

1 **Title:** Spatial synchrony at the extremes: Tail-dependence in temperature drives tail-dependence
2 in birds' spatial synchrony across North America

3

4 **Authors and emails:**

5 Shyamolina Ghosh^{1*}(ghoshshyamolina89@gmail.com),

6 Owen L. Petchey¹(owen.petchey@ieu.uzh.ch)

7

8 **Affiliations:**

9 1. Department of Evolutionary Biology and Environmental Studies, University of Zurich;
10 Winterthurerstrasse 190, 8057 Zurich, Switzerland

11 ***Name, mailing address, email, phone number of corresponding author:**

12 Dr. Shyamolina Ghosh

13 Senior researcher (oberassistentin)

14 Department of Evolutionary Biology and Environmental Studies, University of Zurich

15 Winterthurerstrasse 190, 8057 Zurich, Switzerland

16 Phone (+41) 779567848, email ghoshshyamolina89@gmail.com

17

18 **Short running title:** Spatial synchrony at the extremes

19

20 **Keywords:** Tail-dependent synchrony, Spatial synchrony, Birds, LTER, Copula, Abundance,
21 Time series, Climate extremes, Dispersal

22

23 **Type of article:** Letter

24 **Number of words in the abstract:** 149, **Number of words in the main text:** 4912, **Number of**
25 **words in each text box:** NA, **Number of references:** 56, **Number of figures:** 5, **Number of**
26 **tables:** 0, **Number of text boxes:** 0

27

28 **Statement of authorship:** Conceptualization, Data curation, Formal analysis, Investigation,
29 Methodology, Software, Validation, Project management, Writing – original draft: SG; Funding
30 acquisition, Resources, Supervision: OP; Writing – review & editing: SG, OP.

31

32 **Data and code accessibility statement:** All data used for this analysis were extracted from
33 several public databases (e.g., Breeding Bird Survey: <https://doi.org/10.5066/P9J6QUF6>;
34 CHELSA: <https://chelsa-climate.org/>, AVONET: (Tobias *et al.* 2022); EltonTraits: (Wilman *et al.*
35 2014); Birds of the World: (Billerman *et al.* 2022); BirdTree: <https://birdtree.org/>). Analyses
36 were conducted in Program R (R Core Team 2022); version number 4.2.1, and publicly archived
37 in Zenodo (<https://doi.org/10.5281/zenodo.10840575>).

38

39

40

41

42

43

44

45

46

47 Abstract

48 Environmental change is becoming synchronous across sites with frequent emergence of
49 extremes in recent years, with potential impacts on species' synchronous abundance over large
50 scales. Analyzing 41 years of breeding bird survey data across North America, we observed that
51 some birds showed mostly lower tail-dependent spatial synchrony (i.e., synchrony across sites at
52 low abundances), while others showed mostly upper tail-dependent spatial synchrony (i.e.,
53 synchrony across sites at high abundances). We found that spatial synchrony in climate extremes
54 (i.e., tail-dependence in climate), not the dispersal trait (hand-wing index), drove the spatial
55 synchrony in abundance extremes (i.e., tail-dependence in abundance) up to 250 Km.
56 Tail-dependence in high (or low, respectively) temperature across sites caused lower (or upper,
57 respectively) tail-dependent spatial synchrony in abundance. In a rapidly changing environment,
58 these findings highlight the importance of considering synchronized climatic extremes to assess
59 species' tail-dependent spatial synchrony across large scales.

60

61

62

63

64

65

66

67

68

69

70 Introduction

71 Understanding spatio-temporal patterns in the abundance of natural populations has been
72 a long-standing challenge for ecologists (Gaston & Blackburn 2000). Spatial synchrony - i.e., the
73 correlated fluctuation in abundances of geographically distinct sites within a metapopulation - is
74 a common spatio-temporal pattern widely observed in many taxa (Bjørnstad *et al.* 1999;
75 Liebhold *et al.* 2004). Spatial synchrony can arise due to diverse factors (Haynes & Walter
76 2022), including similar responses to correlated environmental drivers-the mechanism known as
77 the “Moran effect” (Hansen *et al.* 2020; Moran 1953), as well as dispersal within metapopulation
78 (Abbott 2011; Goldwyn & Hastings 2008), and effects of synchronized or mobile predators
79 (Haynes *et al.* 2009; Vasseur & Fox 2009). Studying spatial synchrony for a given species helps
80 ecologists to understand variability in abundance across sites, species’ vulnerability to stochastic
81 events, and spatial prioritization of conservation management (Allen & Lockwood 2020; Heino
82 *et al.* 1997; Koenig & Liebhold 2016; Walter *et al.* 2021; Yang *et al.* 2022).

83 Growing evidence indicates that extreme climatic events are becoming more frequent
84 over large scale (Duffy & Tebaldi 2012; La Sorte *et al.* 2021; Weaver *et al.* 2014). When such an
85 extreme climatic event is synchronized over large scales, it affects metapopulation dynamics,
86 stability, and extinction risk by making population abundances synchronized across sites within a
87 metapopulation network (Jenouvrier *et al.* 2009; Reeve 2018; Sarremejane *et al.* 2021; Tack *et*
88 *al.* 2015). Furthermore, if an extreme climatic event occurs at a large regional scale where many
89 species share similar resources and environment, synchrony in extreme climate has been shown
90 to affect synchrony in population abundances across multiple species, and trophic levels (Hansen
91 *et al.* 2013). As climatic extremes can result in climatic conditions beyond the tolerance range of
92 species (Ummenhofer & Meehl 2017), it is essential to investigate linkages between the spatial

93 synchrony of species' populations and climatic conditions considering the importance of climatic
94 extremes for population extremes.

95 Frequent widespread climatic extremes create considerable concerns for species
96 conservation and lead us to think about the impact of spatial synchrony in climatic conditions on
97 population viability beyond the usual approaches. The usual approach measures pairwise
98 synchrony through correlation between two fluctuating variables from two sites (variables could
99 be two population abundance time series, or could be two temperature time series) and then
100 compares synchrony in abundance and synchrony in temperature for evidence of the “Moran
101 effect”. However, when using correlation to measure pairwise synchrony, the influence of
102 extremes, either in terms of population size or climatic events, may be missed. To elaborate, as
103 correlation is a measure of linear relationship, it is not sufficient to quantify the dependence
104 between two extreme values. Therefore, two correlated time series can have exactly the same
105 correlation coefficient (i.e., same spatial synchrony), irrespective of whether they have
106 significant dependence in their extreme values (i.e., tails) or not, Fig. 1. In such a situation, one
107 cannot differentiate the metapopulation risks for two cases: when populations are overall
108 synchronous and when populations are synchronous particularly at extreme low (or high)
109 abundances. We term this as “synchrony at the extremes”, and also “tail-dependence” since it
110 concerns associations or dependencies in the tails of the distributions of variables.

111 In simple words, measuring “tail-dependence” focuses on the tails (low or high end) of
112 the concerned distribution (e.g., for a joint distribution of population abundances from two sites),
113 rather than the middle part of it - which is the focus for a correlation-based approach. For the
114 same given correlation coefficient two populations can show a variety of tail-dependence (Fig. 1,
115 symmetric tail: A1-A2 no tail-dependence; B1-B2: lower tail-dependence, and for C1-C2: upper

116 tail-dependence) with different implications for extinction risk. A lower tail dependence
117 indicates that populations are synchronous particularly when they are rare at both sites (i.e., their
118 dynamics are more similar when they have low abundance, Fig. 1, B1-B2). Whereas upper tail
119 dependence indicates that populations are synchronous particularly when they are abundant at
120 both sites (i.e., their dynamics are more similar when they are at peak abundance values through
121 time, Fig. 1, C1-C2).

122 Some local-scale studies showed the importance of “tail-dependence” (i.e., considering
123 the synchrony among extreme values beyond the usual correlation coefficient) for synchrony at
124 the extremes in population abundance (Ghosh *et al.* 2020b; Walter *et al.* 2022), stability (Ghosh
125 *et al.* 2021), and metapopulation extinction risk (Ghosh *et al.* 2020c). Since extinction risk is
126 often related to the size of the populations, the risk of regional- to global-scale extinction is
127 increased due to poor rescue effects if populations are synchronous at low abundances across
128 sites (Ghosh *et al.* 2020c) (Fig. 1, B1-B2). On the contrary, lower extinction risk is expected if
129 populations are synchronous at high abundances across sites (Fig. 1, A1-A2) or overall
130 synchronous with symmetric tail dependence (Fig. 1, C1-C2). A recent regional study (Walter *et*
131 *al.* 2022) shows a nonlinear threshold-like relationship between population abundance and its
132 environmental driver as a possible mechanism explaining both types of tail-dependent spatial
133 synchrony in population abundance and is consistent with other theoretical and empirical studies
134 that indicate tail-dependence can arise from threshold like phenomena in ecology (Ghosh *et al.*
135 2020a, b).

