

1 **Adaptation to climate change through seasonal migration revealed by climatic versus**
2 **demographic niche models**

3 **Running Title:** Niche models reveal adaptation via migration

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26 **Abstract**

27 Predicting the geographic range of species and their response to climatic variation and change are
28 entwined goals in conservation and evolutionary ecology. Species distribution models (SDMs) are
29 foundational in this effort and used to visualize the geographic range of species as the spatial
30 representation of its realized niche. SDMs are also used to forecast range shifts under climate change, but
31 often in the absence of empirical evidence that climate limits population growth. We explored the
32 influence of climate on demography, seasonal migration, and the extent of the geographic range in song
33 sparrows (*Melospiza melodia*), a species thought to display marked local adaptation to regional climate.
34 To do so, we developed SDMs to predict the demographic and climate niches of migratory and resident
35 song sparrows across our study area in western North America from California to Alaska, using 48 years
36 of demographic data from a focal population in British Columbia and 1.2 million continental-scale citizen
37 science observations. Spatial agreement of our demographic and climate niche models in the region of our
38 focal population was strong (76%), supporting the hypothesis that demographic performance and the
39 occurrence of seasonal migration varied predictably with climatic conditions. In contrast, agreement at
40 the northern (58%) and southern (40%) extents of our study area was lower, as expected if the factors
41 limiting population growth vary regionally. Our results support the hypothesis that local climate drives
42 spatial variation in the occurrence of seasonal migration in song sparrows by limiting the fitness of year-
43 round residents, and suggest that climate warming has favored range expansions and facilitated an
44 upward shift in elevational range song sparrows that forgo seasonal migration. Our work highlights the
45 potential role of seasonal migration in climate adaptation and limits on the reliability of climate niche
46 models not validated with demographic data.

47

48 **Keywords:** migratory behavior, climate adaptation, species distribution model, climate niche,
49 demographic niche, population growth, *Melospiza melodia*

50

51 **Introduction**

52 Theory and empirical evidence indicate that spatial and temporal heterogeneity in the environment can
53 drive variation in species distributions and life histories by causing variation in individual fitness and
54 thereby driving natural selection and adaptation to local conditions (Wright, 1982; Wade & Kalisz, 1990;
55 Schluter, 2000; Aitken et al., 2008; Hendry et al., 2018). However, the rapid pace of anthropogenic
56 change has raised new questions about the capacity of local populations to accommodate it (e.g., Gaston
57 2003; Mason et al., 2019; reviewed by Root et al., 2003; Parmesan, 2006; Bell, 2017) and elevated the
58 importance of empirical studies which allow us to estimate the pace of climate adaptation and identify
59 underlying processes (e.g., Grant & Grant, 2006; Stoks et al., 2014; Bay et al., 2018; Bontrager & Angert,
60 2019; Radchuk et al., 2019). Theory suggests that species can avoid the negative effects of climate
61 change on demographic performance at a site by (1) adapting via genetic and/or (Aitken et al., 2008; Bay
62 et al., 2018); (2) plastic mechanisms to maintain fitness at a level sufficient to persist *in situ* (Ghalambor
63 et al., 2007; Charmantier et al., 2008; Nicotra et al., 2010); or (3) dispersing to new areas reflecting
64 historical conditions (Angert et al. 2011; Chen et al. 2011; Gillings et al. 2015; *cf* Greenwood & Harvey
65 1982). However, some species also harbor a capacity to respond to deteriorating environments by altering
66 spatial patterns of seasonal migration (i.e., the reversible movement between breeding and non-breeding
67 areas) versus year-round residency; changes which may arise via adaptive migratory plasticity and/or
68 evolution (Reid et al. 2018). Here, we develop and test the hypothesis that migration represents an
69 additional mechanism by which mobile species can adapt to climate change by facilitating their access to
70 spatially and temporally limiting resources whilst avoiding conditions that would preclude their survival
71 at one location throughout the annual cycle. In doing so, we also explicate the demographic mechanisms
72 underlying the climate niche in a focal population of song sparrow (*Melospiza melodia*), and then explore
73 the application of such models to predicting species distribution under climate change.

74 Populations comprising a mix of seasonal migrants and year-round residents occur in diverse taxa
75 (e.g., fish, Chapman et al., 2012; birds, Dingle, 2014; mammals, Avgar et al., 2014; and reptiles and

76 amphibians, Shaw & Levin, 2011; Yackulic et al., 2017) and may harbor sufficient genetic variation
77 and/or capacity for plasticity in migration to enable rapid responses to environmental change (Liedvogel
78 et al., 2011). For example, Pulido & Berthold (2010) used common garden and artificial selection
79 experiments to demonstrate a genetic basis and thereby suggest that residency could evolve rapidly in
80 migratory blackcaps (*Sylvia atricapilla*) if climate change conferred a selective advantage by enhancing
81 the relative fitness of birds that winter closer to their breeding areas. Such responses might be driven by
82 spatial and temporal variation in the costs and benefits of seasonal migration versus residence, which may
83 in turn give rise to correlations between environmental conditions, occurrence of migration, and life
84 history evolution (e.g., Coppack & Both; Reid et al. 2018). In support of such ideas, climate warming,
85 supplemental feeding, and habitat modification have each contributed to the establishment of resident
86 populations in species of birds known previously as obligate migrants (Zuckerberg et al., 2011; Møller et
87 al., 2014; Shephard et al., 2015; Plummer et al., 2015; Vistry et al. 2018) and are now influencing patterns
88 of colonization and local adaptation at the leading and trailing edges of many species (Rushing et al.
89 2020).

90 Such transitions to residency can elevate population growth rate in newly-established residents as
91 compared to sub-populations of migrants by enhancing over-winter survival and annual reproductive rate
92 (Vistry et al., 2018), but may also reveal trade-offs involving individual fitness and climate which can
93 drive variation in migratory phenotype. For example, Acker et al. (2021a; 2021b) reported context-
94 dependent variation in the survival and reproduction of resident and migrant European shags
95 (*Phalacrocorax aristotelis*), wherein selection favored migrants in severe winters but residents in more
96 benign years. However, predicting spatial and temporal changes in the occurrence of migration and the
97 demography and growth rates of populations requires detailed population-level data across wide
98 geographic ranges; two requirements rarely met in free-living species. Alternatively, one can infer
99 continent-wide variation in the growth rates of resident versus migrant populations by extrapolating from
100 long-term climate and demographic data collected at smaller scales (i.e., ‘space-for-time substitutions’,

101 e.g., Pickett 1989; La Sorte et al. 2009). However, because datasets spanning multiple decades and
102 completely enumerated populations are rare, it remains to be demonstrated that temporal variation in
103 climatic factors shown to limit population growth at local scales can be reliably scaled-up to predict the
104 distribution of resident and migratory populations of a species across its historical, contemporary and/or
105 future range. Using such relationships can predict species distribution and evaluating the reliability of
106 those predictions at regional and larger scales thus remain key steps to elucidating mechanisms by which
107 mobile species may respond change in the environment.

