Diverse strategies for tracking seasonal environmental niches at hemispheric scale

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Abstract:

Species depend upon a constrained set of environmental conditions, or niches, for survival and reproduction that are being increasingly perturbed or lost under rapid climatic change. Seasonal environments offer an important system to study the range of biological responses to cope with such change, as they require species to either undergo physiological or behavioral changes to sustain altered conditions or to track their niches via movement. Here we use a uniquely well sampled system of 619 New World bird species to identify the tracking of both environmental niche position and breadth and assess its phylogenetic and functional underpinning. We find a diversity of strategies, including the tracking of niche position, niche breadth, both, or neither. Species that track niche position most often also track niche breadth, but nearly 40% only track one component and 26% only track niche breadth and not position. There was only limited phylogenetic determinism to this variation, but a strong association with ecological and functional attributes that differed between niche position vs. niche breadth tracking. The observed diversity in type and strength of niche tracking strategies points to highly differing sensitivity to ongoing climatic change, with narrow trackers of both position and breadth particularly susceptible. The trait associations of niche tracking imply significant functional consequences for communities and ecosystems as impending climate change affects some strategies more strongly than others. Seasonal environments and their diversity of niche tracking strategies offer exceptionally dynamic systems for understanding the biological responses and consequences of climate change.

Significance Statement:

As climate change progresses, species are increasingly being exposed to novel environmental conditions. Niche tracking, i.e. maintaining exposure to required environmental conditions, is a key mechanism for species persistence under climate change. To date, a general understanding of the causes and consequences of niche tracking across diverse taxonomic groups remains missing. Here, we identify environmental niche tracking strategies in New World birds and assess their phylogenetic and functional underpinnings. Across 619 species – nearly the entire avian diversity of the United States and Canada – we find a diversity of niche tracking strategies that points to highly differing sensitivity to ongoing climatic change, with narrow trackers particularly susceptible, implying significant functional consequences for communities and ecosystems.

Introduction

Species survive and reproduce under a specific set of environmental conditions, known as the environmental niche or *n*-dimensional hypervolume (Blonder et al. 2014; Hutchinson 1957; Lu, Winner, and Jetz 2021). In seasonal environments, species must adjust to a constantly shifting window of available conditions through one of several strategies. When remaining stationary, species must either maintain tolerance to a wide range of conditions or undergo physiological and behavioral changes to survive seasonal variation, known as 'niche-switching' (Nakazawa et al. 2004). Alternatively, seasonally mobile animals can occupy a dynamic niche that remains relatively narrow across the annual cycle, known as 'niche-tracking' (Gómez et al. 2016). Seasonal niche tracking is central to the persistence of species with limited behavioral or physiological capacity to adjust their niches (Fandos et al. 2020; Zurell et al. 2018). Understanding the functional and phylogenetic drivers of niche tracking behavior across diverse species can allow researchers to predict how species mediate exposure to novel, potentially adverse conditions as climate change progresses (Tingley et al. 2009; La Sorte and Jetz 2012).

After the documentation of seasonal niche tracking behavior in single species (Fandos et al. 2020) and smaller clades (Gómez et al. 2016; Eyres et al. 2020), a more general understanding of the patterns, causes and consequences of seasonal niche tracking across diverse taxonomic groups remains missing. For example, the role of phylogeny and functional traits in driving seasonal niche tracking across a diverse species set remains largely unexplored (but see Zurell et al. 2018). Several studies have hypothesized that niche tracking may be phylogenetically conserved (Gómez et al. 2016; Martínez–Meyer, Townsend Peterson, and Navarro–Sigüenza 2004), as is typical of behavioral and migratory traits (Outlaw and Voelker 2006), but this has not been evaluated rigorously or broadly. Alternatively, niche tracking may have repeatedly evolved in tandem with species' functional traits. For example, obligate insectivores or small-bodied species may be most likely to closely track their niche over the annual cycle to satisfy narrow dietary or thermal requirements (Gómez et al. 2016; Huey et al. 2012). Separating these potential drivers will allow researchers to better predict niche flexibility and niche tracking, and thus climate change vulnerability, among rare species or those from under-sampled regions.

Previous work on niche tracking has focused on seasonal similarity in niche positions, or mean environmental conditions, without accounting for niche components such as niche breadth (the volume or range of tolerable conditions), potentially disregarding important behavioral strategies. Niche-tracking species may plausibly track niche position, breadth, or both components depending on life-history strategy. For example, a specialist species with seasonal flexibility in physiology or behavior may track niche breadth but not position. Meanwhile, a species with inflexible thermal or dietary requirements that is specialized only during certain parts of the year (e.g., due to strict breeding requirements) may track niche position but not breadth. Although breadth tracking is typically ignored in niche tracking studies, it is important to consider because climate change is altering both the means and variances of climatic

conditions (Rahmstorf and Coumou 2011). To identify complex variation in niche tracking strategies among species, we suggest that seasonal niche similarity should be partitioned into constituent components. These include *niche position similarity*, or the distance between niche centroids, representing the difference between the average conditions a species experiences in each season; and *niche breadth similarity*, or the proportional difference in niche breadths (Lu, Winner, and Jetz 2021), representing the range of conditions a species can tolerate. Hypervolumes quantified using non-parametric techniques, such as kernel-density estimates or support vector machines (Blonder 2018; Brown, Holland, and Jordan 2020), are difficult to partition into constituent components. However, recently developed parametric methods for quantifying the niche allow for partitioning of these components and direct hypothesis testing against predictions derived from theories (Lu, Winner, and Jetz 2021).

We use these new metrics to distinguish five primary strategies for seasonal niche tracking (Fig.1): i) "Non-trackers" retain neither the position nor the breadth of their niches over the annual cycle; ii) "Breadth trackers" track niche breadth but shift their position; iii) "Position trackers" track niche position but shift breadth; Finally, "complete trackers" track both niche position and breadth, but may do so by either iv) migrating to track weather conditions across the annual cycle or v) remaining stationary in an aseasonal environment. However, a simple comparison of niche space during the breeding and overwintering seasons (henceforth, *seasonal* niche similarity) cannot distinguish these strategies (Fig.1b, columns 4-5), despite obviously divergent dispersal capability and potential for climate change adaptation (Eyres et al. 2020). We therefore include an additional metric, *locational* niche similarity, in which the realized overwintering hypervolume is compared with that had the species remained at its breeding range, its *stationary winter niche* (Fig. 1c). This measure, which emphasizes the similarity of conditions at specific locations, is important for understanding seasonal niche tracking because it accounts for the environmental distance covered by the species through purposeful movement. Among temperate breeders, seasonal and locational niche similarity are likely to have an inverse relationship; for example, a niche tracking species with little difference between its breeding and overwintering niche is likely to experience highly distinct overwintering conditions compared with those at its breeding sites.

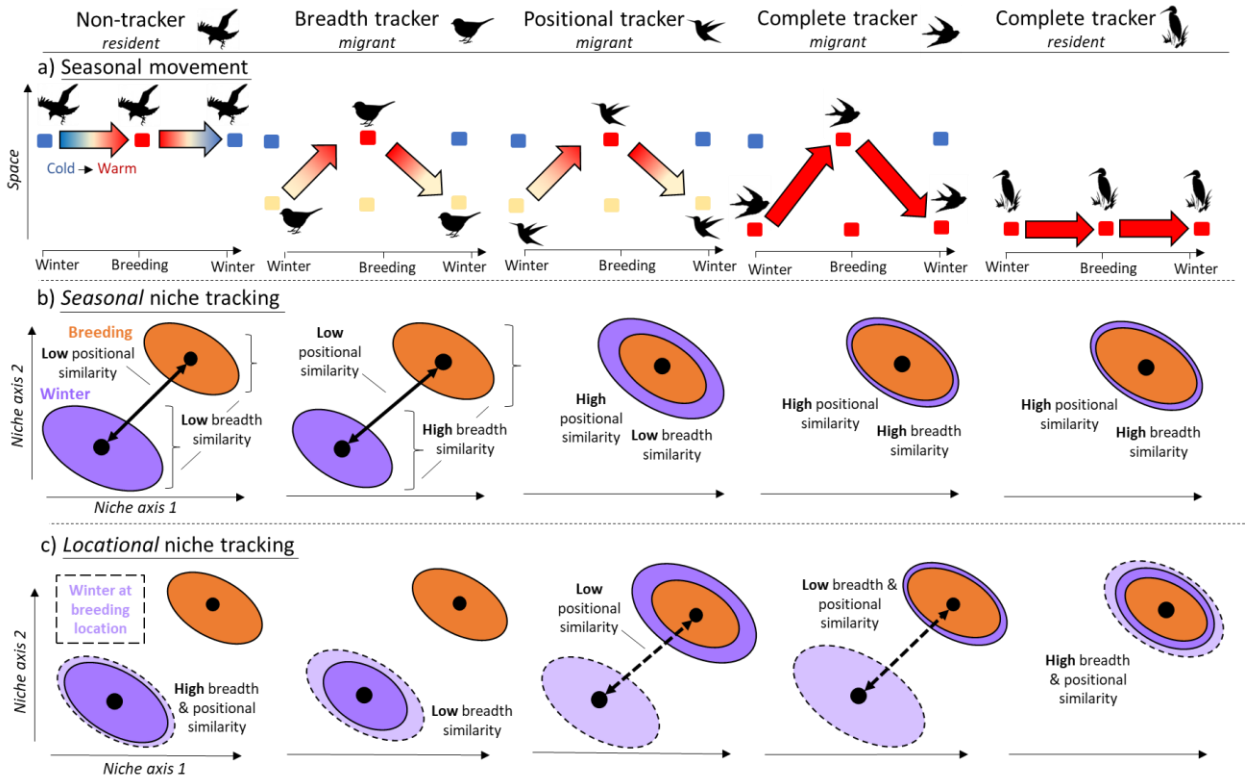

Figure 1: A typology of seasonal niche tracking strategies. Seasonal niche similarity is decomposed into two components, similarity in niche position and niche breadth. A given species may (1) be a non-tracker, tracking neither niche position or breadth, (2) track niche breadth, but not position, (3) track niche position, but not breadth, or (4-5), be a complete tracker, tracking both niche position and breadth. a) shows the differing use of climate zones over space and time; b) compares seasonal niches between the breeding (orange) and overwintering (purple) seasons (solid arrows represent positional similarity, and brackets represent breadth similarity); c) compares the location of the winter conditions at breeding locations (light purple) and the overwintering niche, revealing that for strategy 4 and 5 niche tracking is achievable through multiple life history strategies. Dashed arrows represent locational positional similarity.

Here, we use a hemispheric system to address patterns and drivers of these strategies; specifically, 619 bird species, representing nearly the full diversity of birds breeding in the US and Canada. This species set is ideally suited given its tremendous variation in migratory strategy, diversity of functional trait groups (Barnagaud et al. 2017) and uniquely comprehensive occurrence data. We also leverage a recently developed environmental annotation tool (Li et al. 2021) and a novel parametric hypervolume method (Lu, Winner, and Jetz 2021) to quantify similarity between the environmental niches occupied by each species during both the breeding and overwintering seasons. We use this system to address the following questions:

1) What is the prevalence of different niche tracking strategies? To date, a quantitative multi-species assessment of strategies has been missing.

2) What is the relationship between niche position and niche breadth tracking? In general, we expect species maximizing niche positional similarity across seasons to also maximize breadth similarity, but we expect many species to only track niche position or breadth, demonstrating the importance of considering both metrics.

3) How phylogenetically and functionally determined are niche tracking strategies? Across functional trait groups, we hypothesize seasonal niche tracking to be most common in a) long-distance migrants, because they can physically relocate to suitable locations (Laube, Graham, and Böhning-Gaese 2015; Zurell et al. 2018); b) small-bodied species, because they have low thermal inertia and generally narrow thermal breadths (Huey et al. 2012; Albright et al. 2017), suggesting they cannot tolerate large seasonal variation in the niche; c) insectivores, because abundant insect prey is only available under specific temperature, precipitation and productivity levels (Winkler, Luo, and Rakhimberdiev 2013); and d) species occupying open or water habitats, because they are not shielded from climate variability by forest structure (Jarzyna et al. 2016). Given that behavioral and migratory traits are often phylogenetically conserved (Outlaw and Voelker 2006), we expect a strong phylogenetic signal in seasonal niche tracking behavior (Gómez et al. 2016).

4) Do cross-species comparisons of *locational* niche similarity reveal important behavioral strategies and functional or phylogenetic associations not apparent when quantifying only *seasonal* niche similarity? We predict an inverse relationship between seasonal and locational similarity across species and expect to observe functional trait relationships with locational similarity that are not observed with temporal similarity.

We expect the emerging insights to not only address these questions but more generally offer an assessment of seasonal niche dynamics as a system to understand realized strategies for mitigating exposure to climatic change.

Results

We found all five niche-tracking strategies represented among North American birds (Fig 2). For example, Red-bellied woodpeckers (*Melanerpes carolinus*; Fig. 2a) are largely stationary birds occupying highly seasonal environments, with low seasonal similarity between their breeding and overwintering niches, but high locational similarity between their overwintering and stationary winter niches. In contrast, Pine grosbeaks (*Pinicola enucleator*; Fig. 2b) are short-distance migrants and “breadth trackers”, tracking niche breadth but not position across seasons. Migratory Swainson’s thrushes (*Catharus ustulatus*; Fig. 2c) are “position trackers”, tracking

their niche position across seasons, but occupying a much broader niche during the breeding season. Prothonotary warblers (*Protonotaria citrea*; Fig. 2d) are long-distance migrants that abandon breeding territories to closely track both niche components across seasons, resulting in high seasonal and low locational similarity. Finally, Great kiskadees (*Pitangus sulphuratus*; Fig. 2e) are stationary tropical residents with conserved niches across the annual cycle, resulting in both high seasonal and high locational similarity.

