

1 **Title: Spatial and seasonal variation in thermal sensitivity within North American bird**
2 **species**

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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 **Author contributions:** All authors devised research ideas. JMC compiled eBird data and
17 environmental data. JMC conducted species distribution models and statistical analyses, with
18 input from DF and BZ. All authors wrote the manuscript.

19

20 **Short Title:** Spatiotemporal variation in thermal sensitivity

21 **Keywords:** birds, citizen science, climate change, eBird, macroecology, random forest, species
22 distribution models, thermal sensitivity, thermal ecology, non-stationarity

23 **Article Type:** Letter

24 **Word Count (Abstract):** 150

25 **Word Count (Main Text):** 5125

26 **References:** 57

27 **Figures:** 5

28 **Tables:** 0

29

30 **Data Accessibility Statement:** The data supporting the results will be archived in an appropriate
31 public repository such as Dryad or Figshare and the data DOI will be included at the end of the
32 article.

33

34 **Abstract:**

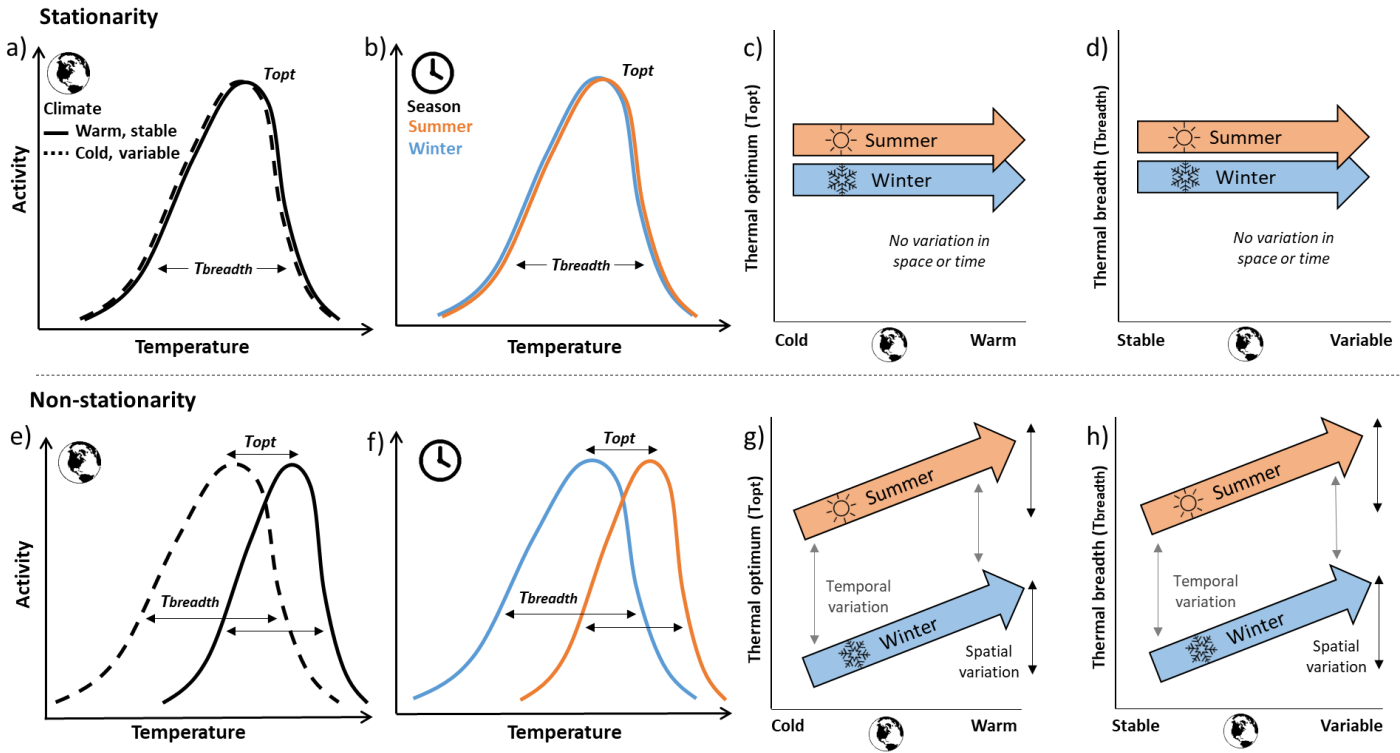
35 Responses of wildlife to climate change are typically quantified at the species level, but
36 physiological evidence suggests significant intraspecific variation in thermal sensitivity (non-
37 stationarity) given adaptation to local and seasonal environments. Non-stationarity carries
38 important implications for climate change vulnerability; for instance, sensitivity to extreme
39 weather may increase in specific regions or seasons. Here, we leverage high-resolution
40 observational data from eBird to understand regional and seasonal variation in thermal sensitivity
41 for 20 bird species. Across their ranges, most birds demonstrated spatial and seasonal variation in
42 both thermal optimum and breadth, or the temperature and range of temperatures of peak
43 occurrence. Some birds demonstrated constant thermal optima or breadths (stationarity) while
44 others varied according to local and current environmental conditions (non-stationarity). Across
45 species, birds typically invested in either geographic or seasonal adaptation to climate.
46 Intraspecific variation in thermal sensitivity is likely an important but neglected aspect of
47 organismal responses to climate change.

48 **Introduction**

49 Anthropogenic climate change is impacting wildlife at all organizational levels, from individuals
50 to populations to species (Scheffers et al., 2016), representing a leading conservation priority for
51 wildlife management (Abrahms et al., 2017; LeDee et al., 2021). Using traditional species
52 distribution models or ecological niche models, ecologists typically operate at the species level to
53 quantify responses to the thermal environment and predict the consequences of climate change
54 (Smith et al., 2019). These approaches generally ignore adaptive capacity and phenotypic
55 plasticity within species, implicitly assuming that thermal sensitivity, or the influence of
56 temperature on behavior, performance, or fitness, is stationary (static) in both space and time
57 (Jarnevich et al., 2015; Smith et al., 2019). However, emerging physiological evidence suggests
58 that populations of a species may be locally adapted to distinct thermal conditions depending on
59 the climate zones they inhabit, and individuals may dynamically alter their response to seasonal
60 changes in temperature via phenotypic flexibility (Bennett et al., 2019; Louthan et al., 2021;
61 Stager et al., 2021). Approaches assuming constant thermal sensitivity across continental spatial
62 extents and the full annual cycle may thus be inadequate to account for the full spectrum of
63 responses to climate change exhibited by a given species (Sultaire et al., 2022). As organisms
64 increasingly face novel climates, understanding variation in thermal sensitivity within species
65 will provide more detailed insights about which populations are most impacted by changing
66 climatic conditions or extreme weather (Louthan et al., 2021; Smith et al., 2019).

67 Populations within a species are likely to exhibit non-stationarity in thermal sensitivity across
68 space and time due to physiological mechanisms and constraints (Bennett et al., 2019; Louthan et
69 al., 2021; Stager et al., 2021; Youngflesh et al., 2022; Fig. 1). Across geographic gradients,
70 populations of wide-ranging species are likely adapted to local climatic conditions (Atkins and
71 Travis, 2010; Stager et al., 2021). Physiological studies have suggested that within species,
72 southern and lowland populations adapted to warm climates demonstrate warmer optimum
73 thermal performance temperatures when compared with northern and high-elevation populations
74 that demonstrate cooler optimums (Richardson et al., 2014; Zillig et al., 2021). Thermal breadth,
75 or the range of tolerable conditions, is associated with the level of variability in the local climate,
76 with ‘thermal specialists’ being found in more stable climates and ‘thermal generalists’ found in
77 more variable climates (Bozinovic et al., 2011; Stevens, 1989). Given that climatic variability is
78 increasing with climate change (Cai et al., 2022; La Sorte et al., 2021; Pendergrass et al., 2017),
79 these findings highlight the importance of considering population-level variation in thermal
80 breadth (Stager et al., 2021). In seasonal environments, non-migratory organisms must adapt to
81 variable weather across the annual cycle via phenotypic plasticity, often undergoing behavioral
82 and physiological changes (foraging during different times of day, seeking out refugia, gaining
83 fat reserves, etc.) to cope with cold winter temperatures (Jimenez et al., 2020; Laplante et al.,
84 2019). Indeed, physiological studies have revealed that organisms often fluctuate in thermal
85 sensitivity depending on time of year (Doucette and Geiser, 2008; Hopkin et al., 2006).

