

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

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31

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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  
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## 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.

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## 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

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

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

Here, we provide an analysis of long-term dynamics (1979-2019) of bird species abundances, temperature (T), and precipitation (P) across North America to explore the effects of 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

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

#### **Trait data**

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

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

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

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

### **Structural equation model considering phylogeny**

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

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

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

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

## 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

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

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

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

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

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

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

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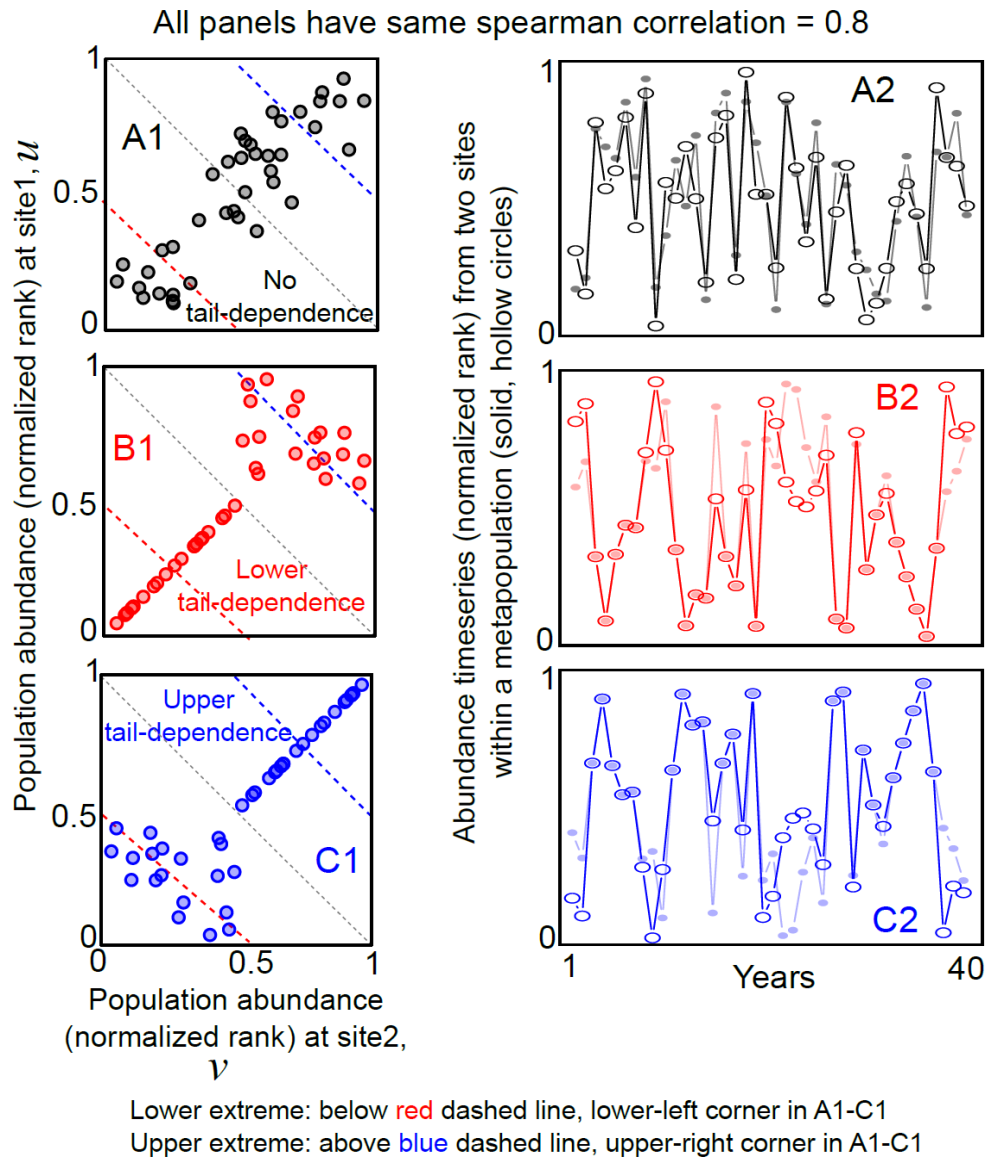
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**Figure 1:** Schematic diagram to visualize tail-dependent spatial synchrony. Left panels (A1-C1) show the copula-plot (scatterplot of normalized ranks) for two population abundances from two sites within a metapopulation network. All three panels have the same Spearman correlation or overall synchrony ( $=0.8$ ), but zero, positive (lower), and negative (upper) tail-dependence, for the top, middle, and bottom panels, respectively. In A1-C1, the data points are divided equally 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.