The 619 bird species analyzed spanned the full diversity of niche tracking strategies (Fig. 3; Table S2). Across seasons, the median positional similarity (-log(Mahalonobis distance)) was -1.95 +/- 0.05 SE (i.e., centroids approximately 3 SDs apart), suggesting that many species are not closely tracking this niche attribute over the annual cycle (Ponti et al. 2020). For 60 species (9.7%), centroids were within 1 SD, suggesting highly similar niches in each season for this subset. The median among-season similarity in niche breadth was 2.17 +/- 0.03, equivalent to a 4:1 ratio in niche breadth between seasons, suggesting that many species shrink or expand their niche breadths as they traverse seasons. Only 18 species (3%) had a niche breadth similarity equivalent to a < 1.5:1 ratio, suggesting roughly equally sized seasonal niches.

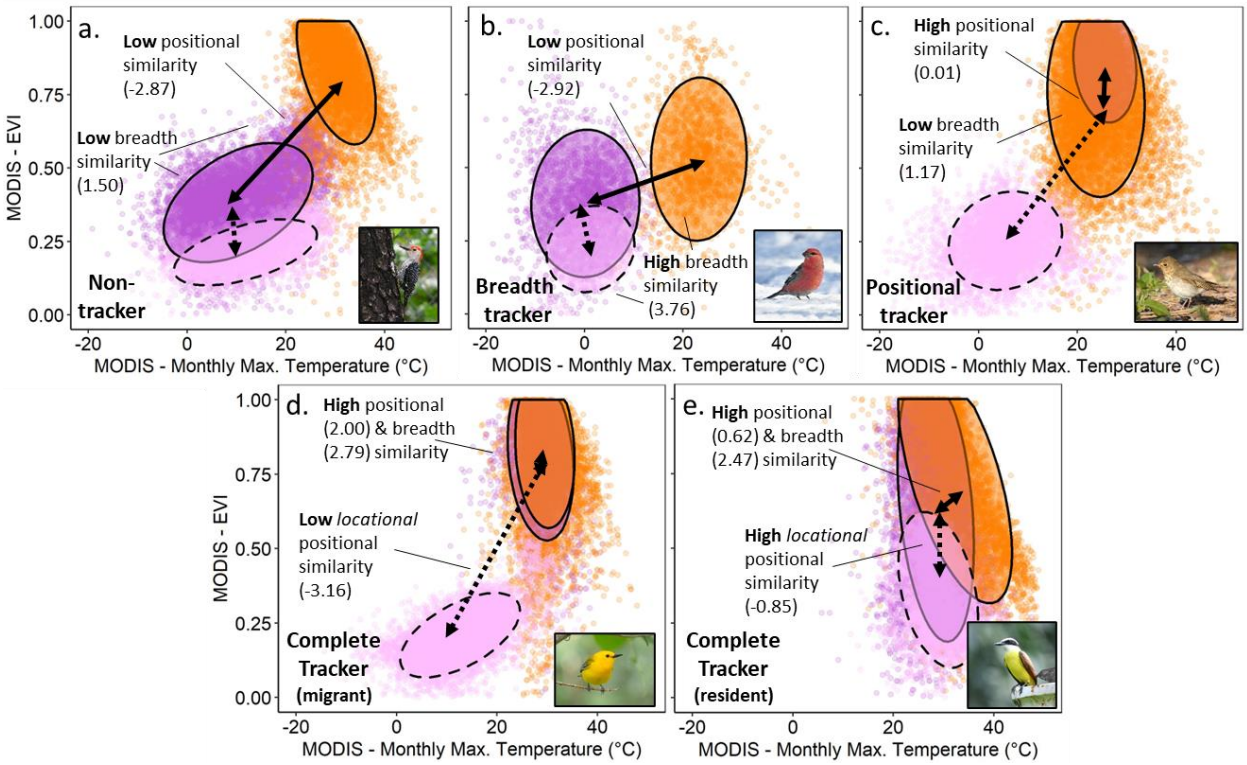

Figure 2: Diverse niche tracking strategies. (**a**) Red-bellied woodpeckers (*Melanerpes carolinus*) are non-trackers, with low *seasonal* similarity (solid arrow) between their breeding (orange points and ellipsoid) and overwintering (dark blue) two-dimensional niche (presented as standardized ellipse area). Meanwhile, the difference between their overwintering niche and winter conditions at breeding locations

(light blue), or *locational* similarity (dotted arrow), is high. (**b**) Pine grosbeaks (*Pinicola enucleator*) track their niche breadth but not position across seasons, while (**c**) Swainson's thrushes (*Catharus ustulatus*) track their niche position, but not breadth. (**d**) Prothonotary warblers (*Protonotaria citrea*) closely track their niche across seasons via migration, resulting in high seasonal and low locational similarity. (**e**) Great kiskadees (*Pitangus sulphuratus*) track their niche by remaining stationary in less seasonal environments, leading to high seasonal and locational similarity. Position and breadth similarity values are provided in parentheses

Tracking niche position was loosely tied to tracking niche breadth; species that tracked niche position more often tracked niche breadth, and *vice versa* (β=0.179, R^2=0.073, $p<0.001$; Fig. 3). 170 (27.5%) species were "complete" niche trackers, tracking both position and breadth more than most species (positive values on both axes in Fig. 3), while 209 (33.8%) were non-trackers, tracking both less than others (negative values in Fig. 3). However, numerous species tracked one but not the other (Fig. 3), suggesting a complex diversity of approaches to seasonal niche tracking across bird species. Only 80 species (12.9%) tracked niche position but not breadth, while double that number – 160 (25.8%) – tracked breadth but not position.

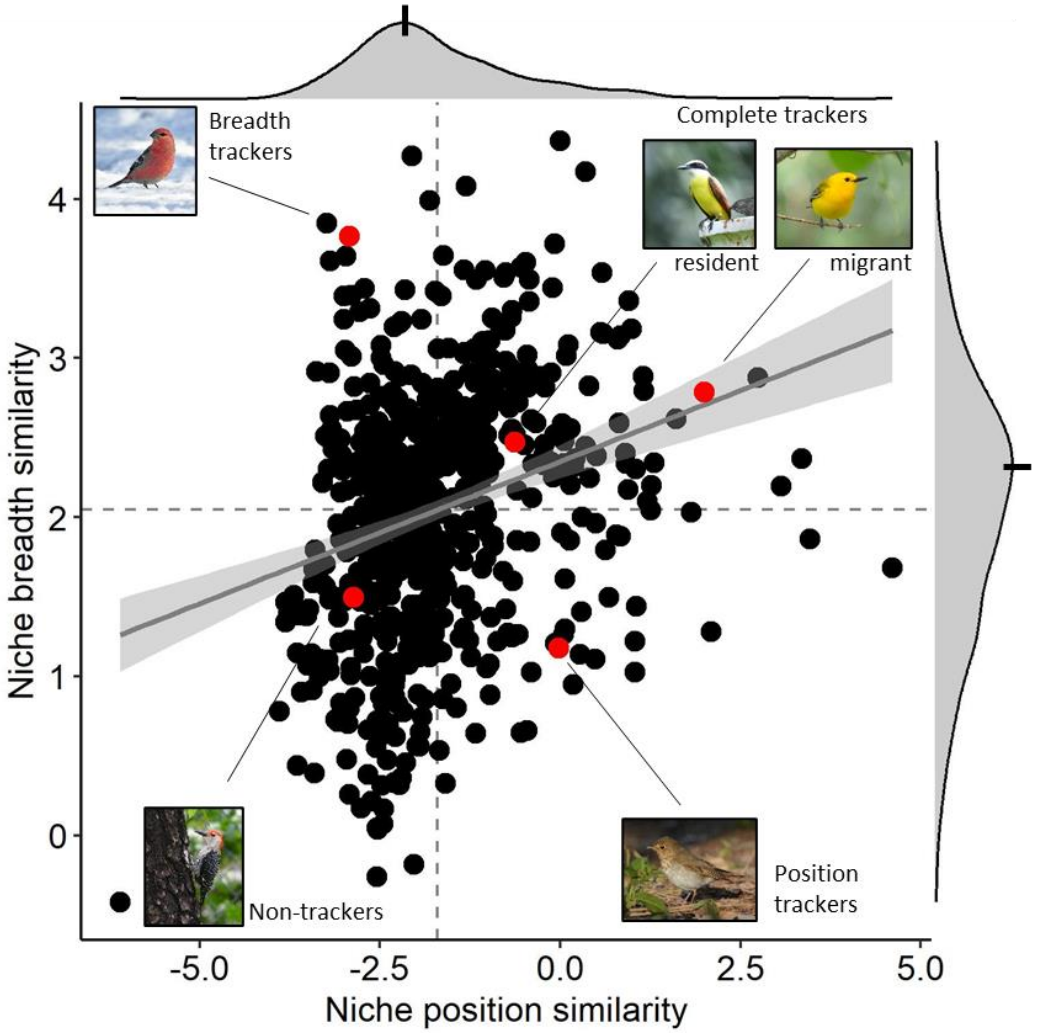

Figure 3: Interspecific variation in tracking niche position and breadth across seasons. The figure shows the niche similarities between the breeding and overwintering seasons for the 619 bird species analyzed (for red highlights, see Fig. 2). Dashed lines highlight the means. Marginal density plots illustrate that species tracking only one niche component often track niche breadth more closely than niche position, with medians represented by notches. See Fig. S2 for equivalent patterns for locational similarity.

We found seasonal niche tracking strategies to be closely associated with functional traits (Fig. 4; Tables S3-S4), and their role to be consistent across multivariate and univariate models (Tables S5-S6). As expected, both niche positional and breadth similarity were very strongly linked to migration distance (both $\beta<0.001$, $p<0.001$), which was the strongest functional predictor; long-distance migrants were most likely to maximize similarity, while residents minimized similarity and others fell in the middle (Fig. 4a,d). Body mass emerged as the second most important functional predictor of seasonal niche tracking, especially with regards to positional similarity. Body mass negatively predicted niche position similarity ($\beta=-0.37$, $p<0.001$) and was positively (though weakly) associated with breadth similarity ($\beta=0.26$, $p<0.001$). Small-bodied birds maximized seasonal similarity, while large-bodied birds minimized it (Fig. 4b,e). Finally, both diet ($F_{1,3}=4.08$, $p<0.01$) and habitat preference ($F_{1,3}=7.09$, $p<0.001$) categories described variation in positional similarity, though only habitat preference drove breadth similarity ($F_{1,3}=4.46$, $p<0.01$). As predicted, insectivores maximized positional and breadth similarity, herbivores minimized these, and omnivores fell in the middle (Fig. 4c,g). Waterbirds tracked their niches more closely than other species (Fig. 4d,h).

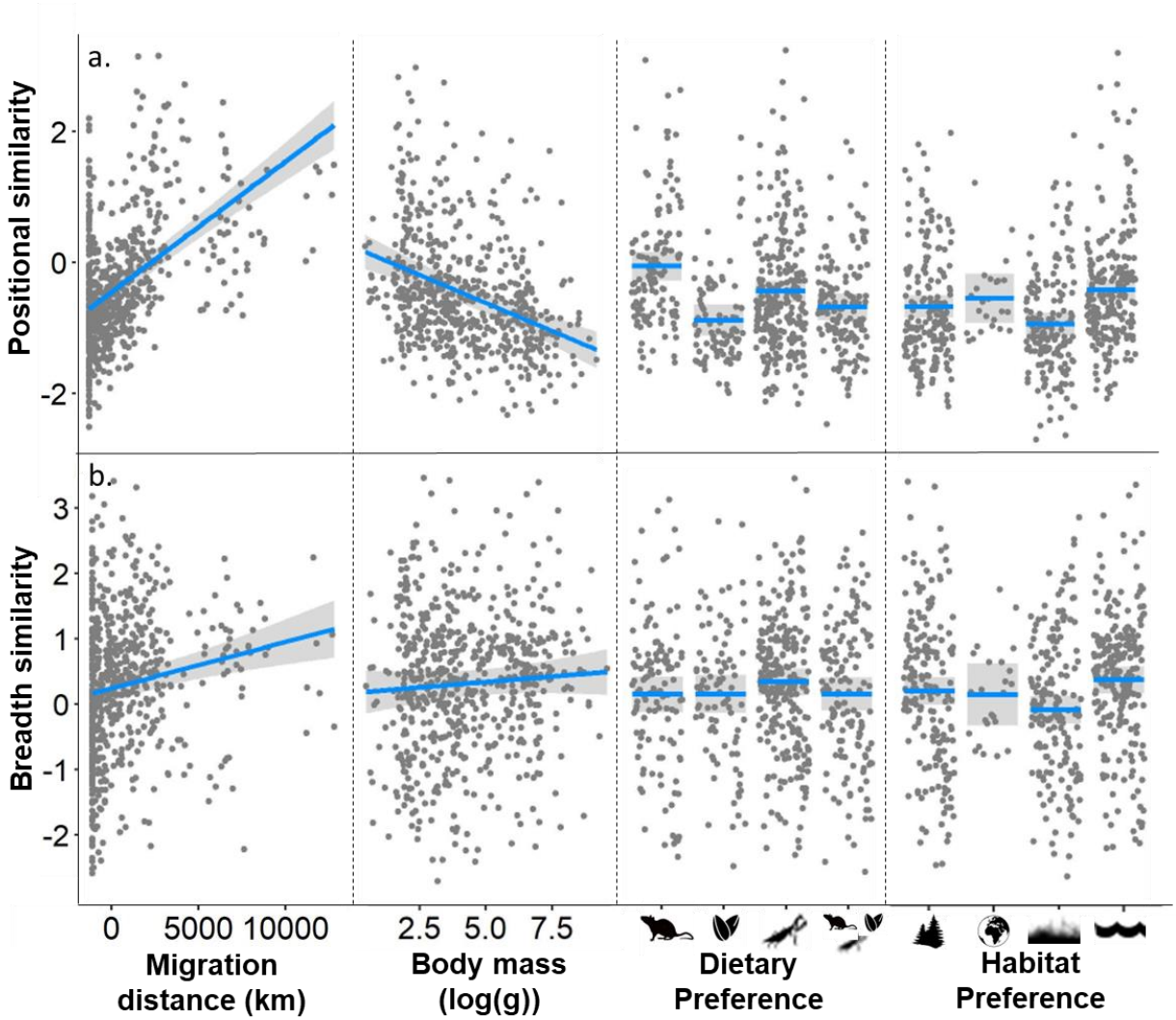

Figure 4: Functional traits predict variation in the seasonal niche, as shown by partial residual plots based on phylogenetic least-squares models. Y-axis values represent (a) positional and (b) breadth similarity. Silhouettes correspond to categorical functional trait values as follows: Dietary preference (left to right: carnivore, herbivore, insectivore, omnivore); Habitat preference (forest, generalist, open/grassland, water).