86



87

88 **Figure 1. Non-stationarity in thermal sensitivity.** Conceptual schematic of spatial and seasonal patterns in
 89 the thermal sensitivity of a species given (a-d) the assumption of stationarity, or lack of variability in thermal
 90 sensitivity within a species, and (e-h) non-stationarity or variation in space and time. In (a,e) curves represent
 91 hypothetical relationships between temperature and activity levels in a warm, stable climate (solid line) or
 92 cold, variable climate (dotted line). In (b,f) curves represent seasons (summer, orange; winter, blue). In right
 93 panels, variation in thermal optimum (T_{opt} , temperature of peak activity; c,g) and thermal breadth ($T_{breadth}$,
 94 range of temperatures at which activity is high; d,h) is driven by climate context only in the non-stationarity
 95 scenario. Black arrows represent the degree of spatial non-stationarity in thermal optimum or breadth, while
 96 gray arrows represent seasonal non-stationarity between seasons.

97

98 Together, evidence from physiological and behavioral studies suggests that non-stationarity in
 99 thermal sensitivity may be widespread, especially among species that occur across a wide
 100 latitudinal or elevational gradient or occupy seasonal environments (Bennett et al., 2019;
 101 Louthan et al., 2021). However, it remains unclear to what extent spatial and seasonal non-
 102 stationarity exists and whether its presence is similar across species (Louthan et al., 2021). Thus,
 103 studies are needed that can determine whether species demonstrate stationarity, meaning
 104 consistent thermal sensitivities across their ranges, or non-stationarity, where sensitivity is
 105 primarily driven by the local environment. Field- or lab-based studies conducted with one or few
 106 species (i.e., most physiological and behavioral studies) rarely capture spatial and seasonal
 107 variation in thermal sensitivity across many species occupying broad geographic regions and are
 108 unable to assess the extent to which non-stationarity is associated with certain traits across
 109 species. To evaluate the stationarity of species' responses to their thermal environments, these

110 relationships must be modeled at high temporal resolutions (to capture dynamic changes in
111 temperature) across multiple seasons, and with high spatial resolution across broad geographic
112 extents to characterize the responses of regionally distinct populations.

113 Across species, variation in thermal sensitivity may be mediated by morphological or life history
114 traits (Ryding et al., 2021). For example, larger-bodied species are more common in cooler
115 climates due to their ability to retain heat more effectively (Bergmann's Rule; Bergmann, 1848)
116 and larger appendages are important for effective heat dissipation for species in warmer climates
117 (Allen's Rule; Allen, 1877). Habitat specialists, which are more often thermal specialists than
118 generalists (Barnagaud, Devictor et al. 2012), and species occupying forested or urban habitats,
119 which may have more microclimates to buffer environmental conditions than open/grassland
120 species (Jarzyna, Zuckerberg et al. 2016), may also be likely to exhibit high spatial and seasonal
121 variation in thermal sensitivity. Thus, we hypothesize that non-stationarity is greatest in birds
122 that 1) are small-bodied, 2) have smaller appendages, 3) are habitat specialists, and 4) occupy
123 forested or urban habitats. Understanding which species have greater non-stationarity in thermal
124 sensitivity – including both thermal optimum and breadth – is an important step towards
125 anticipating organismal responses to climate change. For such species, a cold-adapted northern
126 population may be more sensitive to warming events than a warm-adapted southern population,
127 and a population from a stable climate may be more sensitive to increasing temperature
128 variability than a population from a variable climate.

129 Here, our goal was to analyze how sensitivity to the thermal environment varies across species'
130 ranges and between seasons by quantifying it at high resolution across space and time. Our
131 approach modelled the association between species occurrence rates and daily temperature and
132 used this information to estimate population-level parameters of thermal performance. We
133 measure thermal sensitivity as both thermal optimum, or the temperature at which a species
134 occurs most often, and thermal breadth, or the range of temperatures at which a species occurs at
135 80% of its maximum rate, with daily occurrence rate as a measure of behavioral activity (Cohen
136 et al., 2020) (Fig. 1). We used North American bird species as a case study because they are
137 highly detectable and demonstrate strong sensitivity to weather and climate (Knudsen et al.,
138 2011). We focused on 20 bird species from across the United States that met the following
139 criteria: 1) broad ranges spanning latitudinal and climate zones, enabling comparisons of
140 populations occupying diverse climates; 2) year-round presence in most of their range, enabling
141 direct comparisons of similar populations over different seasons; and 3) ranges that overlap,
142 minimizing variation in available thermal conditions between species that could account for
143 differing relationships between activity levels and climatic conditions. Thus, differences in non-
144 stationarity across species (e.g., if one species demonstrates stationarity and another with nearly
145 the same range demonstrates non-stationarity) are a consequence of an organismal response to
146 temperature and not simply a reflection of available conditions.

147 Specifically, we pose the following questions:

- 148 1. Do species vary in thermal sensitivity across their ranges (spatial non-stationarity)?
- 149 2. Do birds vary in thermal sensitivity across seasons (seasonal non-stationarity)?
- 150 3. Do species with greater spatial non-stationarity have greater seasonal non-stationarity?
- 151 Species that exhibit high spatial and seasonal non-stationarity likely have increased
- 152 adaptive capacity whereas a negative relationship suggests a trade-off (e.g., a species
- 153 with high seasonal non-stationarity is less reliant on local adaptation).
- 154 4. Is non-stationarity mediated by species' traits or phylogeny?

155 To address our questions, we present a novel analytical framework for exploring thermal
156 sensitivity based on observational data from eBird, a citizen science initiative in which users
157 submit bird sightings (Sullivan et al., 2014). eBird is especially useful for our approach because
158 it has a massive data volume in the US (over 500 million records) with dense coverage, and
159 observations are collected throughout the year, at all times of day (La Sorte et al., 2018). We
160 leverage this dataset to identify regional and seasonal non-stationarity in thermal sensitivity for
161 20 species, fitting random forest models as dynamic species distribution models (SDMs) within a
162 STEM wrapper (Fink et al., 2020, Spatio-Temporal Exploratory Models; 2010). STEM is an
163 ensemble modeling approach that fits regional SDMs over broad spatial extents, allowing
164 relationships between weather conditions and observations to vary spatially. We fit models using
165 data across the full annual cycle and generated predictions for both the summer and winter
166 seasons. In doing so, we quantified associations between species occurrence and daily
167 temperature at local and seasonal scales to assess non-stationarity across a continental extent
168 encompassing ~900 million km². Finally, we examined trait and phylogenetic associations with
169 non-stationarity at the species level.

