

1 **Running head:** Cross-species synchrony in survival

2 **Title:**

3 **Synchrony in adult survival is remarkably strong among common**
4 **temperate songbirds across France**

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29

30 **Abstract**

31 Synchronous variation in demographic parameters across species destabilizes populations,
32 metapopulations and metacommunities and increases extinction risks. Revealing the processes
33 that synchronize population dynamics across species allows to identify trans-specific
34 demographic processes that are subject to environmental forcing of overarching importance.
35 Using a Bayesian, hierarchical multi-site, multi-species mark–recapture model, we investigated
36 synchrony in annual adult local survival across 16 species of songbirds over France for the period
37 2001–2016, and the contributions of winter and spring weather conditions to synchrony. Adult
38 annual survival was largely synchronous among species (73% [47–94] of Species-by-Year
39 variance), despite species differing in ecological niche and life-histories. This result was robust to
40 differences in migratory strategy among species, uneven species sample sizes, and time de-
41 trending. Shared synchrony across migratory strategy suggests that environmental forcing during
42 the 4-month temperate breeding season has large-scale, cross-specific impacts among songbirds.
43 At a scale ~1000 km a likely proximate mechanism of synchronization is forcing by weather-
44 driven variation in resources, which, in particular, determines the cost of reproduction. However,
45 the strong synchrony was not easily explained by climate, with spring weather variables
46 explaining only about 1.4% [0.01–5.5] of synchrony, while the contribution of large-scale winter
47 weather indices may be stronger, but uncertain (12% [0.3–37]). Future research should up-scale
48 these results to community dynamics, to understand compensatory intra- and inter-specific
49 demographic processes that preserve meta-communities from synchronization.

50

51 *Keywords : adult survival; common songbirds; demography; mark-recapture; migration;*
52 *Moran effect; precipitation; synchrony; temperature.*

54 **INTRODUCTION**

55 Synchrony corresponds to the coincident change in individual, population or species state over
56 extended areas (up to thousands of km, Liebhold et al. 2004). Understanding the causes of
57 synchronous variations in population size is of importance in ecology and conservation because
58 the higher the synchrony, the higher the risk of population, metapopulation, and metacommunity
59 extinction (Liebhold et al. 2004, Koenig and Liebhold 2016). Indeed, synchronous populations go
60 down in numbers simultaneously, increasing the risk of synchronous local extinctions, and
61 reducing opportunity for subsequent demographic rescue through immigration (Tavecchia et al.
62 2016). If this extinction process undergoes simultaneously for multiple co-occurring species, it
63 can ultimately result in disruptions of ecosystem functioning (Loreau and de Mazancourt 2008,
64 Kahilainen et al. 2018). However, differences in niche and life-histories among the species of a
65 community should decrease synchrony and thereby the risk of extinction (Pandit et al. 2013).

66 Spatial synchrony has mainly been investigated across populations within species, i.e., as the
67 spatial covariance in temporal changes of population properties (Liebhold et al. 2004). There, a
68 major theoretical and empirical challenge is to reveal the respective role of the three processes
69 that can cause spatial synchrony. The most intuitive, and commonly reported, process is extrinsic
70 forcing: individuals that share a common environment are exposed to the same constraints (the
71 Moran effect, Liebhold et al. 2004, Olmos et al. 2019). A first process is climate forcing, where
72 temperatures, precipitations, or other weather properties, drive directly variation in survival and
73 reproduction (Post and Forchhammer 2004, Cattadori et al. 2005, Hansen et al. 2013, Sheppard
74 et al. 2015, Koenig and Liebhold 2016, Black et al. 2018, Kahilainen et al. 2018, but see Vik et
75 al. 2004), in particular by affecting the cost of thermoregulation (Root, 1988, Boyles et al. 2011).
76 A second process is synchronization through interactions with another trophic level, e.g. through
77 synchronous fluctuations in shared preys (e.g., synchronous mast-seeding for seed-eating species;

78 Liebhold et al. 2004, Klapwijk et al. 2018), predators (Huitu et al. 2004) or parasites (Cattadori et
79 al. 2005), which may themselves be driven by climate forcing (Dubos et al. 2018). The third
80 process is dispersal. Dispersal synchronizes fluctuations in size of connected populations
81 proportionally to dispersal distance (over c. 65 kms in common songbirds, Paradis et al. 1999,
82 Liebhold et al. 2004, Martin et al. 2017). But interpopulation dispersal can also desynchronize
83 population fluctuations (Sanz-Aguilar et al. 2016, Tavecchia et al. 2016).