Surprisingly, we found little evidence of a phylogenetic signal in seasonal niche tracking. For both niche position and breadth, Within-group phylogenetic variation was greater and among-group variation lesser than expected by chance (Bloomberg's K always < 0.1; position: $p<0.001$; breadth: $p=0.10$; Table S7) and did not support Ornstein-Uhlenbeck trait evolution. Measurements of lambda indicated a moderate phylogenetic signal for species tracking niche position ($\lambda=0.66$, $p<0.001$), suggesting possible Brownian-motion trait evolution, but little signal for niche breadth ($\lambda=0.28$, $p<0.001$).

Species that maximized seasonal niche similarity typically minimized locational niche similarity, and vice versa (β=-0.408, R^2=0.237, $p<0.001$; Fig. S1). For locational similarity, the link between tracking niche position and niche breadth was stronger than for seasonal similarity, with 42% of species tracking both components and 29% neither (Fig. S2). Only 15% of species tracked locational niche position but not breadth, and 13% tracked locational breadth but not position. Likewise, relationships between functional traits and locational positional similarity were generally opposite to those observed with seasonal positional similarity. Long-distance migrants ($\beta<0.001$, $F_{1,1}$=23, $p<0.001$), small-bodied birds (β=0.31, $F_{1,1}$=25, $p<0.001$), and waterbirds ($F_{1,3}$=8.5, $p<0.001$) each minimized locational positional similarity, though we found no effect of diet. As with seasonal similarity, we found no evidence for a phylogenetic signal in locational niche similarity (Table S7).

Discussion

Seasonal niche tracking behavior plays an important role in mediating exposure to novel climate conditions. Here, we developed a framework to understand the representation of distinct seasonal niche tracking strategies across North American breeding birds and predict the functional and phylogenetic drivers of these strategies. Our analyses revealed five distinct seasonal niche tracking strategies and their key functional drivers. We find that most species can be categorized as “complete trackers”, tracking both niche position and breadth across seasons, or “non-trackers”, tracking neither. However, almost 40% of species only track niche position or breadth, revealing complexity in niche tracking strategies that is previously unexplored in niche-tracking studies. Twice as many species tracked only niche breadth (26%) compared with those that tracked niche position (13%), suggesting that tracking breadth is often a prerequisite for tracking position and that birds may be most specialized in terms of the range of environmental conditions they can tolerate rather than means. Importantly, niche tracking studies that do not consider niche breadth would likely have labeled the 26% of species that are niche breadth trackers as non-trackers.

We found that migration distance was the most important functional driver of seasonal niche tracking, despite this link previously receiving mixed support among cross-species niche tracking studies (Zurell et al. 2018; Laube, Graham, and Böhning-Gaese 2015; Gómez et al. 2016). Although several studies (Gómez et al. 2016; Laube, Graham, and Böhning-Gaese 2015) failed to detect a link between migration and niche tracking, their approaches compared species within single families, including residential species that are exclusively tropical. Because these residents occupy relatively stable environments, they can track their niches despite being stationary (Eyres et al. 2020). This example helps illustrate why migration distance and niche tracking are less correlated than might be intuitively expected – tropical residents can track their niches well while long-distance migrants may experience high seasonal variation if they annually move between

arctic breeding grounds and boreal or temperate wintering grounds. Indeed, although migration distance was the strongest correlate of seasonal niche tracking in our study, the correlation was moderate (R^2=0.249).

Body size was revealed as the next most important functional trait associated with seasonal niche tracking. Small-bodied birds may not be able to tolerate large variation in their thermal niches because they have low thermal inertia (Huey et al. 2012; Albright et al. 2017). Further, small-bodied animals have shown greater sensitivity to extreme weather events (Cohen, Fink, and Zuckerberg 2021) and more rapidly alter phenological timing in tune with interannual weather variability (Cohen, Lajeunesse, and Rohr 2018) compared with large-bodied animals, suggesting that they must carefully maintain thermal limits. Additionally, small-bodied birds may be more likely to evolve niche-tracking strategies dependent on seasonal migration because long-distance flight carries lower energetic costs than it does for large birds (Watanabe 2016).

Finally, diet and habitat preference were meaningful drivers of seasonal niche tracking behavior, with insectivores tracking their niches more than herbivores and waterbirds more so than other species. Insectivores, and to an extent, omnivores (which often rely on insects during parts of annual and life cycles) are dependent upon prey that is most commonly available under specific thermal and productivity limits (Winkler, Luo, and Rakhimberdiev 2013). Surprisingly, carnivores tracked their niche positions even more closely than insectivores, but many of these species are predating on herpetofauna also active during warm weather. Though we predicted both open and water habitat specialists to be the strongest niche trackers, as they are less shielded from the external environment by habitat structure (Jarzyna et al. 2016), only water birds tracked their niche more closely than other groups (Fig 4d,h). Bird species that occupy open habitats may make greater use of microhabitat structure than water birds, which are typically exposed (e.g., (Shew, Nielsen, and Sparling 2019)).

Although many studies have assumed seasonal niche tracking to be phylogenetically conserved (Gómez et al. 2016; Martínez–Meyer, Townsend Peterson, and Navarro–Sigüenza 2004), this has not to our knowledge been evaluated over a large, diverse taxonomic group such as North American breeding birds. There are several explanations as to why we did not detect a phylogenetic signal. First, migratory behavior has arisen in numerous, diverse lineages of birds, and is flexible even within species (Zink 2011). Second, closely related species often occupy distinct climatic zones that vary greatly in seasonality, especially if speciation resulted from character displacement (Newton 2003). Finally, species-level exposure to and adaptation potential for climate change may be quite independent from phylogeny (Khaliq et al. 2015; Davis et al. 2010). Based on our analyses, we conclude that functional traits likely play a larger role than phylogeny in driving seasonal niche tracking in birds.

Complex variation among niche tracking strategies cannot fully be assessed via seasonal niche comparisons; for example, a species that niche-tracks via movement and a stationary species in an aseasonal environment have similar seasonal niches. To parse these strategies, we estimated locational niche similarity, or the similarity between overwintering niches and the *stationary winter niche* for each species. Species with high seasonal similarity often had low locational similarity, and *vice versa*, reflecting a trade-off between conserving niches and ranges throughout the annual cycle. While many species tracked only niche position or breadth between seasons, species adhered to locationally tracking both or neither components much more often, with few tracking just one. Therefore, species may be leaving breeding areas in winter for the purposes of modifying both the mean and variance of environmental conditions. We observed several key differences between functional trait relationships and either seasonal or locational niche similarity. For instance, migration distance and body size were equally important as drivers of locational niche similarity, possibly because large-bodied birds are especially reluctant to energetically invest in movement (Watanabe 2016). Further, there was no effect of diet on locational similarity. Thus, we demonstrate the importance of considering both seasonal and locational similarity in species niches to understand variation in niche tracking strategies.

We estimated niche metrics at the species level to effectively compare niche tracking strategies across a taxonomic group as broad and diverse as birds. However, we did not explore niche variation as experienced at lower levels of organization, including populations, demographic groups, and individuals (Fandos et al. 2020; Fandos and Tellería 2020; Carlson et al. 2021). Populations of species with wide geographic ranges might be adapted to highly distinct environmental conditions (Broggi et al. 2005). Within a population, demographic groups can also occupy different niches – sexes can occupy spatially distinct regions during the nonbreeding season, or young can be shielded in microclimate during breeding season (Shipley et al. 2020). Finally, individuals may track different niche components than populations (Fandos et al. 2020) or might have strong variation in their ecological niches during different parts of the year and thus vary in niche-tracking. For example, individual white storks (*Ciconia ciconia*) and sandhill cranes (*Antigone canadensis*) range from subtropical residents to short-distance migrants to longer-distance migrants moving between northern temperate and tropical zones each year (Krapu et al. 2014; Fandos et al. 2020; Carlson et al. 2021). Here, new technologies such as GPS tracking offer exciting opportunities for assessing individual niches over time and across hierarchies of organismal organization (Jetz et al. 2022; Costa-Pereira et al. 2022) and complement the presented species-level findings.

As climate change progresses, species are increasingly being exposed to conditions that are quite different from those to which they have adapted (Pacifici et al. 2015). Gradual shifts in range boundaries or phenology allow species to keep pace with long-term changes in climatic means (La Sorte and Jetz 2012; Rushing et al. 2020; Koleček, Adamík, and Reif 2020). However, niche tracking is an important tool for species to buffer the increasing interannual variability associated

with climate change by selecting optimal environmental conditions over short time scales (Román-Palacios and Wiens 2020), especially for species with narrow thermal or habitat requirements. Our findings reveal a broad diversity in niche tracking strategies and uncover important functional trait associations with migratory behavior and body size. This has ecological consequences for the assemblages and ecosystems that will see different functional perturbations due to the different susceptibility of niche tracking strategies to climatic change (Barbet-Massin and Jetz 2015). For example, as niche tracking becomes more difficult with climate change, small-bodied and insectivorous birds may be especially likely to fail to maintain their niches, resulting in proportional declines of these species relative to the broader avian community assemblage.

Thus, we provide a framework for future studies to assess the degree of niche tracking and capability for climate change adaptation in many other species globally, including those from understudied regions with limited available data. However, additional work is needed to assess how species have already been keeping up with climate change that has occurred. Understanding how climate change is modifying species' ability to conserve their niches will be a critical step towards determining which species are most likely to adapt to increasing short-term variability in climate.

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Data Sharing and Accessibility

GBIF data is available for public use online at https://www.gbif.org/. Code generated to conduct the analyses will be made available in a public repository such as Dryad or Figshare.

Methods

Species selection and environmental data

We compiled a list of 672 bird species that annually breed or overwinter in the United States and Canada based on American Birding Association birding codes (Association 2008) updated to the Clements bird taxonomy as of 2021 (Clements 2007). These codes are a widely-accepted authority to distinguish regularly occurring species from irregularly occurring vagrants, or those species which sporadically appear on the continent each year but whose occurrence is not predictably tied to a given location. We excluded species not native to the US or Canada or those that are primarily marine, for which weather data is unavailable.

In August 2021, we accessed the Spatiotemporal Observation Annotation Tool (STOAT) v1.0, a novel cloud-based toolbox for flexible biodiversity annotations (Li et al. 2021), to download annotated Global Biodiversity Information Facility data (https://www.gbif.org/) for all species (data compilation, analyses and visualizations were all completed in R 4.1.0 (R Core Team 2021)). To minimize the potential for spatiotemporal sampling bias, we then thinned points by selecting one point from each location (5x5km grid cell) per week.

We annotated observation points with three environmental dimensions: daily maximum temperature (sourced from NASA-MODIS; https://lpdaac.usgs.gov/products/mod11a1v006/), enhanced vegetation index (EVI; from MODIS), and precipitation (from CHELSA v2.1; Karger et al. 2021), each summarized to a 1km buffer (0.5km radius) over 30 days prior to the observation (imported using jsonlite and httr packages; Ooms 2014; Wickham and Wickham 2020). We did not assess *a priori* whether these variables are equally relevant across species; for example, certain species may be limited by precipitation but not temperature within their range, or *vice versa*. Alternatively, some species may be limited by environmental factors not considered in our estimation of species niches. However, this variable set represents the environmental factors that most commonly drive species distributions (Qian 2010), and these variables have low collinearity, allowing each axis to remain independent. Estimating niches with the same variable set for all species was necessary to ensure consistency in cross-species evaluation of seasonal changes to both niche position and breadth.

For each species, we restricted observation points to those with environmental data available for all dimensions. Further, we temporally cropped data to season (December-February for the overwintering season and June-August for breeding season) and spatially cropped points to the American continents (< -30° longitude). Sufficient data for analysis (>20 points per season after filtering) was available for 619 species. Database management was completed using *tidyverse* packages (Wickham et al. 2019).

To quantify locational similarity, we conducted the same niche characterizations for breeding locations during the overwintering season. For each species, we created a hypothetical set of occurrence points corresponding to coordinate locations during the breeding season, each with randomized winter calendar dates (December-February), annotating them with environmental data as described above.

Ecological niche modeling and seasonal similarity

For every species, we calculated parametric measurements of the similarity between the seasonal three-dimensional hypervolumes. The hypervolumes were characterized as multivariate normal distributions, allowing us to derive analytical estimates for the breadth and position of each hypervolume (MVNH package; Lu, Winner, and Jetz 2021). We partitioned niche similarity into two metrics: i) *niche position similarity*, which quantifies the distance among hypervolume centroids in each season based on the sign-flipped, log-transformed Mahalanobis distance, used to assess changes in niche position between seasons; and ii) *niche breadth similarity*, which represents the similarity in *niche breadth* (volume) between seasons and is measured as the sign-flipped, log-transformed determinant ratio.

To quantify seasonal similarity, we calculated positional and breadth similarity between the breeding and overwintering seasonal hypervolumes. To quantify locational similarity, we calculated positional similarity between the overwintering hypervolume and available hypervolume during winter at breeding locations. Thus, we had a total of three metrics of seasonal niche similarity per species. We visualized pairwise two-dimensional hypervolumes for each species using *ggplot2* (Wickham 2011).

Functional traits and phylogeny

We obtained species-level functional trait values and an avian phylogenetic tree to test associations between trait groups, phylogeny, and seasonal niche tracking. We derived migration distances from (La Sorte et al. 2022; La Sorte personal communication), body mass from the Eltonian trait database (Wilman et al. 2014), and habitat preference and diet from Barnagaud et al. (2017). We grouped several categories of each categorical predictor to avoid false positives associated with small sample sizes and to keep our conclusions broad. Diet categories included carnivore, invertebrate, omnivore, and herbivore (combining ‘fruit’, ‘nectar’, ‘vegetation’, and ‘seed’ categories). Habitat categories included water (‘coastal’, ‘open_water’, ‘riparian_wetlands’), open (‘semi-open’, ‘rock’, ‘arid’), generalist (‘urban’, ‘developed’), and forest.