108 Most efforts to predict the response of species to environmental change employ species
109 distribution models (SDMs) to summarise statistical links between the occurrence of species and
110 environmental characteristics at a site (reviewed by Elith & Leathwick, 2009). Climate niche models are a
111 particular case of SDMs that aim to predict species' distribution based solely on climatic factors known or
112 assumed to limit population growth (Andrewartha & Birch, 1954; Wiens et al., 2009). However, such
113 models have been criticized for their opaque assumptions and inability to reveal the biological
114 mechanisms driving variation in demographic performance and species distribution (Elith & Leathwick,
115 2009; Zurell, 2017). For example, although climate niche models make implicit predictions about
116 population growth in versus outside the climate niche, few studies test such assumptions directly (e.g.,
117 Tredennick et al., 2017; Bayly & Angert, 2019; Williams et al., 2021). Moreover, eco-evolutionary
118 studies increasingly indicate that local adaptation to environment is common in nature (e.g., Hoban et al.
119 2016; Delph 2018), implying that some species can be expected to show heterogeneous responses to
120 climatic factors at micro-geographic to regional scales (e.g., Walsh et al., 2019; Mikles et al., 2020).
121 Because many climate niche models assume that the biological and statistical relationships between
122 climate and demography act similarly over the species range (Elith & Leathwick, 2009), testing their
123 underlying mechanisms and predictions will be essential to evaluating their reliability, evaluating the
124 adaptive capacity of species, and predicting how resident and migrant populations may respond to spatial
125 and temporal heterogeneity in climatic conditions.

126 We addressed the knowledge gaps above using 48 years of demographic data, 1.2 million citizen
127 science observations, and climate data spanning two centuries to predict the influence of historical,
128 contemporary, and future climate on population growth, and migration versus residence, in song sparrow
129 populations throughout western North America (comprising Alaska, British Columbia, Washington,
130 Oregon, and California). To do so, we first tested several *a priori* hypotheses (Table 1) on the effects of
131 temporal variation in climate on survival and reproduction in a focal study population which resides year-
132 round in coastal British Columbia (BC), Canada.

133 Second, we then used ‘space-for-time substitution’ (e.g., Pickett 1989; La Sorte et al. 2009) to
134 predict how variation in climate may affect the population growth rate (λ), migratory status, and
135 distribution of song sparrow populations (i.e., the ‘demographic niche’) at larger spatial scales, assuming
136 that song sparrows in our study population and western North America respond similarly to climate. This
137 study area encompasses Mediterranean to Arctic ecosystems, an elevational range of 0 to 3200 m, and 17
138 of 25 extant subspecies (Miller, 1956; Patten & Pruett, 2009), including five of ‘special concern’ (Pruett
139 et al., 2008; Shuford et al., 2008). Because climate is thought to play a key role in local adaptation and the
140 evolution of migration or residence in song sparrows (e.g., Aldrich 1984, Arcese et al. 2002, Mikles et al.
141 2020), they are an excellent species in which to develop and test SDMs.

142 Third, we evaluated the performance of our demographic niche model by comparing it to a
143 climate niche model generated from 1.2 million citizen science observations and contemporary climate
144 data to predict the distributions of migratory and resident populations throughout western North America.
145 Given the large scale of our study area and substantial variation in climate recorded therein, we expected
146 that mismatches between our demographic and climate niche models would increase as climatic
147 conditions diverged from those experienced in our focal study population and reveal practical limits to
148 prediction.

149 Last, we predicted how climate might influence migratory phenotype by using our demographic
150 niche model to predict the historical and future ranges of migratory and resident song sparrow

151 populations in three periods over two centuries: 1901-1910, when winter temperatures in our focal study
152 population averaged 0.9°C cooler than present-day (2010-2018), and 2070-2100, when winter
153 temperatures are predicted to exceed conditions 200 years earlier by 3.1°C. We validated retrospective
154 projections using historical records before speculating on the potential role of migration versus residence
155 in climate adaptation. By doing so, we provide a particularly detailed case study of how population
156 demography, species occurrence, and climate data can be used to explore, predict, and test for the
157 interactive effects of environmental change on the distribution, demography, and migratory dynamics of
158 mobile species.

159

160 **Methods**

161 *Study Species*

162 Twenty-four subspecies of song sparrows breed from Newfoundland to the Aleutian Islands, and south to
163 central Mexico, with 17 subspecies occurring with our study area from Alaska (AK) to California (CA).
164 Variation in size and plumage over the song sparrow range exemplify Bergmann's and Gloger's rules,
165 with the largest individuals residing year-round in near-shore habitats of the Aleutian Islands and the
166 smallest in California salt marshes, and the darkest inhabiting southeast Alaska and lightest the arid
167 southwest of North America (Aldrich, 1984; Zink & Remsen, 1986; Patten and Pruett, 2009; Pruett &
168 Winker, 2010). Because song sparrows are among the world's most polytypic species, display marked
169 local adaptation, and additive genetic variation in traits linked to environmental conditions (e.g., Walsh et
170 al., 2019; Mikles et al., 2020), they are an excellent species to test for spatial and temporal heterogeneity
171 in relationships between climate, population growth, and migration.