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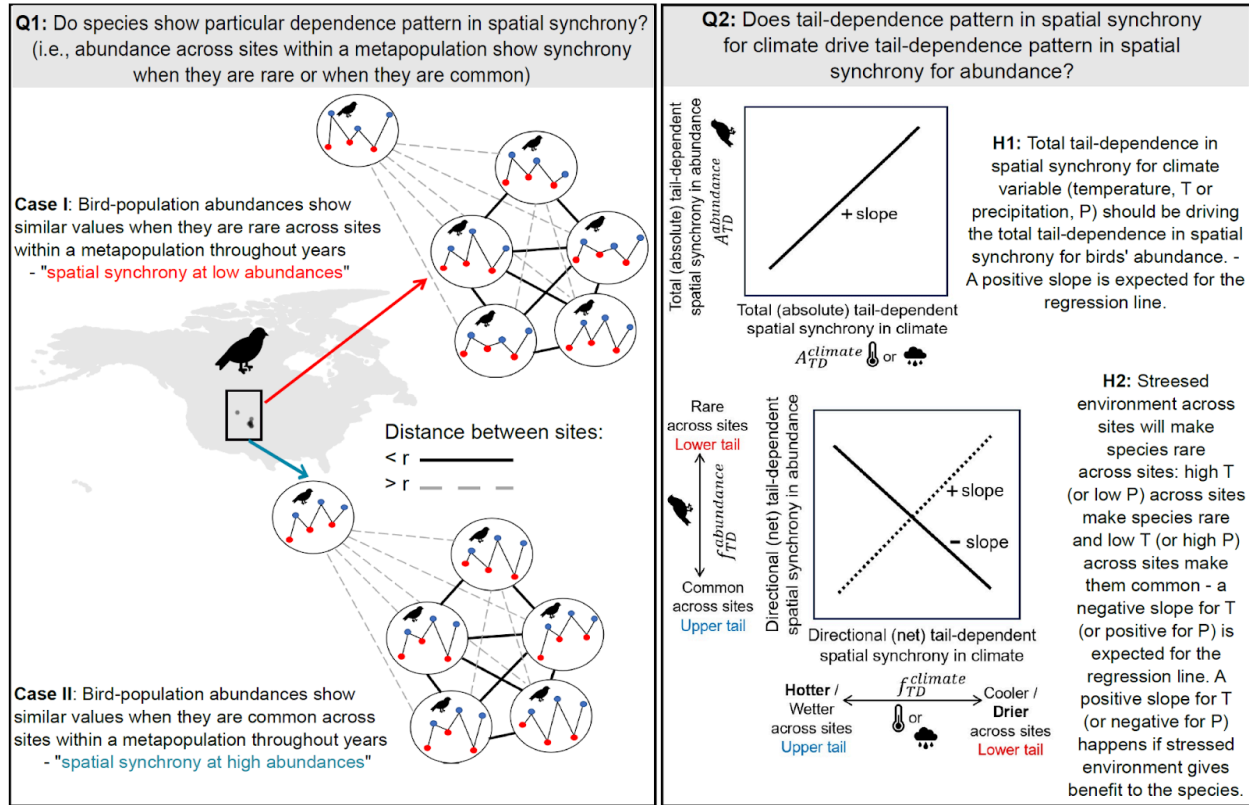
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491 **Figure 2:** Conceptual figure showing two research questions explored in the present study. (Q1)

