1 **Diverse strategies for tracking seasonal environmental niches at hemispheric scale**

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3 **Jeremy Cohen*[1,2] & Walter Jetz[1,2]**

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5 [1]Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New
6 Haven, CT, 06520 USA
7 [2]Center for Biodiversity and Global Change, Yale University, 165 Prospect Street, New Haven,
8 CT, 06520 USA

9

10 *Correspondence to: jeremy3cohen@gmail.com

11

12 **Author emails (in order of authorship):** jeremy3cohen@gmail.com, walter.jetz@yale.edu

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14 **Author statement:** All authors agreed to submission of the manuscript and accept the
15 responsibility for the accuracy and integrity of the manuscript.

16

17 **Author contributions:** All authors devised ideas for the study. JMC compiled annotated GBIF
18 data. JMC calculated niche similarity metrics. JMC accessed functional trait databases and
19 harmonized phylogenetic information. JMC conducted statistical analyses and generated figures.
20 All authors helped write the manuscript.

21

22 **Keywords:** Environmental niche, climatic niche, hypervolume, seasonal niche tracking, birds,
23 big data, seasonality, migration, functional trait groups, phylogenetic signal, GBIF

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25

26   **Abstract:**

27

28   Species depend upon a constrained set of environmental conditions, or niches, for survival and
29   reproduction that are increasingly lost under climatic change. Seasonal environments require
30   species to either track their niches via movement or undergo physiological or behavioral changes
31   to survive. Here we identify the tracking of both environmental niche position and breadth across
32   619 New World bird species and assess their phylogenetic and functional underpinning.
33   Partitioning niche position and breadth tracking can inform whether climatic means or extremes
34   limit seasonal distributions. We uncover diverse strategies, including the tracking of niche
35   position, breadth, both, or neither, suggesting highly variable sensitivity to ongoing climatic
36   change. There was limited phylogenetic determinism to this variation, but a strong association
37   with functional attributes that differed between niche position and breadth tracking. Our findings
38   imply significant functional consequences for communities and ecosystems as impending climate
39   change affects some niche tracking strategies more than others.

40

41 **Introduction**

42

43 Species survive and reproduce under a specific set of environmental conditions, known as the
44 environmental niche or *n*-dimensional hypervolume (Blonder et al. 2014; Hutchinson 1957; Lu,
45 Winner, and Jetz 2021). In seasonal environments, species must adjust to a constantly shifting
46 window of available conditions through one of several strategies. When remaining stationary,
47 species must either maintain tolerance to a wide range of conditions or undergo physiological
48 and behavioral changes to survive seasonal variation, known as 'niche switching' (Nakazawa et
49 al. 2004). Alternatively, seasonally mobile animals can occupy a dynamic niche that remains
50 relatively narrow across the annual cycle, known as 'niche tracking' (Gómez et al. 2016;
51 Somveille, Rodrigues, and Manica 2018; Winger et al. 2019). Seasonal niche tracking is central
52 to the persistence of species with limited behavioral or physiological capacity to adjust their
53 niches (Fandos et al. 2020; Zurell et al. 2018). Understanding the functional and phylogenetic
54 drivers of niche tracking behavior across diverse species can allow researchers to predict how
55 species mediate exposure to novel, potentially adverse conditions as climate change progresses
56 (Tingley et al. 2009; La Sorte and Jetz 2012; Somveille, Rodrigues, and Manica 2015).

57 After the documentation of seasonal niche tracking behavior in single species (Fandos et al.
58 2020) and smaller clades (Gómez et al. 2016; Eyres et al. 2020), a more general understanding of
59 the patterns, causes and consequences of seasonal niche tracking across diverse taxonomic
60 groups remains missing. For example, the role of phylogeny and functional traits in driving
61 seasonal niche tracking across a diverse species set remains largely unexplored (but see Zurell et
62 al. 2018). Several studies have hypothesized that niche tracking may be phylogenetically
63 conserved (Gómez et al. 2016; Martínez–Meyer, Townsend Peterson, and Navarro–Sigüenza
64 2004), as is typical of behavioral and migratory traits (Outlaw and Voelker 2006), but this has
65 not been evaluated rigorously or broadly. Alternatively, niche tracking may have repeatedly
66 evolved in tandem with species' functional traits. For example, obligate insectivores or small-
67 bodied species may be most likely to closely track their niche over the annual cycle to satisfy
68 narrow dietary or thermal requirements (Gómez et al. 2016; Huey et al. 2012). Separating these
69 potential drivers will allow researchers to better predict niche flexibility and niche tracking, and
70 thus climate change vulnerability, among rare species or those from under-sampled regions.

71 Previous work on niche tracking has focused on seasonal similarity in niche positions, or mean
72 environmental conditions, without accounting for niche components such as niche breadth (the
73 volume or range of tolerable conditions). However, niche breadth is a central additional
74 dimension because climate change is altering both the means and variances of climatic
75 conditions (Rahmstorf and Coumou 2011). For example, species may seasonally track niche
76 breadth instead of changing the central niche position when extremes are more limiting to their
77 survival and reproductive success than climatic means, as is the case for numerous species
78 (Albright et al. 2010; Ummenhofer and Meehl 2017). Thus, species may use the tracking of
79 niche breadth as an alternative strategy to niche position tracking to persist in the face of

80   seasonality, one unexplored by the existing niche tracking literature, which instead considers
81   niche breadth as an annually static variable (Gómez et al. 2016; Zurell et al. 2018). To better
82   identify complex variation in niche tracking, seasonal niche similarity should be partitioned into
83   constituent components, including *niche position similarity*, or the distance between niche
84   centroids, representing the difference between the average conditions a species experiences in
85   each season; and *niche breadth similarity*, or the proportional difference in niche breadths (Lu,
86   Winner, and Jetz 2021), representing the range of conditions a species can tolerate.
87   Hypervolumes quantified using non-parametric techniques, such as kernel-density estimates or
88   support vector machines (Blonder 2018; Brown, Holland, and Jordan 2020), are difficult to
89   partition into constituent components. However, recently developed parametric methods for
90   quantifying the niche allow for partitioning of these components and direct hypothesis testing
91   against predictions derived from theories (Lu, Winner, and Jetz 2021).

92   We use these new metrics to distinguish five primary strategies for seasonal niche tracking (Fig.
93   1; Fig. 2): i) "Non-trackers" retain neither the position nor the breadth of their niches over the
94   annual cycle; ii) "Breadth trackers", or "position shifters", track niche breadth but shift their
95   position, suggesting that their seasonal ranges may be limited by environmental variation; iii)
96   "Position trackers", or "breadth expanders", track only niche position and adjust niche breadth
97   between seasons and may be seasonally limited by environmental means; Finally, "complete
98   trackers" track both niche position and breadth, but may do so by either iv) migrating to track
99   weather conditions across the annual cycle or v) remaining stationary in an aseasonal
100   environment.

101   However, a simple comparison of niche space during the breeding and overwintering seasons
102   (henceforth, *seasonal* niche similarity) cannot fully distinguish these strategies (Fig.1b, columns
103   4-5), despite obviously divergent dispersal capability and potential for climate change adaptation
104   (Eyres et al. 2020). We therefore consider an additional metric, *locational* niche similarity, in
105   which the realized overwintering hypervolume is compared with that had the species remained at
106   its breeding range, its *stationary winter niche* (Fig. 1c). This measure, which emphasizes the
107   similarity of conditions at specific locations, is important for understanding seasonal niche
108   tracking because it accounts for the environmental distance covered by the species through
109   purposeful movement. Among temperate breeders, seasonal and locational niche similarity are
110   likely to have an inverse relationship; for example, a niche tracking species with little difference
111   between its breeding and overwintering niche is likely to experience highly distinct
112   overwintering conditions compared with those at its breeding sites.