We updated an avian phylogeny from Jetz et al. (2012) to account for recent taxonomic changes, updating species names to the Clements bird taxonomy as of 2021 (Clements 2007) and treating

recently split species as having no phylogenetic distance (Table S1). We also harmonized species names in all trait datasets to Clements.

Cross-species models

To assess the role of functional traits in seasonal niche tracking, we used multivariate phylogenetic generalized least squares (PGLS) models (caper package; Orme et al. 2013). Phylogenetically correlated model errors in PGLS account for the non-independence of the species due to their phylogenetic relatedness (Symonds and Blomberg 2014). The dependence of the model errors arises from trait axes that we did not include in the analysis and that may be subject to niche conservatism so that model errors reflect the unobserved trait and thus the phylogenetic distance between species. We used species' similarity in niche position and breadth as the response variables in the models and explained their variation with categorical trait variables. Prior to use in models, response variables were log-transformed, standardized and sign-flipped (representing niche similarity rather than dissimilarity) to improve interpretability. We fit three models testing the relationships between the four functional traits and three metrics of niche similarity: seasonal niche position similarity, seasonal niche breadth similarity, and locational niche position similarity. To evaluate the reliability of multivariate models, we also fit univariate models for each combination of functional trait predictor and response variable.

To measure the role of phylogeny in both positional and breadth similarity, we quantified Blomberg's K (Blomberg, Garland Jr et al. 2003) and compared it to a null distribution of K after randomizing species' responses 1,000 times (picante package; Kembel et al. 2010). $K < 1$ suggests greater than expected phylogenetically-correlated variance within clades, while $K > 1$ suggests variance among clades (i.e., phylogenetically-conserved trait). We also quantified lambda to assess the extent of phylogenetic conservation of niche metrics via Brownian motion. We visualized relationships between niche metrics and functional traits using *ggplot2* (Wickham 2011), *ggExtra* (Attali and Baker 2019) and *RcolorBrewer* (Neuwirth and Neuwirth 2011). We visualized partial residuals using *visreg* (Breheny, Burchett, and Breheny 2020).

Supporting Information

Title: Diverse strategies for tracking seasonal environmental niches at hemispheric scale

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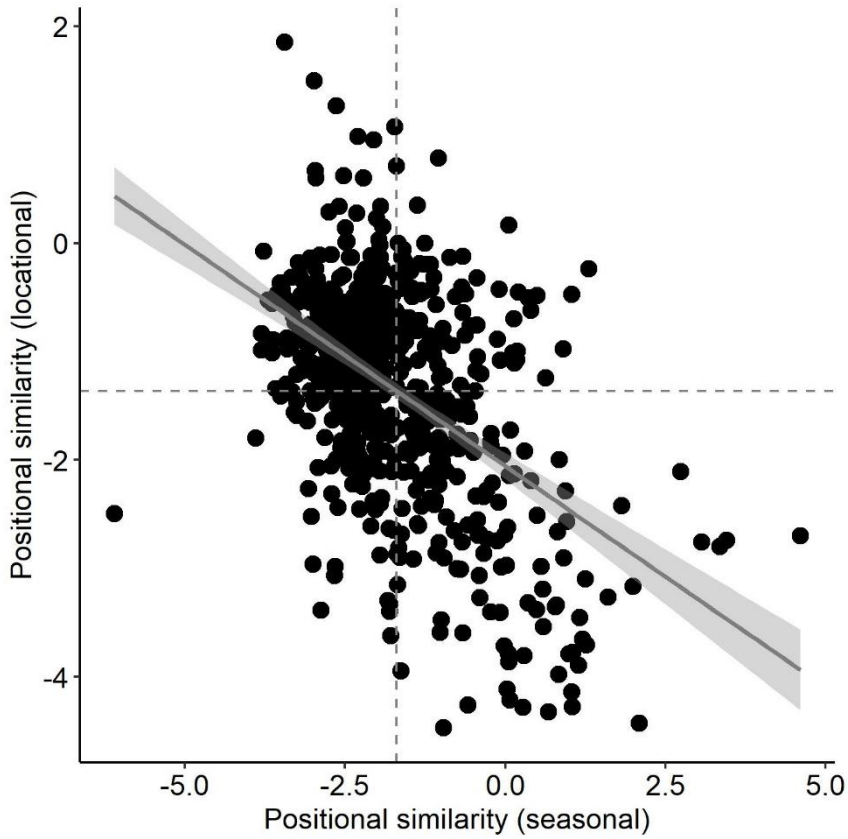

Figure S1. Seasonal and locational niche centroid similarity are inversely related. Niche-tracking species maximize niche similarity between breeding and nonbreeding seasons (defined as seasonal similarity, x-axis) and minimize the similarity between the nonbreeding season niche and the stationary winter niche (defined as locational similarity, y-axis). The reverse is true for non-tracker species. Tropical residents are an exception to this rule; these species have overlapping niche space for all three components, thus maximizing both seasonal and locational similarity. Dashed lines represent means and gray shading represents 95% confidence interval for trend line.

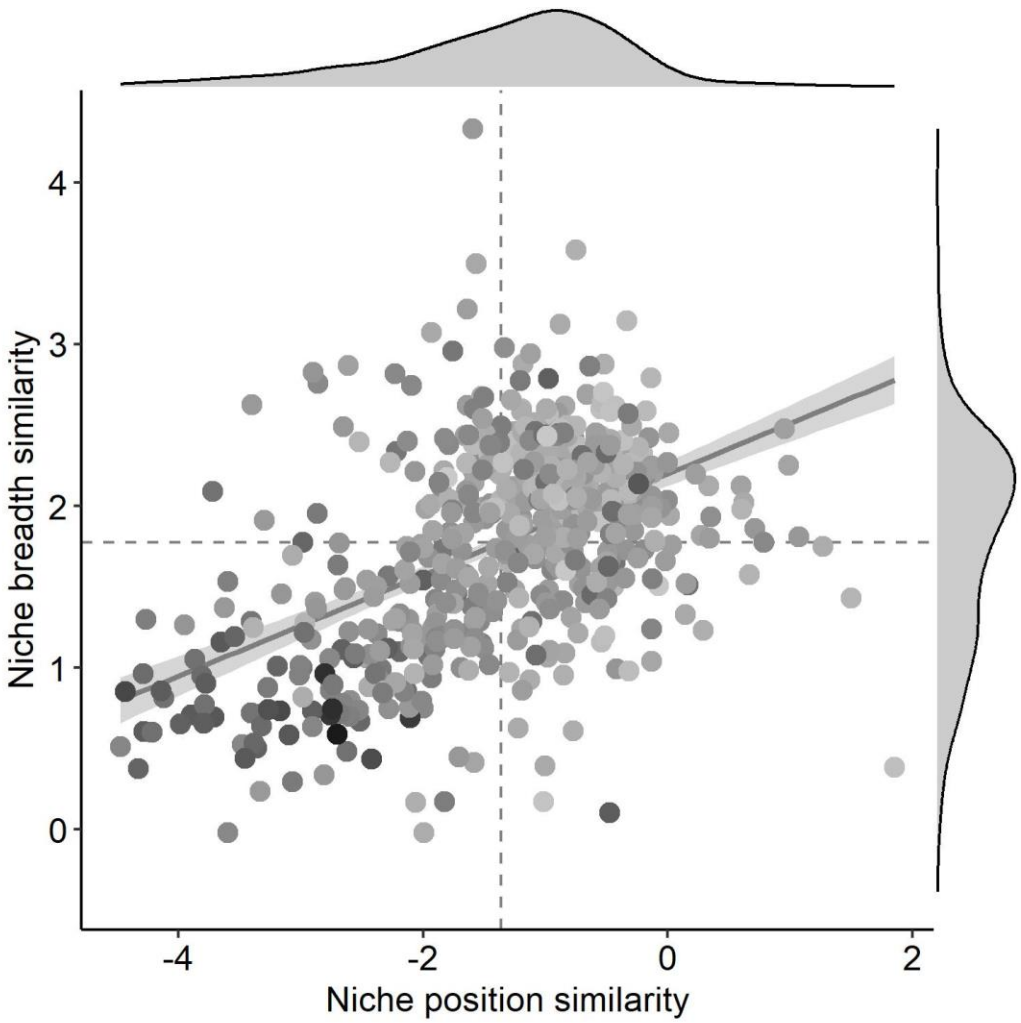

Figure S2: Interspecific variation in locational niche tracking of niche position and breadth. Locational niche similarity represents the similarity of the overwintering niche to the winter conditions at breeding locations. Points represent species-level variation in locational similarity of niche position and breadth between the breeding and overwintering seasons for 619 species of North American birds. Marginal density plots illustrate a positive relationship between tracking locational niche position and breadth. Darker points reflect greater values of seasonal positional niche similarity and are primarily distributed among points with lower values of locational positional similarity.

Table S2 – Updates to avian phylogeny. We updated the avian phylogeny of Jetz et al (2012) to the 2021 Clements taxonomy by harmonizing species names, as follows.

Old names	New names
Carduelis flammea	*Acanthis flammea*
Ammodramus caudacutus	*Ammospiza caudacuta*
Ammodramus leconteii	*Ammospiza leconteii*
Ammodramus maritimus	*Ammospiza maritima*
Ammodramus nelsoni	*Ammospiza nelsoni*
Anas platyrhynchos	*Anas diazi*
Chen caerulescens	*Anser caerulescens*
Chen rossii	*Anser rossii*
Grus canadensis	*Antigone canadensis*
Caprimulgus carolinensis	*Antrostomus arizonae*
Caprimulgus carolinensis	*Antrostomus carolinensis*
Caprimulgus vociferus	*Antrostomus vociferus*
Caprimulgus carolinensis	*Aphelocoma wollweberi*
Caprimulgus carolinensis	*Aphelocoma woodhouseii*
Casmerodius albus	*Ardea alba*
Puffinus creatopus	*Ardenna creatopus*
Puffinus gravis	*Ardenna gravis*
Puffinus gravis	*Ardenna grisea*
Puffinus gravis	*Ardenna pacifica*
Puffinus tenuirostris	*Ardenna tenuirostris*
Amphispiza belli	*Artemisiospiza belli*
Amphispiza belli	*Artemisiospiza nevadensis*
Bubo scandiaca	*Bubo scandiacus*
Buteo nitidus	*Buteo plagiatus*
Tryngites subruficollis	*Calidris subruficollis*
Aphriza virgata	*Calidris virgata*
Wilsonia canadensis	*Cardellina canadensis*
Wilsonia pusilla	*Cardellina pusilla*
Ammodramus bairdii	*Centronyx bairdii*
Ammodramus henslowii	*Centronyx henslowii*
Charadrius alexandrinus	*Charadrius nivosus*
Chasiempis sandwichensis	*Chasiempis sclateri*
Hemignathus flavus	*Chlorodrepanis flava*
Hemignathus kauaiensis	*Chlorodrepanis stejnegeri*
Hemignathus virens	*Chlorodrepanis virens*
Larus philadelphia	*Chroicocephalus philadelphia*
Larus ridibundus	*Chroicocephalus ridibundus*
Circus cyaneus	*Circus hudsonius*

Vestiaria coccinea	*Drepanis coccinea*
Picoides albolarvatus	*Dryobates albolarvatus*
Picoides arizonae	*Dryobates arizonae*
Picoides borealis	*Dryobates borealis*
Picoides nuttallii	*Dryobates nuttallii*
Picoides pubescens	*Dryobates pubescens*
Picoides scalaris	*Dryobates scalaris*
Picoides villosus	*Dryobates villosus*
Dendragapus canadensis	*Falcipennis canadensis*
Gallinago gallinago	*Gallinago delicata*
Gallinula chloropus	*Gallinula galeata*
Sterna nilotica	*Gelochelidon nilotica*
Oporornis formosus	*Geothlypis formosa*
Oporornis philadelphia	*Geothlypis philadelphia*
Oporornis tolmiei	*Geothlypis tolmiei*
Buteo albicaudatus	*Geranoaetus albicaudatus*
Carpodacus cassinii	*Haemorhous cassinii*
Carpodacus mexicanus	*Haemorhous mexicanus*
Carpodacus purpureus	*Haemorhous purpureus*
Larus minutus	*Hydrocoloeus minutus*
Sterna caspia	*Hydroprogne caspia*
Zoothera naevia	*Ixoreus naevius*
Lanius excubitor	*Lanius borealis*
Vermivora crissalis	*Leiothlypis crissalis*
Vermivora luciae	*Leiothlypis luciae*
Larus atricilla	*Leucophaeus atricilla*
Larus pipixcan	*Leucophaeus pipixcan*
Hemignathus parvus	*Magumma parva*
Anas americana	*Mareca americana*
Anas penelope	*Mareca penelope*
Anas strepera	*Mareca strepera*
Melanitta nigra	*Melanitta americana*
Melanitta fusca	*Melanitta deglandi*
Pipilo aberti	*Melozone aberti*
Pipilo crissalis	*Melozone crissalis*
Pipilo fuscus	*Melozone fusca*
Sterna anaethetus	*Onychoprion anaethetus*
Sterna fuscata	*Onychoprion fuscatus*
Vermivora ruficapilla	*Oreothlypis ruficapilla*
Seiurus motacilla	*Parkesia motacilla*
Seiurus noveboracensis	*Parkesia noveboracensis*
Aimophila aestivalis	*Peucaea aestivalis*
Aimophila botterii	*Peucaea botterii*