136 Here, we provide an analysis of long-term dynamics (1979-2019) of bird species
137 abundances, temperature (T), and precipitation (P) across North America to explore the effects of
138 extreme climates on birds’ spatial synchrony (173 species, 161 sites). We focused on birds

139 because of data availability for a variety of species across a wide geography, but our research
140 questions and methods are equally applicable to any other taxa. Birds are often considered
141 important for ecosystem service and excellent indicators of environmental health (Cohen & Jetz
142 2023; Furness *et al.* 1993; Jetz *et al.* 2022).

143 First, we investigated Q1) if species showed any particular tail-dependence pattern in
144 spatial synchrony for their abundances, i.e., lower tail-dependence when spatial synchrony
145 happens at low abundances across sites, or upper tail-dependence when spatial synchrony
146 happens at high abundances across sites, Fig. 2 (left panel). Moreover, we did an exploratory
147 analysis to see if any patterns are emerging from birds' dietary preferences or IUCN status. We
148 expected insectivorous birds would show mainly lower tail-dependence patterns (rare) if stressed
149 environments limited their resource insects' abundances similarly. We also expected that the
150 species listed as "least concerned" (LC) as per IUCN status should not be rare or lower
151 tail-dependent in abundance across sites.

152 Next, we explored Q2) if tail-dependence patterns in spatial synchrony for climate caused
153 the tail-dependence patterns in spatial synchrony for abundances (Fig. 2, right panel). In a
154 metapopulation network, some patches could show lower tail-dependence in spatial synchrony
155 while others could show upper tail-dependence. Total tail-dependence considers the absolute
156 values of lower and upper tail-dependence in total, whereas directional or net tail-dependence
157 considers the difference of their absolute values (scaled to total tail-dependence) to decide if the
158 metapopulation network, as a whole, is lower or upper tail-dependent. We tested two hypotheses
159 to answer Q2. First hypothesis **H1** tests if the variation in total tail-dependent spatial synchrony
160 of climate explains the total tail-dependent spatial synchrony of abundance across species. If yes,
161 then that would be a direct support of the extended "Moran effect" considering the impact of

162 climatic extremes. Second, hypothesis **H2** tests if species that experience climatic stress (high T
163 or low P) across sites become rare and species that experience low T or high P across sites
164 become common, or vice-versa (i.e. when a stressed environment gives benefit to species). The
165 former situation is more likely to happen and in that case, a negative relationship is expected
166 between directional (or net) tail-dependent spatial synchrony in climate and the directional (or
167 net) tail-dependent spatial synchrony in abundance across species.

168 Since dispersal can also influence spatial synchrony in abundance (Abbott 2011;
169 Goldwyn & Hastings 2008), we asked if species dispersal ability influences tail-dependence in
170 abundance under extreme climate conditions. We expected species with higher dispersal ability
171 to have an advantage in a stressed environment, but we did not know if that advantage would be
172 able to nullify any negative impact due to extreme climate on tail-dependent spatial synchrony in
173 abundance. In our study, we did not quantify the dispersal directly as it requires additional data,
174 for example, by tracking individuals. Rather, we used a trait-based approach with the expectation
175 that species with traits for better dispersal ability (larger value for hand-wing index) would be
176 common across sites, whereas species with limited dispersal ability (smaller value for hand-wing
177 index) would be rare across sites. In particular, we used the trait hand-wing index (HWI) which
178 is considered as a proxy for birds' dispersal ability and a determinant of their geographical range
179 size (Sheard *et al.* 2020). A recent study showed traits like HWI can influence population
180 responses to ongoing climate warming (Germain *et al.* 2023). Therefore, we examined the
181 relative importance of such dispersal-mediated and climate-driven pathways as possible
182 mechanisms causing tail-dependent spatial synchrony in birds' abundances.

183

184 **Materials and Methods**

185 **Data**

186 *Abundance data*

187 We used 41 years (1979-2019) of the North American Breeding Bird Survey (BBS)
188 dataset. It contains information on species-level bird counts in 62 states, provinces, or territories
189 in the U.S. and Canada (Pardieck *et al.* 2020), for details see Section S1 in the supplement. We
190 considered BBS data for two reasons. First, it is open-access, long-term, and well-monitored
191 throughout the years, and many studies have been published with this dataset. Second, BBS data
192 have been collected during the breeding season over the summer (April to August) giving a
193 window for us to test the effect of extreme temperature. We considered 161 routes (sites) which
194 were sampled for a minimum of 40 years. 498 species were observed at least once during the
195 study period across those sites. Finally, the species list was reduced to 173 species based on the
196 criterion that they were sampled at least at two sites (among a total of 161 sites) for a minimum
197 of 40 years. Species-level abundance time series data were used to compute spatial synchrony for
198 birds at their extreme low or high abundance (i.e., <25% or >75% values of joint rank
199 distributions, respectively, see Fig. 1).

200 *Climate data*

201 For climate variables, we used annual temperature and precipitation data for 41 years at
202 161 sampling sites. CHELSA, version 2.1 (Karger *et al.* 2017) is an open-access database with
203 records for monthly climate time series data since 1979 at ~1 Km resolution. For a given year,
204 we averaged climate data across five months (April to August) extracted from CHELSA. Those
205 five months correspond to the surveying period for BBS. Precipitation data were not available

206 for all months of 2019, so we considered the timespan 1997-2018 for precipitation data. These
207 annual climate time series data were used to compute spatial synchrony for precipitation and
208 temperature at their extreme values (i.e., <25% or >75% values of joint rank distributions,
209 respectively).

210 ***Trait data***

211 We gathered information about species' diet type (total 5 categories: invertebrates,
212 omnivores, plants & seeds, vertebrates & fish & carrion, fruit & nectar), mainly from the
213 *EltonTraits* database (Wilman *et al.* 2014), and if for some species diet type was not found there,
214 then we also searched on Birds of the World (Billerman *et al.* 2022). We used the morphological
215 trait hand-wing index (HWI), extracted from the AVONET database (Tobias *et al.* 2022), as a
216 proxy for birds' dispersal ability (Sheard *et al.* 2020).

217 ***Quantifying (tail-dependent) spatial synchrony***

218 First, we detrended each species' abundance time series to remove linear temporal trends
219 using “detrend” function from *pracma* R-package (Borchers & Borchers 2022), otherwise, it
220 could lead to spurious correlations. We computed Spearman correlation with two detrended
221 abundance time series from two sites - and called them overall synchronous if found them
222 significantly positively correlated (i.e., p-value <0.05). For a given species and for any two
223 positively correlated (overall synchronous) detrended abundance time series taken from two
224 sites, we then computed spatial synchrony at the extremes (i.e., tail-dependence) in the following
225 ways. We used a *partial Spearman correlation* (Ghosh *et al.* 2020a) approach to estimate
226 dependence for simultaneous low abundances (as Cor_l) and simultaneous high abundances (as
227 Cor_u) of those two detrended population time series. See the next section “*Computing partial*
228 *Spearman correlation* (Cor_l , Cor_u)” for a detailed description.

229 A finite value of $(Cor_l - Cor_u)$ that is significantly different from zero indicates
 230 populations across two sites have significant tail-dependence in their extreme abundances (see
 231 section S2 “*Assessing the significance of tail-dependence*” in the supplement for details). We
 232 only considered significantly positive or negative values of $(Cor_l - Cor_u)$. If $(Cor_l - Cor_u)$ is
 233 positive, then populations are synchronous across sites only at their low abundances. Conversely,
 234 if $(Cor_l - Cor_u)$ is negative, then populations are synchronous across sites only at their high
 235 abundances. If $(Cor_l - Cor_u)$ is not significantly different than zero, the populations show
 236 significant spatial synchrony across two sites (measured by usual correlation) but no
 237 tail-dependence. We repeated the analysis for all pairwise combinations of sampling sites for a
 238 given species. Spatial synchrony (usual correlation) showed a gradual decay as between-sites
 239 distance increased and then saturated beyond 250 Km. (Fig. S1). Therefore, for subsequent
 240 analysis, we focused on a subset of 78 species that showed spatial synchrony within 0-250 Km
 241 distance between sites. We later repeated the whole analysis also for 0-100 Km. and 100-250
 242 Km. to see how the findings would vary within 250 Km. depending on our choice of spatial scale
 243 (Table S1-S2).