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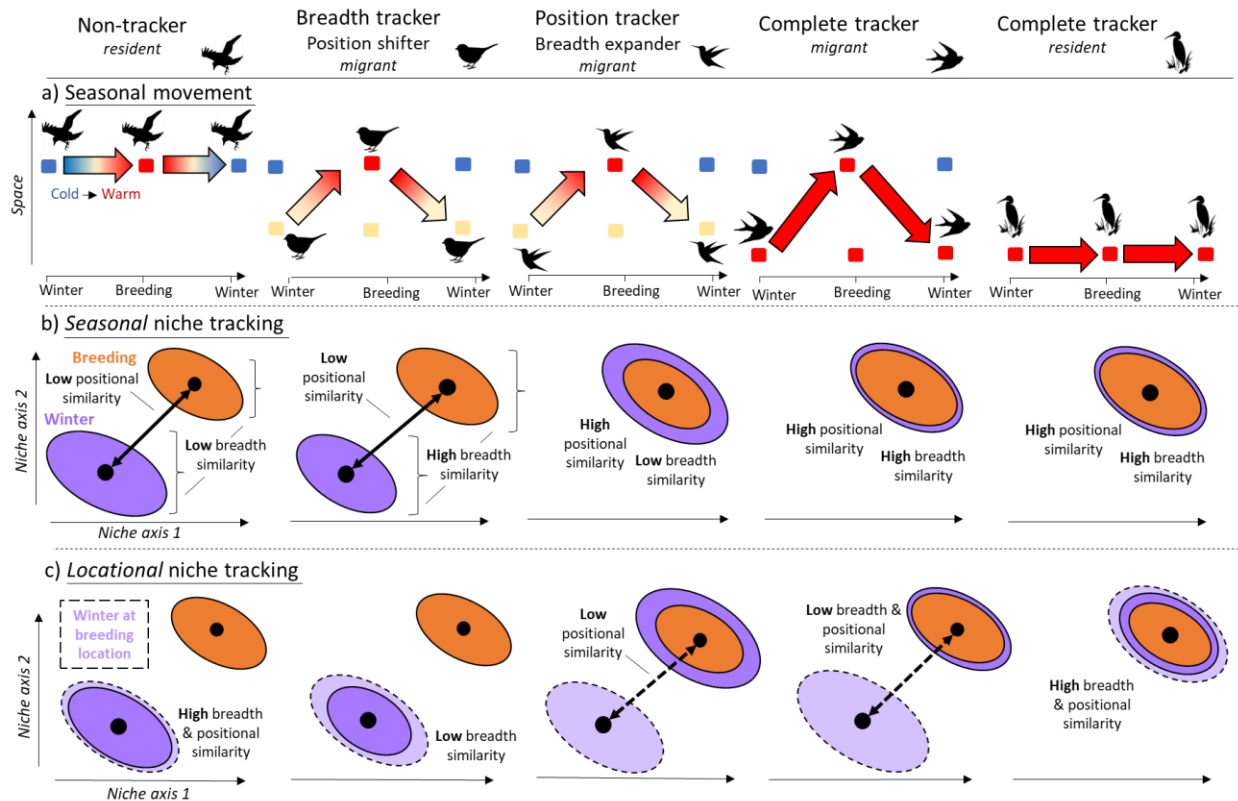
Figure 1: A typology of seasonal niche tracking strategies. Seasonal niche similarity is decomposed into two components, similarity in niche position and niche breadth. A given species may (1) be a non-tracker, tracking neither niche position or breadth, (2) track niche breadth, but shift position, (3) track niche position, but expand 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.
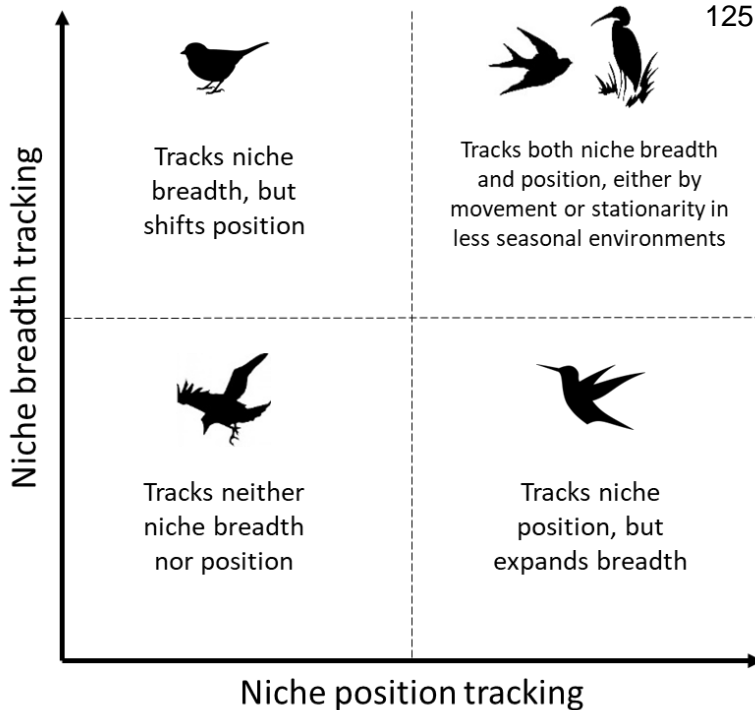
Figure 2. Five niche tracking strategies. Conceptual schematic outlining the contribution of niche breadth and position tracking to each of five possible niche tracking strategies.

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 while accounting for both niche position and breadth? To date, a quantitative multi-species assessment of strategies across a diverse taxonomic group has been missing.

2) What is the relationship between the tracking of niche position and the tracking of niche breadth? Do species that maximize niche positional similarity across seasons also tend to retain similar niche breadth, or do species largely track only one or the other?

144   3) How phylogenetically and functionally determined are niche tracking strategies? Across
145   functional trait groups, we hypothesize seasonal niche tracking to be most common in a) long-
146   distance migrants, because they can physically relocate to suitable locations (Laube, Graham,
147   and Böhning-Gaese 2015; Zurell et al. 2018); b) small-bodied species, because they have low
148   thermal inertia and generally narrow thermal breadths (Huey et al. 2012; Albright et al. 2017),
149   suggesting they cannot tolerate large seasonal variation in the niche; c) insectivores, because
150   abundant insect prey is only available under specific temperature, precipitation and productivity
151   levels (Winkler, Luo, and Rakhimberdiev 2013); and d) species occupying open or water
152   habitats, because they are not shielded from climate variability by forest structure (Jarzyna et al.
153   2016). Given that behavioral and migratory traits are often phylogenetically conserved (Outlaw
154   and Voelker 2006), we expect a strong phylogenetic signal in seasonal niche tracking behavior
155   (Gómez et al. 2016).

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

161   We expect the emerging insights to not only address these questions but more generally offer an
162   assessment of seasonal niche dynamics as a system to understand realized strategies for
163   mitigating exposure to climatic change.
164
165   **Material and Methods**
166
167   *Species selection and environmental data*

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

175   In August 2021, we accessed the Spatiotemporal Observation Annotation Tool (STOAT) v1.0, a
176   novel cloud-based toolbox for flexible biodiversity annotations (Li et al. 2021), to download
177   annotated Global Biodiversity Information Facility data (https://www.gbif.org/) for all species
178   (data compilation, analyses and visualizations were all completed in R 4.1.0; R Core Team
179   2021). To minimize the potential for spatiotemporal sampling bias, we then thinned points by
180   selecting one point from each location (5x5km grid cell) per week.