172

173 *Focal population*

174 Our focal dataset on song sparrow demography was collected on Mandarte (XO, XDEL) Is., BC, Canada
175 (48.8°N, 123.8°W; c. 6 ha in area), where all song sparrows were identified individually and monitored

176 from 1960-1962 and 1975-2018 using nearly identical methods (Tompa, 1963; Smith et al., 2006).
177 Briefly, territories were monitored each 2-5 days from mid-March to July in all years to record the
178 behavior, survival, and reproductive success of all birds. Nestlings were uniquely color-banded after
179 hatching, observed to independence from parental care (~24-32 days of age), and recorded as having
180 recruited to or disappeared from the population in late April the following year. High annual re-sighting
181 probabilities (> 99%; Wilson et al., 2007), the enumeration of immigrants by color-banding (< 0.5
182 female/yr on average; Reid & Arcese 2020), continuous monitoring of breeding activity, and genetic
183 confirmation of a 50:50 sex ratio at hatching (Postma et al., 2011) facilitated high precision in our
184 estimates of survival, reproduction, and population growth. For simplicity, we only considered females
185 when estimating demographic rates and population growth here (Arcese et al., 1992; Arcese & Marr,
186 2006). Smith et al. (2006), Sardell et al. (2012), and Lameris et al. (2016) describe the current and
187 historical change in vegetation on the island.

188

189 *Climate data*

190 All climate data were obtained via ClimateNA (version 6.00; Wang et al. 2016), which generates scale-
191 free point data for specific locations through dynamic local downscaling of gridded historical and future
192 climate variables for individual years and periods between 1901 and 2100. Historical and contemporary
193 periods were selected based on the most recently available decadal data from ClimateNA. For building
194 climate niche and demographic models, climate data were generated for specific sample locations for the
195 contemporary period (2010-2018). For spatial predictions, monthly climate data obtained by querying
196 ClimateNA using an input file of the latitude, longitude and elevation each of 35,118,256 rasterized cells
197 in our study area (1 km² DEM; Amatulli et al., 2018). Historical (1901-1910) and future climate (2070-
198 2100) was estimated similarly. To account for uncertainty in future climate, we selected an ensemble of
199 15 General Circulation Models (GCM; Coupled Model Intercomparison Project) included in the IPCC

200 Fifth Assessment Report (IPCC, 2014), and an intermediate greenhouse gas emission scenario (RCP 4.5)
201 which assumes emissions start declining around 2040 (IPCC, 2014).

202

203 ***Demographic niche models***

204 We characterized the effects of monthly weather on demographic performance using our focal population
205 dataset from Mandarte Is. using variables shown previously to predict adult survival (S_a), juvenile
206 survival (S_j), reproductive success (RS), and population growth rate (λ) (Table 1, S1). These variables are
207 thought to reflect extreme winter and/or summer conditions influencing energy and water balance,
208 respectively (e.g., Arcese et al., 1992; Wilson & Arcese, 2003; Tarwater & Arcese, 2018). S_a was
209 estimated annually as the fraction of females alive in late April each year that survived to the next April.
210 S_j was estimated as the fraction of female yearlings that became independent from parental care and
211 survived on Mandarte to late April the next year. RS equaled the mean number of female young that
212 became independent of parental care per adult female in each year (see Fig. S1 for timeline).
213 Deterministic population growth rate was then calculated as $\lambda = (S_j * RS) + S_a$ following Arcese & Marr
214 (2006; see also Vistry et al., 2018), assuming no further age structure or immigration.

215 We employed normal regression to quantify relationships between S_j , S_a , RS and climate. All
216 models initially included linear and second-order polynomial terms of each *a priori* predictor identified in
217 Table 1. We then reduced models using supervised backward selection to eliminate variables sequentially
218 with the least influence on model fit, such that final models only included predictors with influence ($p <$
219 0.1) that were not closely correlated ($r < 0.7$). Model selection using Akaike information criterion (AICc)
220 returned equivalent or identical models in all cases (i.e., delta AICc < 1). All response variables were
221 mean-centered and natural log-transformed to facilitate climate mapping and because doing so led us to
222 models that explained more variance and exhibited better diagnostics than other approaches (Table S3).
223 Values of S_j and S_a predicted from generalized linear models assuming binomial errors and a logit link

224 were well correlated to values derived above ($r = 0.99$ and 0.770 , respectively); we employed the former
225 here because similar methods generated our *a priori* predictions (Table 1).

226 We then used our fitted demographic models to predict contemporary λ across our study area
227 spanning western USA and Canada given climate (Table S3; see ‘Climate data’). To do so, predicted
228 values of S_a , S_j , and RS were back-transformed, centered on their observed means in our focal population,
229 and bounded between 0 and 0.99 for S_a , 0 and 0.69 for S_j , and 0 and 4.34 for RS , which represent ranges
230 spanning ± 3 SEs. We used the same procedure to predict historical and future λ in relation to climate.
231 Each map cell was classified as supporting a ‘resident’ population if the predicted value of λ given local
232 climate at the site was ≥ 1 (i.e., resident demographic niche), or a ‘migrant’ population if $\lambda < 1$ (i.e.,
233 migrant demographic niche), given our assumption that the long-term persistence such populations at a
234 site can only be achieved via seasonal migration. For each demographic model based on contemporary
235 climate, and used to predict S_a , S_j , and RS , we also calculated prediction uncertainty and error
236 propagation (Taylor, 1997) to estimate the 95% confidence limits and prediction uncertainty in λ .

237

238 ***Climate niche models***

239 To characterize relationships between migration or residence and climate at the continental scale using
240 our ‘climate niche model,’ we first obtained all observations of song sparrows from the eBird Basic
241 Dataset (version Sep 2019; www.ebird.org/science/download-ebird-data-products) to extract presence and
242 absence data from individual checklists. eBird is a large semi-structured citizen science depository of
243 high-quality observations of birds year-round. We filtered 49,972,482 checklists for our study area
244 (comprising Alaska, British Columbia, Washington, Oregon, and California) to include only those
245 recorded from January 1, 2010 to September 1, 2019, representing ‘complete checklists’, with a
246 maximum distance travelled of 5 km, and ≤ 5 hrs of effort, and complete documentation; yielding
247 5,137,845 informative checklists (using *Auk* package in R; Strimas-Mackey et al., 2018). Because eBird
248 checklists are not randomly distributed in space or time and often suffer ‘class imbalance’ due to more

249 absences than presences recorded, we generated a 1 km hexagonal grid over the study area and randomly
250 subsampled the filtered dataset to reduce bias, following Johnston et al. (2019). Subsampling had little
251 influence on prevalence but reduced checklists to 3,424,036 (detection rate before subsampling = 33.3%;
252 after= 33.9%). Checklists were further sorted to create ‘winter’ and ‘breeding’ distributions based on the
253 date in which observations were made, such that observations in January-February were assumed to
254 reflect the distribution of overwintering populations (N = 543,837) and those in May-June the distribution
255 of the breeding populations (N = 693,751), respectively (N_{total} = 1,237,588). Ten climate variables
256 describing annual variation in temperature and precipitation were used to predict the occurrence of
257 migration and residence in song sparrows at each sample location (Table S2; 2010-18).