244 For a given species sampled at S number of sites, we calculated the overall lower tail
 245 dependence $L = \sum_i (Cor_l - Cor_u)$ where i is the index for site-pair having significant positive
 246 value for $(Cor_l - Cor_u)$, and overall upper tail dependence $U = \sum_j (Cor_l - Cor_u)$ where j is the
 247 index for site-pair having significant negative value for $(Cor_l - Cor_u)$. We computed total or
 248 absolute tail-dependent spatial synchrony in abundance as $A_{TD}^{abundance} = L + |U|$. Subscript TD
 249 is a short-hand notation for tail-dependence. Next, we computed $f_{TD}^{abundance}$ as directional or net

250 tail-dependent spatial synchrony in abundance, defined as the proportion of lower minus upper
251 tail-dependence, $f_{TD}^{abundance} (= \frac{L-|U|}{L+|U|})$. The maximum value of $f_{TD}^{abundance}$ is 1 when across-site
252 synchrony happens only at low abundances. The minimum value of $f_{TD}^{abundance}$ is -1 when
253 across-site synchrony happens only at high abundances.

254 To compute the spatial synchrony for climate extremes (precipitation, P, and temperature,
255 T), we followed a similar approach as computing spatial synchrony at extreme abundances. We
256 first detrended the climate time series. Then with those detrended climate time series, we
257 computed tail-dependence (as $Cor_l - Cor_u$) for any two given sites, and checked its significance.
258 Finally, we calculated total (or absolute) tail-dependent spatial synchrony in climate (as $A_{TD}^{climate,P}$
259 and $A_{TD}^{climate,T}$), and directional (or net) tail-dependent spatial synchrony in climate (as $f_{TD}^{climate,P}$
260 and $f_{TD}^{climate,T}$), where P is precipitation and T is temperature.

261 **Computing partial Spearman correlation (Cor_l , Cor_u)**

262 The partial Spearman correlation approach (Ghosh *et al.* 2020a), a non-parametric
263 measure of tail-dependence, uses “copula” (Joe 2014; Nelsen 2007) and recently has been used
264 in ecological field to measure tail-dependent synchrony (Ghosh *et al.* 2020b, c, 2021). Copula is
265 a statistical tool that computes dependence between any two variables at their simultaneous low
266 or high ranks. Ranking individual time series makes the marginal distribution uniform and thus
267 helps to extract the dependence information for the joint distribution (Sklar 1959). For example,
268 if two population abundance time series from two sites are $\{x_t, y_t\}$; $t = 1, \dots, n$, then the
269 corresponding copula would be $\{u_t, v_t\} = \{rank(x_t), rank(y_t)\}/(n + 1)$, so that the range

270 of the ranked time series variables $\{u_t, v_t\}$ lies within 0 to 1. Here, the lowest value would get
271 rank 1 whereas the highest value would get a rank n . Following (Ghosh *et al.* 2020a), one then
272 can calculate the dependence between $\{u_t, v_t\}$ for the lower and upper extremes of the unit box
273 as Cor_l and Cor_u , respectively. In our study, for lower tail (or extreme) we computed dependence
274 for the data points that lie below the red dashed line as shown in Fig. 1(A1-C1), i.e., satisfying
275 two conditions: $u + v > 0$ and $u + v < 0.5$. For the upper tail (or extreme) we computed
276 dependence for the data points that lie above the blue dashed line as shown in Fig. 1(A1-C1), i.e.,
277 satisfying two conditions: $u + v > 1.5$ and $u + v < 2$. This definition of extremes
278 corresponds to <25% and >75% of the joint distribution as we split the unit box into 4 diagonal
279 bins and roughly 10 data points within each tail. With more data availability one could use a
280 higher threshold (e.g., <5% and >95% if one split the unit box into 10 bins) to define the
281 extremes.

282 ***Structural equation model considering phylogeny***

283 We use structural equation modeling to answer Q2. We hypothesized $A_{TD}^{abundance}$ (or
284 $f_{TD}^{abundance}$) would be driven both by the patterns in $A_{TD}^{climate}$ (or $f_{TD}^{climate}$) and dispersal trait HWI.
285 To test which hypothesized path would best explain the variation in the response variable, we
286 used a structural equation model (SEM) considering species' phylogenetic relationships, i.e.,
287 phylogenetic path analysis (PPA) (Gonzalez-Voyer & von Hardenberg 2014). Considering
288 phylogenetic relatedness in regression analysis across species is crucial because species that are
289 closely related tend to share more similar traits due to their common ancestry. Traditional
290 regression analysis assumes that data points are statistically independent. Ignoring phylogenetic
291 relatedness can lead to violating the assumption of independence among data points, which can

292 result in biased parameter estimates and inaccurate confidence intervals. Therefore, for the
293 phylogeny, we subsampled 1,000 ‘Ericson All Species: a set of 10,000 trees with 9993 OTU
294 each’ trees pruned for our set of species considered (species matched from BirdTree database,
295 source: <https://birdtree.org/subsets/>; species-level information is provided in the
296 “DATA/BirdTree” folder of the code repository). All 1,000 trees were well-behaved (i.e., rooted,
297 binary, ultrametric, and strictly bifurcating). Then we made a consensus tree from those 1,000
298 trees to look primarily if there were any patterns for $A_{TD}^{abundance}$, $f_{TD}^{abundance}$, trait HWI (Fig. S2,
299 A-C). Finally, We implemented PPA for our data with the *phylopath* R-package (van der Bijl
300 2018). As temperature T and precipitation P are negatively correlated, we did not include two
301 correlated climatic predictors into a single model to avoid the collinearity issue, rather we ran the
302 model separately for each climatic driver.

303

304 Results

305 Within 0-250 Km distance between sites, 78 out of 173 species showed significant spatial
306 synchrony (usual correlation approach). We found significant tail-dependence (based on 75% CI)
307 in birds’ spatial synchrony for 59 out of those 78 species (Fig. 3). Of those 59 species, some
308 species (N=27) showed spatial synchrony mainly at their low abundances (i.e., more contribution
309 in $A_{TD}^{abundance}$ from site-pairs where species were synchronous at low abundances;
310 $L/(L + |U|) > |U|/(L + |U|)$; higher proportion of red colors in bars, Fig. 3). The rest of the
311 species (N=32) showed spatial synchrony mainly at their high abundances (i.e., more
312 contribution in $A_{TD}^{abundance}$ from site-pairs where species were synchronous at high abundances;
313 $|U|/(L + |U|) > L/(L + |U|)$; higher proportion of blue colors in bars, Fig. 3). This

314 observation confirmed (Q1) of Fig. 2 that, indeed, birds across North America showed
315 tail-dependence patterns in spatial synchrony.

316 We did not find any particular preference for lower or upper tail-dependence patterns
317 based on species' diets or IUCN status. In particular, contrary to our expectation as stated in the
318 introduction, the insectivorous group (diet = "invertebrates") consisted of a significant number of
319 species that showed spatial synchrony mainly at high abundances, as well as the species that
320 showed spatial synchrony mainly at low abundances. Nearly 93% of species (N=55) in our study
321 belong to "Least Concerned" as per IUCN status. Even if some species were listed as "Least
322 Concerned", some of them (N=19 out of 55) had more than 70% of tail-dependence in the lower
323 extreme of abundances (i.e., $L * 100 / (L + |U|) > 70$) meaning spatial synchrony happened
324 mainly when those species were rare across sites within a metapopulation network.

325 We found total tail-dependent spatial synchrony in climate, $A_{TD}^{climate}$, was driving the total
326 tail-dependent spatial synchrony in abundances, $A_{TD}^{abundance}$, across species (significant positive
327 regression slopes in Fig. 4). This finding supports hypothesis **H1**, answering (Q2) of Fig. 2. In
328 particular, total tail-dependent spatial synchrony in temperature $A_{TD}^{climate, T}$ explained 76%
329 variation in total tail-dependent spatial synchrony in abundances across species, whereas total
330 tail-dependent spatial synchrony in precipitation $A_{TD}^{climate, P}$ explained 72% variation of the same.
331 Though we did not observe any significant phylogenetic signal for abundance, we did find a
332 significantly strong phylogenetic signal (mean Pagel's $\lambda \sim 1$, all p-values < 0.00001) in the trait
333 HWI, as observed in the consensus tree (Fig. S2). Phylogenetic path analysis showed the
334 climate-driven pathway as relatively more important to explain variation in $A_{TD}^{abundance}$, whereas

335 the dispersal-mediated pathway appeared as the non-significant one. We found similar findings
336 supporting **H1** when we repeated this analysis for two other between-sites distance categories:
337 0-100 Km, and 100-250 Km. as summarized in Table S1.