181 We annotated observation points with three environmental dimensions: daily maximum
182 temperature (sourced from NASA-MODIS; https://lpdaac.usgs.gov/products/mod11a1v006/),
183 enhanced vegetation index (EVI; from MODIS), and precipitation (from CHELSA v2.1; Karger
184 et al. 2021), each summarized to a 1km buffer (0.5km radius) over 30 days prior to the
185 observation (imported using jsonlite and httr packages; Ooms 2014; Wickham and Wickham
186 2020). We did not assess *a priori* whether these variables are equally relevant across species; for
187 example, certain species may be limited by precipitation but not temperature within their range,
188 or *vice versa*. Alternatively, some species may be limited by environmental factors not
189 considered in our estimation of species niches. However, this variable set represents the
190 environmental factors that most commonly drive species distributions (Qian 2010), and these
191 variables have low collinearity, allowing each axis to remain independent. Estimating niches
192 with the same variable set for all species was necessary to ensure consistency in cross-species
193 evaluation of seasonal changes to both niche position and breadth.

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

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

205 *Ecological niche modeling and seasonal similarity*

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

215 To quantify seasonal similarity, we calculated positional and breadth similarity between the
216 breeding and overwintering seasonal hypervolumes. To quantify locational similarity, we
217 calculated positional similarity between the overwintering hypervolume and available

218 hypervolume during winter at breeding locations. Thus, we had a total of three metrics of

219 seasonal niche similarity per species. We visualized pairwise two-dimensional hypervolumes for

220 each species using *ggplot2* (Wickham 2011).

Functional traits and phylogeny

222 We obtained species-level functional trait values and an avian phylogenetic tree to test

223 associations between trait groups, phylogeny, and seasonal niche tracking. We derived migration

224 distances from (La Sorte et al. 2022; La Sorte personal communication), body mass from the

225 Eltonian trait database (Wilman et al. 2014), and habitat preference and diet from Barnagaud et

226 al. (2017). We grouped several categories of each categorical predictor to avoid false positives

227 associated with small sample sizes and to keep our conclusions broad. Diet categories included

228 carnivore, invertebrate, omnivore, and herbivore (combining 'fruit', 'nectar', 'vegetation', and

229 'seed' categories). Habitat categories included water ('coastal', 'open_water',

230 'riparian_wetlands'), open ('semi-open', 'rock', 'arid'), generalist ('urban', 'developed'), and

231 forest.

232 We updated an avian phylogeny from Jetz et al. (2012) to account for recent taxonomic changes,

233 updating species names to the Clements bird taxonomy as of 2021 (Clements 2007) and treating

234 recently split species as having no phylogenetic distance (Appendix 2). We also harmonized

235 species names in all trait datasets to Clements.

Cross-species models

237 To assess the role of functional traits in seasonal niche tracking, we used weighted multivariate

238 phylogenetic generalized least squares (PGLS) models (caper package; Orme et al. 2013).

239 Phylogenetically correlated model errors in PGLS account for the non-independence of the

240 species due to their phylogenetic relatedness (Symonds and Blomberg 2014). The dependence of

241 the model errors arises from trait axes that we did not include in the analysis and that may be

242 subject to niche conservatism so that model errors reflect the unobserved trait and thus the

243 phylogenetic distance between species. We used species' similarity in niche position and breadth

244 as the response variables in the models and explained their variation with categorical trait

245 variables. Prior to use in models, continuous predictor variables (migration distance and log-

246 transformed body mass) were scaled to improve model fit and response variables were log-

247 transformed and sign-flipped (representing niche similarity rather than dissimilarity) to improve

248 interpretability. We weighted all species points in models by log-transformed minimum sample

249 size (number of points in the season with less data) to account for uncertainty in seasonal niche

250 dissimilarity estimates (true error estimates are unavailable when estimating niche dissimilarity).

251 We fit three models testing the relationships between the four functional traits and three metrics

252 of niche similarity: seasonal niche position similarity, seasonal niche breadth similarity, and

253 locational niche position similarity. To evaluate the reliability of multivariate models, we also fit

254 univariate models for each combination of functional trait predictor and response variable.

255   To measure the role of phylogeny in both positional and breadth similarity, we quantified
256   Blomberg's K (Blomberg, Garland Jr et al. 2003) and compared it to a null distribution of K after
257   randomizing species' responses 1,000 times (picante package; Kembel et al. 2010). K < 1
258   suggests greater than expected phylogenetically-correlated variance within clades, while K > 1
259   suggests variance among clades (i.e., phylogenetically-conserved trait). We also quantified
260   lambda to assess the extent of phylogenetic conservation of niche metrics via Brownian motion.
261   We visualized relationships between niche metrics and functional traits using *ggplot2* (Wickham
262   2011), *ggExtra* (Attali and Baker 2019) and *RcolorBrewer* (Neuwirth and Neuwirth 2011). We
263   visualized partial residuals using *visreg* (Breheny, Burchett, and Breheny 2020).

264
265   **Results**
266
267   We found all five niche-tracking strategies represented among North American birds (Fig 3). For
268   example, Red-bellied woodpeckers (*Melanerpes carolinus*; Fig. 3a) are largely stationary birds
269   occupying highly seasonal environments, with low seasonal similarity between their breeding
270   and overwintering niches, but high locational similarity between their overwintering and
271   stationary winter niches. In contrast, Pine grosbeaks (*Pinicola enucleator*; Fig. 3b) are short-
272   distance migrants and "breadth trackers", tracking niche breadth while shifting position across
273   seasons. Migratory Swainson's thrushes (*Catharus ustulatus*; Fig. 3c) are "position trackers",
274   tracking their niche position across seasons, but expanding their niche during the breeding
275   season. Prothonotary warblers (*Protonotaria citrea*; Fig. 3d) are long-distance migrants that
276   abandon breeding territories to closely track both niche components across seasons, resulting in
277   high seasonal and low locational similarity. Finally, Great kiskadees (*Pitangus sulphuratus*; Fig.
278   3e) are stationary tropical residents with conserved niches across the annual cycle, resulting in
279   both high seasonal and high locational similarity. We select these species for visualizations
280   because they represent each strategy well in both two-dimensional niche space (temperature and
281   EVI only; Fig. 3) and three-dimensional space (remainder of results).