258 To predict the contemporary, historical, and future ranges of migratory and resident song sparrow
259 populations in western North America, we used Random Forest (*ranger* R package; Wright & Ziegler,
260 2017). Random Forest models are considered one of the most credible statistical methods for species
261 distribution modelling, and are highly flexible and easy to implement (Elith et al. 2008; Iverson et al.
262 2011; Laube et al. 2015; Wang et al. 2012). Random Forest works by producing a ‘forest’ of decision
263 trees and aggregating the results over all trees. The decision trees are constructed with a bootstrap sample
264 of the input data such that the resulting ‘bagged’ dataset contains about 64% of the original observations,
265 and the remaining samples comprise the ‘out-of-bag’ (OOB) data. Using the trees grown from a bootstrap
266 sample, each of the independent observations in the OOB data is classified as either presence or absence
267 and a model prediction error (OOB error) as the percent of incorrectly classed observations is calculated.
268 We built a Random Forest model for resident and breeding song sparrows, respectively. The species
269 occurrence (presence or absence) was used as the dependent variable, and the 10 climate variables were
270 used as predictors.

271 We evaluated OOB error rates using Brier Score (Brier, 1950), which employs the mean squared
272 error of the probabilistic model predictions and the true presence or absence in OOB data. We also
273 evaluated performance using sensitivity, specificity, AUC, and Kappa metrics calculated by comparing

274 predictions to the actual observations in unseen data (OOB data; Table S4). Random Forest also provides
275 measures of variable importance defined as the mean decrease in model accuracy (DMA; Altmann et al.,
276 2010). To reduce prediction bias, we fit a balanced random forest model using the ‘sample.fraction’
277 argument to grow each tree from random samples of the data with an equal number of detections and non-
278 detections. Because the effect of number of predictors selected at each node was minor, we used the
279 default square-root of the number of predictors included (Breiman, 2001). By repeated testing, we found
280 that 500 trees per model generated consistency in model accuracy.

281 After the models were built and tested, we first predicted the climate niche for both resident and
282 breeding song sparrows across western North America using the predict function in the *ranger* package to
283 produce maps in response to the contemporary, historical, and future climate periods (see ‘Climate data’).
284 We then created the migrant niche by classifying ‘migrant’ pixels as those which were occupied during
285 the breeding period and absent in winter. The resident niche was determined by classifying ‘resident’
286 pixels as those which were occupied during both breeding and winter periods, assuming the same
287 individuals are present in both seasons. All maps showing the niche spatial distributions were generated
288 in ArcGIS (v10.7.1).

289

290 ***Spatial and temporal map comparisons***

291 To assess agreement of our climate and demographic niche models we first calculated the percentage of
292 grid cells predicted to host resident or migrant song sparrow populations given the climate niches of each
293 within each of the three regions of interest at the northern (AK), central (BC), and southern (CA) extents
294 of our study area. To estimate how much prediction uncertainty of the demographic models affects
295 agreement between climate and demographic models, we used the 95% upper and lower confidence limits
296 to calculate agreement as stated above. We then compared these climate niches to the demographic niche
297 model derived from the demographic variation observed on Mandarte Is. and projected across the study
298 area (i.e., assuming that all song sparrows respond to climatic conditions in ways similar to those

299 documented on Mandarte Is. over the last half century). To do so, we also classified grid cells by the
300 expected rate of population growth given local climatic variation as noted above. Agreement between
301 mapped predictions was estimated by first sampling 1,000 grid cells at random and calculating the
302 Pearson's correlation coefficient, r , between the difference in predicted probabilities of occurrence and
303 population growth rate at a site versus the Euclidian distance from our focal location. We report the mean
304 value of r ($\pm 1SD$) given 10,000 replicated comparisons and the mean percentage of grid cells across our
305 study area. Statistical description of seasonal and spatial climate variation in these regions appear in Fig
306 S5 and Table S6.

307 We also estimated the correlation between maps in climatic space by collapsing the 10 climate
308 variables (Table S2) into principal components (PCs; Table S5). PC1 and PC2 together described 78% of
309 observed variation and were used here to define climate space independent of location. Coastal areas
310 scored higher than their adjacent continental space, indicating that PC1 reflected 'continentality', whereas
311 PC2 reflected a 'temperature – wetness' gradient (Fig. S3). Spatial correlations between our climate and
312 demographic niche models were explored by assembling three bins of equal width wherein climate was
313 similar, ensuring the smallest bin had $\geq 100,000$ pixels with predictions (Fig. S4). Agreement between
314 maps was estimated as described above.

315

316 **Results**

317 *Demographic models*

318 We predicted the growth rate (λ) of song sparrow populations in western North America using a
319 deterministic model based on relationships between climatic conditions and juvenile and adult survival
320 (S_j , S_a) and reproductive success (RS) fit to 48 years of data from an intensively studied focal population.
321 Eight climate variables hypothesized to influence the demography of our focal population accounted for
322 47, 44 and 56% of variation in annual S_j , S_a , and RS observed, respectively (Table 1, S1, S3). S_j was

323 predicted to decrease as July heating degree days ($\text{Jul DD} > 18 = -0.390 \pm 0.125$; $(\text{Jul DD} > 18)^2 = 0.195$
324 ± 0.133) and February cooling degree days increased ($\text{Feb DD} < 0 = 0.057 \pm 0.137$; $(\text{Feb DD} < 0)^2 = -$
325 0.457 ± 0.106), and to increase with precipitation in August ($\beta \pm \text{SE}$; $\text{Aug PPT} = 0.254 \pm 0.105$), and
326 slightly with cooling degree days in December ($\text{Dec DD} < 0 = 0.190 \pm 0.109$), and to). S_a was similarly
327 predicted to decrease as cooling degree days in February ($\text{Feb DD} < 0 = -0.065 \pm 0.086$; $(\text{Feb DD} < 0)^2 =$
328 -0.331 ± 0.082) and precipitation in August ($\text{Aug PPT} = 0.134 \pm 0.059$) increased, and to increase slightly
329 with December ($\text{Dec DD} < 0 = 0.112 \pm 0.061$). RS was predicted to increase with increasing heating
330 degree days and precipitation in spring ($\text{Jun DD} > 18 = 0.207 \pm 0.059$; $\text{Mar PPT} = 0.151 \pm 0.055$; Jun
331 $\text{PPT} = 0.175 \pm 0.059$).