84 Disentangling these three causes of synchrony is a notoriously complex topic in ecology.
85 Cross-specific synchrony (or “interspecific synchrony”, Liebhold et al. 2004). Evidence
86 accumulates that a few taxa can show a strong degree of synchrony over wide areas, even when
87 they are ecologically, functionally and phylogenetically divergent (Post and Forchhammer 2004,
88 Hansen et al. 2013, Black et al. 2018). Interspecific synchrony has been mainly revealed in two
89 systems that are subject to trivial environmental forcing: species thriving in cold-driven
90 environments (Post and Forchhammer 2004, Jones et al. 2003, Hansen et al. 2013, Koenig and
91 Liebhold 2016, with cyclic dynamics, e.g. Huitu et al. 2004, Liebhold et al. 2004), and predatory
92 marine seabirds that aggregate at a few colonies surrounding shared areas of high oceanic
93 productivity (Lahoz-Monfort et al. 2011, 2013, 2017, Robinson et al. 2013). Evidence of cross-
94 specific synchronous demography across a wide range of species are very few, and come from
95 large-scale census of common wintering birds (6 species from UK, Swallow et al. 2016; 49
96 species from North-America, Koenig and Liebhold 2016).

97 Population size fluctuations can be asynchronous despite synchrony in some vital rates.
98 Indeed, vital rates taken separately are expected to be more commonly synchronized than
99 population sizes, due to life-history trade-offs (e.g. increased fecundity may decrease survival due
100 to the cost of reproduction) and to demographic buffering, when the synchronous vital rate has a
101 limited contribution to the population growth rate (Schaub et al. 2015, Saether et al. 2016).

102 Dispersal can also desynchronize population sizes (Tavecchia et al. 2016). Identifying synchrony
103 in some vital rates, rather than in population size, is nonetheless important because it points
104 towards a demographic weakness: if the compensatory mechanism was to fail, then synchrony
105 may scale-up to population size, increasing the risk of extinction (Sanz-Aguilar et al. 2016).

106 To the best of our knowledge, until recently, cross-species synchrony in vital rates had been
107 studied only for a small number of species (2 to 6) at a single site or region : one on two duck
108 species (Péron and Koons 2012), two on two salmon species (Malick and Cox 2016, Malick et al.
109 2017), all others on marine predatory birds (Lahoz-Monfort et al. 2011, 2013, 2017, Robinson et
110 al. 2013). The reduced taxonomic coverage in those studies may have facilitated the detection of
111 cross-species synchrony. Recently, Telensky et al. (2020) estimated the synchronizing effect of
112 weather variables on breeding sites and winter sites for migrants for the survival of 16 songbird
113 species and 42 sites located in the Czech Republic during 2004–2014. In addition, Morrisson et
114 al. (2021), studied patterns of demographic and vital rates changes across European songbirds
115 and in particular estimated the covariation in population trends, reproductive rates and survival
116 between migrant species vs. resident species using 26 songbird species across 10 areas
117 comprising 336 sites. These two studies did not explicitly estimate synchrony in vital rates
118 though. The lack of research on cross-species synchrony of vital rates likely results from (i) the
119 lack of theories and methods to root (meta)community dynamics in processes operating at
120 individual level (but see Lahoz-Monfort et al. 2017), and (ii) the complexity and computational
121 intensiveness of pioneer methods to analyze multi-species, multi-site, long-term vital rate dataset
122 (Grosbois et al. 2009, Lahoz-Monfort et al. 2011, 2013, 2017, Swallow et al. 2016). The reward
123 for by-passing these limits is that evidencing cross-specific demographic processes reveal
124 regulating mechanisms of overarching importance.