282
283   The 619 bird species analyzed spanned the full diversity of niche tracking strategies (Fig. 4;
284   Appendix 1). Across seasons, the median positional similarity (-log[Mahalonobis distance]) was
285   -1.95 +/- 0.05 SE (i.e., centroids approximately 3 SDs apart), suggesting that many species are
286   not closely tracking this niche attribute over the annual cycle (Ponti et al. 2020). For 60 species
287   (9.7%), centroids were within 1 SD, suggesting highly similar niches in each season for this
288   subset. The median among-season similarity in niche breadth was 2.17 +/- 0.03, equivalent to a
289   4:1 ratio in niche breadth between seasons, suggesting that many species expand their niche
290   breadths as they traverse seasons. 129 species (22%) had a niche breadth similarity equivalent to
291   a < 2:1 ratio, suggesting similarly-sized seasonal niches.
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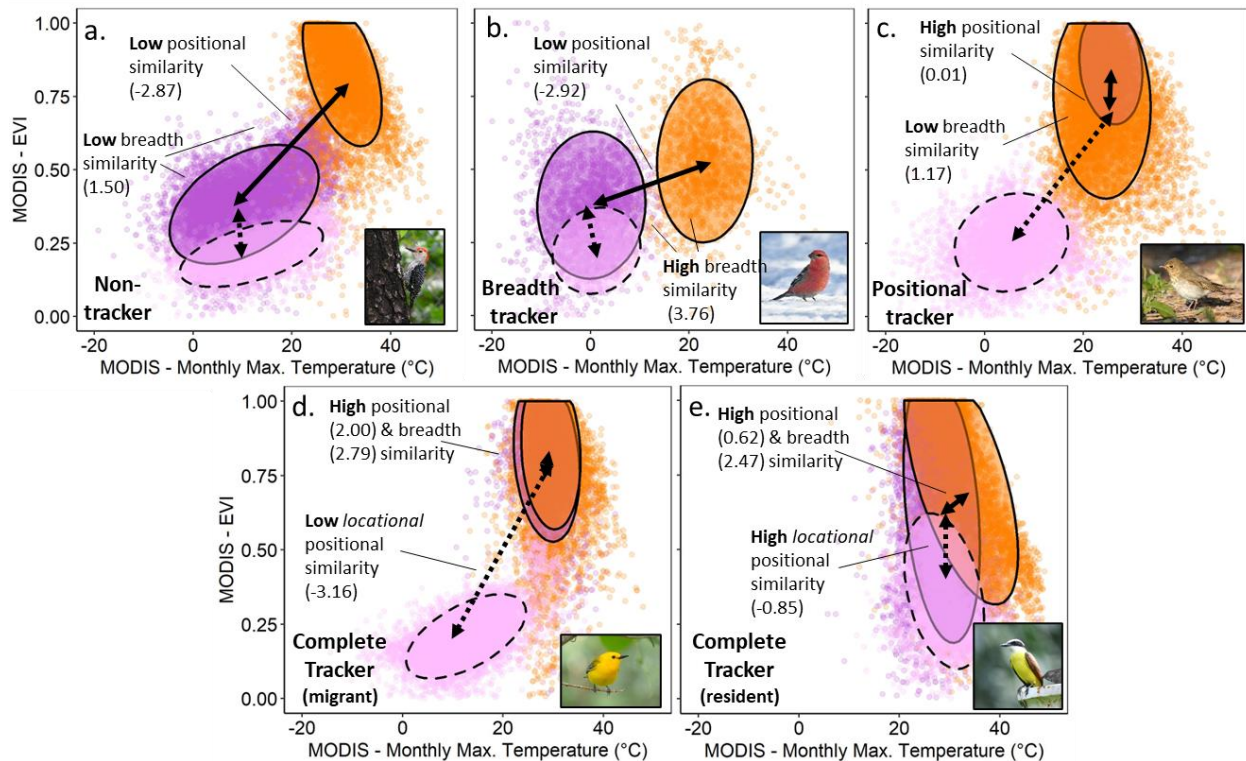
Figure 3: Diverse niche tracking strategies. (**a**) Red-bellied woodpeckers (*Melanerpes carolinus*) are non-trackers, with low *seasonal* similarity (solid arrow) between their breeding (orange points and ellipsoid) and overwintering (dark purple) two-dimensional niche (presented as standardized ellipse area). Meanwhile, the difference between their overwintering niche and winter conditions at breeding locations (light purple, dotted ellipsoid), or *locational* similarity (dotted arrow), is high. (**b**) Pine grosbeaks (*Pinicola enucleator*) track their niche breadth but shift position across seasons, while (**c**) Swainson's thrushes (*Catharus ustulatus*) track their niche position but expand niche 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. Note that this figure displays two-dimensional niche space, though our statistical analyses consider three-dimensional niches, including precipitation as additional dimension.

Tracking niche position was loosely tied to tracking niche breadth; species that tracked niche position more often tracked niche breadth, and *vice versa* (Generalized linear model: β=0.179, R^2=0.073, p<0.001; Fig. 4). 170 (27.5%) species were "complete" niche trackers, tracking both position and breadth more than most species (positive values on both axes in Fig. 4), while 209 (33.8%) were non-trackers, tracking both less than others (negative values in Fig. 4). However, numerous species tracked one but not the other (Fig. 4), suggesting a complex diversity of approaches to seasonal niche tracking across bird species. Only 80 species (12.9%) tracked niche

316 position but expanded breadth, while double that number – 160 (25.8%) – tracked breadth but
317 shifted position.
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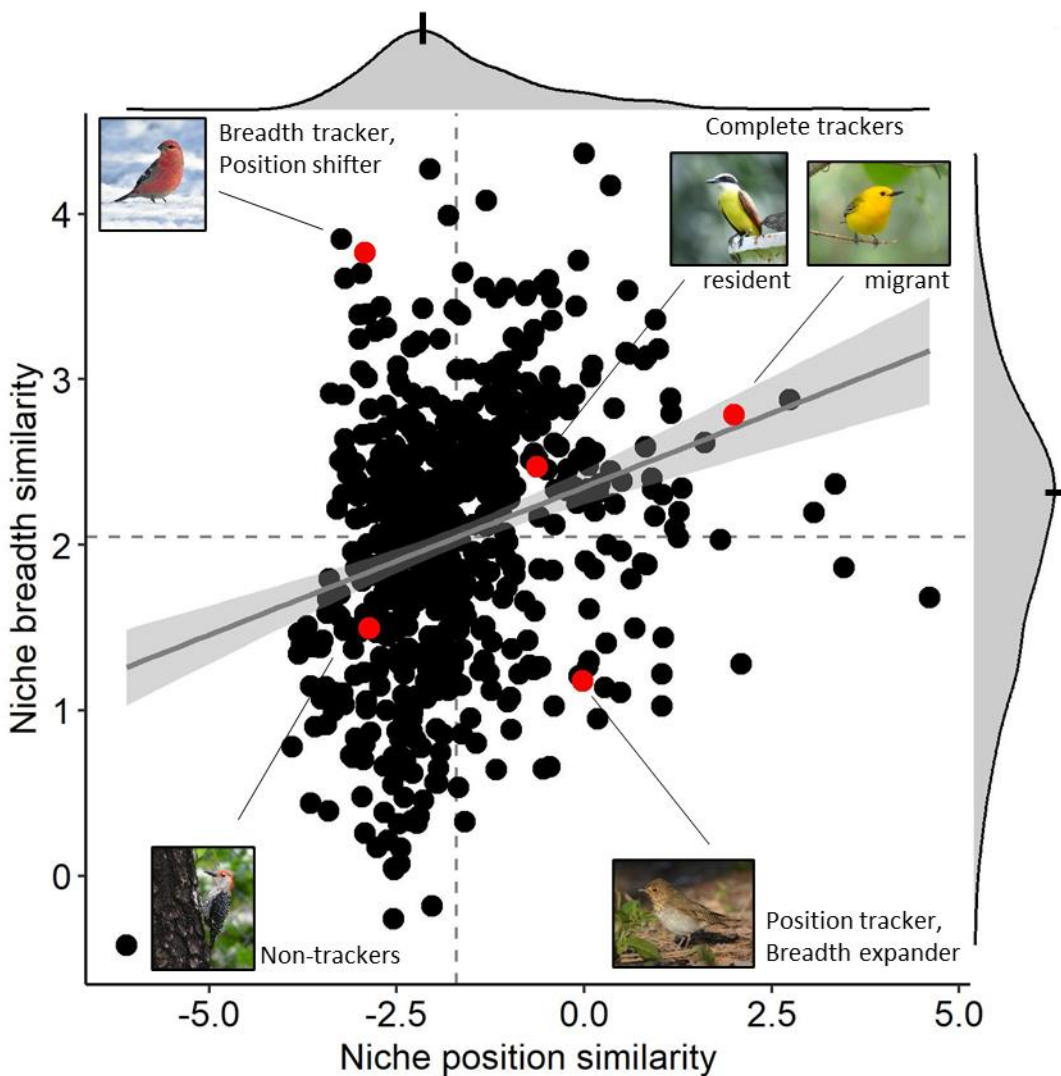
319
320 **Figure 4: Interspecific variation in tracking niche position and breadth across seasons.** The figure
321 shows niche similarities between the breeding and overwintering seasons for the 619 bird species
322 analyzed based on three niche dimensions (for red highlights, see Fig. 3). Strategies of tracking niche
323 position, breadth, both, or neither are partitioned into four categories (boxes separated by dashed lines).
324 Dashed lines highlight the means. Marginal density plots illustrate that species tracking only one niche
325 component often track niche breadth more closely than niche position, with medians represented by
326 notches. The trendline represents a linear relationship between niche position and breadth similarity with
327 associated 95% confidence interval (shading). See Fig. S2 for equivalent patterns for locational similarity.
328
329 We found seasonal niche tracking strategies to be closely associated with functional traits, and
330 their role to be consistent across weighted multivariate models accounting for all traits and
331 phylogenetic structure simultaneously (Fig. 5; Tables S1-S2) as well as univariate models