332

333 *Climate niche models*

334 Climate niche models for resident and migrant song sparrows throughout western North America, based
335 on eBird data fit to 10 climate variables using Random Forest, displayed high accuracy (OOB error:
336 15.5% and 13.9%), sensitivity (81.1% and 83.0%), and specificity (78.4% and 80.3%), respectively
337 (Table S4). Climate variables reflecting ambient and extreme temperatures had the largest influence on
338 model accuracy in our resident niche model (e.g., $\text{DD} > 5$, T_{max} , T_{min} , T_{ave}) with DMA ranging from
339 11.5 to 12.7% (Fig. S2). The predicted migrant niche also depended strongly on local climate, especially
340 temperature in late winter to early spring (Fig. S2; T_{max} , $\text{DD} > 5$, T_{min} , $\text{DD} > 18$; $\text{DMA} = 12.4$ to
341 13.5%.) Precipitation also influenced resident and migrant niches strongly (e.g., see below; Fig. S2; DMA
342 $= 10.6$ and 12.2% , respectively).

343 However, variables used to develop climate niche models affected migrant and resident niche
344 differently over our study area in western North America (Fig S5). In all cases, warmer winter
345 temperatures prevailed in the resident versus migrant niche, but these differences were much smaller in
346 California than Alaska, causing a statistical interaction between location and migratory status (Table S6).
347 In contrast, winter precipitation was higher in the migrant than resident niche in AK and BC whereas an

348 opposite pattern prevailed in niche CA (Table S6). Variables reflecting heat load in spring also influenced
349 resident and migrant climate niches unequally. For example, degree-days of warming ($DD > 18$) in the
350 migrant niche in CA exceeded values recorded in the resident niche. Warming was also higher in the
351 resident than migrant niche in BC but similar in migrant and resident niches in AK (Table S6).

352

353 *Spatial agreement of demographic and climate niches*

354 The parallel effects of climate on the demography of our focal population and modeled distributions of
355 resident and migratory populations of song sparrows in western North America led to strong agreement
356 between the resulting climate and demographic niches predicted in Cartesian space in the region of our
357 focal population (BC; 95% CI [LL, UL]; 75.8% [63.3%, 72.3%]; Fig. 1c, f). However, the agreement
358 between the predictions of each was slightly to much weaker at the northern (AK; 57.6% [24.6%, 31.0%])
359 and southern (CA; 39.5% [36.5%, 39.8%]) extents of the study area, respectively. In the BC region,
360 prediction uncertainty of the demographic model was strongly correlated with winter cold (Dec and Feb
361 $DD < 0^{\circ}\text{C}$: 0.89 and 0.88, respectively) but much weaker for spring and summer precipitation and
362 summer heat (range = -0.19 – 0.06; Fig. S6). Spatial correlations between the predicted distributions of
363 resident and migratory sparrows also decreased as the Euclidean distance from our focal population
364 increased ($r = -0.29 \pm 0.02$), as expected if locally adapted populations respond to climatic conditions
365 differently than year-round residents in our focal study population.

366 The agreement between our climate and demographic niche models also decreased as climatic
367 conditions in our focal population diverged from those experienced by song sparrows elsewhere in
368 western North America. Across western North American variation in climate space was largely accounted
369 for by PC1 (56.2%; Table S5), reflecting differences in ‘continentality;’ e.g., coastal areas with positive
370 values of PC1 experience much less variation in annual temperature and precipitation than montane, high
371 plains, and deserts, all with negative values of PC1 (Fig. S3). PC2 described a complimentary but less

372 variable (21.8%; Table S5) gradient of warmer, drier (positive values) to cooler, wetter conditions
373 (negative values; Fig. S3).

374 Strong spatial correlations between the demography and predicted distribution of resident and
375 migratory song sparrows at regional to larger scales similar to those estimated between continentality
376 (PC1, Fig S4) and the spatial overlap of the predictions of demographic and climate niche models in the
377 region surrounding our focal population (bin 2: $r = 0.78 \pm 0.01$). However, as predicted, we observed
378 smaller positive correlations in the northern region of our study area (AK), where variation in
379 continentality was very high (bin 1: $r = 0.53 \pm 0.02$), and in the southern region of our study area (CA)
380 where variation in continentality was less but variation in aridity was high (bin 3: $r = 0.32 \pm 0.02$).
381 Despite accounting for a substantial fraction of variation in climate over the study area, PC2 was weakly
382 related to the predicted ranges of resident and migrant song sparrows based on our climate niche model
383 (Fig S4).

384

385 *Historical and future variation in the spatial distribution of the climate niche*

386 General agreement of our demographic and climate-based niche models allowed us to ask how migratory
387 and resident niches may have shifted due to climate warming after the period 1901-1910, when winter
388 temperatures at our focal population averaged 0.9°C less than conditions in 2010-2018, but still 3.1°C less
389 than averages expected in 2070-2100. To predict how such changes could affect the demography and
390 distribution of song sparrows in the region of our focal population, we therefore compared our climate
391 and demographic niche models parameterized to historical, contemporary, and future conditions to
392 quantify consequence shifts in the range of resident and migrant song sparrow populations. In particular,
393 we expected that climate warming has facilitated range expansion by song sparrows, particularly those
394 displaying resident life histories.