Aimophila carpalis	*Peucaea carpalis*
Aimophila cassinii	*Peucaea cassinii*
Steganopus tricolor	*Phalaropus tricolor*
Parus atricapillus	*Poecile atricapillus*
Parus carolinensis	*Poecile carolinensis*
Parus gambeli	*Poecile gambeli*
Parus hudsonicus	*Poecile hudsonicus*
Parus rufescens	*Poecile rufescens*
Parus sclateri	*Poecile sclateri*
Parus sclateri	*Poecile sclateri*
Otus flammeolus	*Psiloscops flammeolus*
Rallus longirostris	*Rallus crepitans*
Rallus longirostris	*Rallus obsoletus*
Calcarius mccownii	*Rhynchophanes mccownii*
Stellula calliope	*Selasphorus calliope*
Parula americana	*Setophaga americana*
Dendroica caerulescens	*Setophaga caerulescens*
Dendroica castanea	*Setophaga castanea*
Dendroica cerulea	*Setophaga cerulea*
Dendroica chrysoparia	*Setophaga chrysoparia*
Wilsonia citrina	*Setophaga citrina*
Dendroica coronata	*Setophaga coronata*
Dendroica discolor	*Setophaga discolor*
Dendroica dominica	*Setophaga dominica*
Dendroica fusca	*Setophaga fusca*
Dendroica graciae	*Setophaga graciae*
Dendroica kirtlandii	*Setophaga kirtlandii*
Dendroica magnolia	*Setophaga magnolia*
Dendroica nigrescens	*Setophaga nigrescens*
Dendroica occidentalis	*Setophaga occidentalis*
Dendroica palmarum	*Setophaga palmarum*
Dendroica pensylvanica	*Setophaga pensylvanica*
Dendroica aestiva	*Setophaga petechia*
Dendroica pinus	*Setophaga pinus*
Dendroica striata	*Setophaga striata*
Dendroica tigrina	*Setophaga tigrina*
Dendroica townsendi	*Setophaga townsendi*
Dendroica virens	*Setophaga virens*
Anas clypeata	*Spatula clypeata*
Anas cyanoptera	*Spatula cyanoptera*
Anas discors	*Spatula discors*
Carduelis lawrencei	*Spinus lawrencei*
Carduelis pinus	*Spinus pinus*

Carduelis psaltria	*Spinus psaltria*
Carduelis tristis	*Spinus tristis*
Sterna antillarum	*Sternula antillarum*
Synthliboramphus hypoleucus	*Synthliboramphus scrippsi*
Sterna elegans	*Thalasseus elegans*
Sterna maxima	*Thalasseus maximus*
Sterna sandvicensis	*Thalasseus sandvicensis*
Heteroscelus incanus	*Tringa incana*
Catoptrophorus semipalmatus	*Tringa semipalmata*
Troglodytes troglodytes	*Troglodytes hiemalis*
Troglodytes troglodytes	*Troglodytes pacificus*
Vermivora pinus	*Vermivora cyanoptera*

Table S2 – Seasonal niche dissimilarity for 619 species of North American birds (sorted taxonomically). Dissimilarity is partitioned into Mahalanobis distance and determinant ratio for both seasonal (breeding/overwintering comparison) and locational (overwintering/winter at breeding sites comparison) dissimilarity. Position and breadth similarity (visualized and used in analyses) was generated from these values by ln-transforming and sign-flipping.

		Seasonal dissimilarity		Locational dissi	
Species	**Common name**	**Mahalonobis distance**	**Determinant ratio**	**Mahalonobis distance**	**De**
Pandion haliaetus	Osprey	2.772	0.080	4.611	
Elanus leucurus	White-tailed Kite	6.358	0.065	1.604	
Elanoides forficatus	Swallow-tailed Kite	2.966	0.080	10.750	
Aquila chrysaetos	Golden Eagle	9.449	0.078	1.500	
Circus hudsonius	Northern Harrier	7.571	0.111	1.800	
Accipiter striatus	Sharp-shinned Hawk	8.661	0.120	1.802	
Accipiter cooperii	Cooper's Hawk	11.529	0.166	2.203	
Accipiter gentilis	Northern Goshawk	18.113	0.034	1.116	
Haliaeetus leucocephalus	Bald Eagle	9.371	0.070	1.360	
Ictinia mississippiensis	Mississippi Kite	2.718	0.090	32.300	
Parabuteo unicinctus	Harris's Hawk	7.192	0.202	1.594	
Buteo lineatus	Red-shouldered Hawk	10.814	0.215	3.201	
Buteo platypterus	Broad-winged Hawk	0.286	0.129	22.102	
Buteo swainsoni	Swainson's Hawk	3.727	0.113	5.413	
Buteo jamaicensis	Red-tailed Hawk	11.993	0.132	1.727	
Buteo lagopus	Rough-legged Hawk	15.647	0.290	0.749	
Buteo regalis	Ferruginous Hawk	10.335	0.126	4.869	
Dendrocygna autumnalis	Black-bellied Whistling-Duck	7.130	0.157	3.965	
Dendrocygna bicolor	Fulvous Whistling-Duck	5.148	0.094	3.297	
Anser caerulescens	Snow Goose	8.903	0.077	2.028	
Anser rossii	Ross's Goose	16.063	0.095	1.927	
Anser albifrons	Greater White-fronted Goose	10.928	0.111	2.322	
Branta bernicla	Brant	8.996	0.040	1.469	
Branta hutchinsii	Cackling Goose	16.280	0.111	2.696	
Branta canadensis	Canada Goose	15.896	0.085	1.768	
Cygnus buccinator	Trumpeter Swan	26.911	0.109	1.722	
Cygnus columbianus	Tundra Swan	19.995	0.034	1.559	
Aix sponsa	Wood Duck	11.742	0.106	2.934	
Spatula discors	Blue-winged Teal	2.419	0.065	6.650	
Spatula cyanoptera	Cinnamon Teal	5.407	0.168	2.819	
Spatula clypeata	Northern Shoveler	5.565	0.100	2.255	
Mareca strepera	Gadwall	7.089	0.105	2.093	
Mareca americana	American Wigeon	5.190	0.132	2.607	

Anas platyrhynchos	Mallard	13.267	0.077	1.380
Anas rubripes	American Black Duck	24.559	0.055	1.230
Anas fulvigula	Mottled Duck	11.618	0.123	3.621
Anas acuta	Northern Pintail	6.417	0.102	1.632
Anas crecca	Green-winged Teal	6.478	0.111	2.463
Aythya valisineria	Canvasback	6.725	0.073	1.614
Aythya americana	Redhead	7.065	0.072	1.017
Aythya collaris	Ring-necked Duck	5.719	0.095	2.426
Aythya marila	Greater Scaup	7.807	0.076	0.386
Aythya affinis	Lesser Scaup	4.249	0.079	1.641
Somateria mollissima	Common Eider	24.244	0.027	1.614
Histrionicus histrionicus	Harlequin Duck	13.401	0.140	0.714
Melanitta perspicillata	Surf Scoter	7.444	0.155	0.795
Melanitta deglandi	White-winged Scoter	12.137	0.063	0.869
Melanitta americana	Black Scoter	9.144	0.069	0.548
Clangula hyemalis	Long-tailed Duck	13.943	0.036	0.282
Bucephala albeola	Bufflehead	8.120	0.184	1.127
Bucephala clangula	Common Goldeneye	10.170	0.097	0.760
Bucephala islandica	Barrow's Goldeneye	9.252	0.130	1.934
Lophodytes cucullatus	Hooded Merganser	10.713	0.109	1.860
Mergus merganser	Common Merganser	12.492	0.077	0.537
Mergus serrator	Red-breasted Merganser	5.630	0.033	0.342
Oxyura jamaicensis	Ruddy Duck	7.253	0.080	1.345
Archilochus colubris	Ruby-throated Hummingbird	3.009	0.049	11.176
Archilochus alexandri	Black-chinned Hummingbird	9.312	0.113	9.421
Calypte anna	Anna's Hummingbird	11.041	0.295	2.527
Calypte costae	Costa's Hummingbird	18.791	0.150	1.401
Selasphorus calliope	Calliope Hummingbird	3.873	0.157	13.544
Selasphorus rufus	Rufous Hummingbird	5.638	0.154	7.905
Selasphorus sasin	Allen's Hummingbird	9.268	0.729	3.786
Selasphorus platycercus	Broad-tailed Hummingbird	3.940	0.087	13.356
Chordeiles acutipennis	Lesser Nighthawk	9.718	0.139	11.661
Chordeiles minor	Common Nighthawk	0.667	0.106	8.947
Phalaenoptilus nuttallii	Common Poorwill	7.533	0.120	8.009
Antrostomus carolinensis	Chuck-will's-widow	2.884	0.126	7.380
Antrostomus vociferus	Eastern Whip-poor-will	5.376	0.066	23.402
Chaetura vauxi	Vaux's Swift	0.441	0.075	14.331
Aeronautes saxatalis	White-throated Swift	9.359	0.068	3.498
Coragyps atratus	Black Vulture	7.141	0.248	2.957
Cathartes aura	Turkey Vulture	7.679	0.128	3.064
Uria aalge	Common Murre	7.199	0.301	1.203

Uria lomvia	Thick-billed Murre	11.842	0.164	0.986
Alca torda	Razorbill	13.295	0.090	3.269
Cepphus grylle	Black Guillemot	25.298	0.021	1.195
Cepphus columba	Pigeon Guillemot	18.212	0.348	3.075
Brachyramphus marmoratus	Marbled Murrelet	9.276	0.190	1.445
Ptychoramphus aleuticus	Cassin's Auklet	3.560	0.294	1.562
Cerorhinca monocerata	Rhinoceros Auklet	8.411	0.271	2.060
Fratercula arctica	Atlantic Puffin	20.502	0.101	2.276
Rissa tridactyla	Black-legged Kittiwake	7.808	0.146	2.825
Xema sabini	Sabine's Gull	0.942	0.084	0.848
Chroicocephalus philadelphia	Bonaparte's Gull	5.343	0.062	2.159
Leucophaeus atricilla	Laughing Gull	4.725	0.075	2.027
Leucophaeus pipixcan	Franklin's Gull	1.040	0.102	7.057
Larus heermanni	Heermann's Gull	3.220	0.526	1.216
Larus canus	Mew Gull	6.335	0.127	2.221
Larus delawarensis	Ring-billed Gull	8.350	0.093	1.638
Larus occidentalis	Western Gull	4.883	0.722	1.168
Larus californicus	California Gull	5.517	0.310	1.873
Larus argentatus	Herring Gull	12.011	0.046	0.990
Larus glaucoides	Iceland Gull	5.448	0.099	0.492
Larus glaucescens	Glaucous-winged Gull	11.766	0.278	2.455
Larus hyperboreus	Glaucous Gull	9.938	0.054	0.374
Larus marinus	Great Black-backed Gull	19.190	0.070	0.548
Sternula antillarum	Least Tern	0.064	0.056	8.212
Gelochelidon nilotica	Gull-billed Tern	2.947	0.045	1.760
Hydroprogne caspia	Caspian Tern	2.047	0.081	4.560
Chlidonias niger	Black Tern	0.162	0.131	11.267
Sterna hirundo	Common Tern	0.432	0.043	7.369
Sterna forsteri	Forster's Tern	6.766	0.095	2.647
Thalasseus maximus	Royal Tern	4.509	0.081	1.991
Thalasseus sandvicensis	Sandwich Tern	3.238	0.058	2.354
Thalasseus elegans	Elegant Tern	0.937	0.199	8.524
Rynchops niger	Black Skimmer	5.523	0.088	1.324
Himantopus mexicanus	Black-necked Stilt	4.305	0.083	1.519
Recurvirostra americana	American Avocet	6.370	0.108	1.961
Haematopus palliatus	American Oystercatcher	3.499	0.159	1.002
Haematopus bachmani	Black Oystercatcher	6.790	0.474	1.261
Pluvialis squatarola	Black-bellied Plover	3.537	0.055	1.219
Pluvialis dominica	American Golden-Plover	1.255	0.092	6.254

Charadrius vociferus	Killdeer	7.991	0.094	2.529
Charadrius semipalmatus	Semipalmated Plover	2.295	0.041	2.575
Charadrius wilsonia	Wilson's Plover	3.742	0.114	1.546
Charadrius nivosus	Snowy Plover	4.904	0.097	1.062
Bartramia longicauda	Upland Sandpiper	1.337	0.096	9.795
Numenius phaeopus	Whimbrel	1.099	0.105	1.533
Numenius americanus	Long-billed Curlew	5.817	0.128	1.633
Limosa haemastica	Hudsonian Godwit	1.227	0.060	9.163
Limosa fedoa	Marbled Godwit	5.324	0.084	1.418
Arenaria interpres	Ruddy Turnstone	1.967	0.064	1.500
Arenaria melanocephala	Black Turnstone	7.015	0.571	1.139
Calidris canutus	Red Knot	2.637	0.045	2.204
Calidris virgata	Surfbird	3.796	0.272	1.208
Calidris himantopus	Stilt Sandpiper	2.706	0.070	4.642
Calidris alba	Sanderling	3.037	0.086	1.374
Calidris alpina	Dunlin	3.939	0.075	2.244
Calidris bairdii	Baird's Sandpiper	0.867	0.111	3.034
Calidris minutilla	Least Sandpiper	4.674	0.072	2.280
Calidris fuscicollis	White-rumped Sandpiper	0.534	0.167	3.467
Calidris subruficollis	Buff-breasted Sandpiper	0.739	0.135	6.834
Calidris melanotos	Pectoral Sandpiper	2.791	0.175	3.471
Calidris pusilla	Semipalmated Sandpiper	0.384	0.035	13.023
Calidris mauri	Western Sandpiper	4.942	0.094	1.415
Limnodromus griseus	Short-billed Dowitcher	3.050	0.049	2.822
Limnodromus scolopaceus	Long-billed Dowitcher	6.375	0.103	2.169
Scolopax minor	American Woodcock	12.791	0.088	4.942
Gallinago delicata	Wilson's Snipe	4.133	0.069	5.924
Actitis macularius	Spotted Sandpiper	1.736	0.059	4.939
Tringa solitaria	Solitary Sandpiper	1.394	0.075	10.366
Tringa incana	Wandering Tattler	0.667	0.059	1.861
Tringa flavipes	Lesser Yellowlegs	3.203	0.071	4.548
Tringa semipalmata	Willet	3.781	0.048	1.598
Tringa melanoleuca	Greater Yellowlegs	4.498	0.071	2.281
Phalaropus tricolor	Wilson's Phalarope	2.007	0.053	3.712
Phalaropus lobatus	Red-necked Phalarope	0.921	0.049	5.608
Phalaropus fulicarius	Red Phalarope	5.136	0.317	1.523
Stercorarius pomarinus	Pomarine Jaeger	2.830	0.102	0.457
Stercorarius parasiticus	Parasitic Jaeger	2.175	0.030	1.641
Mycteria americana	Wood Stork	7.630	0.118	4.883
Patagioenas fasciata	Band-tailed Pigeon	4.627	0.068	4.458