170

171 **Materials and Methods**

172 *eBird observational data*

173 Our overarching goal was to examine spatial and seasonal variation in the responses of North
174 American bird species to variation in daily temperature. We compiled all 'complete checklists'
175 contributed to eBird in the contiguous United States (bounding box with dimensions 25° to 47°
176 N and 60° to 125° W) between 2004-2018. When submitting 'complete checklists', users
177 indicate that all identified species were recorded, allowing the inference of non-detection for
178 presence-absence modeling. We applied a number of filters to the data in accordance with
179 established best practices outlined in Johnston et al. (Johnston et al. 2019). We limited checklists
180 to "traveling" or "stationary" observations, excluding exhaustive area-counts, which are less
181 numerous and not directly comparable with the bulk of the eBird dataset. In all checklists,
182 subspecies information was discarded, and observations were summarized at the species level.
183 Likewise, we excluded checklists with extreme high values of effort (> 3 hours or > 5 km
184 traveled, to mitigate positional uncertainty in eBird data) or extreme Checklist Calibration Index
185 (CCI) scores (z-score < -4 or > 4), an index designed to capture inter-observer variation among

186 eBird checklists (Johnston et al. 2019). To mitigate site selection and temporal bias, we also
187 filtered eBird checklists by randomly selecting one observation per 5 km² grid cell during each
188 calendar week (Johnston et al. 2019). Database management was completed using *tidyverse*
189 packages (Wickham et al., 2019).

190 *Distribution models*

191 We included environmental features in each model to account for the many factors that influence
192 species' detection and occurrence rates. To account for variation in detection rates associated
193 with search effort, and varying activity levels among birds at different times of the day and
194 among observers, we included time spent birding, number of birders, whether a checklist was
195 categorized as traveling or stationary, distance traveled, and CCI as features in species
196 distribution models (SDMs, see below) following established best practices for modeling eBird
197 data (Johnston et al. 2019). Further, we accounted for seasonal and daily timing by including
198 calendar date and the time difference from solar noon in models.

199 To account for species preferences in landscape composition and configuration, we gathered land
200 and water cover and topographic data corresponding to each checklist. We obtained annual
201 landcover data from the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover
202 Type (MCD12Q1) Dataset, version 6
203 (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd12q1). For each
204 checklist, we calculated the proportion of land and water classes within a neighborhood with 1.4
205 km radius occupied by a variety of landcover types (Hansen et al., 2000), including grasslands,
206 croplands, mixed forests, woody savannahs, urban/built, barren, evergreen broadleaf, evergreen
207 needle, deciduous broadleaf, deciduous needle, closed shrubland, open shrubland, herbaceous
208 wetlands, and open savannah. Land-cover data varied annually, although we used 2017 land-
209 cover values for checklists recorded in 2018. We also collected topographical information
210 (median aggregations of elevation, eastness, northness, roughness, and topographic position
211 index or TPI at a 1 km² resolution) from the Global Multi-Terrain Elevation Dataset, a product of
212 the U.S. Geological Survey and the National Geospatial-Intelligence Agency (Danielson and
213 Gesch, 2011).

214 Daily mean temperatures and total daily precipitation corresponding to each checklist were
215 compiled from Daymet, a high-resolution, interpolated grid-based product from NASA that
216 offers daily, 1 km² scale weather data across North America (Thornton et al., 2017). To account
217 for the climate zone of each observation point, we included mean seasonal (DJF=winter,
218 MAM=spring, JJA=summer, SON=fall) temperature and precipitation (via Worldclim; Fick and
219 Hijmans, 2017) as additional features in random forests. The spatial resolution of our
220 environmental features is similar to the typical radius of search effort in eBird checklists within
221 our filters (Auer et al. *pers. comm.*).

222 *Species distribution models: Random Forest*

223 The objective of the analysis was to study the relationship between species' local occurrence
224 rates and daily temperature for widespread, commonly detected species. We modeled responses
225 to daily temperature in common, widespread species with sufficient data to ensure enough power
226 to detect regional-scale variation in the relationships between temperature and occurrence across
227 the study extent. We excluded long-distance migratory species from our analysis because winter
228 and summer populations at the same locations are not directly comparable, although our species
229 do move semi-locally within our spatial extent. Within the eastern or western US and Canada,
230 we selected species with sympatric ranges to ensure that species-level differences in spatial and
231 seasonal thermal sensitivity were not due to differences in weather availability. We divided the
232 continent in this way to increase the similarity and overlap between species' range extents. In the
233 east ($< 100^\circ$ W), we modeled Northern cardinal (*Cardinalis cardinalis*), Blue jay (*Cyanocitta*
234 *cristata*), American crow (*Corvus brachyrhynchos*), Mourning dove (*Zenaida macroura*), White-
235 breasted nuthatch (*Sitta carolinensis*), Black-capped chickadee (*Poecile atricapillus*), Carolina
236 chickadee (*Poecile carolinensis*), Tufted titmouse (*Baeolophus bicolor*), Carolina wren
237 (*Thryothorus ludovicianus*), Downy woodpecker (*Dryobates pubescens*), Hairy woodpecker
238 (*Dryobates villosus*), Red-bellied woodpecker (*Melanerpes carolinus*), and Northern
239 mockingbird (*Mimus polyglottos*). In the west ($> 100^\circ$ W), we modeled Mountain chickadee
240 (*Poecile gambeli*), Chestnut-backed chickadee (*Poecile rufescens*), Pygmy nuthatch (*Sitta*
241 *pygmaea*), Bewick's wren (*Thryomanes bewickii*), Black-billed magpie (*Pica hudsonia*), Steller's
242 jay (*Cyanocitta stelleri*), Anna's hummingbird (*Calypte anna*), and Acorn woodpecker
243 (*Melanerpes formicivorus*).

244 For each species, we individually fit occurrence models using Random Forests (RF; ranger
245 package; Wright et al., 2018), a flexible machine learning method that has been used in a number
246 of species distribution modeling problems (Mi et al., 2017) and is designed to analyze large
247 datasets with many features, adjust automatically to complex, nonlinear relationships, and
248 consider high-order interactions between all features. To account for spatiotemporal variation in
249 species responses to climate across broad spatial extents, we fit RF models within a
250 spatiotemporal exploratory models (STEM) as a wrapper (Fink et al., 2020, 2010). We used
251 STEM to generate a randomized ensemble of partially overlapping regional models consisting of
252 $10^\circ \times 10^\circ$ cells ('stixels') across our spatial extent and fit independent RF models within each
253 cell with a minimum of 20,000 checklists, producing a uniformly distributed ensemble of
254 hundreds of partially overlapping models. Within each stixel, we assume relationships between
255 species' occurrence and environmental variables to be stationary. We generated spatially explicit
256 occurrence estimates by averaging predictions from all regional RF overlapping a given location.
257 STEM is established as an effective method for measuring non-stationary relationships between
258 environmental features and observations (Fink et al., 2010; Johnston et al., 2015; La Sorte et al.,
259 2017; Zuckerberg et al., 2016).

260 Before modeling, all data was split 75/25 into training/testing subsamples. Initial training data
261 were further split 75/25 for model training and validation (see below). For each set, we used

262 case-weights to equalize weighting by year, accounting for the increasing sample sizes by year
263 generated by eBird (submissions increase 30% annually). For each model, we calibrated
264 predicted probabilities based on a validation set calibration adjustment. Finally, we assessed the
265 fit of each model based on a series of predictive performance metrics computed with the test
266 data, including specificity, sensitivity, Kappa, and area under the curve (AUC).

267 *Partial dependence and non-stationarity metrics*

268 To examine the regional-scale relationships between species occurrence rates and daily mean
269 temperature, we calculated the partial dependence (Hastie et al., 2009) within each stixel. Partial
270 dependence statistics describe how occurrence varies as a function of certain focal features,
271 averaging across the values all other features in models (except date, see below). By averaging in
272 this way, the partial dependence estimates capture systematic changes in occurrence associated
273 with temperature while averaging out all other sources of variation captured by the models,
274 including variation in detection rates and heterogeneity in search effort and among observers. For
275 each species, we generated partial dependence estimates for both summer and winter seasons for
276 every stixel by predicting at the median date within season (December-February dates were
277 adjusted to a continuous scale).

