assemblage structure patterns may have been promoted by the mixing of Nearctic and Neotropical biotas along the elevational

gradient of the Mexican Highlands (see Sánchez-González & Navarro, 2009; Escalante et al., 2013). Hummingbird assemblages in medium elevations show a species composition including species from tropical lowlands and from temperate highlands exhibiting both a high species richness assemblage, and a higher degree of feeding specialization and niche partitioning (López-Segoviano et al., 2021). The biotic mixing and habitat heterogeneity across the elevation gradient may explain overdispersed patterns by allowing species from different lineages to coexist, while trait lability and habitat filtering would explain the distribution of phenotypically similar species toward higher elevations.

Mexican Neotropical ecoregions showed a phylogenetic random pattern (Fig. 3) which may be due to the presence of species from mainly South American clades (i.e., Topazas, Hermits, Mangoes, and Coquettes) that are distantly related to the primarily North American Bees, Mountain Gems and the Emeralds clades (McGuire et al., 2014). Two ecoregions, however (Pantanos de Centla and Veracruz Dry Forest), showed an overdispersed phylogenetic (MPD) pattern (Fig. 3, Table S4). This may be explained by the presence of many Emerald clade species and other distantly related South American taxa, such as the Topazas and Hermits. Similarly, in the Tehuacan Valley ecoregion, clustered (pMNTD) and overdispersed (pMPD) trends were observed, suggesting the co-occurrence of highly and intermediate phenotypically similar species, which may be a response to niche partitioning by body size, and therefore probably to phenotypic repulsion to reduce strong interspecific competition (Mayfield & Levine, 2010); but, simultaneously allowing phenotypically highly similar species to coexist, likely mediated by character displacement, such as foraging strategies (Lara et al., 2011; López-Segoviano et al., 2018; Ornelas et al., 2002; Wolowski et al., 2017).

Neotropical and Transitional regions showed similar structure values, which may be due to factors such as a lower species richness in Neotropical assemblages in comparison with Transitional ecoregions. For example, Neotropical ecoregions showed higher variability in the community structure values, suggesting a finer niche partition likely associated with interspecific competition (Martin-González et al., 2015). However, due to the generally broader scales of our study, some factors operating at local scales, such as niche partitioning mediated by floral abundance and seasonal availability or local movements linked to flowers' phenology, may not be easily interpreted from our data.

We evaluated whether phylogenetic and phenotypic structure patterns may be explained by factors indirectly related to interspecific competition or habitat filtering. Values of  $\lambda$  phylogenetic signal of body size (PC1) and wing shape (PC3) indicate that these are conserved traits. In the case of the proportion of species in high-diversification rate clades, assemblages mainly composed of species from only

one of the three North American clades (Bees, Emeralds and Mountain Gems) may indicate that the assemblage is younger than mixed assemblages (i.e., composed of species from all clades). Interspecific competition in young lineages with high rate of diversification may generate high trait disparity between co-occurring species (Aristide & Morlon, 2019). On the other hand, when traits are conserved, habitat filtering favors fewer and more highly similar species from the same clade, and negative values in both phylogenetic and phenotypic structure measures may be thus obtained, however habitat filtering may keep a lower species richness depending on ecological conditions (p.e., seasonal flower availability). Thus, with increase in species richness, phylogenetic diversity and the proportion of species in high-diversification rate clades should present negative relationships (Emerson & Gillespie, 2008; Webb et al., 2002). In the case of convergent traits, habitat filtering favors highly similar species from different clades, and overdispersion values in phylogenetic structure and clustered in phenotypic structure. The proportion of species in high-diversification rate clades should have negative and positive relationship with phylogenetic and phenotypic structure, respectively (see Emerson & Gillespie, 2008).

Our results partially fit these patterns. The best supported models for MPD and MNTD for the breeding season included species richness and phylogenetic diversity (Table 5), but the coefficients were negative and positive respectively, which may be due to inclusion of most species in North American ecoregions in only three clades (Emeralds, Bees, and Mountain Gems; McGuire et al., 2014), therefore pulling toward MPD and MNTD negative values in ecoregions with high species richness. For pMPD and pMNTD, the best supported models included species richness and phylogenetic diversity, and only for pMNTD, proportion of species in high-diversification rate clades (Table 4). In these cases, species from the Bee clade increased the species richness in the northernmost ecoregions, showing relatively minor phenotypic differences with other clades, such as the Emeralds (Fig. 1). Breeding season models and structuring pattern suggest that habitat filtering may have been the main assembly process in the northernmost ecoregions where habitat conditions are highly variable among seasons. Conversely, in the southern ecoregions, overdispersion patterns and positive coefficient of phylogenetic diversity indicate the accumulation of phylogenetic histories from different clades, suggesting that factors, such as the diversity and abundance of resources or niche partitioning, may drive the assembly process (Weinstein & Graham, 2016; Wolowski et al., 2017; Martín-Gonzalez et al., 2018).