338 Directional (or net) tail-dependent spatial synchrony in temperature, $f_{TD}^{climate,T}$, showed a
339 significant negative relationship with the directional (or net) tail-dependent spatial synchrony in
340 birds' abundances, $f_{TD}^{abundance}$ (Fig. 5). This finding supports hypothesis **H2** from Fig. 2 that a
341 stressful environment (high temperature across sites) limits species abundance across sites,
342 making them rare (lower tail-dependent), while cooler temperature across sites makes them
343 common (upper tail-dependent). Only high temperature, not low precipitation, appeared as a
344 significant factor in limiting species' abundance ($R^2 \sim 9.2\%$ in Fig. 5B). Phylogenetic path
345 analysis also showed climate-driven pathway as the only significant determinant for net
346 tail-dependent spatial synchrony in birds' abundances. Further exploration showed the
347 significant negative relationship between $f_{TD}^{abundance}$ and $f_{TD}^{climate,T}$, as hypothesized in **H2**, was
348 actually driven by the sites within 0-100 Km (Table S2).

349 When we repeated the analysis considering a more conservative criterion (95% CI) to
350 assess significance for tail-dependence, we found N=25, 29, and 35 species with significant
351 tail-dependent spatial synchrony in abundance for 0-100 Km, 100-250 Km, and 0-250 Km of
352 between-sites distance, respectively. In all distance categories, we got similar results supporting
353 **H1** (Table S3), but we could not test hypothesis **H2** because of the limited sample size.

354

355

356 Discussion

357 Overall, we found birds across North America showed tail-dependence patterns in spatial
358 synchrony (i.e., simultaneously rare or common across sites). This large-scale pattern (up to 250
359 Km) was driven by tail-dependence patterns in spatial synchrony for climate, whereas a
360 dispersal-related trait (HWI) played no significant role in driving tail-dependent spatial
361 synchrony in abundance.

362 These findings are practically significant in at least three important ways. First,
363 tail-dependence patterns in metapopulation ecology are known to be linked to extinction risk
364 (Ghosh *et al.* 2020c). Hence our findings highlight species that showed mainly simultaneous low
365 abundance across sites are at higher risk than is estimated in usual analysis. For example, some
366 species (N=19) with >70% lower tail-dependence in spatial synchrony might have higher risk
367 though they are listed as “least concerned” in IUCN status. It could be useful to include
368 tail-dependent spatial synchrony in future assessments of a species’ vulnerability.

369 Second, here we proposed an extension of the classic Moran effect considering
370 tail-dependence beyond the usual correlation between two population or climate time series. As
371 the earlier study (Koenig 2002) found spatial synchrony in animal populations is driven by
372 spatial synchrony in environments over a large scale (i.e., classic Moran effect), we found a
373 similar conclusion that over large scale tail-dependence in population abundance is driven by
374 tail-dependence in climate (this is extension of classic Moran effect). Tail-dependent spatial
375 synchrony patterns in birds’ abundance could be caused by resource limitations or extreme
376 environmental conditions that limit some species’ growth. This finding highlights the underlying
377 nonlinearity (beyond linear correlation) as a mechanism to understand how tail-dependence in

378 climate synchrony translates into tail-dependence in population synchrony, as found by a recent
379 study (Walter *et al.* 2022).

380 Third, we attempted to disentangle the relative contributions of tail-dependent spatial
381 synchrony in climate and dispersal. Dispersal and correlated environmental fluctuation (“Moran
382 effect”) are both known as important drivers for spatial synchrony (Liebhold *et al.* 2004) and
383 their contribution often depends on spatial scale (Lande *et al.* 1999), with the environmental
384 correlation being of greater importance at larger scales (Peltonen *et al.* 2002). For tail-dependent
385 spatial synchrony in abundance, we found similar results: large-scale patterns (~250 Km apart)
386 are driven by tail-dependent spatial synchrony in climate, but not by a dispersal-related trait. To
387 our knowledge, this is the first study to assess the contribution of two co-occurring mechanisms
388 for tail-dependent spatial synchrony in abundance.

389 Like any other landscape pattern, tail-dependent spatial synchrony also depends on
390 spatial and temporal scales. We found that over a large scale, climatic extremes across sites
391 appeared as a significant predictor for simultaneous population extremes across sites, and this
392 finding appears reasonable as climatic extremes are also becoming more frequent over large
393 scales (Duffy & Tebaldi 2012; La Sorte *et al.* 2021; Weaver *et al.* 2014). However, if the climatic
394 extreme happens only at a given site, then that local-scale environmental stochasticity might not
395 be able to synchronize the population dynamics across sites over a large scale, and lead to
396 demographic stochasticity for that population patch only. Similarly, to find a causal relationship
397 between tail-dependence in climate and abundance, considering an appropriate time span is
398 important. For example, most of the bird species we studied (62 out of 78 species, and in
399 particular 52 out of 59 species within 0-250 Km.) were migratory and observed at survey sites
400 from April to August each year. Therefore, we found support for hypothesis **H2**, only when we

401 considered those 5 months in our analysis, rather than all 12 months, despite tail-dependence in
402 climates being higher for the latter case (Fig. S3).

403 Our study offers an improved understanding of the underlying mechanism of how
404 spatio-temporal patterns in metapopulation synchrony for North American birds are shaped by
405 climatic synchrony at the extremes, and the approach could be generalized to any taxa. We
406 provide a mechanism beyond the classic “Moran effect”, to explain such patterns and also
407 compare its importance with respect to an alternate dispersal-mediated (or trait-mediated)
408 pathway. We believe our findings will encourage further exploration of detecting the role of
409 environmental filtering and natural selection to understand macro-scale patterns in the field of
410 ecology and evolutionary biology.

411 Future studies could focus on two directions. First, exploration of another possible
412 mechanistic explanation for tail-dependent synchrony in metapopulation abundances: either by a
413 bottom-up effect or by a top-down effect in the multi-trophic food web context. In a bottom-up
414 approach, due to limited food resources at the primary producer levels, the consumer could be
415 simultaneously rare across sites. A similar result has been found for red squirrels’
416 metapopulation synchrony over a large scale that was mainly driven by synchrony in their
417 primary resource: spruce cones (Turkia *et al.* 2020). In a top-down approach, one could test if
418 tail-dependent spatial synchrony in a prey population happens because of the extreme pressure of
419 predation. Synchronized predation is a known factor causing spatial synchrony in prey
420 populations (Ims & Andreassen 2000; Vasseur & Fox 2009), and a recent study showed
421 behavioral synchrony amplified in a group of prey populations due to fear of predation (Aguilar
422 de Soto *et al.* 2020). Tail-dependence has not been studied in this context.

423 Second, dispersal could be limited by habitat fragmentation due to land-use change
424 (Moore *et al.* 2008). In the current study, we did not consider the anthropogenic impact on birds'
425 dispersal ability or on the tail-dependent synchrony in climatic extremes. As land-use change and
426 climate change are coupled together (Oliver & Morecroft 2014), and climatic extremes are
427 projected to increase due to anthropogenic pressure globally (Zhou *et al.* 2023), considering both
428 aspects in explaining tail-dependent spatial synchrony for abundance would be a logical avenue
429 for future study (Holyoak & Heath 2016). In this context, we think studying connectivity in
430 meta-population networks could help in understanding tail-dependence in population
431 abundances. For example, we found some species showed a similar proportion of
432 tail-dependence (say, 40% lower and 60% upper) within a network meaning they were
433 simultaneously rare across 40% of between-sites connections and simultaneously common across
434 60% of between-sites connections. This might indicate that the network has two different clusters
435 of patches showing two different kinds of vulnerability to the same climatic extremes. Future
436 studies on habitat quality, connectivity, and nutrient flow across the network would help identify
437 the target sites needed to prioritize for species' conservation.

438 In sum, we found significant tail-dependent spatial synchrony (for abundance) in bird
439 population dynamics. We evaluated the relative importance of co-occurring mechanisms
440 (tail-dependent climatic variables and dispersal) to find out that it was the environmental effects
441 that prevailed on large-scale patterns. Our study is possible because of long-term data (a
442 minimum of 40 years) availability for bird count, climate time series, and species-level traits
443 information. Long-term monitoring data are immensely important in ecological research (Willis
444 *et al.* 2007), including detecting the effect of extremes (i.e., tail-dependence). We hope that with

445 the increasing accessibility of long-term monitoring data, scientists will continue such
446 mechanistic exploration of spatio-temporal macroecological patterns.

447

448 **Acknowledgments** SG and OP were supported by funding from the University of Zurich. SG
449 would like to thank Dr. Imran Khaliq for the helpful discussion on phylogeny and feedback on
450 the initial draft.

451 **Competing interests** The authors declare that they have no competing interests.