278 We derived two measures of thermal sensitivity from partial dependence plots fit for
279 temperature-occurrence relationships within each stixel: 1) Thermal optimum, the value of daily
280 temperature at which predicted occurrence is maximized; 2) Thermal breadth, equal to the
281 difference between the value of daily temperature above the thermal optimum at which predicted
282 occurrence falls below 80% of the maximum value and the value below the thermal optimum at
283 which occurrence falls below 80% of the maximum value. The 80% threshold is in line with
284 many physiological studies (e.g., Angilletta Jr et al., 2002).

285 For both measures, we quantified the spatial and seasonal non-stationarity within each species by
286 summarizing how thermal optimum and breadth varied across the species range and between
287 seasons. To estimate spatial non-stationarity, we regressed mean annual temperature (bio1 from
288 worldclim) on the thermal optimum to calculate the slope across all stixels spanning a
289 geographic-climatic gradient within the given season, summer or winter. Similarly, we regressed
290 mean annual temperature range (bio7) against thermal breadth to calculate the slope of thermal
291 breadth spanning a geographic-climatic gradient within the season. A slope closer to one
292 suggests that stixel-level thermal optimum or breadth is closely associated with local
293 environmental conditions, while a slope closer to zero suggests that each is consistent across the
294 species' range. To estimate seasonal non-stationarity, we recorded the mean stixel-level
295 difference in thermal optimum or breadth between seasons and computed a Welch's two-sample
296 t-test (Welch, 1938) to evaluate whether the difference in thermal optimum or breadth between
297 winter and summer are statistically different. Greater differences suggest greater seasonal non-
298 stationarity. Thus, we compiled six metrics of non-stationarity for each species: spatial (two
299 seasons) and seasonal variation in thermal optimum and breadth.

300 All plots visualizing metrics were generated using *ggplot2* (Wickham, 2011) and *RcolorBrewer*
301 (Neuwirth and Neuwirth, 2011).

302 *Influence of human observers*

303 We explored the possible confounding influence of daily temperature on eBird observers by
304 fitting a random forest model with daily temperature as the dependent variable and effort, CCI,
305 landcover, topography, and mean climate features and all model parameters identical to our
306 primary models. We then examined the explanatory power of this model, using root mean
307 squared error (RMSE), Spearman's rank correlation, and the partial dependency of daily
308 temperature based on effort variables and CCI.

309 *Spatial predictions*

310 We generated maps depicting spatial variation in thermal optimum throughout the range of each
311 species across both the winter and summer seasons. First, we created a gridded dataset with 2.8
312 km² resolution and generated model predictions of occurrence in each cell assuming 12 evenly
313 spaced values of daily temperature ranging between 0° and 36°C, assigning a thermal optimum
314 to each cell corresponding to the temperature at which occurrence in the cell was maximized. We
315 held all the observation process features constant to remove variation in detectability, resulting in
316 occurrence predictions for a standardized eBird search defined as a checklist reported by an
317 average observer traveling 1 km over one hour. For each cell, we compiled values of land cover,
318 elevation, and topographic features for use when generating predictions. For each species, we
319 generated these predictions at the hour of the day when the species is most often observed based
320 on our data, and on a day with mean annual 1970-2000 temperatures and total precipitation.
321 Maps were generated using the *purrr* package (Wickham et al., 2019) and plotted using
322 *RColorBrewer*.

323 *Species trait and phylogeny assessment*

324 Our final goal was to determine whether spatial and seasonal variation in thermal sensitivity is
325 associated with various avian life-history traits. We compiled information on preferred habitat
326 (merging forest with woodland and grassland with shrubland categories), body mass (which was
327 log-transformed) and hand-wing index from AVONET (Tobias et al., 2022). Further, we
328 calculated species-level landcover diversity index (following Zuckerberg, Fink et al. 2016) to
329 represent habitat generalism, based on mean partial effects of all landcover features in
330 independent continent-wide SDMs (Cohen and Jetz *in prep*). Thus, we compiled four traits.

331 To assess phylogeny as a driver of non-stationarity, we calculated Blomberg's K (Blomberg,
332 Garland Jr et al. 2003) using an avian phylogeny (Jetz, Thomas et al. 2012) and comparing it to a
333 null distribution of K after randomizing species' responses 1,000 times ('picante' package;
334 Kembel, Cowan et al. 2010). Finally, we fit six multivariate phylogenetic generalized least-
335 squares (PGLS) models to assess the simultaneous influence of traits and phylogeny on each of

336 the six non-stationarity metrics. We then fit ANOVAs to each model to assess the importance of
337 the categorical variable (habitat preference).