332   (Tables S3-S4). As expected, both niche positional and breadth similarity were very strongly

333   linked to migration distance (Phylogenetic generalized least-squares models: position, β=0.43,

334   p<0.001; breadth, β=0.25, p<0.001), which was the strongest functional predictor; long-distance

335   migrants were most likely to maximize similarity, while residents minimized similarity and

336   others fell in the middle (Fig. 5a,d). Body mass emerged as another important functional

337   predictor of seasonal niche tracking, especially with regards to positional similarity. Body mass

338   negatively predicted niche position similarity (β=-0.80, p<0.001) and was positively associated

339   with breadth similarity (β=0.53, p<0.001). Small-bodied birds maximized seasonal similarity,

340   while large-bodied birds minimized it (Fig. 5b,e). Finally, both diet ($F_{1,3}$=5.70, p<0.005) and

341   habitat preference ($F_{1,3}$=9.68, p<0.001) categories described variation in positional similarity,

342   though only habitat preference drove breadth similarity ($F_{1,3}$=10.15, p<0.005). As predicted,

343   insectivores maximized positional and breadth similarity, herbivores minimized these, and

344   omnivores fell in the middle (Fig. 5c,g). Waterbirds tracked their niches more closely than other

345   species (Fig. 5d,h).

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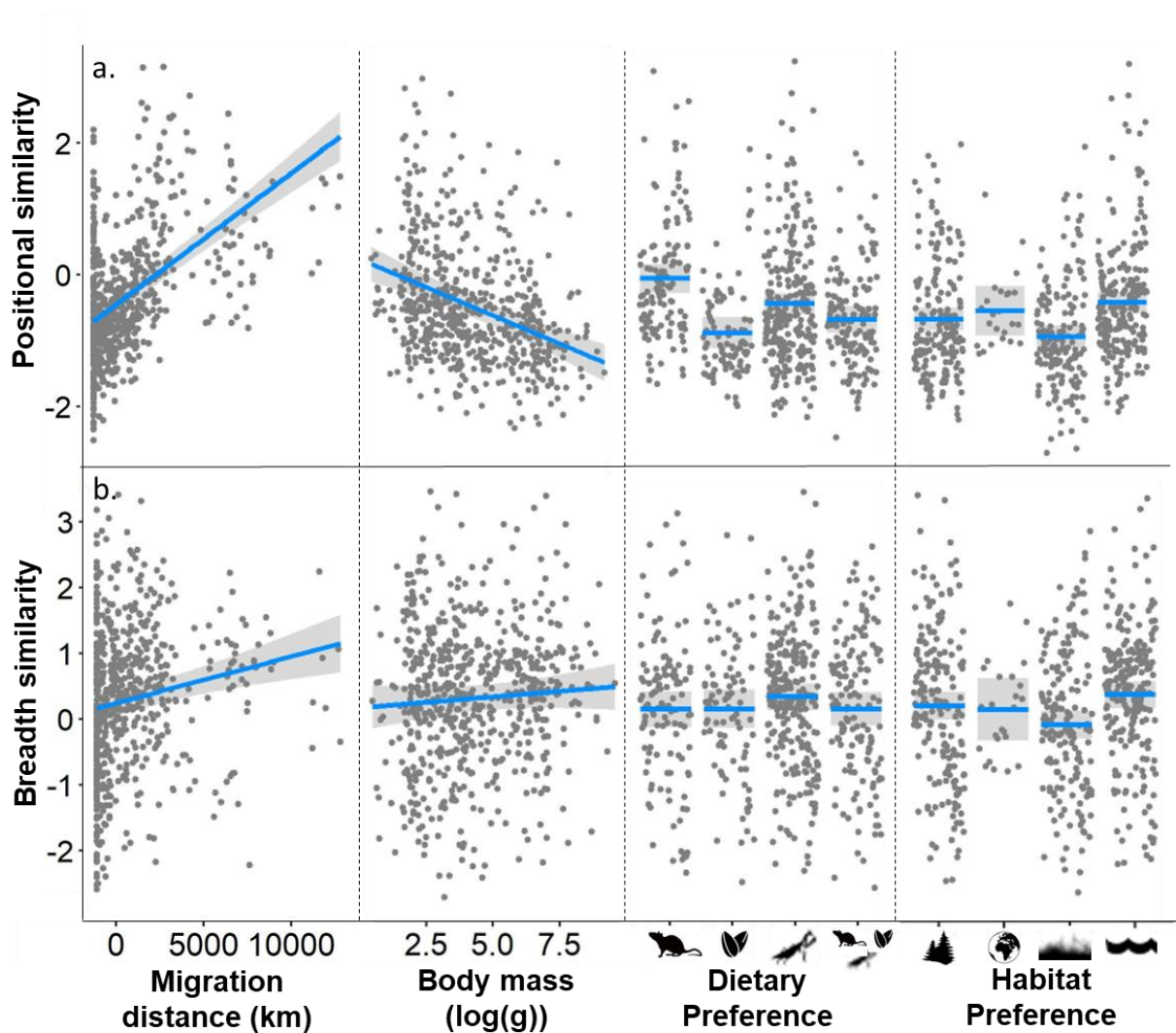
Figure 5: Functional traits predict variation in seasonal niche tracking, as shown by partial residual plots based on phylogenetic least-squares models. Y-axis values represent (a) positional and (b) breadth similarity. Silhouettes correspond to categorical functional trait values as follows: Dietary 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 S5) and did not support Ornstein-Uhlenbeck trait evolution. Measurements of lambda indicated a moderate phylogenetic signal for species tracking niche position (λ=0.66, p<0.001), suggesting possible Brownian-motion trait evolution, but little signal for niche breadth (λ=0.28, p<0.001).