125 In the present study, we investigated synchrony in yearly fluctuations in annual adult local
126 survival across a set of common songbirds (16 species), at a country level (242 sites across
127 France, see Fig. 1), over a period of 16 years. Cross-specific synchrony was analyzed using the
128 variance partitioning method of Lahoz-Monfort *et al.* (2011), splitting between-year variance into
129 a synchronous component, common to all species, and a species-specific, asynchronous
130 component. We expected annual variations of survival to be largely species-specific (i.e.
131 asynchronous) since our analyses involved a large number of species with distinct niches (Table
132 S1; the higher the diversity, the lower the expected synchrony, Pandit et al. 2013). These species
133 differ in terms of migratory strategy and wintering range: 9 species are resident or short-distance
134 migrants, with year-round exposure to temperate climate, whereas 7 species are trans-Saharan
135 migrants that winter under the west-African climate. Therefore, we expected that synchrony
136 would be stronger within migratory strategy and that migratory strategy would explain a
137 significant portion of year-to-year variation among species. If that was the case, it would point to
138 a role of conditions on wintering grounds. Winter harshness is commonly proposed to explain a
139 large proportion of year-round mortality in small organisms like songbirds (Grosbois et al. 2006,
140 Robinson et al. 2007, Salewski et al. 2013, Johnston et al. 2016, Saether et al. 2016), including in
141 migratory songbirds (Robinson et al. 2007, Woodworth et al. 2017b). Factors explaining winter
142 mortality could include water availability in arid wintering areas (Telenský et al. 2020) and the
143 cost of thermoregulation in extreme cold or hot conditions (Boyles et al. 2011).

144 On the other hand, if survival was to covary more synchronously and across migration
145 strategies, it would point towards a role of conditions on the breeding grounds, and climate
146 forcing during the breeding season would be a likely synchronizing process. In addition to factors
147 that explain mortality during winter, climate forcing during the breeding season could
148 synchronize species through its effect on primary and secondary productivity. During nestling

149 rearing, all songbirds feed their chicks exclusively with invertebrates. High precipitations and
150 mild to hot temperatures favor high invertebrate production (Eglington et al. 2015, Dubos et al.
151 2018, 2019), minimizing the foraging effort for chick rearing by breeding adults, and decreasing
152 exposure to predators (Eglington et al. 2015). Aphids and Lepidoptera are subject to spatial
153 synchronization of their abundance by climate forcing (Jones et al. 2003, Sheppard et al. 2015,
154 Kahilainen et al. 2018). A remarkable food-supplementation experiment demonstrated that food
155 availability during breeding has a direct effect on annual adult survival in a long-distance
156 migratory species: simply increasing food availability during reproduction (i.e. over 4–5 months)
157 increased survival by 5% (Seward et al. 2013). Moreover, in highly productive years, a higher
158 proportion of adults engage in rearing a second brood (Visser et al. 2003), potentially at a
159 supplementary cost in terms of survival (Woodworth et al. 2017a). If facultative multi-brooding
160 species (62% of studied species; Appendix S1) are synchronous in their choice to lay a second
161 brood, their adult survival could be synchronized by the cost of reproduction. Schaub et al.
162 (2015) demonstrated that the probability of double brooding was actually the most synchronous
163 vital rates across the 9 populations of an aerial insectivorous songbird, the Barn Swallow
164 (*Hirundo rustica*). All these lines of evidence support that the environmental conditions during
165 the short period of reproduction could have a major incidence on year-round survival in
166 temperate songbirds.

167 To assess the respective role of climate forcing during the breeding (i.e. common to all
168 species) vs. non-breeding seasons (i.e. common to species wintering in the same climatic region),
169 we tested for the dependence of survival on local temperatures and precipitations at the breeding
170 sites during the breeding season, and on global climate indices related to conditions on the
171 wintering grounds during the non-breeding season (the winter North Atlantic Oscillation and the
172 summer Sahel rainfalls, see Methods). We predicted that, if climate exerts forcing on adult

173 mortality during the breeding season, survival probability variations should be synchronous to
174 some extent across species. These synchronous peaks of mortality or high survival should depend
175 on spring weather conditions. On the other hand, if climate forcing operates mainly during the
176 ‘harsh’ season (winter), survival variations should be synchronous among species sharing the
177 same migratory behavior (but not across all species), and should depend on yearly fluctuations in
178 winter harshness indices.