452

453

454

455

456

457

458

459

460

461

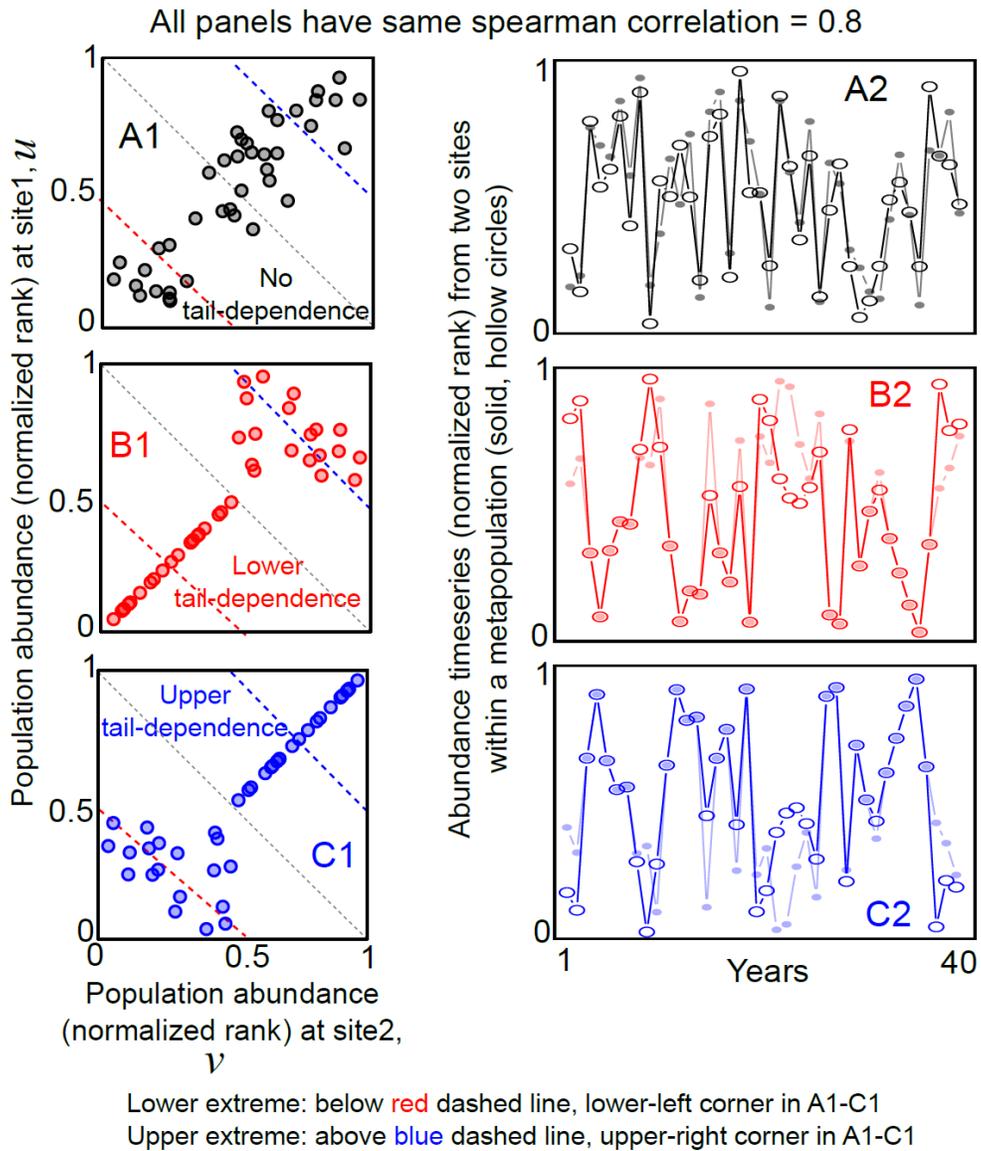
462

463

464

465

466



468

469 **Figure 1:** Schematic diagram to visualize tail-dependent spatial synchrony. Left panels (A1-C1)
 470 show the copula-plot (scatterplot of normalized ranks) for two population abundances from two
 471 sites within a metapopulation network. All three panels have the same Spearman correlation or
 472 overall synchrony (=0.8), but zero, positive (lower), and negative (upper) tail-dependence, for
 473 the top, middle, and bottom panels, respectively. In A1-C1, the data points are divided equally
 474 into four bins separated by three broken diagonal lines. The lower extreme corresponds to less

475 than 25%, and the upper extreme corresponds to more than 75% of the joint distribution. For B1,
476 the dependence measured as *partial Spearman correlation* in the lower extreme (Cor_l) is larger
477 than the same in the upper extreme (Cor_u), i.e., $(Cor_l - Cor_u) > 0$, whereas for C1 it is opposite,
478 i.e., $(Cor_l - Cor_u) < 0$. The right panels (A2-C2) show population abundance time series from two
479 sites corresponding to their left panel analog. One can see for asymmetric copula like B1 and C1,
480 mostly all the hollow and solid circles exactly coincide in B2 and C2 for their troughs and peaks,
481 respectively.

482

483

484

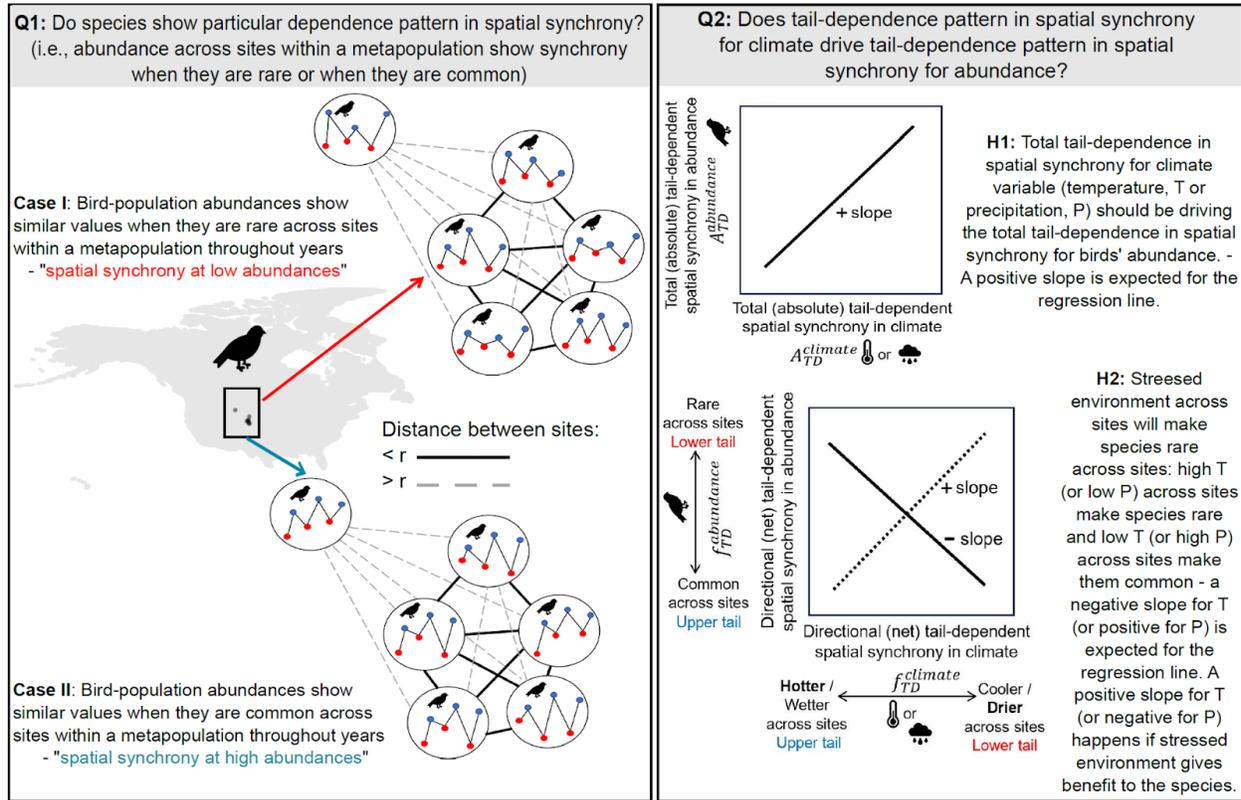
485

486

487

488

489



490

491 **Figure 2:** Conceptual figure showing two research questions explored in the present study. (Q1)

492 asks if species show lower tail-dependent (Case I: spatial synchrony at low abundances) and

493 upper tail-dependent (Case II: spatial synchrony at high abundances) spatial synchrony. In Case