362   Species that maximized seasonal niche similarity typically minimized locational niche similarity,
363   and vice versa (β=-0.408, R^2=0.237, p<0.001; Fig. S1). For locational similarity, the link
364   between tracking niche position and niche breadth was stronger than for seasonal similarity, with
365   42% of species tracking both components and 29% neither (Fig. S2). Only 15% of species
366   tracked locational niche position but not breadth, and 13% tracked locational breadth but not
367   position. Likewise, relationships between functional traits and locational positional similarity
368   were generally opposite to those observed with seasonal positional similarity. Long-distance
369   migrants (β=-0.331, p<0.001), small-bodied birds (β=0.95, p<0.001), and waterbirds ($F_{1,3}$=7.75,
370   p<0.001) each minimized locational positional similarity, though we found no effect of diet. As
371   with seasonal similarity, we found no evidence for a phylogenetic signal in locational niche
372   similarity (Table S5).

373

374

375   **Discussion**

376   For mobile organisms, seasonal niche tracking is a central part of the behavioral repertoire for
377   mediating exposure to novel climate conditions. Here, we assessed the representation of distinct
378   seasonal niche tracking strategies across North American breeding birds and evaluated the
379   functional and phylogenetic drivers of these strategies. Our analyses revealed five distinct
380   seasonal niche tracking strategies and their key functional drivers. We find that only a bit more
381   than half of species can be categorized as either "complete trackers", tracking both niche position
382   and breadth across seasons, or "non-trackers", tracking neither. However, almost 40% of species
383   only track niche position or breadth, revealing complexity in niche tracking strategies that is
384   previously unexplored in niche-tracking studies. Twice as many species tracked only niche
385   breadth (26%) compared with those that tracked niche position and expanded niche breadth
386   (13%), suggesting that tracking breadth is often a prerequisite for tracking position and that birds
387   may be most specialized in terms of the range of environmental conditions they can tolerate
388   rather than means. Importantly, niche tracking studies that do not consider niche breadth would
389   likely have labeled the 26% of species that are niche breadth trackers as non-trackers, ignoring
390   the role that niche breadth tracking and expansion plays in allowing species to persist over
391   seasons. Species limited by extreme or highly variable weather conditions rather than climatic
392   means may be more apt to prioritize niche breadth tracking while allowing niche position to
393   seasonally fluctuate. Meanwhile, a species with inflexible thermal or dietary requirements that is
394   specialized only during certain parts of the year (e.g., due to strict breeding requirements) may
395   track niche position but not breadth. However, further work is needed to pinpoint the ecological
396   motivations behind selection of breadth tracking as a niche tracking strategy.

397   We found that migration distance was the most important functional driver of seasonal niche
398   tracking, despite this link previously receiving mixed support among cross-species niche tracking
399   studies (Zurell et al. 2018; Laube, Graham, and Böhning-Gaese 2015; Gómez et al. 2016).
400   Although several studies (Gómez et al. 2016; Laube, Graham, and Böhning-Gaese 2015) failed

401   to detect a link between migration and niche tracking, their approaches compared species within
402   single families, including residential species that are exclusively tropical. Because these residents
403   occupy relatively stable environments, they can track their niches despite being stationary (Eyres
404   et al. 2020). This example helps illustrate why migration distance and niche tracking are less
405   correlated than might be expected – tropical residents can track their niches well despite their
406   stationarity, while long-distance migrants may experience high seasonal variation despite their
407   migration if they annually move between arctic breeding grounds and boreal or temperate
408   wintering grounds. Indeed, although migration distance was the strongest correlate of seasonal
409   niche tracking in our study, the correlation was moderate (R^2=0.249).
410
411   Body size was revealed as the next most important functional trait associated with seasonal niche
412   tracking when controlling for other traits. Small-bodied birds may not be able to tolerate large
413   variation in their thermal niches because they have low thermal inertia (Huey et al. 2012;
414   Albright et al. 2017). Further, small-bodied animals have shown greater sensitivity to extreme
415   weather events (Cohen, Fink, and Zuckerberg 2021) and more rapidly alter phenological timing
416   in tune with interannual weather variability (Cohen, Lajeunesse, and Rohr 2018) compared with
417   large-bodied animals, suggesting that they must carefully maintain thermal limits. Additionally,
418   small-bodied birds may be more likely to evolve niche-tracking strategies dependent on seasonal
419   migration because long-distance flight carries lower energetic costs than it does for large birds
420   (Watanabe 2016).
421
422   Finally, diet and habitat preference were additional meaningful drivers of seasonal niche tracking
423   behavior, with insectivores and carnivores tracking their niches more than herbivores and
424   omnivores, and waterbirds more so than other species. Insectivores may prioritize niche-tracking
425   because they are dependent upon prey that is most commonly available under specific thermal
426   and productivity limits (Winkler, Luo, and Rakhimberdiev 2013). Surprisingly, carnivores
427   tracked their niche positions even more closely than insectivores, but many of these species are
428   predating on herpetofauna also active during warm weather. Though we predicted both open and
429   water habitat specialists to be the strongest niche trackers, as they are less shielded from the
430   external environment by habitat structure (Jarzyna et al. 2016), only water birds tracked their
431   niche more closely than other groups (Fig 4d,h). Bird species that occupy open habitats may
432   make greater use of microhabitat structure than water birds, which are typically exposed (e.g.,
433   (Shew, Nielsen, and Sparling 2019)).
434
435   Although many studies have assumed seasonal niche tracking to be phylogenetically conserved
436   (Gómez et al. 2016; Martínez–Meyer, Townsend Peterson, and Navarro–Sigüenza 2004), this
437   has not to our knowledge been evaluated over a large, diverse taxonomic group such as North
438   American breeding birds. There are several explanations as to why we did not detect a
439   phylogenetic signal. First, migratory behavior has arisen in numerous, diverse lineages of birds,
440   and is flexible even within species (Zink 2011). Second, closely related species often occupy

441 distinct climatic zones that vary greatly in seasonality, especially if speciation resulted from
442 character displacement (Newton 2003). Finally, species-level exposure to and adaptation
443 potential for climate change may be quite independent from phylogeny (Khaliq et al. 2015;
444 Davis et al. 2010). Based on our analyses, we conclude that functional traits likely play a larger
445 role than phylogeny in driving seasonal niche tracking in birds.
446
447 Complex variation among niche tracking strategies cannot fully be assessed via seasonal niche
448 comparisons; for example, a species that niche-tracks via movement and a stationary species in
449 an aseasonal environment have similar seasonal niches. To parse these strategies, we estimated
450 locational niche similarity, or the similarity between overwintering niches and the *stationary*
451 *winter niche* for each species. Species with high seasonal similarity often had low locational
452 similarity, and *vice versa*, reflecting a trade-off between conserving niches and ranges
453 throughout the annual cycle. While many species tracked only niche position or breadth between
454 seasons, species adhered to locationally tracking both or neither components much more often,
455 with few tracking just one. Therefore, species may be leaving breeding areas in winter for the
456 purposes of modifying both the mean and variance of environmental conditions. We observed
457 several key differences between functional trait relationships and either seasonal or locational
458 niche similarity. For instance, migration distance and body size were equally important as drivers
459 of locational niche similarity, possibly because large-bodied birds are especially reluctant to
460 energetically invest in movement (Watanabe 2016). Further, in contrast with seasonal niche
461 similarity, there was no effect of diet on locational similarity, perhaps because food availability
462 depends more on environmental conditions themselves rather than the distance birds travel to
463 track them. Thus, we demonstrate the importance of considering both seasonal and locational
464 similarity in species niches to understand variation in niche tracking strategies.
465
466 We estimated niche metrics at the species level to effectively compare niche tracking strategies
467 across a taxonomic group as broad and diverse as birds and to make use of the enormous
468 quantity of available species-level occurrence data. However, we did not explore niche variation
469 as experienced at lower levels of organization, including populations, demographic groups, and
470 individuals (Fandos et al. 2020; Fandos and Tellería 2020; Carlson et al. 2021). Populations of
471 species with wide geographic ranges might be adapted to highly distinct environmental
472 conditions (Broggi et al. 2005). Within a population, demographic groups can also occupy
473 different niches – sexes can occupy spatially distinct regions during the nonbreeding season, or
474 young can be shielded in microclimate during breeding season (Shipley et al. 2020). Finally,
475 individuals may track different niche components than populations (Fandos et al. 2020) or might
476 have strong variation in their ecological niches during different parts of the year and thus vary in
477 niche-tracking. For example, individual white storks (*Ciconia ciconia*) and sandhill cranes
478 (*Antigone canadensis*) range from subtropical residents to short-distance migrants to longer-
479 distance migrants moving between northern temperate and tropical zones each year (Krapu et al.
480 2014; Fandos et al. 2020; Carlson et al. 2021). Summarizing niche tracking strategies at the