395 In support of our predictions, the combined area of the resident and migrant song sparrow niches
396 in the BC region was predicted to have increased by 27.7% (39,668 km²; Fig. 2a, b) and 24.1% (36,309

397 km²; (Fig. 2d, e) from 1901-1910 to present (demographic and climate niche model, respectively). The
398 demographic and climate niche model predicted further increases of 27.4% (50,003 km²; Fig. 2b, c) and
399 10.1% (18,511 km²; Fig. 2e, f), respectively, given climate in 2070-2100. Similarly, the resident niche
400 was predicted to have increased by 36.3% (24,467 km²; Fig. 2a, b) from the historical to present period
401 under our demographic model, or by 38.8% (37,471 km²; Fig. 2d, e) in climate niche model. The resident
402 niche was also projected to increase by 12.8% (17,015 km²; Fig. 2e, f) from the present to future period
403 by our climate niche model, but by 69.1% under our demographic niche model (63,384 km²; Fig. 2b, c).
404 Demographic and climate models also predicted upward expansions in elevation range for song sparrows,
405 with the mean elevation of resident populations rising 171 m over 200 years (i.e., 1900 to 2100; historical
406 = 365 m, current = 475 m, future = 536 m) according to our climate model versus 258 meters (historical =
407 240 m, current = 281 m, future = 498 m) by our demographic model, confirming close correspondence of
408 these predictive models proximal to our focal study population.

409

410 **Discussion**

411 Predicting how species distributions will shift in response to climate change depends in part on how life-
412 history traits such as seasonal migration versus residence reflect variation in environmental conditions,
413 influence individual and population fitness and thereby affect species occurrence (e.g., Reid et al. 2018,
414 Vistry et al. 2018, Acker et al., 2021a; 2021b). By contrasting the predicted climate and demographic
415 niches of song sparrows spanning a substantial geographical range in western North America, we
416 highlighted uncertainties in the application and empirical basis of commonly-used species distribution
417 models, whilst exploring the potential for variation in seasonal migration versus residence to facilitate
418 climate adaptation. We found substantial agreement in the predictions of our demographic and climate
419 niche models in the region of our focal study population in Canada, but also quantified a predicted
420 deterioration in model agreement in regions that differ in climatic conditions. Our results thus support the
421 idea that climate niche models based on species occupancy and climate averages can reproduce broadly

422 the predictions of detailed empirical models which link demographic performance to species distribution
423 and migration via space for time substitution. However, we also revealed limits on this approach when
424 extrapolating an empirical demographic model of our focal song sparrow population to predict population
425 growth, migration behavior, and distribution in AK and CA, as expected if song sparrow in these regions
426 have adapted *in situ* to maximize fitness within their regional environment. Taken together, these results
427 also support our overarching suggestion that climate has and will continue to affect the distribution of
428 song sparrows via its influence on demography and migratory behavior. Our findings highlight the
429 potential role of seasonal migration in climate adaptation and offer strong support to the assumption that
430 climate niche models reflect demographic processes that drive local population persistence. But they also
431 point to limits in our ability to predict species distributions in the absence of reliable knowledge on the
432 factors limiting population growth.

433

434 ***Demographic versus climate niches***

435 We found strong agreement between our demographic and climate niche models particularly in the BC
436 region where our focal population resides (Fig. 1). These results strongly support the general hypothesis
437 that climate plays a key role in the demography, distribution, and life history of species (Hutchinson,
438 1957). More importantly, they extend understanding by demonstrating that empirical demographic
439 models driven by climatic conditions can predict migratory phenotype given historical, current, or future
440 climatic conditions (Fig. 2).

441 Dybala et al. (2013) suggested that the climate niche of song sparrows at a long-term monitoring
442 site in coastal California was strongly influenced by winter temperature and precipitation in the preceding
443 wet season via their effects on survival and population growth. Our demographic model predicted a
444 declining population growth rate ($\lambda = 0.80$) in coastal California, similar to Dybala et al.'s (2013)
445 prediction given averaged climatic conditions ($\lambda = 0.88$). However, because we arbitrarily classified
446 populations predicted to decline ($\lambda < 1$) based on local climate and modeled relationships between

447 demography and climate in our focal population, our demographic niche model predicted that this coastal
448 California population should migrate, whereas our climate niche model accurately predicted their status
449 as year-round residents. It is plausible that some song sparrow populations in coastal California exist as
450 metapopulations comprising a mix of migratory phenotypes. Although, these comparisons suggest our
451 empirical demographic niche model under-predicted the range of resident song sparrows in western North
452 America, they generally support suggestions that climate niche models can be used to elucidate factors
453 contributing to variation in the historical, contemporary, and future distributions of partial migrant
454 species.

455 Across western North America our climate and demographic niche models yielded moderate to
456 excellent predictions of the migratory status of song sparrow populations (Fig. 1; Table S3; S4). In
457 particular, models built on an *a priori* understanding of the effects of climate on local survival,
458 reproduction, and population growth predicted the observed distribution of resident and migratory
459 populations in the BC region with high precision. This supports the hypothesis that variation in the
460 occurrence of seasonal migration represents an adaptive response to temporal variation in climate and its
461 influence on resource availability and osmotic and/or thermal stress. Moreover, the close correspondence
462 of our empirical climate niche model with observed patterns of spatial variation seasonal migration in BC
463 imply that this variation is shaped by natural selection (e.g., Arcese et al., 2002; Peters et al., 2017; Reid
464 et al., 2018; Delmore et al., 2020).

465

466 ***Spatio-temporal shifts in resident and migrant niches***

467 Links between climate, demography, and distribution observed in BC also allowed us to predict that
468 climate warming in the last century should have facilitated range expansion by song sparrows expressing
469 resident phenotypes as the amelioration of winter cold and relaxed its effects on juvenile and adult
470 survival (e.g, Arcese et al. 1992). Similar examples of range expansion and upward shifts in elevation in
471 response to climate warning have been reported in many taxa (birds, La Sorte & Thompson, 2007;

472 insects, Hickling et al., 2005; plants, Holzinger et al., 2008; mammals, Moritz et al., 2008). Although
473 song sparrows have resided year-round in our focal study population since at least 1960 (Tompa, 1963),
474 our demographic niche model suggests that a population comprised of residents would decline rapidly
475 given historical climatic conditions due to a much higher frequency of freezing temperatures in winter.
476 We therefore expect migratory phenotypes to have predominated in our focal population in the early
477 1900s, as is currently the case in song sparrow populations breeding above 500 m elevation in BC (Fig. 2,
478 our unpubl. observations). Although historical data from BC do not allow a direct test of this hypothesis,
479 a shift from migratory to residential phenotype has occurred at Interpont, Ohio, where Nice (1933) used
480 color-banded birds to confirm the migratory status of all but a single male song sparrow in the 1930s, but
481 wherein most or all birds now reside year-round (Chris Tonra, pers. comm.). Historical records in British
482 Columbia also suggest resident populations of song sparrows were restricted to warm coastal sites on
483 Vancouver Island prior to the 1890s (e.g., Fannin, 1891).