Columbina inca	Inca Dove	7.599	0.269	1.903
Columbina passerina	Common Ground Dove	7.207	0.153	2.753
Zenaida asiatica	White-winged Dove	10.842	0.256	2.065
Zenaida macroura	Mourning Dove	11.312	0.195	2.732
Megaceryle alcyon	Belted Kingfisher	7.661	0.092	2.563
Geococcyx californianus	Greater Roadrunner	19.262	0.169	1.270
Coccyzus americanus	Yellow-billed Cuckoo	1.128	0.055	15.625
Falco sparverius	American Kestrel	7.587	0.160	2.002
Falco columbarius	Merlin	5.444	0.117	3.743
Falco peregrinus	Peregrine Falcon	4.816	0.098	1.290
Falco mexicanus	Prairie Falcon	9.437	0.065	1.730
Oreortyx pictus	Mountain Quail	8.186	0.342	5.225
Colinus virginianus	Northern Bobwhite	10.351	0.253	1.697
Callipepla squamata	Scaled Quail	24.525	0.356	1.357
Callipepla californica	California Quail	11.645	0.437	2.543
Callipepla gambelii	Gambel's Quail	30.721	0.204	1.725
Meleagris gallopavo	Wild Turkey	13.933	0.188	3.010
Bonasa umbellus	Ruffed Grouse	23.776	0.078	3.254
Centrocercus urophasianus	Greater Sage-Grouse	43.355	0.249	1.077
Gavia stellata	Red-throated Loon	6.994	0.092	0.712
Gavia pacifica	Pacific Loon	5.030	0.255	1.138
Gavia immer	Common Loon	8.906	0.106	1.272
Antigone canadensis	Sandhill Crane	5.528	0.132	2.507
Rallus crepitans	Clapper Rail	8.791	0.181	2.419
Rallus elegans	King Rail	8.789	0.164	4.497
Rallus limicola	Virginia Rail	8.341	0.098	3.257
Porzana carolina	Sora	3.010	0.076	6.488
Gallinula galeata	Common Gallinule	4.866	0.170	3.071
Fulica americana	American Coot	6.574	0.091	1.585
Porphyrio martinica	Purple Gallinule	3.342	0.079	4.196
Xanthocephalus xanthocephalus	Yellow-headed Blackbird	4.668	0.047	4.260
Dolichonyx oryzivorus	Bobolink	12.548	0.963	2.721
Sturnella magna	Eastern Meadowlark	9.115	0.166	2.016
Sturnella neglecta	Western Meadowlark	9.999	0.082	3.309
Icterus spurius	Orchard Oriole	1.004	0.013	14.730
Icterus cucullatus	Hooded Oriole	5.328	0.187	5.499
Icterus bullockii	Bullock's Oriole	3.692	0.121	6.477
Icterus galbula	Baltimore Oriole	0.607	0.140	12.352
Icterus parisorum	Scott's Oriole	13.048	0.142	6.595
Agelaius phoeniceus	Red-winged Blackbird	9.109	0.105	2.207
Molothrus aeneus	Bronzed Cowbird	5.089	0.209	2.605

Molothrus ater	Brown-headed Cowbird	9.054	0.151	2.791
Euphagus carolinus	Rusty Blackbird	5.921	0.148	4.906
Euphagus cyanocephalus	Brewer's Blackbird	7.277	0.157	2.776
Quiscalus quiscula	Common Grackle	7.739	0.181	3.578
Quiscalus major	Boat-tailed Grackle	6.918	0.154	3.301
Quiscalus mexicanus	Great-tailed Grackle	7.331	0.190	1.372
Piranga rubra	Summer Tanager	2.206	0.190	14.203
Piranga olivacea	Scarlet Tanager	1.494	0.359	21.498
Piranga ludoviciana	Western Tanager	0.863	0.078	8.425
Cardinalis cardinalis	Northern Cardinal	15.349	0.208	3.142
Cardinalis sinuatus	Pyrrhuloxia	27.487	0.332	1.957
Pheucticus ludovicianus	Rose-breasted Grosbeak	0.459	0.152	28.663
Pheucticus melanocephalus	Black-headed Grosbeak	3.199	0.069	10.508
Passerina caerulea	Blue Grosbeak	3.711	0.112	11.346
Passerina amoena	Lazuli Bunting	5.705	0.276	5.507
Passerina cyanea	Indigo Bunting	2.822	0.046	15.838
Passerina ciris	Painted Bunting	4.742	0.157	6.908
Spiza americana	Dickcissel	3.449	0.326	4.495
Dumetella carolinensis	Gray Catbird	3.307	0.099	8.892
Toxostoma curvirostre	Curve-billed Thrasher	20.980	0.436	1.730
Toxostoma rufum	Brown Thrasher	13.177	0.140	4.031
Oreoscoptes montanus	Sage Thrasher	9.148	0.056	8.437
Mimus polyglottos	Northern Mockingbird	10.332	0.202	2.488
Cinclus mexicanus	American Dipper	8.189	0.154	1.537
Coccothraustes vespertinus	Evening Grosbeak	15.927	0.103	2.436
Pinicola enucleator	Pine Grosbeak	18.533	0.023	1.570
Leucosticte tephrocotis	Gray-crowned Rosy-Finch	13.185	0.117	2.411
Haemorhous mexicanus	House Finch	14.181	0.156	2.652
Haemorhous purpureus	Purple Finch	12.797	0.126	3.065
Haemorhous cassinii	Cassin's Finch	10.281	0.063	3.886
Acanthis flammea	Common Redpoll	19.341	0.114	3.307
Loxia curvirostra	Red Crossbill	9.493	0.096	2.407
Spinus pinus	Pine Siskin	8.169	0.070	3.062
Spinus psaltria	Lesser Goldfinch	10.330	0.062	2.326
Spinus tristis	American Goldfinch	16.525	0.154	3.836
Polioptila caerulea	Blue-gray Gnatcatcher	6.916	0.111	6.833
Polioptila melanura	Black-tailed Gnatcatcher	33.637	0.252	1.444
Perisoreus canadensis	Canada Jay	14.245	0.148	3.292
Gymnorhinus cyanocephalus	Pinyon Jay	29.872	0.166	2.652

Cyanocitta stelleri	Steller's Jay	11.859	0.143	3.472
Cyanocitta cristata	Blue Jay	16.595	0.163	3.506
Aphelocoma californica	California Scrub-Jay	12.835	0.577	3.304
Aphelocoma woodhouseii	Woodhouse's Scrub-Jay	21.204	0.298	2.615
Nucifraga columbiana	Clark's Nutcracker	16.096	0.037	1.923
Pica hudsonia	Black-billed Magpie	24.824	0.100	1.714
Corvus brachyrhynchos	American Crow	13.448	0.124	2.172
Corvus ossifragus	Fish Crow	8.323	0.271	3.233
Corvus cryptoleucus	Chihuahuan Raven	24.858	0.332	1.366
Corvus corax	Common Raven	7.642	0.113	1.724
Regulus satrapa	Golden-crowned Kinglet	10.022	0.067	2.278
Regulus calendula	Ruby-crowned Kinglet	2.814	0.029	9.277
Eremophila alpestris	Horned Lark	15.211	0.127	1.528
Calcarius lapponicus	Lapland Longspur	7.211	0.264	0.969
Calcarius ornatus	Chestnut-collared Longspur	13.597	0.092	11.478
Psaltriparus minimus	Bushtit	10.121	0.113	2.822
Riparia riparia	Bank Swallow	0.035	0.094	16.438
Tachycineta bicolor	Tree Swallow	4.419	0.065	7.039
Tachycineta thalassina	Violet-green Swallow	3.027	0.109	6.382
Stelgidopteryx serripennis	Northern Rough-winged Swallow	1.632	0.086	6.905
Progne subis	Purple Martin	4.380	0.120	5.385
Hirundo rustica	Barn Swallow	1.244	0.086	6.490
Petrochelidon pyrrhonota	Cliff Swallow	2.420	0.063	5.052
Petrochelidon fulva	Cave Swallow	8.218	0.180	2.502
Peucaea cassinii	Cassin's Sparrow	18.240	0.365	3.385
Peucaea aestivalis	Bachman's Sparrow	20.577	0.224	12.450
Ammodramus savannarum	Grasshopper Sparrow	7.039	0.129	8.208
Amphispiza bilineata	Black-throated Sparrow	24.484	0.227	2.247
Chondestes grammacus	Lark Sparrow	9.998	0.041	4.368
Calamospiza melanocorys	Lark Bunting	14.884	0.187	5.099
Spizella passerina	Chipping Sparrow	9.687	0.080	7.193
Spizella pallida	Clay-colored Sparrow	5.000	0.179	11.543
Spizella atrogularis	Black-chinned Sparrow	22.559	0.482	2.500
Spizella pusilla	Field Sparrow	21.004	0.156	3.908
Spizella breweri	Brewer's Sparrow	9.322	0.337	8.582
Passerella iliaca	Fox Sparrow	7.059	0.109	2.773
Junco hyemalis	Dark-eyed Junco	12.781	0.100	1.927
Zonotrichia leucophrys	White-crowned Sparrow	3.927	0.118	3.861
Zonotrichia atricapilla	Golden-crowned Sparrow	4.033	0.094	4.693

Zonotrichia querula	Harris's Sparrow	10.297	0.271	2.315
Zonotrichia albicollis	White-throated Sparrow	11.611	0.151	4.793
Artemisiospiza nevadensis	Sagebrush Sparrow	12.950	0.135	6.211
Artemisiospiza belli	Bell's Sparrow	14.347	0.682	1.588
Pooecetes gramineus	Vesper Sparrow	7.575	0.072	11.700
Ammospiza leconteii	LeConte's Sparrow	5.696	0.113	14.060
Ammospiza maritima	Seaside Sparrow	9.635	0.121	2.497
Ammospiza nelsoni	Nelson's Sparrow	5.045	0.026	14.650
Ammospiza caudacuta	Saltmarsh Sparrow	7.317	0.145	4.866
Passerculus sandwichensis	Savannah Sparrow	5.921	0.069	4.898
Melospiza melodia	Song Sparrow	14.297	0.082	2.436
Melospiza lincolnii	Lincoln's Sparrow	3.181	0.030	8.378
Melospiza georgiana	Swamp Sparrow	9.370	0.122	5.291
Melozone fusca	Canyon Towhee	18.594	0.450	1.888
Melozone aberti	Abert's Towhee	40.308	0.221	1.691
Melozone crissalis	California Towhee	11.550	0.846	2.932
Aimophila ruficeps	Rufous-crowned Sparrow	18.935	0.098	2.462
Pipilo chlorurus	Green-tailed Towhee	7.890	0.235	10.820
Pipilo maculatus	Spotted Towhee	12.802	0.189	2.810
Pipilo erythrophthalmus	Eastern Towhee	19.547	0.142	4.393
Sitta canadensis	Red-breasted Nuthatch	15.092	0.079	3.011
Sitta carolinensis	White-breasted Nuthatch	27.990	0.176	3.931
Sitta pygmaea	Pygmy Nuthatch	12.015	0.050	3.195
Sitta pusilla	Brown-headed Nuthatch	26.889	0.108	4.777
Chamaea fasciata	Wrentit	9.007	0.698	3.891
Auriparus flaviceps	Verdin	32.529	0.242	1.541
Lanius ludovicianus	Loggerhead Shrike	12.186	0.167	1.953
Lanius borealis	Northern Shrike	16.320	0.153	3.670
Phainopepla nitens	Phainopepla	23.277	0.088	1.590
Sialia sialis	Eastern Bluebird	18.966	0.156	3.319
Sialia mexicana	Western Bluebird	10.950	0.086	2.453
Sialia currucoides	Mountain Bluebird	6.762	0.058	4.053
Myadestes townsendi	Townsend's Solitaire	13.807	0.080	1.785
Catharus minimus	Gray-cheeked Thrush	1.065	0.300	19.812
Catharus ustulatus	Swainson's Thrush	1.016	0.308	41.142
Catharus guttatus	Hermit Thrush	6.684	0.089	5.142
Hylocichla mustelina	Wood Thrush	0.317	0.056	49.065
Turdus migratorius	American Robin	12.035	0.089	2.718
Ixoreus naevius	Varied Thrush	5.922	0.194	3.788
Poecile carolinensis	Carolina Chickadee	25.908	0.209	4.326
Poecile atricapillus	Black-capped Chickadee	29.392	0.054	2.534