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

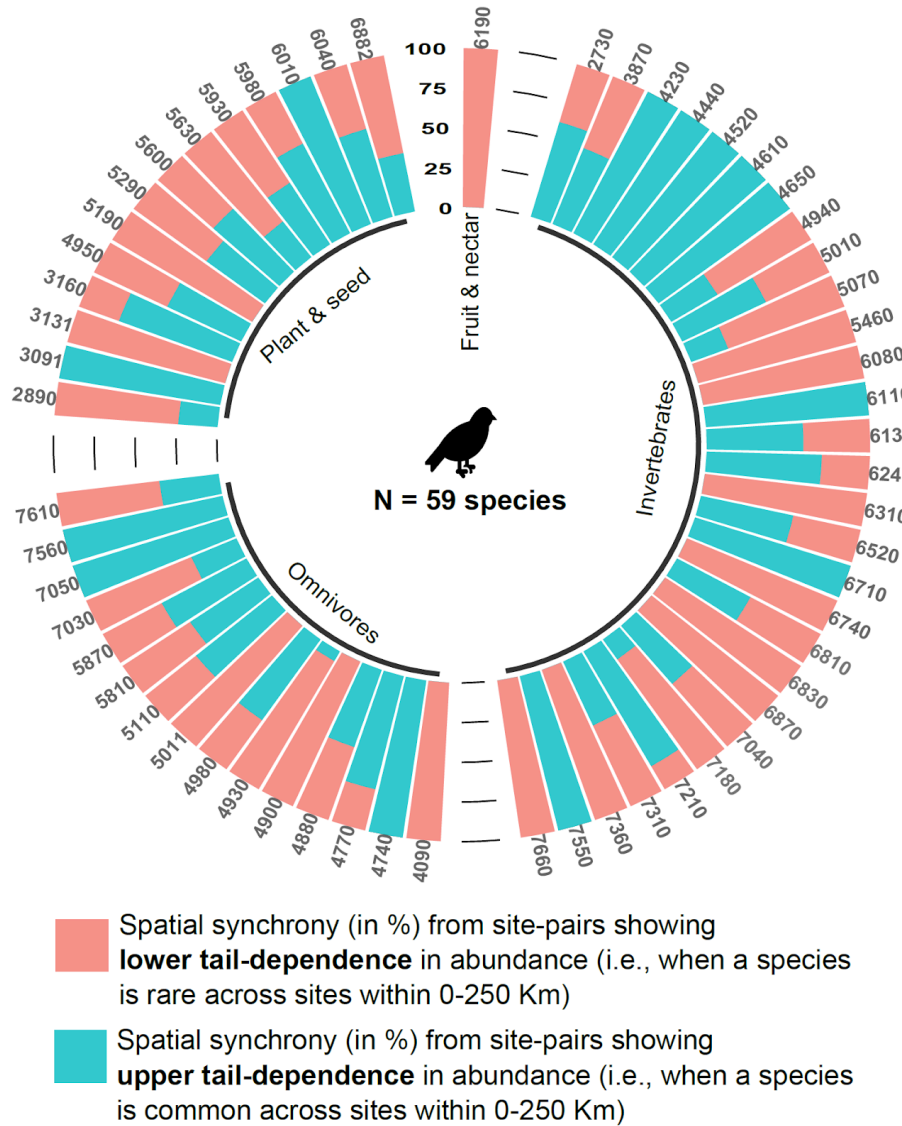
496 series across sites. Spatial synchrony would be high among sites that are closer ( $< r$ , solid lines).

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).

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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.