484 Overall, the distribution of resident song sparrow populations predicted by our models has
485 expanded substantially since historical surveys (Fig. 1), implying a marked expansion over the last
486 century. Similarly, Visty et al. (2018) reported that fox sparrows (*Passerella unalaschcensis*), formerly an
487 obligate migrant throughout its range, established year-round residence on Mandarte Is. after 1960-63,
488 when Tompa (1963) initiated our song sparrow study. Interestingly, Visty et al. (2018) reported that
489 resident fox sparrows produced more broods, and displayed higher survival and population growth rates
490 on Mandarte Is. than migrant populations studied to date, suggesting that higher relative fitness in birds
491 displaying resident versus migrant phenotypes facilitated an expansion of the breeding range.

492

493 ***Local adaptation***

494 In European shags (*Phalacrocorax aristotelis*), harsh climatic events in winter contributed to mortality
495 and caused natural selection on the migratory phenotype of individuals, supporting the idea that micro-
496 evolutionary processes can influence the composition of populations with respect to migratory phenotype

497 (Acker et al., 2021a; 2021b) and influence species distribution. Our results underscore this idea by
498 demonstrating links between climate, population demography, species distribution, and dynamics of
499 seasonal migration in response to historic and ongoing climate change (Aitken et al., 2008; Sexton et al.,
500 2009; Hendry et al., 2018; Bay et al., 2018). Specifically, we suggest that variation in the occurrence of
501 migration represents one route by which mobile species can adapt to rapid climate change, particularly in
502 partial migrants subject to climatic limits on survival and/or reproduction.

503 Song sparrows are among the most polytypic vertebrates known (Aldrich, 1984; Arcese et al.,
504 2002; Patten & Pruett, 2009) and vary markedly in expression of migration and correlated behavioral,
505 morphological and physiological traits including body dimensions (Pruett & Winker, 2010), clutch size
506 (Johnston, 1954), and osmoregulatory capacity (Mikles et al., 2020). Song sparrows also vary predictably
507 in traits widely recognized as adaptations to climatic variation in seasonality and primary production
508 (Sæther et al., 2016) including territorial, dispersal, and breeding behaviors, and demographic traits linked
509 to fecundity, parental effort, and longevity (Arcese, 1989; Arcese et al., 2002; Germain & Arcese, 2014;
510 Tarwater & Arcese, 2017; Reid & Arcese, 2020). Because such traits often have an additive genetic basis
511 (e.g., Schluter & Smith, 1986; Wolak & Reid, 2016; Reid & Arcese, 2020), it is plausible that spatial
512 variation in natural selection has contributed to heritable variation in migratory phenotype, as extensively
513 described in blackcaps (*Sylvia atricapilla*; e.g., Berthold, 1991; Berthold & Pulido, 1994; Delmore et al.,
514 2020), along with the divergence of subspecies (Aldrich, 1984). If so, the pace of adaptation to climate
515 warming in song sparrows might first be measured as the rate by which residency has become established
516 in local populations known to have been migrants historically, and secondarily by estimating the rate of
517 change in allele frequencies at functional loci (Rellstab et al., 2016; Capblancq et al., 2020). Phenotypic
518 changes in migration behavior may also arise plastically, but influence subsequent genetic change
519 (Coppack & Pulido, 2004; Pulido, 2007; Teplitsky & Millien, 2014). Quantitative genetic approaches
520 (Kruuk, 2004; Wolak et al., 2018; Reid et al., 2021) to estimate the genetic basis of partial migration and
521 pedigree-based comparison of individuals displaying residence versus migration should help elucidate the

522 contributions of phenotypic plasticity versus micro-evolution in local adaptation to rapid environmental
523 change and the divergence of populations.

524 Finally, we made several assumptions in this study that could influence our results and warrant
525 further work. First, climate niche models depict correlations between species occurrence and climate, but
526 do not account for biotic interactions known to vary spatially, temporally, and in response to climate
527 change. Thus, because density, inter- and intra-specific competition, parasitism, depredation, inbreeding,
528 and dispersal all interacted with climate to affect fitness in our focal song sparrow population (e.g., Marr
529 et al. 2002, 2006; Jewell & Arcese 2008; Germain & Arcese 2014; Johnson et al. 2018; Crombie &
530 Arcese 2020; Reid et al. 2021), more work is need needed to determine if such knowledge can improve
531 predictions of distribution models (e.g., Sinclair et al. 2010). For example, data from across the song
532 sparrow range could be used to identify climatic factors most influential of local demography to
533 characterize spatial dynamics more precisely. However, because doing so will add assumptions that may
534 be challenging to test, we advise that comparative analysis, external validations (this study), and adaptive
535 management (Walters 1986) offer more direct paths to reliable knowledge in conservation planning (e.g.,
536 Romesburg 1981). Our models also assumed niche conservatism, whereas capacities for rapid adaptation
537 are increasingly being reported in nature (e.g., Hendry et al. 2018; Radichuck et al. 2019; Skaeien &
538 Arcese 2022; Bonnett et al. 2022), including via gene flow and directional selection in song sparrows
539 (Walsh-Emond et al. 2019; Mickles et al. 2020; Reid & Arcese 2020; Reid et al. 2021). Initial findings
540 imply that a relatively small number of loci influence osmoregulation and body size (Mickles et al. 2020;
541 Carbeck et al. unpubl. res.) in this species. Last, we used random forest to predict climate niches of
542 migratory and resident song sparrows. Although it is also common to use an ‘ensemble’ of different
543 models to avoid potential biases in each (Elith & Leathwick 2009), or to consolidate individually
544 uncertain projections to create ‘consensus’ decisions in management (Wang et al. 2012), Hao et al. (2019,
545 2020) found no particular benefit to using ensembles over individual models.