338

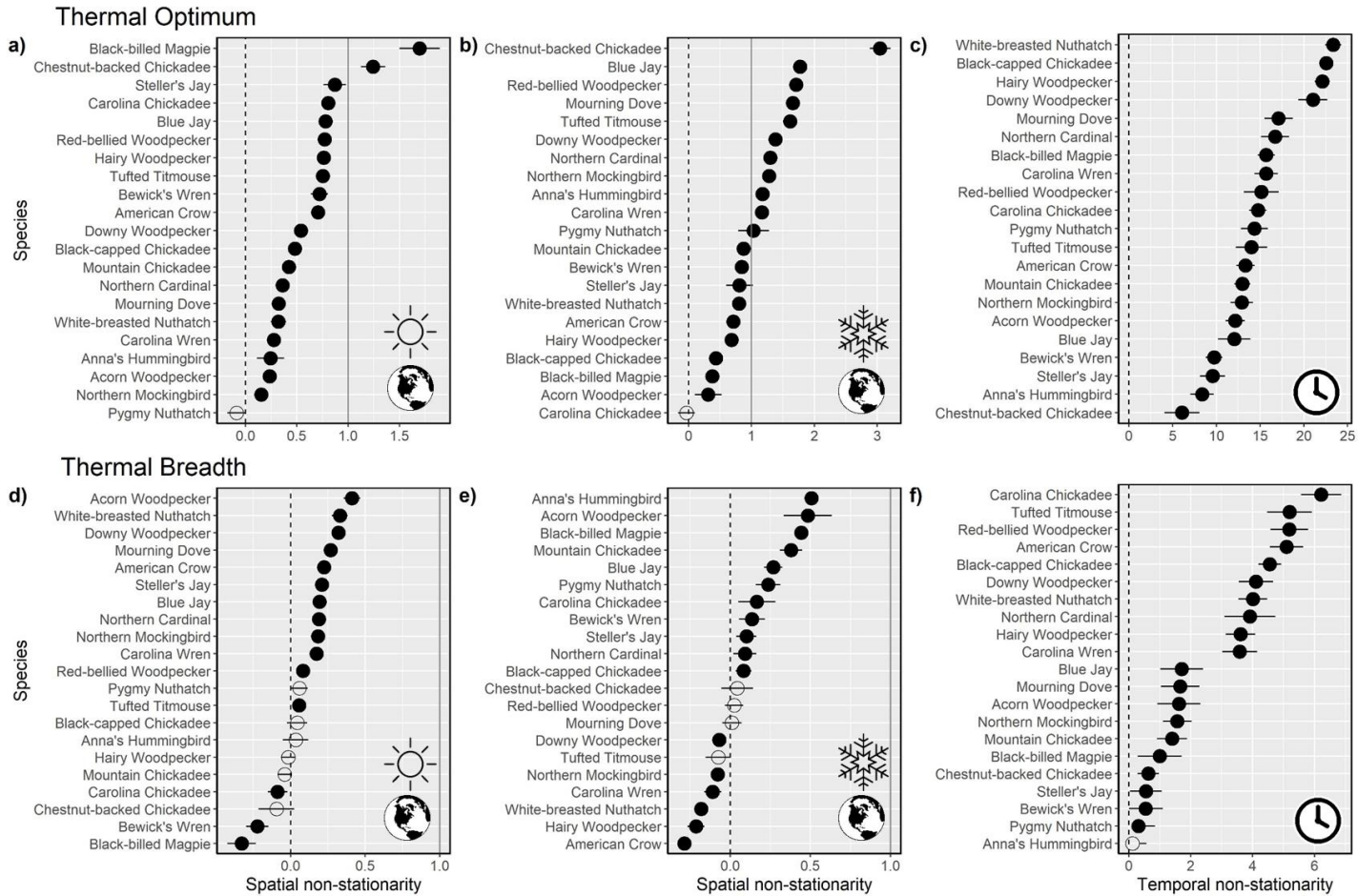
339 **Results**

340 Overall, species demonstrated both spatial and seasonal non-stationarity, though with
341 considerable variation among species (Table 1; Figs. 2 & 3). During both seasons, species
342 exhibited higher thermal optimums in warmer climates, although this relationship was stronger
343 during winter (summer: mean $\beta = 0.59 \pm 0.09$; winter: 1.09 ± 0.14). Birds also exhibited
344 wider thermal breadths in more variable climates (summer: mean $\beta = 0.1 \pm 0.04$; winter: 0.09
345 ± 0.05), and greater optimums (mean sample difference = $14.74 \text{ }^\circ\text{C} \pm 1.01$) and narrower
346 breadths ($-2.69 \text{ }^\circ\text{C} \pm 0.43$) in summer than winter.

347 In both summer and winter, all but one bird species exhibited spatial non-stationarity in thermal
348 optimum (based on a model coefficient \pm SE not overlapping zero) across climate zones. In
349 summer, thermal optima of two species (10%) perfectly matched that of their environment
350 (based on a model coefficient > 1), but this increased to 11 species (55%) during winter. Spatial
351 non-stationarity in thermal breadth was mixed, with 55% of species demonstrating shifts in
352 winter and 60% in summer (Fig. 2). Meanwhile, seasonal non-stationarity in thermal optimum
353 (the difference in thermal optimum between summer and winter) was observed in all birds but
354 varied in magnitude across species, and seasonal non-stationarity in thermal breadth was
355 observed in all species except for Pygmy nuthatch and Anna's hummingbird (Fig. 2). Across
356 species, we observed that birds with greater spatial non-stationarity generally had lower seasonal
357 non-stationarity, especially in winter (optimum, $\beta = -2.47 \pm 1.50$ SE; breadth, $\beta = -4.82 \pm$
358 1.62 ; Fig. 4). We did not detect consistent effects of daily temperature on human observer effort
359 or variation (RMSE = 8.05; Spearman's $\rho = 0.54$; Fig. S1).

360 We found no evidence that phylogeny is associated with spatial or seasonal non-stationarity
361 across species ($K < 0.39$, $\lambda < 0.32$, $p > 0.1$ for all metrics; Table S1). Most species traits were not
362 associated with stationarity or non-stationarity either. However, habitat diversity consistently
363 emerged as associated with spatial or seasonal non-stationarity in thermal optimum and breadth
364 after controlling for phylogeny. For example, habitat generalists were less likely to exhibit
365 spatial non-stationarity in thermal breadth in winter (PGLS: $\beta = -1.70$, $p < 0.01$), while more
366 likely to show seasonal non-stationarity in thermal optimum ($\beta = 36.73$, $p < 0.05$) and thermal
367 breadth ($\beta = 18.19$, $p < 0.01$; Figs. 5-6; Tables S2-3).

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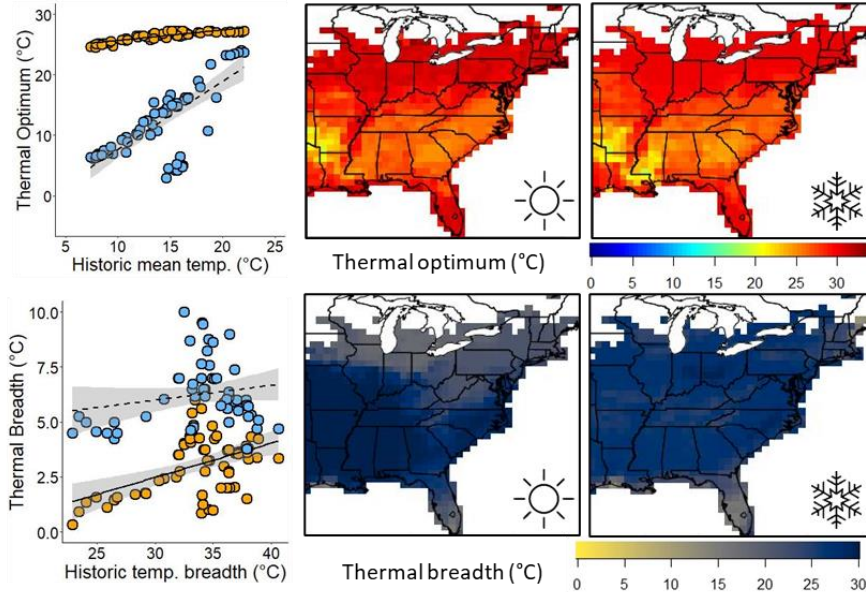


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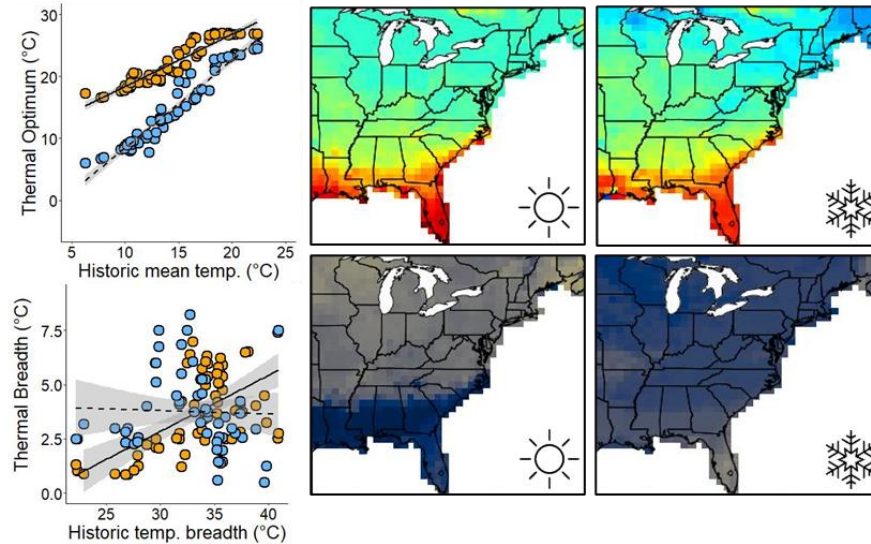
370 **Figure 2. Spatial non-stationarity across 20 North American bird species.** Estimates of spatial and
 371 seasonal non-stationarity in thermal optimum (a-c) and breadth (d-f). Spatial non-stationarity is defined as
 372 the slope coefficient (+/- SE) describing the regional-scale relationship between a species' thermal
 373 optimum or breadth and the regional mean temperature or temperature range and is presented for summer
 374 (a,d) and winter (b,e) seasons. Seasonal non-stationarity is defined as the mean stixel-level difference in
 375 °C (+/- 95CI) between a species' thermal optimum (c) or thermal breadth (f) during summer and winter
 376 seasons. The black dotted lines correspond to a value of zero, or no relationship between thermal
 377 optimum/breadth and local climate (i.e., stationarity) and gray lines correspond to one, or a 1:1
 378 relationship, or strong spatial non-stationarity. Open circles denote species with error overlapping zero.