Poecile gambeli	Mountain Chickadee	11.508	0.052	2.202
Poecile rufescens	Chestnut-backed Chickadee	11.208	0.336	3.594
Poecile hudsonicus	Boreal Chickadee	24.152	0.071	1.395
Baeolophus inornatus	Oak Titmouse	18.570	0.772	4.285
Baeolophus ridgwayi	Juniper Titmouse	30.376	0.188	3.678
Baeolophus bicolor	Tufted Titmouse	25.880	0.182	4.894
Certhia americana	Brown Creeper	14.280	0.076	1.888
Myiarchus cinerascens	Ash-throated Flycatcher	6.775	0.164	3.413
Myiarchus crinitus	Great Crested Flycatcher	0.963	0.097	13.760
Myiarchus tyrannulus	Brown-crested Flycatcher	6.985	0.138	11.023
Tyrannus vociferans	Cassin's Kingbird	12.443	0.074	4.322
Tyrannus verticalis	Western Kingbird	4.877	0.087	8.287
Tyrannus tyrannus	Eastern Kingbird	0.448	0.044	28.215
Tyrannus forficatus	Scissor-tailed Flycatcher	3.748	0.048	8.919
Contopus cooperi	Olive-sided Flycatcher	1.938	0.288	36.454
Contopus sordidulus	Western Wood-Pewee	5.077	0.424	51.781
Contopus virens	Eastern Wood-Pewee	0.281	0.111	40.720
Empidonax flaviventris	Yellow-bellied Flycatcher	0.951	0.282	44.013
Empidonax virescens	Acadian Flycatcher	0.351	0.100	72.138
Empidonax alnorum	Alder Flycatcher	0.615	0.331	29.356
Empidonax traillii	Willow Flycatcher	0.299	0.122	38.571
Empidonax minimus	Least Flycatcher	0.558	0.029	24.326
Empidonax hammondii	Hammond's Flycatcher	1.947	0.037	15.734
Empidonax wrightii	Gray Flycatcher	7.753	0.169	7.506
Empidonax oberholseri	Dusky Flycatcher	2.508	0.153	12.533
Empidonax difficilis	Pacific-slope Flycatcher	0.010	0.186	14.877
Empidonax occidentalis	Cordilleran Flycatcher	2.113	0.241	20.176
Sayornis nigricans	Black Phoebe	9.412	0.090	1.672
Sayornis phoebe	Eastern Phoebe	9.973	0.091	6.295
Sayornis saya	Say's Phoebe	13.942	0.067	3.088
Pyrocephalus rubinus	Vermilion Flycatcher	8.034	0.287	1.876
Vireo griseus	White-eyed Vireo	7.654	0.117	6.589
Vireo bellii	Bell's Vireo	5.851	0.188	8.243
Vireo huttoni	Hutton's Vireo	10.116	0.088	3.511
Vireo flavifrons	Yellow-throated Vireo	0.312	0.061	31.665
Vireo cassinii	Cassin's Vireo	1.785	0.066	13.456
Vireo solitarius	Blue-headed Vireo	6.117	0.100	13.901
Vireo plumbeus	Plumbeous Vireo	3.994	0.289	9.770
Vireo philadelphicus	Philadelphia Vireo	0.758	0.321	72.495
Vireo gilvus	Warbling Vireo	1.491	0.073	26.277
Vireo olivaceus	Red-eyed Vireo	1.725	0.523	6.186
Anthus rubescens	American Pipit	1.250	0.095	5.799
Bombycilla cedrorum	Cedar Waxwing	9.475	0.130	4.868

Seiurus aurocapilla	Ovenbird	1.324	0.056	15.389
Helmitheros vermivorum	Worm-eating Warbler	1.079	0.081	30.111
Parkesia motacilla	Louisiana Waterthrush	1.484	0.120	14.630
Parkesia noveboracensis	Northern Waterthrush	0.047	0.111	15.779
Vermivora cyanoptera	Blue-winged Warbler	0.371	0.041	44.259
Mniotilta varia	Black-and-white Warbler	1.112	0.032	10.947
Protonotaria citrea	Prothonotary Warbler	0.135	0.062	23.669
Geothlypis tolmiei	MacGillivray's Warbler	0.400	0.097	18.268
Geothlypis philadelphia	Mourning Warbler	0.932	0.273	67.688
Geothlypis formosa	Kentucky Warbler	0.970	0.075	61.339
Geothlypis trichas	Common Yellowthroat	4.692	0.065	6.657
Setophaga citrina	Hooded Warbler	0.702	0.087	27.677
Setophaga ruticilla	American Redstart	0.200	0.073	26.164
Setophaga tigrina	Cape May Warbler	0.570	0.042	19.712
Setophaga americana	Northern Parula	2.116	0.051	8.649
Setophaga magnolia	Magnolia Warbler	0.947	0.097	47.590
Setophaga castanea	Bay-breasted Warbler	0.742	0.245	44.995
Setophaga fusca	Blackburnian Warbler	0.347	0.237	43.608
Setophaga petechia	Yellow Warbler	0.031	0.155	15.504
Setophaga pensylvanica	Chestnut-sided Warbler	0.433	0.153	53.458
Setophaga striata	Blackpoll Warbler	1.252	0.098	30.052
Setophaga caerulescens	Black-throated Blue Warbler	2.015	0.068	20.318
Setophaga palmarum	Palm Warbler	1.397	0.057	17.470
Setophaga pinus	Pine Warbler	9.355	0.098	4.398
Setophaga coronata	Yellow-rumped Warbler	3.279	0.047	6.353
Setophaga dominica	Yellow-throated Warbler	5.679	0.121	7.125
Setophaga discolor	Prairie Warbler	4.355	0.057	8.173
Setophaga graciae	Grace's Warbler	4.185	0.143	18.449
Setophaga nigrescens	Black-throated Gray Warbler	2.658	0.151	7.447
Setophaga townsendi	Townsend's Warbler	2.588	0.050	4.870
Setophaga occidentalis	Hermit Warbler	1.535	0.035	12.828
Setophaga virens	Black-throated Green Warbler	0.551	0.043	34.314
Cardellina canadensis	Canada Warbler	0.355	0.295	62.745
Cardellina pusilla	Wilson's Warbler	0.391	0.114	9.850
Salpinctes obsoletus	Rock Wren	7.846	0.055	3.132
Catherpes mexicanus	Canyon Wren	11.396	0.191	2.003
Troglodytes aedon	House Wren	2.700	0.061	6.291
Troglodytes pacificus	Pacific Wren	13.324	0.216	2.691
Troglodytes hiemalis	Winter Wren	13.152	0.172	4.579
Cistothorus platensis	Sedge Wren	6.849	0.039	10.495
Cistothorus palustris	Marsh Wren	6.884	0.079	3.433

Thryothorus ludovicianus	Carolina Wren	20.053	0.230	4.192
Thryomanes bewickii	Bewick's Wren	11.430	0.139	2.369
Campylorhynchus brunneicapillus	Cactus Wren	26.759	0.206	2.074
Icteria virens	Yellow-breasted Chat	2.061	0.280	6.686
Botaurus lentiginosus	American Bittern	3.352	0.109	5.203
Ixobrychus exilis	Least Bittern	2.833	0.147	4.286
Ardea herodias	Great Blue Heron	7.285	0.109	1.936
Ardea alba	Great Egret	4.723	0.068	2.476
Egretta thula	Snowy Egret	4.458	0.066	2.166
Egretta caerulea	Little Blue Heron	5.463	0.060	3.763
Egretta tricolor	Tricolored Heron	6.408	0.081	3.192
Egretta rufescens	Reddish Egret	8.367	0.133	1.314
Bubulcus ibis	Cattle Egret	4.029	0.068	3.770
Butorides virescens	Green Heron	3.358	0.084	4.828
Nycticorax nycticorax	Black-crowned Night-Heron	3.804	0.067	2.047
Nyctanassa violacea	Yellow-crowned Night-Heron	3.670	0.017	4.191
Eudocimus albus	White Ibis	9.125	0.115	3.212
Plegadis falcinellus	Glossy Ibis	3.661	0.099	5.644
Plegadis chihi	White-faced Ibis	5.831	0.077	2.424
Platalea ajaja	Roseate Spoonbill	7.736	0.107	2.384
Pelecanus erythrorhynchos	American White Pelican	3.897	0.072	2.943
Pelecanus occidentalis	Brown Pelican	3.172	0.094	1.532
Melanerpes lewis	Lewis's Woodpecker	10.812	0.065	5.741
Melanerpes erythrocephalus	Red-headed Woodpecker	14.298	0.180	2.947
Melanerpes formicivorus	Acorn Woodpecker	10.799	0.098	3.115
Melanerpes uropygialis	Gila Woodpecker	38.114	0.317	1.744
Melanerpes aurifrons	Golden-fronted Woodpecker	7.981	0.285	1.796
Melanerpes carolinus	Red-bellied Woodpecker	17.552	0.224	4.154
Sphyrapicus thyroideus	Williamson's Sapsucker	7.842	0.014	5.711
Sphyrapicus varius	Yellow-bellied Sapsucker	10.075	0.168	6.806
Sphyrapicus nuchalis	Red-naped Sapsucker	8.153	0.068	13.621
Sphyrapicus ruber	Red-breasted Sapsucker	8.236	0.259	5.743
Dryobates pubescens	Downy Woodpecker	19.761	0.146	3.317
Dryobates nuttallii	Nuttall's Woodpecker	15.759	0.841	3.280
Dryobates scalaris	Ladder-backed Woodpecker	18.821	0.293	1.722
Dryobates villosus	Hairy Woodpecker	20.666	0.092	3.018
Dryobates albolarvatus	White-headed Woodpecker	12.329	0.229	3.629
Colaptes auratus	Northern Flicker	12.813	0.079	2.629
Dryocopus pileatus	Pileated Woodpecker	11.982	0.142	3.857

Podilymbus podiceps	Pied-billed Grebe	6.693	0.119	1.930
Podiceps auritus	Horned Grebe	7.769	0.094	1.133
Podiceps grisegena	Red-necked Grebe	15.065	0.135	1.684
Podiceps nigricollis	Eared Grebe	5.822	0.171	2.698
Aechmophorus occidentalis	Western Grebe	6.097	0.224	1.639
Aechmophorus clarkii	Clark's Grebe	7.489	0.285	1.276
Phoebastria nigripes	Black-footed Albatross	3.471	0.138	2.617
Fulmarus glacialis	Northern Fulmar	3.946	0.226	0.705
Ardenna grisea	Sooty Shearwater	1.943	0.078	1.132
Ardenna gravis	Great Shearwater	11.845	0.119	2.494
Ardenna creatopus	Pink-footed Shearwater	2.379	0.295	1.140
Puffinus lherminieri	Audubon's Shearwater	2.675	0.341	6.633
Oceanites oceanicus	Wilson's Storm-Petrel	18.591	0.205	7.951
Oceanodroma leucorhoa	Leach's Storm-Petrel	3.804	0.080	2.209
Tyto alba	Barn Owl	6.473	0.109	1.808
Megascops kennicottii	Western Screech-Owl	13.803	0.235	2.323
Megascops asio	Eastern Screech-Owl	15.550	0.286	3.949
Bubo virginianus	Great Horned Owl	10.738	0.141	2.280
Athene cunicularia	Burrowing Owl	9.304	0.040	2.206
Strix varia	Barred Owl	13.986	0.141	3.732
Asio flammeus	Short-eared Owl	12.466	0.110	1.341
Anhinga anhinga	Anhinga	9.559	0.108	4.337
Phalacrocorax penicillatus	Brandt's Cormorant	5.314	0.587	1.001
Phalacrocorax pelagicus	Pelagic Cormorant	7.175	0.412	1.188
Phalacrocorax carbo	Great Cormorant	20.917	0.083	1.149
Phalacrocorax auritus	Double-crested Cormorant	4.388	0.076	2.178
Phalacrocorax brasilianus	Neotropic Cormorant	4.362	0.141	1.293
Fregata magnificens	Magnificent Frigatebird	1.727	0.028	2.137
Morus bassanus	Northern Gannet	6.136	0.084	5.182
Phoebastria immutabilis	Laysan Albatross	0.876	0.157	2.014
Synthliboramphus scrippsi	Scripps's Murrelet	12.744	1.295	3.395
Synthliboramphus antiquus	Ancient Murrelet	4.815	0.209	1.988
Icterus gularis	Altamira Oriole	6.178	0.253	2.402
Icterus graduacauda	Audubon's Oriole	12.091	0.417	2.114
Agelaius tricolor	Tricolored Blackbird	11.017	0.623	2.069
Piranga flava	Hepatic Tanager	3.746	0.221	6.118
Passerina versicolor	Varied Bunting	15.043	0.267	10.102

Toxostoma longirostre	Long-billed Thrasher	16.473	0.191	2.613
Toxostoma bendirei	Bendire's Thrasher	44.828	0.262	2.305
Toxostoma redivivum	California Thrasher	11.647	0.931	3.243
Toxostoma lecontei	LeConte's Thrasher	30.985	0.402	1.676
Toxostoma crissale	Crissal Thrasher	35.025	0.245	1.598
Ortalis vetula	Plain Chachalaca	6.996	0.266	2.983
Grus americana	Whooping Crane	11.009	0.200	1.140
Crotophaga sulcirostris	Groove-billed Ani	2.878	0.045	4.014
Coccyzus minor	Mangrove Cuckoo	1.969	0.039	4.856
Caracara cheriway	Crested Caracara	7.050	0.170	1.815
Paroreomyza montana	Maui Alauahio	5.701	0.282	14.134
Himatione sanguinea	Apapane	1.602	0.027	3.904
Drepanis coccinea	Iiwi	2.818	0.047	5.995
Magumma parva	Anianiau	6.217	0.079	27.061
Chlorodrepanis virens	Hawaii Amakihi	1.537	0.030	2.862
Chlorodrepanis flava	Oahu Amakihi	2.946	0.186	17.374
Chlorodrepanis stejnegeri	Kauai Amakihi	6.061	0.079	29.917
Leucosticte atrata	Black Rosy-Finch	19.369	0.621	4.301
Leucosticte australis	Brown-capped Rosy-Finch	12.696	0.955	6.948
Loxia leucoptera	White-winged Crossbill	16.327	0.111	2.113
Spinus lawrencei	Lawrence's Goldfinch	11.628	0.482	2.977
Sula leucogaster	Brown Booby	0.812	0.094	1.570
Sula sula	Red-footed Booby	0.702	0.015	1.657
Polioptila californica	California Gnatcatcher	13.736	0.805	4.452
Tachybaptus dominicus	Least Grebe	4.932	0.200	2.178
Cyrtonyx montezumae	Montezuma Quail	36.069	0.407	3.832
Falcipennis canadensis	Spruce Grouse	20.982	0.116	2.116
Lagopus lagopus	Willow Ptarmigan	15.911	0.230	2.337
Lagopus leucura	White-tailed Ptarmigan	31.310	0.319	0.157
Dendragapus obscurus	Dusky Grouse	24.142	0.220	2.880
Dendragapus fuliginosus	Sooty Grouse	11.873	0.262	6.881
Tympanuchus phasianellus	Sharp-tailed Grouse	37.220	0.251	2.441
Tympanuchus cupido	Greater Prairie-Chicken	21.815	0.490	3.195
Hydrocoloeus minutus	Little Gull	8.602	0.032	1.380
Larus fuscus	Lesser Black-backed Gull	6.742	0.100	0.860
Anous stolidus	Brown Noddy	0.272	0.096	1.271
Anous minutus	Black Noddy	1.558	0.053	1.382
Gygis alba	White Tern	1.930	0.202	1.897
Onychoprion fuscatus	Sooty Tern	1.856	0.080	1.596
Onychoprion anaethetus	Bridled Tern	0.826	0.099	2.710