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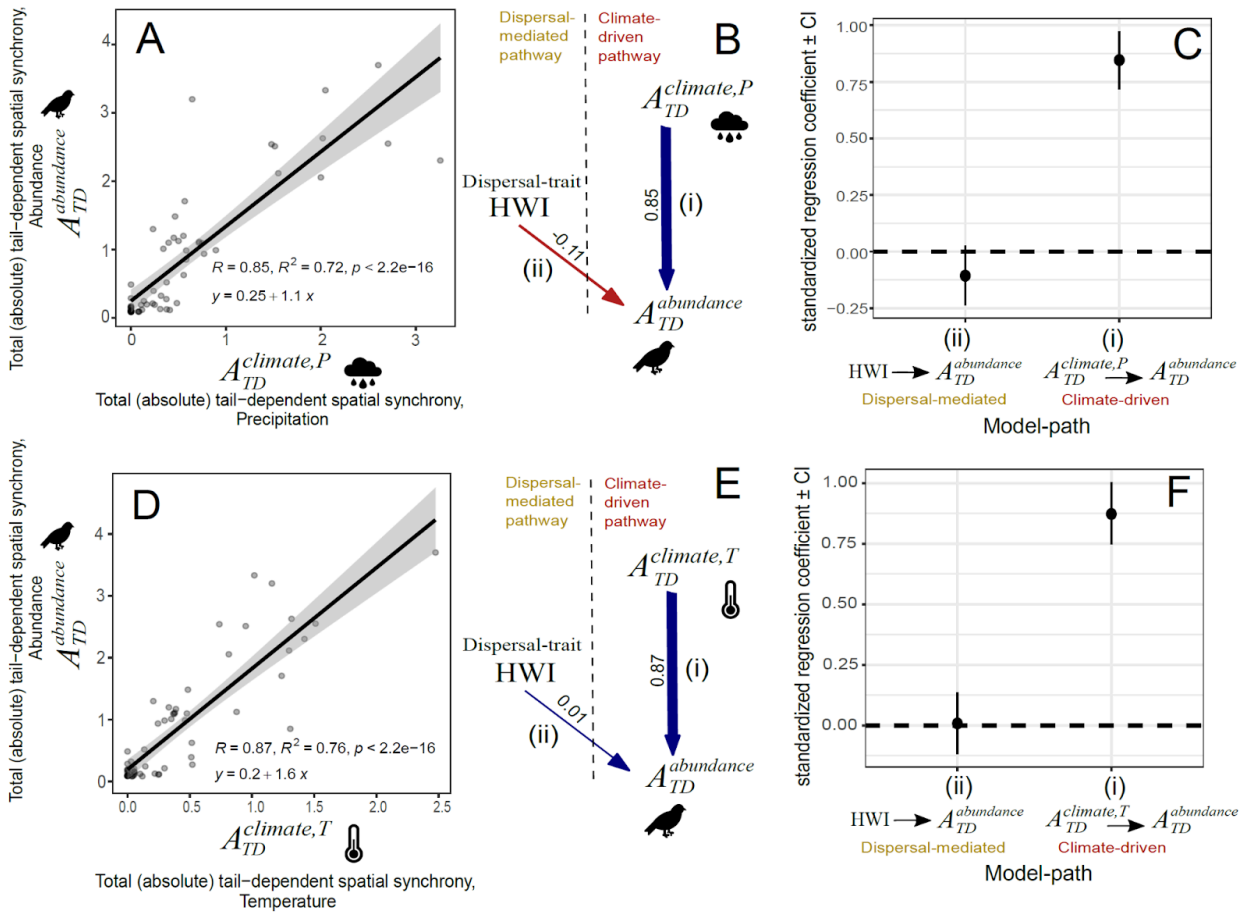
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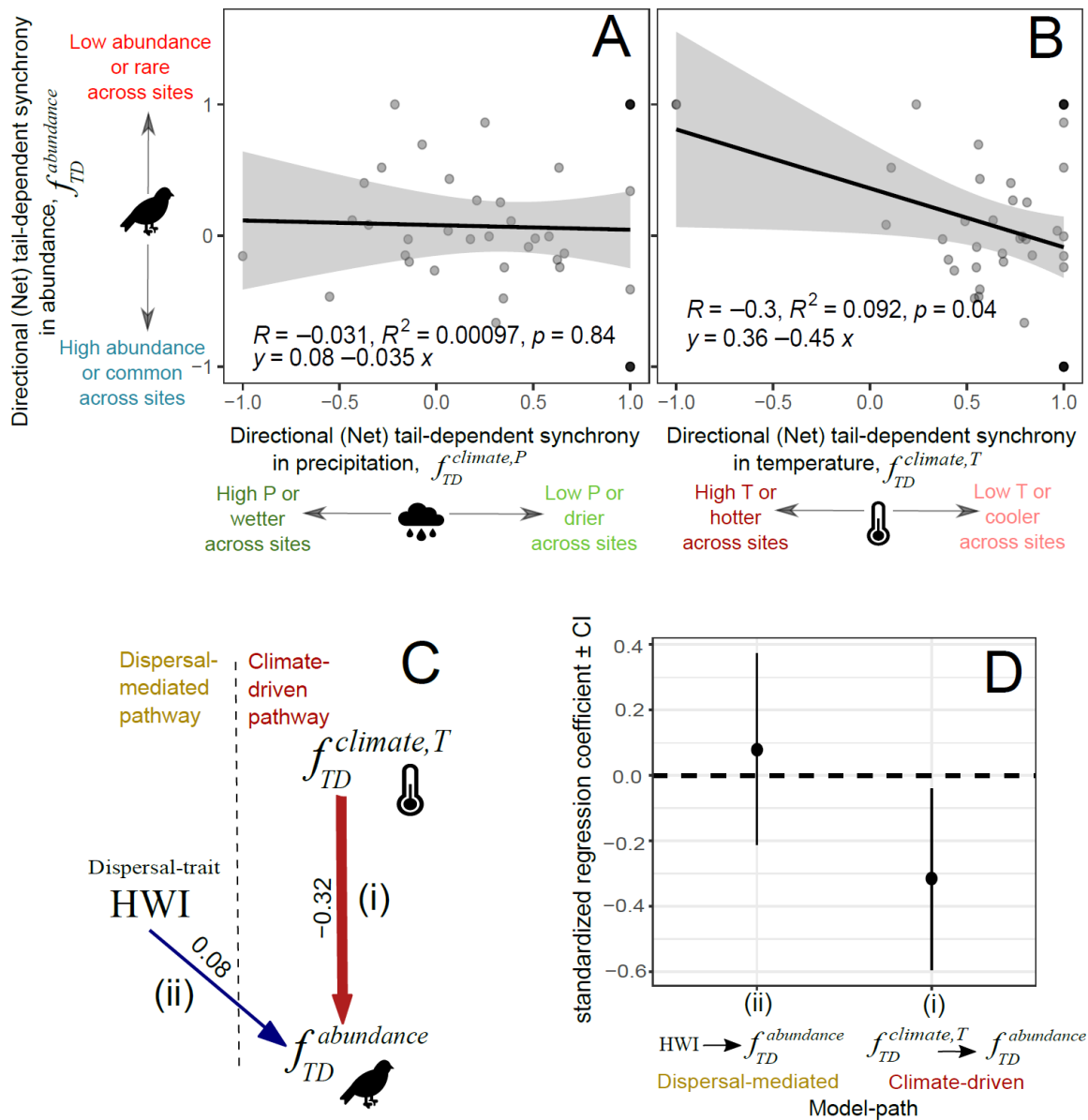
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525 **Figure 4:** Results support hypothesis **H1** that variation in total tail-dependent spatial synchrony  
 526 for climate (precipitation P, panels A-C or temperature T, panels D-F) explains the variation in  
 527 total tail-dependent spatial 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  $p=0.189$ ).



**Figure 5:** Results support hypothesis **H2** that stressed environments across sites make species synchronous at their low abundances. High-temperature extremes across sites limit species abundances significantly (panel B-D), whereas low-temperature extremes across sites make species common: a significant negative slope for panel B as hypothesized in Fig. 2, Q2. 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).

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