379

a) Carolina wren
Thryothorus ludovicianus



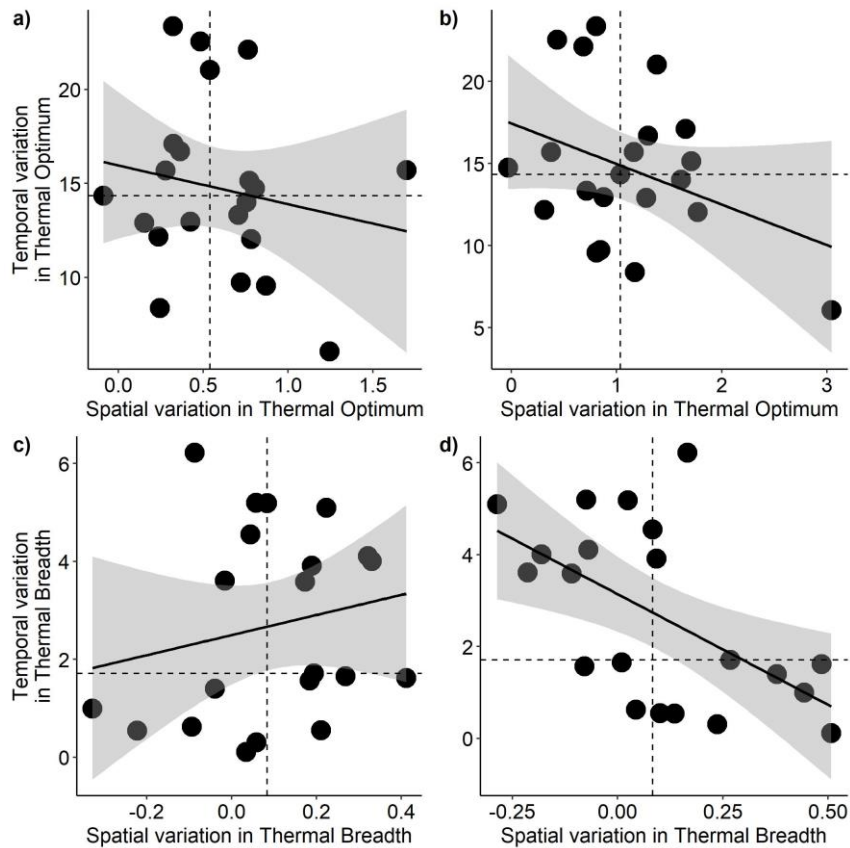
b) Blue jay
Cyanocitta cristata



380

381 **Figure 3. Spatial and seasonal non-stationarity differs between species.** Left panels illustrate
 382 relationships between annual seasonal mean temperature and thermal optimum (the daily temperature at
 383 which activity level is greatest in each region based on model predictions; points), or relationships
 384 between historic seasonal temperature range and thermal breadth (the range of temperatures at which
 385 activity levels are above 80% of maximum) for each stixel. Patterns are given across summer (orange
 386 points, solid trendline) and winter (blue points, dashed line), with shaded 95% confidence bands. Maps
 387 visualize thermal optimums in space for each species across both seasons. (a) Carolina wren (*Thryothorus*
 388 *ludovicianus*) has a consistent optimum at warm temperatures with moderate spatial variation across the
 389 map, with seasonal variation in optimum occurring only in cold climates. It has moderate variation in
 390 breadth during both seasons. (b) Blue jay (*Cyanocitta cristata*) has high spatial and low seasonal variation
 391 in optimum, but more seasonal variation in breadth. Note that patterns in scatterplots may not directly
 392 correspond to those on maps because scatterplots summarize thermal sensitivity at the stixel level while
 393 maps average multiple (10-20) stixels at the point level.

394

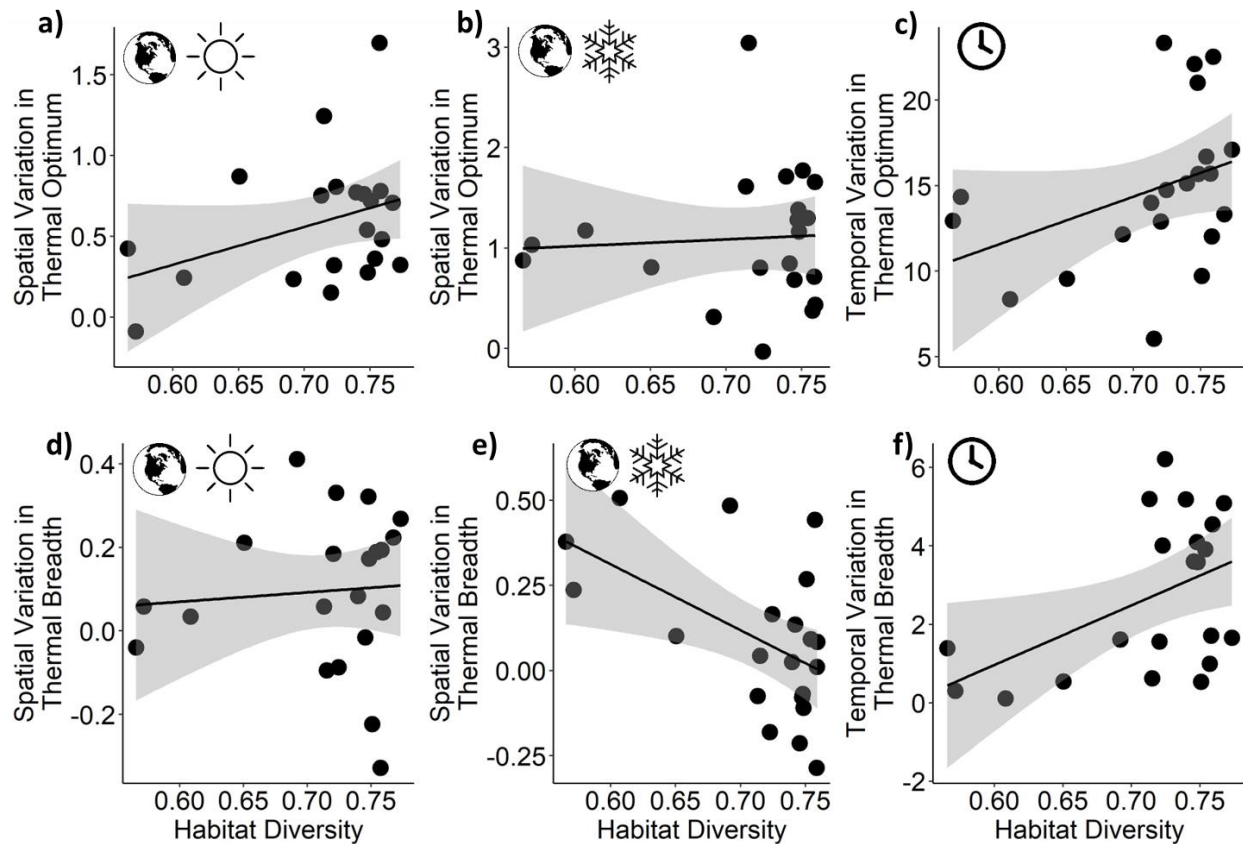


395

396 **Figure 4. Relationships between spatial and seasonal non-stationarity in thermal sensitivity.** Spatial
397 non-stationarity (x-axes), or the slope coefficient describing the stixel-level relationship between a
398 species' thermal optimum or breadth and the local mean temperature or temperature range, is compared
399 against seasonal non-stationarity (y-axes), or the mean stixel-level difference in thermal sensitivity across
400 seasons, with points representing species. In (a-b), these comparisons are visualized for thermal optimum;
401 in (c-d), thermal breadth. Panels (a,c) visualize trends in summer and (b,d) do so in winter. All variables
402 were standardized to increase interpretability. Linear trendlines are given with gray shading representing
403 95% confidence bands. Dotted lines represent medians.