Sterna dougallii	Roseate Tern	0.353	0.358	1.608
Eugenes fulgens	Rivoli's Hummingbird	7.328	0.568	5.638
Lampornis clemenciae	Blue-throated Mountain-gem	8.738	0.460	4.796
Calothorax lucifer	Lucifer Hummingbird	10.824	0.495	9.246
Cynanthus latirostris	Broad-billed Hummingbird	11.502	0.373	2.665
Amazilia violiceps	Violet-crowned Hummingbird	9.408	0.439	2.624
Amazilia yucatanensis	Buff-bellied Hummingbird	11.055	0.175	2.827
Cyanocorax yncas	Green Jay	6.099	0.326	1.855
Aphelocoma coerulescens	Florida Scrub-Jay	16.720	0.069	6.001
Aphelocoma insularis	Island Scrub-Jay	7.622	1.197	5.143
Aphelocoma wollweberi	Mexican Jay	33.273	0.344	4.107
Pica nuttalli	Yellow-billed Magpie	30.154	0.676	2.400
Megaceryle torquata	Ringed Kingfisher	1.129	0.096	2.432
Chloroceryle americana	Green Kingfisher	2.566	0.158	2.484
Aramus guarauna	Limpkin	7.870	0.106	4.542
Gavia arctica	Arctic Loon	446.941	1.519	12.148
Gavia adamsii	Yellow-billed Loon	12.699	0.487	2.084
Chasiempis sclateri	Kauai Elepaio	5.189	0.034	18.127
Chasiempis sandwichensis	Hawaii Elepaio	2.121	0.029	5.821
Rhynchophanes mccownii	Thick-billed Longspur	15.093	0.032	7.821
Peucaea carpalis	Rufous-winged Sparrow	49.061	0.458	6.054
Peucaea botterii	Botteri's Sparrow	13.974	0.368	2.166
Arremonops rufivirgatus	Olive Sparrow	9.880	0.388	1.928
Junco phaeonotus	Yellow-eyed Junco	11.228	0.529	5.758
Centronyx bairdii	Baird's Sparrow	14.407	0.515	21.456
Centronyx henslowii	Henslow's Sparrow	20.042	0.039	19.361
Chordeiles gundlachii	Antillean Nighthawk	1.580	0.049	3.237
Nyctidromus albicollis	Common Pauraque	1.828	0.156	4.500
Antrostomus arizonae	Mexican Whip-poor-will	7.035	0.326	17.820
Peucedramus taeniatus	Olive Warbler	6.988	0.522	5.822
Psiloscops flammeolus	Flammulated Owl	5.284	0.226	16.571
Megascops trichopsis	Whiskered Screech-Owl	11.896	0.730	5.100
Bubo scandiacus	Snowy Owl	19.424	0.026	0.514
Glaucidium gnoma	Northern Pygmy-Owl	8.119	0.137	2.716
Micrathene whitneyi	Elf Owl	9.887	0.417	9.245
Strix nebulosa	Great Gray Owl	38.148	0.644	2.761
Asio otus	Long-eared Owl	15.120	0.163	1.111
Aegolius funereus	Boreal Owl	28.103	0.370	1.375
Aegolius acadicus	Northern Saw-whet Owl	10.575	0.078	1.641

Ardenna pacifica	Wedge-tailed Shearwater	0.606	0.092	1.626
Puffinus puffinus	Manx Shearwater	17.995	0.049	3.658
Puffinus opisthomelas	Black-vented Shearwater	10.044	0.717	1.526
Patagioenas leucocephala	White-crowned Pigeon	3.780	0.029	3.808
Patagioenas flavirostris	Red-billed Pigeon	3.052	0.053	6.209
Leptotila verreauxi	White-tipped Dove	1.818	0.114	3.954
Rallus obsoletus	Ridgway's Rail	11.390	0.431	1.140
Fulica alai	Hawaiian Coot	3.061	0.066	2.621
Coturnicops noveboracensis	Yellow Rail	5.435	0.047	17.577
Laterallus jamaicensis	Black Rail	7.517	0.074	2.099
Pluvialis fulva	Pacific Golden-Plover	1.557	0.060	2.129
Charadrius melodus	Piping Plover	2.574	0.039	3.398
Charadrius montanus	Mountain Plover	13.950	0.058	7.341
Numenius tahitiensis	Bristle-thighed Curlew	2.530	0.057	4.220
Calidris ptilocnemis	Rock Sandpiper	7.386	0.235	3.285
Oceanodroma furcata	Fork-tailed Storm-Petrel	8.539	0.634	4.998
Oceanodroma castro	Band-rumped Storm-Petrel	0.838	0.388	2.936
Oceanodroma melania	Black Storm-Petrel	1.580	0.518	10.288
Cypseloides niger	Black Swift	0.982	0.149	19.535
Myadestes obscurus	Omao	2.133	0.042	6.481
Catharus bicknelli	Bicknell's Thrush	1.789	0.283	71.056
Turdus grayi	Clay-colored Thrush	2.781	0.061	5.094
Poecile sclateri	Mexican Chickadee	9.816	0.538	7.386
Baeolophus wollweberi	Bridled Titmouse	28.066	0.331	2.554
Baeolophus atricristatus	Black-crested Titmouse	21.893	0.141	5.172
Trogon elegans	Elegant Trogon	4.523	0.386	4.051
Phaethon lepturus	White-tailed Tropicbird	1.077	0.024	2.948
Camptostoma imberbe	Northern Beardless-Tyrannulet	8.286	0.308	4.285
Myiarchus tuberculifer	Dusky-capped Flycatcher	2.508	0.162	8.209
Pitangus sulphuratus	Great Kiskadee	1.869	0.085	2.346
Myiodynastes luteiventris	Sulphur-bellied Flycatcher	1.526	0.158	14.836
Tyrannus melancholicus	Tropical Kingbird	1.459	0.097	3.338
Tyrannus couchii	Couch's Kingbird	10.490	0.221	2.162
Tyrannus crassirostris	Thick-billed Kingbird	9.832	0.373	8.053
Tyrannus dominicensis	Gray Kingbird	2.690	0.103	5.089
Contopus pertinax	Greater Pewee	4.209	0.449	5.715
Empidonax fulvifrons	Buff-breasted Flycatcher	6.490	0.426	6.807
Vireo atricapilla	Black-capped Vireo	14.239	0.161	19.704
Vireo vicinior	Gray Vireo	11.484	0.526	7.962

Vireo altiloquus	Black-whiskered Vireo	2.760	0.133	8.112
Gymnogyps californianus	California Condor	15.248	0.317	2.107
Rostrhamus sociabilis	Snail Kite	2.863	0.055	3.092
Buteogallus anthracinus	Common Black Hawk	3.401	0.243	4.695
Geranoaetus albicaudatus	White-tailed Hawk	6.579	0.182	1.595
Buteo plagiatus	Gray Hawk	5.907	0.210	5.847
Buteo solitarius	Hawaiian Hawk	0.403	0.091	2.653
Buteo brachyurus	Short-tailed Hawk	2.495	0.095	4.271
Buteo albonotatus	Zone-tailed Hawk	3.817	0.178	6.591
Anthus spragueii	Sprague's Pipit	6.079	0.019	27.920
Branta sandvicensis	Hawaiian Goose	0.890	0.046	2.757
Mareca penelope	Eurasian Wigeon	6.241	0.139	1.744
Anas wyvilliana	Hawaiian Duck	2.061	0.056	4.540
Anas diazi	Mexican Duck	18.983	0.496	1.437
Somateria spectabilis	King Eider	19.678	0.047	0.224
Picoides dorsalis	American Three-toed Woodpecker	17.389	0.060	2.280
Picoides arcticus	Black-backed Woodpecker	25.891	0.081	3.362
Dryobates borealis	Red-cockaded Woodpecker	21.654	0.254	9.635
Dryobates arizonae	Arizona Woodpecker	17.271	0.420	3.104
Colaptes chrysoides	Gilded Flicker	44.811	0.230	2.679
Vermivora chrysoptera	Golden-winged Warbler	0.123	0.278	83.927
Limnothlypis swainsonii	Swainson's Warbler	2.604	0.254	18.243
Oporornis agilis	Connecticut Warbler	2.629	0.414	87.559
Setophaga kirtlandii	Kirtland's Warbler	2.760	0.349	36.323
Setophaga cerulea	Cerulean Warbler	0.509	0.224	75.458
Setophaga chrysoparia	Golden-cheeked Warbler	17.794	0.135	29.481
Cardellina rubrifrons	Red-faced Warbler	5.963	0.262	37.486
Myioborus pictus	Painted Redstart	6.522	0.319	5.713

Table S3. Model tables (pgls and ANOVA) summarizing functional trait drivers of seasonal niche position and breadth similarity across species in multivariate models.

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-2.989	0.584	-5.120	<0.001
Migration distance	<0.001	<0.001	10.040	<0.001
Body mass (log)	-0.370	0.056	-6.568	<0.001
Diet (herbivore)	-0.494	0.175	-2.818	0.005
Diet (insectivore)	-0.140	0.171	-0.820	0.412
Diet (omnivore)	-0.349	0.137	-2.540	0.011
Habitat (generalist)	-0.166	0.159	-1.041	0.298
Habitat (open)	-0.440	0.104	-4.213	<0.001
Habitat (water)	0.003	0.166	0.015	0.988

Mahalonobis distance ANOVA table	DF	F-value	p-value
Intercept	1	279.549	<0.001
Migration distance	1	116.014	<0.001
Body mass (log)	1	53.663	<0.001
Diet	3	4.084	0.007
Habitat preference	3	7.088	<0.001

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
Intercept	-0.877	0.591	-1.485	0.138
Migration distance	<0.001	<0.001	8.900	<0.001
Body mass (log)	0.264	0.057	4.643	<0.001
Diet (herbivore)	-0.016	0.177	-0.091	0.928
Diet (insectivore)	0.193	0.173	1.115	0.265
Diet (omnivore)	0.143	0.139	1.028	0.304
Habitat (generalist)	-0.231	0.161	-1.437	0.151
Habitat (open)	-0.380	0.106	-3.600	<0.001
Habitat (water)	-0.144	0.168	-0.855	0.393

Determinant ratio ANOVA table	DF	F-value	p-value
Intercept	1	0.697	0.404
Migration distance	1	98.287	<0.001
Body mass (log)	1	34.321	<0.001
Diet	3	1.794	0.147
Habitat preference	3	4.462	0.004

Table S4. Model tables (pgls and ANOVA) summarizing functional trait drivers of locational niche position similarity across species in multivariate models.

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-1.038	0.651	-1.595	0.111
Migration distance	<0.001	<0.001	-4.012	<0.001
Body mass (log)	0.314	0.063	5.002	<0.001
Diet (herbivore)	-0.116	0.195	-0.591	0.555
Diet (insectivore)	-0.063	0.191	-0.329	0.742
Diet (omnivore)	-0.046	0.153	-0.301	0.763
Habitat (generalist)	0.626	0.177	3.531	<0.001
Habitat (open)	0.491	0.116	4.221	<0.001
Habitat (water)	0.152	0.185	0.819	0.413

Mahalonobis distance ANOVA table	DF	F-value	p-value
Intercept	1	8.175	0.004
Migration distance	1	23.076	<0.001
Body mass (log)	1	24.569	<0.001
Diet	3	0.089	0.966
Habitat preference	3	8.545	<0.001

Table S5. Model tables (pgls) summarizing functional trait drivers of seasonal niche position and breadth similarity across species in univariate models.

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-6.405	0.432	-14.817	<0.001
Migration distance	<0.001	<0.001	10.133	<0.001

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-4.296	0.585	-7.348	<0.001
Body mass (log)	-0.382	0.058	-6.633	<0.001

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
(Intercept)	-5.507	0.547	-10.060	<0.001
Diet (herbivore)	-0.777	0.195	-3.980	<0.001
Diet (insectivore)	-0.065	0.193	-0.334	0.738
Diet (omnivore)	-0.478	0.149	-3.206	0.001

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-6.515	0.463	-14.072	<0.001
Habitat (generalist)	-0.414	0.178	-2.332	0.020
Habitat (open)	-0.456	0.117	-3.887	<0.001
Habitat (water)	-0.075	0.186	-0.401	0.689

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
Intercept	0.687	0.427	1.610	0.108
Migration distance	<0.001	<0.001	9.563	<0.001

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
Intercept	-1.646	0.579	-2.842	0.005
Body mass (log)	0.306	0.057	5.369	<0.001

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
(Intercept)	0.271	0.534	0.508	0.612

Diet (herbivore)	-0.024	0.190	-0.127	0.899
Diet (insectivore)	0.312	0.188	1.658	0.098
Diet (omnivore)	0.387	0.145	2.663	0.008

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
Intercept	0.640	0.451	1.419	0.156
Habitat (generalist)	-0.439	0.173	-2.535	0.011
Habitat (open)	-0.465	0.114	-4.067	<0.001
Habitat (water)	0.025	0.182	0.139	0.890

Table S6. Model tables (pgls) summarizing functional trait drivers of seasonal niche position similarity across species in univariate models.

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	1.108	0.469	2.362	0.019
Migration distance	<0.001	0.000	-4.643	<0.001

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-0.576	0.607	-0.949	0.343
Body mass (log)	0.288	0.060	4.810	<0.001

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
(Intercept)	1.029	0.569	1.809	0.071
Diet (herbivore)	0.137	0.203	0.675	0.500
Diet (insectivore)	-0.109	0.200	-0.544	0.586
Diet (omnivore)	0.104	0.155	0.669	0.504

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	1.012	0.471	2.148	0.032
Habitat (generalist)	0.710	0.181	3.925	<0.001
Habitat (open)	0.462	0.119	3.871	<0.001
Habitat (water)	0.221	0.190	1.167	0.244

Table S7. Metrics describing phylogenetic signal in seasonal niche tracking. Asterisks denote significance level (*** < 0.001 < ** < 0.01 < * < 0.05).

	Blomberg's K		Lambda	
	Seasonal dissimilarity	**Locational dissimilarity**	**Seasonal dissimilarity**	**Locational dissimilarity**
Mahalonobis distance	0.083***	0.115***	0.664***	0.663***
Determinant Ratio	0.057*		0.278***	

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