481 species level may limit our inferential ability in two ways: 1) species-level niche breadth is likely

482 greater than individual niche breadth given variability in individual niches (Carlson et al. 2021),

483 and 2) the accuracy of species-level niche centroids for individuals likely depends on the

484 variation in climate zones at which the species exists, so long as individuals and populations are

485 locally adapted (Araújo and Costa-Pereira 2013). Although most occurrence data is still available

486 at the species level, new technologies such as GPS tracking offer exciting opportunities for

487 assessing individual niches over time and across hierarchies of organismal organization (Jetz et

488 al. 2022; Costa-Pereira et al. 2022) and complement the presented species-level findings.

489

490 As climate change progresses, species are increasingly being exposed to conditions that are quite

491 different from those to which they have adapted (Pacifici et al. 2015). Gradual shifts in range

492 boundaries or phenology allow species to keep pace with long-term changes in climatic means

493 (La Sorte and Jetz 2012; Rushing et al. 2020; Koleček, Adamík, and Reif 2020). However, niche

494 tracking is an important tool for species to buffer both the changing mean environmental

495 conditions and increasing interannual variability associated with climate change by selecting

496 optimal environmental conditions over short time scales (Román-Palacios and Wiens 2020),

497 especially for species with narrow thermal or habitat requirements. Our findings reveal a broad

498 diversity in niche tracking strategies and uncover important functional trait associations with

499 migratory behavior and body size. This has ecological consequences for the assemblages and

500 ecosystems that will see different functional perturbations due to the different susceptibility of

501 niche tracking strategies to climatic change (Barbet-Massin and Jetz 2015). For example, as

502 niche tracking becomes more difficult with climate change, small-bodied and insectivorous birds

503 may be especially likely to fail to maintain their niches, resulting in proportional declines of

504 these species relative to the broader avian community assemblage.

505

506 Thus, we provide a framework for future studies to assess the degree of tracking both niche

507 position and breadth and capability for climate change adaptation in many other species globally,

508 including those from understudied regions with limited available data. However, additional work

509 is needed to assess how species have already been keeping up with climate change that has

510 occurred. Understanding how climate change is modifying species' ability to conserve their

511 niches will be a critical step towards determining which species are most likely to adapt to

512 increasing short-term variability in climate.

513

514

515 **Acknowledgements**

516

521 distances. We acknowledge funding from NSF grant DEB-1441737 and NASA grants
522 80NSSC17K0282 and 80NSSC18K0435.
523

524 **Data Sharing and Accessibility**
525

526 GBIF data is available for public use online at https://www.gbif.org/. Code generated to conduct
527 the analyses will be made available in a public repository such as Dryad or Figshare.
528

529 **References**
530

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697

Supporting Information

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

Jeremy Cohen*[1,2] & Walter Jetz[1,2]

[1]Department of Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New Haven, CT, 06520 USA
[2]Center for Biodiversity and Global Change, Yale University, 165 Prospect Street, New Haven, CT, 06520 USA

*Correspondence to: jeremy3cohen@gmail.com
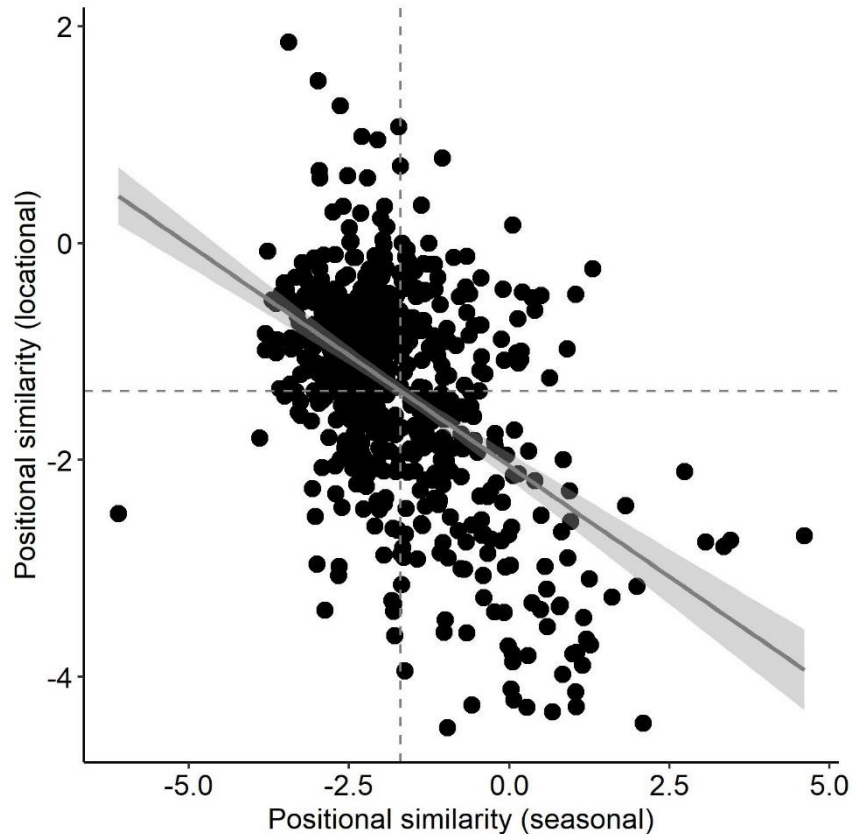
Figure S1. Seasonal and locational niche centroid similarity are inversely related. Niche-tracking species maximize niche similarity between breeding and nonbreeding seasons (defined as seasonal similarity, x-axis) and minimize the similarity between the nonbreeding season niche and the stationary winter 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.
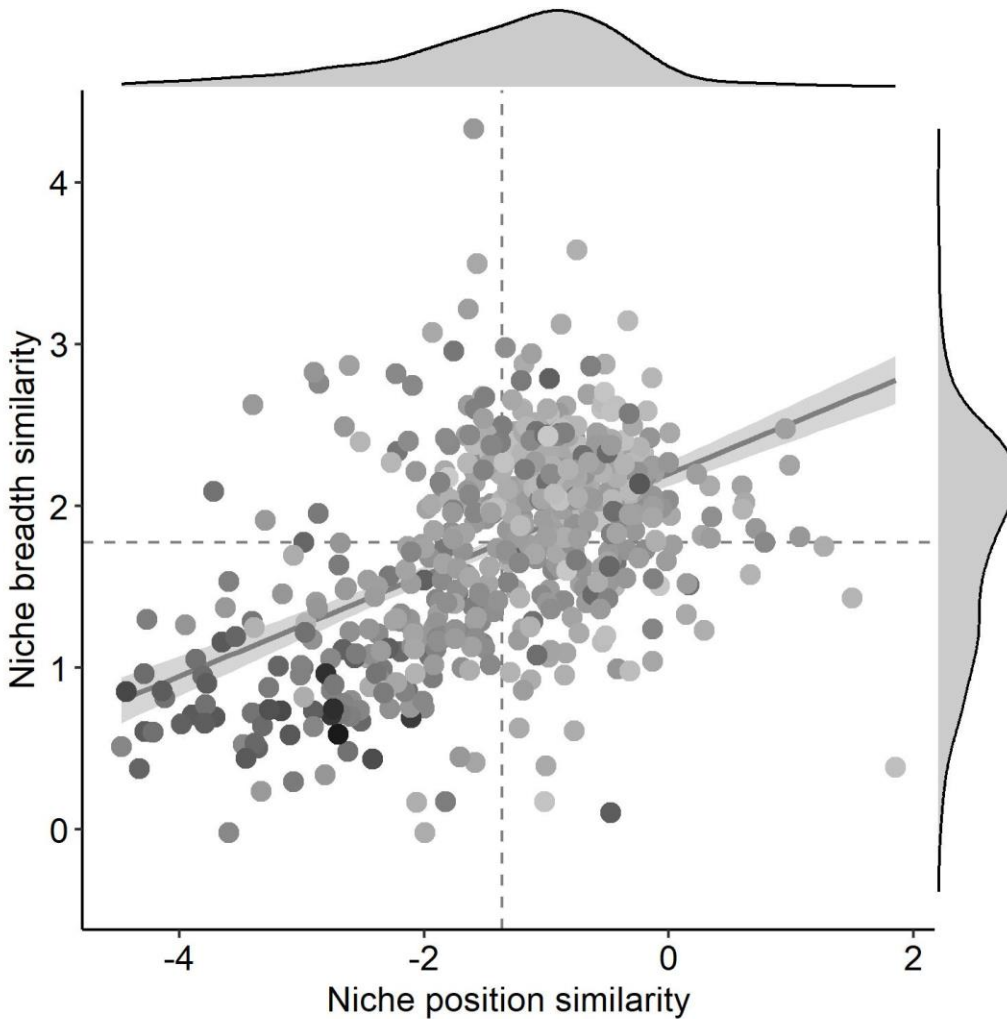
Figure S2: Interspecific variation in locational niche tracking of niche position and breadth.
Locational niche similarity represents the similarity of the overwintering niche to the winter conditions at breeding locations. Points represent species-level variation in locational similarity of niche position 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.