## The role of migratory behavior in the assembly process

The evolution of migratory behavior is a relatively recent trait in North American hummingbirds (Licona-Vera & Ornelas, 2017). It has been suggested that migratory movements may have evolved in different avian lineages to avoid competition (Laube et al., 2013; Salewski & Bruderer, 2007); however, migration in hummingbirds has been related to resource availability (Malpica & Ornelas, 2014; Licona-Vera & Ornelas, 2017). In North America, migrant hummingbird species modify the structure of hummingbird communities in ecoregions from the southernmost Nearctics to the Neotropics, and migrants adjust their niche width during winter season (Martín González et al., 2018). Therefore, it is necessary to evaluate differences in phylogenetic and phenotypic structure between assemblages in the breeding and winter season. At the scale of biogeographic regions, phylogenetic and phenotypic structure did not shift between the two seasons (Table 1). However, at the ecoregional level, our results showed that migratory species shift phylogenetic (MPD) and phenotypic (pMPD and pMNTD) structure patterns in several ecoregions in the Nearctics toward less negative (clustered) values compared to the winter season (Table 2; Fig. 3), indicating that migratory species (Bee clade) arrive to ecoregions with distantly related and phenotypically differentiated taxa, such as Emeralds and Mountain Gems. This pattern is similar to the ecological distribution patterns in *Sylvia* warblers, where the potential of habitat occupancy is greater where there are few congeneric species (Laube et al., 2013); and to Andean hummingbird co-occurrence patterns (Weinstein et al., 2017). However, migratory species movements did not significantly shift MNTD of Nearctic ecoregions, but tended to negative values, suggesting that winter assemblages are composed by not closely related. An interesting trend in northern Nearctic ecoregions during the wintering season is the presence of at least two migratory hummingbird species (Fig. 3), which may be due to the relatively recent range expansion related to climatic change and supplementary feeding by humans (Greig et al., 2017; Winker & Gibson, 2018).

Boxplots showed that in Transitional and Neotropical ecoregions, winter communities changed phylogenetically toward more negative values in MPD and MNTD (Figs. 2–3), due to the arrival of species from the Bees clade sharing wintering locations (e.g., *S. rufus* and *S. platycercus*). Values of pMPD and pMNTD in these bioregions did not change between seasons (Table 2). Given that migratory species are usually classified as generalists (Rodríguez-Flores & Arizmendi, 2016), the phenotypic structure of assemblages is not expected to change (see

Malpica et al., 2017), at least at the ecoregional scale, likely due to niche expansion in long distance migratory species, which feed from even no-ornithophilic species in their wintering grounds (Martín González et al., 2018; Waser et al., 2018), while more specialized species move across the elevational gradient (altitudinal migration) following seasonal flowering patterns (López-Segoviano et al., 2021).

The best models fitting the winter season assemblages showed negative relationships between species richness and phylogenetic and phenotypic structure measures (Tables 4–5). Phylogenetic diversity showed positive coefficients for phylogenetic (MPD and MNTD) and phenotypic structure (pMPD and pMNTD), while the proportion of species in high diversification rates clades coefficient were positive for phenotypic structure (pMPD and pMNTD) models and negative for phylogenetic structure (MPD) model. This combination of coefficients did not clearly fit predictions for competition or habitat filtering assembly processes; however, the negative coefficient of species richness in all models suggests that the habitat filtering may be the main factor for the assemblage of winter communities, since migratory species belong to the Bee clade and are phenotypically similar to each other (Fig. S4). For example, *S. platycercus*, *S. calliope*, and *S. rufus* co-occur during the winter season across their migratory grounds are phenotypically highly similar (although they differ slight in bill size PC4 and PC6, Fig. 1). The lability of traits such as bill curvature and size may be key to the rearrangement of winter communities, because bill traits are closely related to the partitioning of floral resources (López-Segoviano et al., 2021).

In summary, our results suggest that the assembly process of North American hummingbird assemblages may have been significantly influenced by either habitat filtering or interspecific competition, which may have operated differentially depending on time and scale in the North American biogeographic regions. Results from phylogenetic signal analysis and from the phenotypic dendrogram showed that curvature and size of the bill are labile, while body size and wing shape are conserved for most North American hummingbird species. Phylogenetic clustering patterns together with mostly random phenotypic structure suggest that migratory behavior and morphological differentiation may release competitive stress at local scales, while LM suggest that habitat filtering is the main factor in the assembly processes across North America. Finally, it is important to point out that hummingbirds have established an important mutualistic interaction with plants, which has been described as a main driver of their morphological evolution and diversity patterns, and that may be helpful to disentangle random structure across Transitional and Neotropical ecoregions, which are a highly heterogeneous mosaic of distinctive

habitats (Maruyama et al., 2018; Martín-Gonzalez et al., 2018; Rodriguez-Flores et al., 2019).

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**Author's contribution** AP-C and LAS-G conceived and designed the study; AP-C collected, analyzed the data, and wrote the manuscript; LAS-G supervised, edited, and wrote the manuscript. All authors discussed the results, contributed, and wrote the final manuscript.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the first author on reasonable request. Morphological data were obtained from specimens at the Colección Nacional de Aves, Instituto de Biología-UNAM, and at the Museo de Zoología “Alfonso L. Herrera,” Facultad de Ciencias-UNAM.

**Code availability** Not applicable.

## Declarations

**Ethics approval** Not applicable.

**Consent to participate** The authors declare consent to participate in this paper.

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