404

405



406

407 **Figure 5. Habitat diversity is associated with the extent of non-stationarity across species.** At the
408 species level (points), partial residual plots visualize relationships between an index of habitat diversity
409 (x-axes) and (a) spatial non-stationarity in thermal optimum in summer, (b) spatial non-stationarity in
410 winter, or (c) seasonal non-stationarity across seasons (y-axes), based on phylogenetic least-squares
411 models. In (d-f), equivalent relationships are presented for thermal breadth. Linear trendlines are shown
412 with gray shading representing 95% confidence bands.

413

414

415 Discussion

416 Thermal sensitivity and responses to climate change are typically quantified at the species level
417 (Smith et al., 2019), but recent evidence suggests significant physiological and morphological
418 variation among individuals below the species level (Bennett et al., 2019; Louthan et al., 2021;
419 Stager et al., 2021; Youngflesh et al., 2022). Thus, researchers require a better understanding of
420 variation in thermal sensitivity within species to assess when and where populations are more
421 likely to be sensitive to weather-related effects (Louthan et al., 2021; Smith et al., 2019; Sultaire
422 et al., 2022). However, thermal sensitivity is difficult to measure across numerous populations
423 and multiple seasons for many species. Here, we use dynamic species distribution models that

424 allow spatial and seasonal variation in temperature responses to identify patterns of spatial and
425 seasonal non-stationarity in thermal sensitivity across common North American resident birds.
426 We found that birds exhibit both stationarity and non-stationarity in responses to variation in
427 temperature across space and time.

428 Our findings support recent physiological work suggesting that populations of a species vary in
429 their thermal optimum and breadth based on geography. For both thermal optimum and breadth,
430 most species occupied an intermediate space between complete spatial stationarity (coefficient =
431 0), or no variation among locations where non-stationarity that perfectly matches the local
432 environment (coefficient = 1). Thermal optimum was more likely than thermal breadth to match
433 local environmental conditions, with 95% of species (19 of 20) demonstrating a relationship
434 between thermal optimum and local climate that differed from zero, and only 55% (11 of 20)
435 demonstrating such a relationship for thermal breadth. In fact, 10 of 20 species (50%)
436 demonstrated thermal optimums closer to one than zero, suggesting that their thermal sensitivity
437 more closely matches the local environment than conspecifics in different regions – however, 2
438 of 20 species (10%) reflected a coefficient ~ 1 , or thermal sensitivity that matches the local
439 environment. It has long been known that thermal breadth is highly important in terms of
440 constraining organismal distributions, likely more so than thermal optimum (Buckley, 2010;
441 Huey and Stevenson, 1979), and our results may suggest that thermal breadth is a more
442 hardwired physiological constraint than thermal optimum across populations of many bird
443 species. Across species, we found that spatial non-stationarity was infrequently associated with
444 phylogeny or species traits, although the limited sample of 20 species limited our ability to draw
445 broad inferences. We also found limited evidence that spatial non-stationarity in thermal breadth
446 was greater in habitat specialists than generalists, though only during the winter season. This link
447 was predicted because habitat and thermal generalism is often observed in the same species
448 (Barnagaud, Devictor et al. 2012), and thermal generalists may be less likely to adapt to the local
449 environment.

450 Surprisingly, all species reflected different thermal optima and 90% (18 of 20) displayed
451 different thermal breadths across seasons, despite substantial overlap in conditions across
452 seasons in most species' ranges. However, this pattern may not be representative of all bird
453 species; the species in our selection are mostly residential and thus more likely than other bird
454 species to be seasonally flexible in thermal sensitivity. Interestingly, habitat generalism was
455 more closely associated with seasonal non-stationarity in both thermal optimum and breadth.
456 Therefore, habitat generalists may be selecting a strategy in which they eschew adaptation to
457 local climates in space in favor of seasonal flexibility across the annual cycle. Finally, during
458 winter, species with greater spatial variation in thermal sensitivity had reduced seasonal
459 variation, suggesting a trade-off; for example, a species with seasonal non-stationarity in thermal
460 sensitivity may not need to rely on local adaptation to climate.

461 Variation in thermal sensitivity across space and time may be more difficult to quantify in
462 species that seasonally move long distances, occupy smaller ranges, or are reported less

463 frequently, which we avoided exploring in this study. Within species that seasonally migrate
464 long distances, seasonal variation in thermal sensitivity is difficult to measure because without
465 knowing which sets of locations have the same individuals (e.g., information on migratory
466 connectivity; Fuentes et al., 2022), making direct comparisons between populations over time
467 difficult. However, recent improvements in animal tracking, even for smaller birds, will allow
468 for direct comparisons of thermal sensitivity at the population or individual level even for
469 migratory species (Costa-Pereira et al., 2022). Some genetic evidence suggests that populations
470 with are northerly during the breeding season also northerly during the overwintering period
471 (Bay et al., 2021), although this is not reliable for species which compress their ranges during
472 winter, as do many neotropical migrants (Rushing et al., 2020). Species that occupy small ranges
473 may exhibit little spatial variation in thermal sensitivity, as climate generally varies across large
474 spatial scales. Although local adaptation to different climates is possible along elevational
475 gradients, differences in data abundance between lowlands and uplands may inhibit direct
476 comparisons between adjacent populations inhabiting each zone. Finally, assessing non-
477 stationarity in thermal sensitivity may be more difficult for species with limited data coverage in
478 space and time, including birds outside of North America or most other animal taxa, although
479 citizen science observations are increasing exponentially every year (Callaghan et al., 2021).
480 Despite these limitations, our results provide a framework to predict how widespread, residential
481 species with continuous data coverage may vary in population and seasonal thermal sensitivity at
482 fine scales.

483 Although bird species varied in their extent of spatial and seasonal non-stationarity, it remains
484 unclear whether non-stationarity translates to increased or decreased climate change
485 vulnerability. Plausible explanations exist for either scenario. For example, a species exhibiting
486 non-stationarity in space may be more vulnerable to climate change if populations are adapted to
487 distinct thermal conditions and climates become more homogenous (e.g., northern latitudes
488 warming faster than southern latitudes). Given non-stationarity, a continent-wide heat wave may
489 pose a greater risk of disturbance to a northern population of a given species if it has less heat
490 tolerance than a southern population. Alternatively, populations of a species exhibiting
491 stationarity may be more vulnerable if southern populations already living on the edge of their
492 thermal tolerance experience an extreme weather event, such as a heat wave. A species
493 exhibiting seasonal stationarity may face a greater disturbance from warm weather during winter,
494 when individuals have undergone physiological changes to suppress heat loss, than summer.
495 Further work should explore how variation in thermal sensitivity along a climatic gradient is
496 related to population-level consequences to aid finer-scale conservation approaches.

497 *Conclusions*

498 Researchers typically predict and measure static responses to climate change at the species level
499 (Smith et al., 2019). In standard species distribution and niche modeling approaches, the thermal
500 niche is treated as a static “envelope”, with climate-occurrence relationships assumed to be
501 stationary over both species entire ranges and throughout the year (Jarnevich et al., 2015; Smith

502 et al., 2019). Even in “dynamic” distribution modeling approaches, responses to a temporally
503 shifting feature (e.g., weather) are assumed to be consistent across the spatial and temporal
504 extent of the modeling domain (Milanesi et al., 2020). Further, conservationists and managers
505 typically develop climate change vulnerability assessments and adaptation plans at species level,
506 ignoring population-level variability. However, with the modern availability of high-resolution,
507 high-volume, continuous observational and environmental datasets, variation in species’
508 responses to environmental variables, such as temperature, can now be modeled over large
509 spatial extents and across the annual cycle to detect variation in responses to climate change as
510 higher resolutions (Carlson et al., 2021; Latimer et al., 2018). Our results suggest that many
511 species-level assessments of thermal sensitivity may be missing significant variability over space
512 and time, leading to misleading climatic vulnerability assessments. Researchers must consider
513 variation in thermal sensitivity across populations and seasons to improve understanding of
514 climate change adaptation (Smith et al., 2019).