Appendix 1. 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.

(appendix_1.csv)

Appendix 2. 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.

(appendix_2.csv)

Table S1. 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	-1.745	0.270	-6.472	<0.001
Migration distance	0.428	0.041	10.359	<0.001
Body mass (log)	-0.798	0.097	-8.233	<0.001
Diet (herbivore)	-0.647	0.178	-3.626	<0.001
Diet (insectivore)	-0.048	0.177	-0.275	0.784
Diet (omnivore)	-0.394	0.139	-2.836	0.005
Habitat (generalist)	0.001	0.174	0.005	0.996
Habitat (open)	-0.381	0.110	-3.470	0.001
Habitat (water)	0.364	0.172	2.110	0.035

Mahalonobis distance

ANOVA table	DF	F-value	p-value
Intercept	1	121.713	<0.001
Migration distance	1	197.317	<0.001
Body mass (log)	1	93.094	<0.001
Diet	3	5.702	0.001
Habitat preference	3	9.675	<0.001

Determinant ratio

PGLS table	Coefficient	SE	t-value	p-value
Intercept	1.360	0.262	5.183	<0.001
Migration distance	0.250	0.040	6.212	<0.001
Body mass (log)	0.525	0.094	5.565	<0.001
Diet (herbivore)	-0.053	0.174	-0.305	0.760
Diet (insectivore)	0.206	0.172	1.196	0.232
Diet (omnivore)	0.102	0.135	0.754	0.451
Habitat (generalist)	-0.081	0.169	-0.481	0.631
Habitat (open)	-0.400	0.107	-3.738	<0.001
Habitat (water)	0.319	0.168	1.905	0.057

Determinant ratio

ANOVA table	DF	F-value	p-value
Intercept	1	185.261	<0.001
Migration distance	1	37.702	<0.001
Body mass (log)	1	51.669	<0.001
Diet	3	2.201	0.087

Habitat preference	3	10.145	<0.001

Table S2. 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	0.182	0.282	0.645	0.519
Migration distance	-0.331	0.043	-7.660	<0.001
Body mass (log)	0.952	0.101	9.389	<0.001
Diet (herbivore)	-0.215	0.187	-1.155	0.249
Diet (insectivore)	-0.176	0.185	-0.956	0.340
Diet (omnivore)	-0.092	0.145	-0.637	0.524
Habitat (generalist)	0.822	0.182	4.519	<0.001
Habitat (open)	0.415	0.115	3.609	<0.001
Habitat (water)	0.515	0.180	2.861	0.004

Mahalonobis distance

ANOVA table	DF	F-value	p-value
Intercept	1	11.162	0.001
Migration distance	1	111.730	<0.001
Body mass (log)	1	111.154	<0.001
Diet	3	0.703	0.551
Habitat preference	3	7.757	<0.001

Table S3. 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	-3.060	0.214	-14.291	0.000
Migration distance	0.539	0.042	12.747	0.000

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-1.039	0.219	-4.744	0.000
Body mass (log)	-1.057	0.097	-10.883	0.000

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
(Intercept)	-1.254	0.257	-4.876	0.000
Diet (herbivore)	-1.287	0.202	-6.380	0.000
Diet (insectivore)	0.085	0.208	0.410	0.682
Diet (omnivore)	-0.681	0.155	-4.409	0.000

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-1.864	0.260	-7.168	0.000
Habitat (generalist)	-0.356	0.211	-1.684	0.093
Habitat (open)	-0.375	0.134	-2.796	0.005
Habitat (water)	0.121	0.208	0.578	0.563

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
Intercept	1.891	0.201	9.393	<0.001
Migration distance	0.229	0.040	5.770	<0.001

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
Intercept	1.938	0.201	9.659	<0.001
Body mass (log)	0.480	0.089	5.397	<0.001

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
(Intercept)	2.092	0.227	9.213	<0.001
Diet (herbivore)	0.071	0.178	0.401	0.688
Diet (insectivore)	0.354	0.183	1.934	0.054
Diet (omnivore)	0.435	0.136	3.190	0.001

Determinant ratio PGLS table	Coefficient	SE	t-value	p-value
Intercept	2.304	0.218	10.572	<0.001
Habitat (generalist)	-0.161	0.177	-0.909	0.364
Habitat (open)	-0.437	0.113	-3.881	<0.001
Habitat (water)	0.499	0.175	2.858	0.004

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

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	1.485	0.224	6.643	<0.001
Migration distance	-0.424	0.044	-9.610	<0.001

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	-0.357	0.215	-1.658	0.098
Body mass (log)	1.119	0.095	11.721	<0.001

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
(Intercept)	0.331	0.265	1.252	0.211
Diet (herbivore)	0.521	0.208	2.510	0.012
Diet (insectivore)	-0.255	0.214	-1.194	0.233
Diet (omnivore)	0.351	0.159	2.207	0.028

Mahalonobis distance PGLS table	Coefficient	SE	t-value	p-value
Intercept	0.091	0.256	0.354	0.723
Habitat (generalist)	1.068	0.208	5.124	<0.001
Habitat (open)	0.408	0.132	3.085	0.002
Habitat (water)	0.774	0.205	3.770	<0.001

Table S5. 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***	