546

547 ***Conclusions***

548 The ability of song sparrows to persist over a wide range of climatic conditions in western North America
549 indicates their broad tolerance for a diverse range of factors with the potential to limit individual fitness
550 and population growth. By engaging in seasonal migration from sites where residents are unlikely to
551 persist year-round, song sparrows encompass a larger range in North America than could otherwise be
552 accommodated in species displaying less flexibility in migration and life history. Fryxell et al. (1988)
553 reached similar conclusions after comparing range size and abundance in migrant, resident, and partial
554 migrant ungulate populations by attributing such differences to spatial variation in demographic processes
555 that limit individual survival in the non-breeding period (Fryxell & Sinclair 1988). The rapid evolution of
556 populations comprised of migrant, partial migrant, or resident song sparrows, as evidenced by transitions
557 to residency in areas experiencing climate warming, thus appears to be a common mechanism by which
558 mobile species that display phenotypic plasticity and/or additive genetic variance for migratory behavior
559 may adapt to environmental change (e.g., Coppack & Both 2002, Pulido & Berthold 2010, Reid et al.
560 2018, Vistry et al. 2018, Rushing et al. 2020).

561 However, regardless of taxa, phenotypic change in migratory status could be facilitated or
562 constrained by correlations between physiological, morphological, and behavioral processes influenced
563 by developmental plasticity and genetic evolution, and thereby affecting fitness. For example, individual
564 differences in conspecific attraction, diet, vagility, phenology, immune status, brain size, or other traits
565 may all interact to influence the capacity of species to colonize and persist in novel habitats, including
566 those becoming suitable via climate amelioration (e.g., Coppack & Both 2002, Ord et al. 2015, Whytock
567 et al. 2018, Sayol et al., 2020, Veit et al. 2021). This implies that careful assessments of a species'
568 capacity to colonize and persist in such habitats may be necessary to identify species that are sufficiently
569 canalized or sessile as to require human assistance to keep pace with anthropogenic change (Aitken et al.
570 2008, Franklin 2010, Wang et al. 2012). In contrast, for species like song sparrows, which display marked
571 local adaptation despite contemporary gene flow and reinforcing directional selection (e.g., Nelson-

572 Flower et al. 2018, Walsh et al. 2018, Mikles et al. 2020, Reid & Arcese 2020), best management practice
573 may be to ensure sufficient gene flow to maintain additive genetic variance in local populations. In all
574 such cases, Franklin (2010) suggested the static predictions of SDMs be combined with dynamic
575 landscape and demographic models to forecast species performance and range more precisely to advise
576 management. We suggest that song sparrows offer a model system for understanding the evolution of
577 seasonal migration and local adaption, and that future studies will benefit from the integration of fine-
578 scale demographic parameters across the species range. Our current results highlight the potential role of
579 long-term studies and demographic data in explicating the climatic factors which limit population growth
580 and species distribution, complement approaches based on temporal and spatial correlations of climate,
581 habitat composition, and species occurrence over time (Rushing et al. 2020), while also responding to
582 calls for increased biological realism (Seaborn et al. 2020) and more rigorous validations (Sinclair et al.
583 2010) of species distribution models applied to conservation.

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602

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604

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609

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611 analysed the data and wrote the manuscript. K.C., T.W., J.R. and P.A. edited and improved the
612 manuscript.

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Table 1. Predicted response of demographic vital rates to climatic variables, their hypothesized mode of action, and references to the prior results on which predictions are based.

Vital Rate	Variable (Abbreviation)	Months	Rationale	References	Prediction
Survival	Degree days < 0°C (DD < 0)	Dec, Jan, Feb	Influences energy required for thermoregulation and reduces access to food	Arcese, 1989; Keller et al. 1994; Ketterson and King 1977	Survival rates decrease as degree days below freezing increase
	Spring precipitation (PPT) in mm	Apr, May	Influences level of environmental stress and reduces foraging opportunities	Öberg et al. 2015; McDonald et al. 2004	Survival rates decrease with high precipitation in spring
	Summer precipitation (PPT) in mm	Jun, Jul, Aug	Dry, hot summers reduce food abundance and may increase intraspecific competition for access to water	Arcese and Smith 1985; Arcese and Smith 1988; Smith et al. 2006	Survival rates decrease with low precipitation in late summer/degree days greater than 18°C
	Degree days > 18°C (DD > 18)				
Reproductive success	Degree days < 0°C (DD < 0)	Jan, Feb, Mar, April (prior to breeding)	Influences length of breeding season	Tarwater and Arcese 2018; Wilson and Arcese 2003	Reproductive success decreases as degree days below freezing increase
	Spring precipitation (PPT) in mm	Mar, Apr, May	Influences level of environmental stress during nesting period, reduces foraging opportunities, and is correlated with nest abandonment	Öberg et al. 2015; Wingfield 1985; McDonald et al. 2004; Crombie and Arcese 2018	Reproductive success decreases with high levels of precipitation in spring
	Summer precipitation (PPT) in mm	Jun, July	Dry, hot summers reduce food abundance and may increase intraspecific competition for access to water, especially among fledged young. May also influence length of breeding season	Arcese and Smith 1985; Arcese and Smith 1988; Smith et al. 2006; Tarwater and Arcese 2018	Reproductive success decreases with low precipitation in late summer/degree days greater than 18°C
	Degree days > 18°C (DD > 18)				

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Figure 1. Present-day ranges of the expected population growth wherein the migrant demographic niche is indicated in purple ($\lambda < 1$), and resident demographic niche is indicated in orange ($\lambda > 1$) predicted using demographic models (insets a-c), and migratory (purple) and resident song sparrow populations (orange) predicted using climate niche models (insets d-f; see Methods). AK (inset a and d; Aleutian Islands, AK), BC (inset b and e; Georgia Basin, BC), and CA (inset c and f; San Francisco Bay, CA) regions highlight areas wherein the observed ranges are more and less similar. Climate data was acquired from ClimateNA (version 6.00; Wang et al. 2016). Scale bar: 50km.

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Figure 2. Projected distribution of song sparrows for past (1901-1910; a, d), current (2010-2018; b, e) and future (2070-2100 under scenario RCP 4.5; c, f) using two modelling approaches: demographic modelling (GLM; a-c), and climate niche modelling (Random Forest; d-f) for the BC region. In the demographic models, the migrant niche ($\lambda < 1$) is indicated in purple and resident niche ($\lambda > 1$) in orange, and in the climate niche models the migrant niche is shown in purple and resident niche in orange. Climate data was acquired from ClimateNA (version 6.00; Wang et al. 2016).