515

516 **Acknowledgments**

517 We thank S. Keyser, M. Lu, and S. Sharma for their thoughtful comments on the analyses.
518 Funding was provided by the Data Science Initiative through the Office of the Vice Chancellor
519 for Research and Graduate Education at the University of Wisconsin. We thank the many eBird
520 participants for their contributions and the eBird team for their support. This work was funded in
521 part by The Leon Levy Foundation, The Wolf Creek Foundation, NASA (80NSSC19K0180),
522 and the National Science Foundation (DBI-1939187; CCF-1522054; and computing support
523 from CNS-1059284).

524

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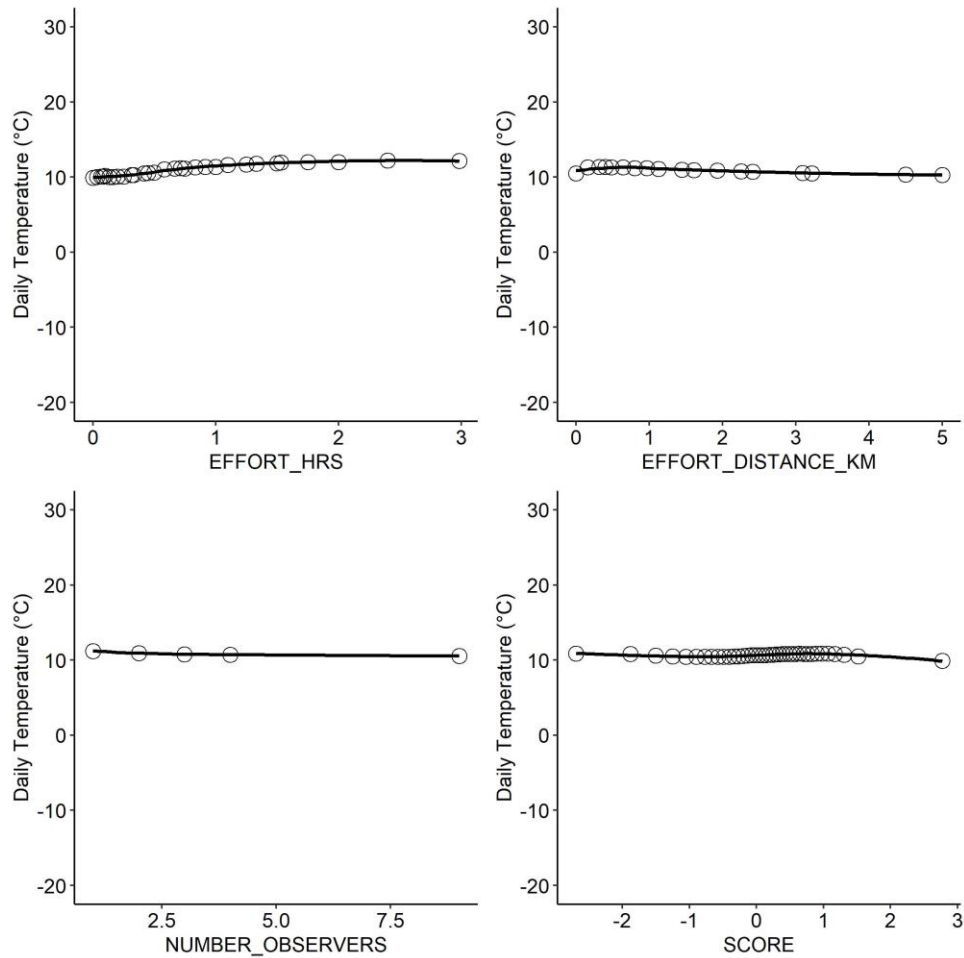
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684

685

686 **Supplementary Materials**

687



688

689 **Figure S1. The relationship between daily temperature and human observers.** Partial dependence
690 plots based on a random forest model explicitly testing the relationship between daily temperature and
691 metrics of human observation, including (a) number of hours birding, (b) distance traveled (km), (c) the
692 number of observers, and (d) Checklist Calibration Index, which reflects inter-observer variation (see
693 methods).

694

695 **Table S1.** Metrics describing phylogenetic signal (Lambda and Blomberg's k) in spatial or seasonal non-
696 stationarity.

Non-stationarity metric	lambda	lambda p-value	k	k p-value
Spatial Optimum (summer)	0.317	0.786	0.388	0.149
Spatial Optimum (winter)	<0.001	1	0.152	0.959
Seasonal Optimum	<0.001	1	0.217	0.744
Spatial Breadth (summer)	<0.001	1	0.278	0.408
Spatial Breadth (winter)	<0.001	1	0.260	0.483
Seasonal Breadth	<0.001	1	0.216	0.787

697

698

699 **Table S2.** Summary tables from phylogenetic least-squares models associating species functional traits
700 with spatial and seasonal non-stationarity in thermal optimum while controlling for phylogenetic
701 structure.

Spatial (summer)	Coefficient	SE	t-value	p-value
(Intercept)	-0.939	1.508	-0.623	0.543
Body Mass	0.064	0.146	0.439	0.667
Habitat diversity	1.398	1.037	1.349	0.197
Hand-Wing Index	0.069	0.373	0.185	0.856
Habitat (Grassland)	0.347	0.245	1.415	0.177
Habitat (Human Modified)	-0.453	0.498	-0.910	0.377

Spatial (winter)	Coefficient	SE	t-value	p-value
(Intercept)	3.644	4.507	0.809	0.431
Body Mass	-0.338	0.438	-0.772	0.452
Habitat diversity	1.000	3.131	0.320	0.754
Hand-Wing Index	-0.607	1.117	-0.543	0.595
Habitat (Grassland)	-0.255	0.734	-0.348	0.733
Habitat (Human Modified)	0.667	1.489	0.448	0.661

Seasonal	Coefficient	SE	t-value	p-value
(Intercept)	-27.989	22.054	-1.269	0.224
Body Mass	1.368	2.135	0.641	0.531
Habitat diversity	36.725	15.164	2.422	0.029
Hand-Wing Index	4.033	5.453	0.740	0.471
Habitat (Grassland)	-3.783	3.583	-1.056	0.308
Habitat (Human Modified)	-7.227	7.277	-0.993	0.336

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704 **Table S3.** Summary tables from phylogenetic least-squares models associating species functional traits
 705 with spatial and seasonal non-stationarity in thermal breadth while controlling for phylogenetic structure.

Spatial (summer)	Coefficient	SE	t-value	p-value
(Intercept)	-0.180	0.769	-0.234	0.818
Body Mass	0.032	0.074	0.435	0.670
Habitat diversity	0.232	0.529	0.439	0.667
Hand-Wing Index	0.024	0.190	0.127	0.901
Habitat (Grassland)	-0.326	0.125	-2.613	0.020
Habitat (Human Modified)	0.040	0.254	0.156	0.878

Spatial (winter)	Coefficient	SE	t-value	p-value
(Intercept)	0.858	0.828	1.036	0.317
Body Mass	-0.025	0.081	-0.309	0.762
Habitat diversity	-1.698	0.575	-2.952	0.010
Hand-Wing Index	0.186	0.205	0.906	0.379
Habitat (Grassland)	0.212	0.135	1.571	0.137
Habitat (Human Modified)	-0.405	0.274	-1.482	0.159

Seasonal	Coefficient	SE	t-value	p-value
(Intercept)	-15.256	8.219	-1.856	0.083
Body Mass	0.435	0.795	0.547	0.592
Habitat diversity	18.193	5.651	3.219	0.006
Hand-Wing Index	1.000	2.032	0.492	0.630
Habitat (Grassland)	-2.411	1.335	-1.806	0.091
Habitat (Human Modified)	-0.154	2.712	-0.057	0.955

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