494 I, red points (i.e., the troughs) show similar fluctuation in the abundance time series across sites,

495 whereas in Case II, blue points (i.e., the peaks) show similar fluctuation in the abundance time

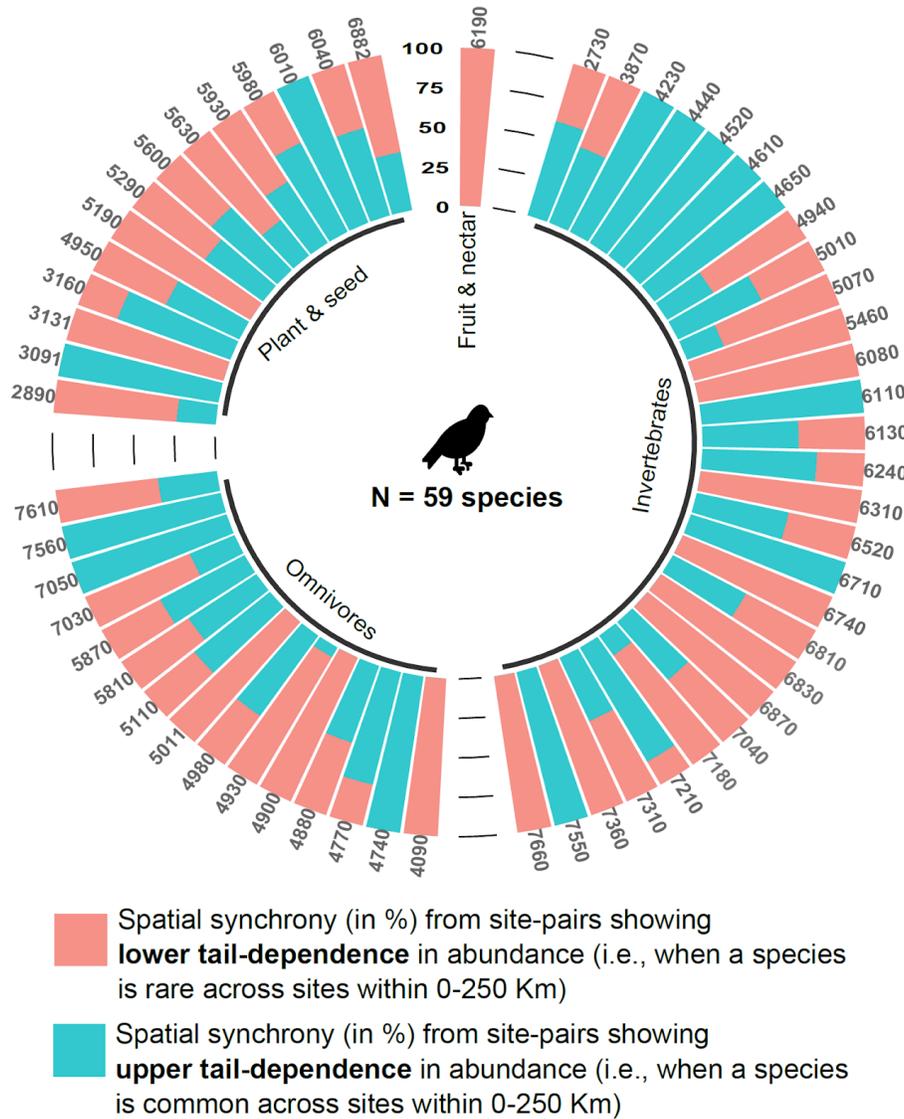
496 series across sites. Spatial synchrony would be high among sites that are closer ($< r$, solid lines).

497 With two hypotheses **H1-H2** as shown in the right panel, (Q2) tests if tail-dependence patterns in

498 spatial synchrony for climate (temperature or precipitation) drive the tail-dependence patterns in

499 spatial synchrony for abundances (for details see Introduction).

500



501

502 **Figure 3:** Tail-dependence patterns in spatial synchrony for birds' abundances within 0-250 Km
 503 between-sites distance. Each bar in the circular stacked bar plots is color-coded based on the
 504 proportion of lower-tail dependence $L/(L + |U|)$ (in red) and upper-tail dependence
 505 $|U|/L + |U|$ (in blue) in abundance multiplied by 100 to show in percentage. The numeral
 506 4-digit code written on top of each bar is the AOU code for each species and can be found from
 507 the complete species list as supplied with BBS data (Pardieck *et al.* 2020). Species with a higher
 508 proportion of red color in bars means those species have more site-pair interactions for spatial

509 synchrony at low abundances. Conversely, species with a higher proportion of blue color in bars
510 means those species have more site-pair interactions for spatial synchrony at high abundances.
511 Bars are grouped into dietary preferences (invertebrates, omnivores, plants & seeds, fruit &
512 nectar). Based on IUCN status, 3 species (AOU = 2890, 5010, 5110) belong to nearly
513 threatened, and 1 species (AOU = 4230) belongs to the vulnerable group, and the rest are least
514 concerned. No clear pattern was found for either of the diet or IUCN-based categories.

515

516

517

518

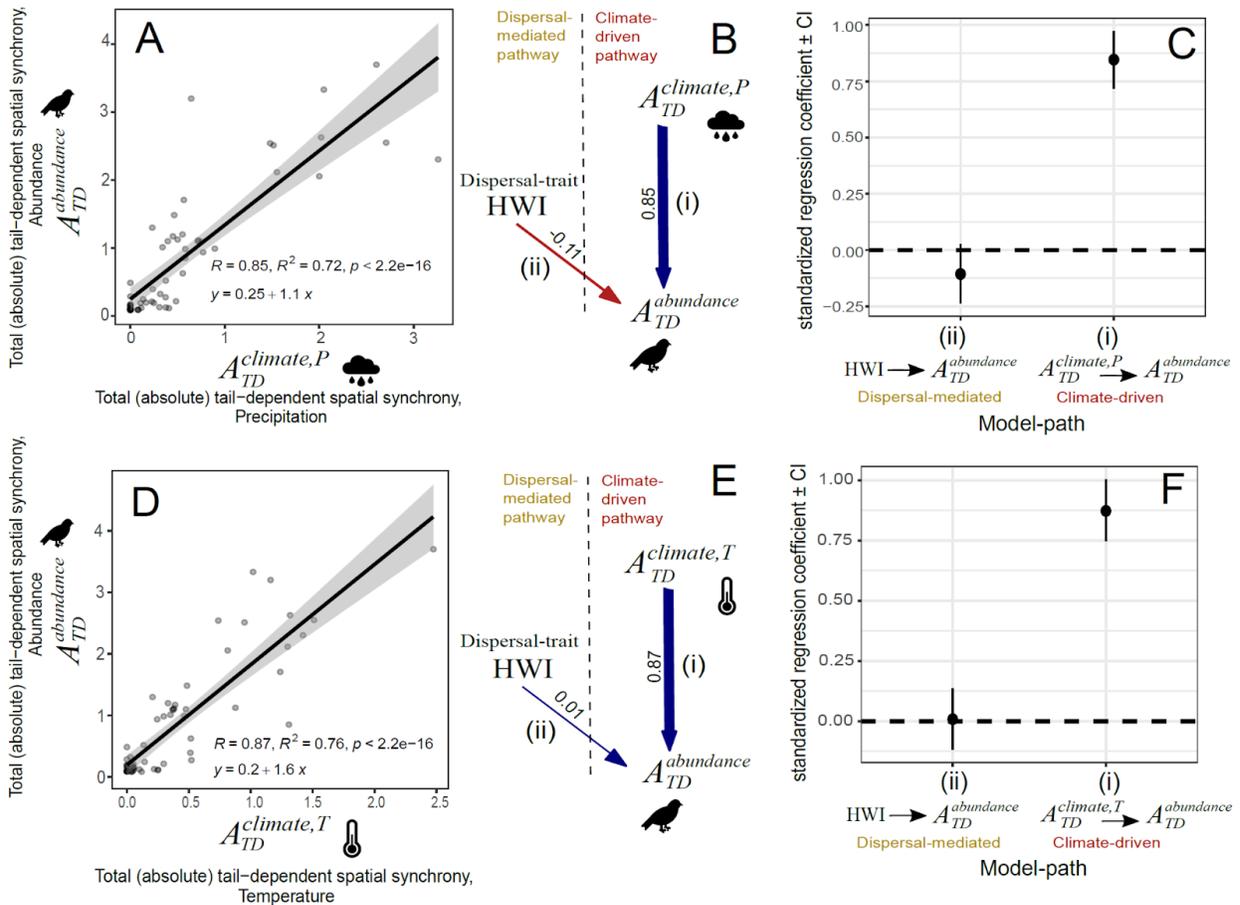
519

520

521

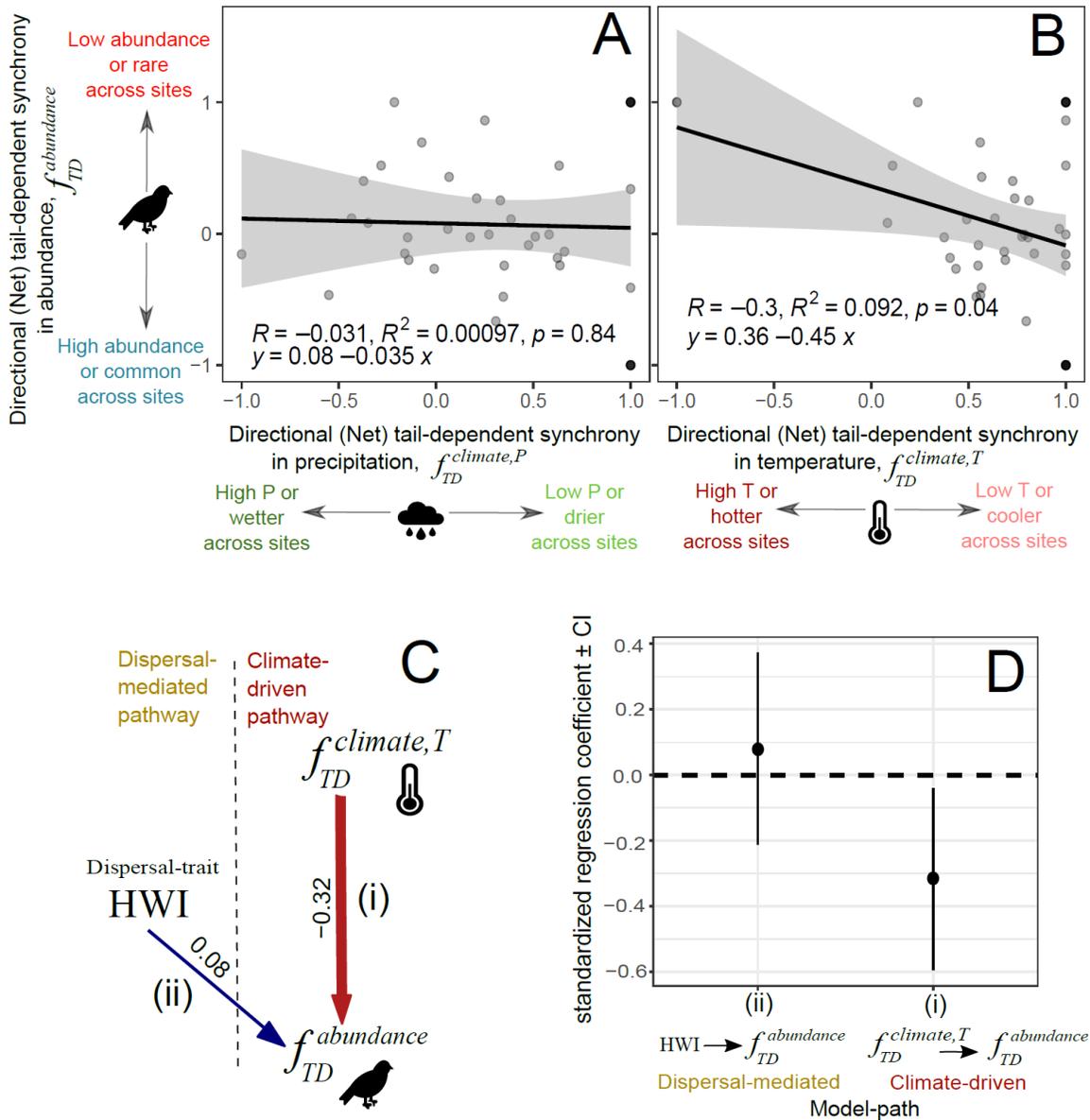
522

523



524

525 **Figure 4:** Results support hypothesis **H1** that variation in total tail-dependent spatial synchrony
 526 for climate (precipitation P, panels A-C or temperature T, panels D-F) explains the variation in
 527 total tail-dependent spatial synchrony for abundances across species. Each dot in panels A and D
 528 represents each species, a total of 59 species within 0-250 Km. between-sites distance.
 529 Climate-driven pathways appear as the significant ones compared to the non-significant and
 530 weaker dispersal-driven pathways in panels B and E. Panels C and F show the regression
 531 coefficients and 95% CI from 1,000 bootstraps. If the bar crosses the horizontal dashed line, then
 532 that is not significant. Models' goodness of fit test was checked with p-value from C-statistic: in
 533 both cases, it was >0.05 (for B-C: C-statistic=0.591, $p=0.744$; for E-F: C-statistic=3.33,
 534 $p=0.189$).



537 **Figure 5:** Results support hypothesis **H2** that stressed environments across sites make species
 538 synchronous at their low abundances. High-temperature extremes across sites limit species
 539 abundances significantly (panel B-D), whereas low-temperature extremes across sites make
 540 species common: a significant negative slope for panel B as hypothesized in Fig. 2, Q2.
 541 Precipitation did not appear as a significant limiting factor for abundance (panel A). Panels C

542 and D summarize the results from phylogenetic path analysis that the climate-driven
543 (temperature, in particular) pathway is the only significant factor for explaining variation in net
544 tail-dependent spatial synchrony for abundances, compared to the dispersal-mediated one. Panel
545 D shows the regression coefficients and 95% CI from 1,000 bootstraps. If the bar crosses the
546 horizontal dashed line, then that is not significant. The model's goodness of fit test was checked
547 with a p-value from Fisher's C-statistic (C-statistic=3, p=0.223).

548

549

550

551

552

553

554

555

556

557

558

559

560

561

562

563

564

565 References

- 566 Abbott, K.C. (2011). A dispersal-induced paradox: synchrony and stability in stochastic
567 metapopulations. *Ecol. Lett.*, 14, 1158–1169.
- 568 Aguilar de Soto, N., Visser, F., Tyack, P.L., Alcazar, J., Ruxton, G., Arranz, P., *et al.* (2020). Fear
569 of Killer Whales Drives Extreme Synchrony in Deep Diving Beaked Whales. *Sci. Rep.*, 10,
570 13.
- 571 Allen, M.C. & Lockwood, J.L. (2020). Mapping shifts in spatial synchrony in grassland birds to
572 inform conservation planning. *Conserv. Biol.*
- 573 van der Bijl, W. (2018). phylopath: Easy phylogenetic path analysis in R. *PeerJ*, 6, e4718.
- 574 Billerman, M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (2022). *Birds of the World*.
575 *Cornell Lab of Ornithology, Ithaca*. Available at: <https://birdsoftheworld.org/bow/home>.
576 Last accessed 2023.
- 577 Bjørnstad, O.N., Ims, R.A. & Lambin, X. (1999). Spatial population dynamics: analyzing
578 patterns and processes of population synchrony. *Trends Ecol. Evol.*, 14, 427–432.
- 579 Borchers, H.W. & Borchers, M.H.W. (2022). Package “pracma.” *accessed on*, 4.
- 580 Cohen, J. & Jetz, W. (2023). Diverse strategies for tracking seasonal environmental niches at
581 hemispheric scale. *Glob. Ecol. Biogeogr.*, 32, 1549–1560.
- 582 Duffy, P.B. & Tebaldi, C. (2012). Increasing prevalence of extreme summer temperatures in the
583 US Climatic Change, 111, 487--495.
- 584 Furness, R.W., Greenwood, J.J.D. & Jarvis, P.J. (1993). Can birds be used to monitor the
585 environment? In: *Birds as Monitors of Environmental Change* (eds. Furness, R.W. &
586 Greenwood, J.J.D.). Springer Netherlands, Dordrecht, pp. 1–41.
- 587 Gaston, K.J. & Blackburn, T.M. (Eds.). (2000). *Pattern and Process in Macroecology*.

588 Ghosh, S., Cottingham, K.L. & Reuman, D.C. (2021). Species relationships in the extremes and
589 their influence on community stability. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 376,
590 20200343.

591 Ghosh, S., Sheppard, L.W., Holder, M.T., Loecke, T.D., Reid, P.C., Bever, J.D., *et al.* (2020a).
592 Copulas and their potential for ecology. In: *Advances in Ecological Research*. Elsevier, pp.
593 409–468.

594 Ghosh, S., Sheppard, L.W., Reid, P.C. & Reuman, D. (2020b). A new approach to interspecific
595 synchrony in population ecology using tail association. *Ecol. Evol.*, 10, 12764–12776.

596 Ghosh, S., Sheppard, L.W. & Reuman, D.C. (2020c). Tail associations in ecological variables
597 and their impact on extinction risk. *Ecosphere*, 11.

598 Goldwyn, E.E. & Hastings, A. (2008). When can dispersal synchronize populations? *Theor.*
599 *Popul. Biol.*, 73, 395–402.

600 Gonzalez-Voyer, A. & von Hardenberg, A. (2014). An Introduction to Phylogenetic Path
601 Analysis. In: *Modern Phylogenetic Comparative Methods and Their Application in*
602 *Evolutionary Biology: Concepts and Practice* (ed. Garamszegi, L.Z.). Springer Berlin
603 Heidelberg, Berlin, Heidelberg, pp. 201–229.

604 Hansen, B.B., Grøtan, V., Aanes, R., Sæther, B.-E., Stien, A., Fuglei, E., *et al.* (2013). Climate
605 events synchronize the dynamics of a resident vertebrate community in the high Arctic.
606 *Science*, 339, 313–315.

607 Hansen, B.B., Grøtan, V., Herfindal, I. & Lee, A.M. (2020). The Moran effect revisited: spatial
608 population synchrony under global warming. *Ecography* .

609 Haynes, K.J., Liebhold, A.M., Fearer, T.M., Wang, G., Norman, G.W. & Johnson, D.M. (2009).
610 Spatial synchrony propagates through a forest food web via consumer–resource

611 interactions. *Ecology*.

612 Haynes, K.J. & Walter, J.A. (2022). Advances in understanding the drivers of population spatial
613 synchrony. *Curr Opin Insect Sci*, 53, 100959.

614 Heino, M., Kaitala, V., Ranta, E. & Lindström, J. (1997). Synchronous dynamics and rates of
615 extinction in spatially structured populations. *Proceedings of the Royal Society of London.
616 Series B: Biological Sciences*, 264, 481–486.

617 Holyoak, M. & Heath, S.K. (2016). The integration of climate change, spatial dynamics, and
618 habitat fragmentation: A conceptual overview. *Integr. Zool.*, 11, 40–59.

619 Ims, R.A. & Andreassen, H.P. (2000). Spatial synchronization of vole population dynamics by
620 predatory birds. *Nature*, 408, 194–196.

621 Jenouvrier, S., Thibault, J.-C., Viallefont, A., Vidal, P., Ristow, D., Mougín, J.-L., *et al.* (2009).
622 Global climate patterns explain range-wide synchronicity in survival of a migratory seabird.
623 *Glob. Chang. Biol.*, 15, 268–279.

624 Jetz, W., Tertitski, G., Kays, R., Mueller, U., Wikelski, M. & Supporting authors. (2022).
625 Biological Earth observation with animal sensors. *Trends Ecol. Evol.*, 37, 293–298.

626 Joe, H. (2014). *Dependence Modeling with Copulas*. CRC Press.

627 Karger, D.N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., *et al.* (2017).
628 Climatologies at high resolution for the earth’s land surface areas. *Sci Data*, 4, 170122.

629 Koenig, W.D. (2002). Global patterns of environmental synchrony and the Moran effect.
630 *Ecography*, 25, 283–288.

631 Koenig, W.D. & Liebhold, A.M. (2016). Temporally increasing spatial synchrony of North
632 American temperature and bird populations. *Nat. Clim. Chang.*, 6, 614–617.

633 Lande, R., Engen, S. & Sæther, B.-E. (1999). Spatial Scale of Population Synchrony:

634 Environmental Correlation versus Dispersal and Density Regulation. *Am. Nat.*, 154,
635 271–281.

636 La Sorte, F.A., Johnston, A. & Ault, T.R. (2021). Global trends in the frequency and duration of
637 temperature extremes. *Clim. Change*, 166, 1.

638 Liebhold, A., Koenig, W.D. & Bjørnstad, O.N. (2004). Spatial Synchrony in Population
639 Dynamics. *Annu. Rev. Ecol. Evol. Syst.*, 35, 467–490.

640 Moore, R.P., Robinson, W.D., Lovette, I.J. & Robinson, T.R. (2008). Experimental evidence for
641 extreme dispersal limitation in tropical forest birds. *Ecol. Lett.*, 11, 960–968.

642 Moran, P.A.P. (1953). The statistical analysis of the Canadian Lynx cycle. *Aust. J. Zool.*, 1,
643 291–298.

644 Nelsen, R.B. (2007). *An Introduction to Copulas*. Springer Science & Business Media.

645 Oliver, T.H. & Morecroft, M.D. (2014). Interactions between climate change and land use
646 change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdiscip.*
647 *Rev. Clim. Change*, 5, 317–335.

648 Pardieck, K.L., Ziolkowski, D.J., Jr, Lutmerding, M., Aponte, V.I. & Hudson, M.A.R. (2020).
649 North American breeding bird survey dataset 1966--2019: US Geological Survey data
650 release. *Reston, VA: US Geological Survey, doi*, 10, P9J6QUF6.

651 Peltonen, M., Liebhold, A.M., Bjørnstad, O.N. & Williams, D.W. (2002). Spatial synchrony in
652 forest insect outbreaks: Roles of regional stochasticity and dispersal. *Ecology*, 83,
653 3120–3129.

654 R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation
655 *for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.*

656 Reeve, J.D. (2018). Synchrony, Weather, and Cycles in Southern Pine Beetle (Coleoptera:

657 Curculionidae). *Environ. Entomol.*, 47, 19–25.

658 Sarremejane, R., Stubbington, R., England, J., Sefton, C.E.M., Eastman, M., Parry, S., *et al.*
659 (2021). Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk
660 in an intermittent river network. *Glob. Chang. Biol.*, 27, 4024–4039.

661 Sheard, C., Neate-Clegg, M.H.C., Alioravainen, N., Jones, S.E.I., Vincent, C., MacGregor,
662 H.E.A., *et al.* (2020). Ecological drivers of global gradients in avian dispersal inferred from
663 wing morphology. *Nat. Commun.*, 11, 2463.

664 Sklar, M. (1959). Fonctions de repartition a n dimensions et leurs marges. *Publ. Inst. Statist.*
665 *Univ. Paris*, 8, 229–231.

666 Tack, A.J.M., Mononen, T. & Hanski, I. (2015). Increasing frequency of low summer
667 precipitation synchronizes dynamics and compromises metapopulation stability in the
668 Glanville fritillary butterfly. *Proc. Biol. Sci.*, 282, 20150173.

669 Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., *et al.* (2022).
670 AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.*, 25,
671 581–597.

672 Turkia, T., Jousimo, J., Tiainen, J., Helle, P., Rintala, J., Hokkanen, T., *et al.* (2020). Large-scale
673 spatial synchrony in red squirrel populations driven by a bottom-up effect. *Oecologia*, 192,
674 425–437.

675 Ummenhofer, C.C. & Meehl, G.A. (2017). Extreme weather and climate events with ecological
676 relevance: a review. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 372.

677 Vasseur, D.A. & Fox, J.W. (2009). Phase-locking and environmental fluctuations generate
678 synchrony in a predator-prey community. *Nature*, 460, 1007–1010.

679 Walter, J.A., Castorani, M.C.N., Bell, T.W., Sheppard, L.W., Cavanaugh, K.C. & Reuman, D.C.

680 (2022). Tail-dependent spatial synchrony arises from nonlinear driver-response
681 relationships. *Ecol. Lett.*, 25, 1189–1201.

682 Walter, J.A., Shoemaker, L.G., Lany, N.K., Castorani, M.C.N., Fey, S.B., Dudley, J.C., *et al.*
683 (2021). The spatial synchrony of species richness and its relationship to ecosystem stability.
684 *Ecology*, 102, e03486.

685 Weaver, S.J., Kumar, A. & Chen, M. (2014). Recent increases in extreme temperature occurrence
686 over land. *Geophys. Res. Lett.*, 41, 4669–4675.

687 Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, B., Froyd, C.A. & Myers, N. (2007).
688 How can a knowledge of the past help to conserve the future? Biodiversity conservation and
689 the relevance of long-term ecological studies. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 362,
690 175–186.

691 Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014).
692 EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals.
693 *Ecology*, 95, 2027–2027.

694 Yang, Q., Hong, P., Luo, M., Jiang, L. & Wang, S. (2022). Dispersal Increases Spatial Synchrony
695 of Populations but Has Weak Effects on Population Variability: A Meta-analysis. *Am. Nat.*,
696 200, 544–555.

697 Zhou, S., Yu, B. & Zhang, Y. (2023). Global concurrent climate extremes exacerbated by
698 anthropogenic climate change. *Sci Adv*, 9, eabo1638.

699