179

180 **METHODS**

181 *Study site and species*

182 Mark-recapture data were collected by volunteer bird ringers under the French Constant-
183 ringing-Effort-Site (CES) banding scheme (Julliard and Jiguet 2002) over the period 2001–2016,
184 with the goal of estimating annual local survival and recapture probabilities. We consider “local
185 survival”, rather than “true survival”, as our data cannot distinguish between mortality and
186 permanent emigration. At each CES site, the local bird community is sampled 3.17 ± 1.06 SD
187 times per breeding season (first session in May 21 ± 15 days) and July (last session in July 4 ± 12
188 days), with 14 ± 7 mist nets (12-m long), spread over an area of ~ 3 hectares (4 to 5 mist nets per
189 hectare). A capture session typically starts at dawn, and lasts until midday. For every site, the
190 number, dates and hours of capture sessions, as well as the mist net locations, are held constant
191 across sessions and years. Sites are monitored for an average of 6 ± 4 years. Sites are
192 typically located in low canopy habitats such as shrub lands, open woodlands and reed beds,
193 where birds are easily trapped with 3.5-m high mist nets. Each captured bird is marked with a
194 metal band bearing a unique identifier, identified at the species level, aged (juvenile or adult),
195 sexed (Svensson 1992), and released at the point of capture. All recaptures of marked individuals

196 are recorded. To secure minimal robustness of site-level estimates, we retained only those species
197 with at least five individuals captured, on average, per year. Juvenile mortality is highly
198 confounded with dispersal and was not considered (Johnston et al. 2016). Overall, our mark-
199 recapture dataset consists of 20,912 adults from 16 species, including 5,198 individuals
200 recaptured across years at least once (see Appendix S1) and 242 sites (Fig. 1 and Appendix S10
201 Fig. S1), over a period of 16 years (Dehorter and CRBPO 2017).

202 *Bayesian survival data analysis*

203 We modelled annual local survival and recapture probabilities using mark-recapture history of
204 individual birds with species- and time-dependent Cormack-Jolly-Seber (CJS) models (Lahoz-
205 Monfort et al. 2011). Inter-annual adult local survival probability (ϕ) is the probability that a bird
206 alive in year (t) is still alive and present at the same CES site in year ($t+1$). The recapture
207 probability (p) is the probability that a bird alive and present in the same CES site where it was
208 formerly captured (year ($t-1$) or before) is recaptured in year (t). Transient individuals that do not
209 pertain to the local population (i.e. that were captured only once, Johnston et al. 2016) were
210 discarded by starting capture history only at the second capture of each individual. We also
211 attempted to retain transients and model them, but the models were prohibitively long to run.
212 Goodness-of-fit tests for the general group-by-time-dependent CJS model were then run
213 separately for each species using the R2ucare package (Gimenez et al. 2018; Appendix S2).

214 We built a Bayesian formulation of the CJS model applying a Markov Chain Monte Carlo
215 (MCMC) sampling procedure (Lahoz-Monfort et al. 2011) implemented in JAGS (Plummer
216 2003) called from R version 3.5.1 (R Development Core Team 2015) using the R-package R2jags
217 version 4.2.0 (Su and Yajima 2015). We chose weakly informative priors for all parameters
218 (Appendix S3). Details on specification of prior distributions for the parameters and satisfactory

219 convergence criteria are provided in Appendix S3. All models accounted for the variation of local
220 survival and recapture probabilities between sexes (effect common to all species), species and
221 sites (see Appendix S3). We addressed only synchrony across all sites, ignoring the spatio-
222 temporal (i.e. Site:Year random variance) and the species-specific spatio-temporal variances (i.e.
223 Species:Site:Year random variance) in local adult survival probability. Such a full, hierarchical
224 partitioning of variance was not achievable with the amount of mark-recapture data available
225 within year-site-species. We report posterior modes as point estimates and 95% highest posterior
226 density credible intervals to show estimation uncertainty.

227 *Temporal synchrony in survival across species*

228 We estimated the between-year synchrony in annual survival probability across species using
229 two complementary random effects (as in Grosbois et al. 2009): a Year random variance (σ_δ^2) that
230 quantifies the amount of between-year variation that is common to all species, across all sites
231 (synchronous, country-scale, inter-annual variation) and a Year-by-Species random variance (σ_ϵ^2)
232 that quantifies the between-year variation that differs between species (asynchronous, country-
233 scale, inter-annual variation). Note that σ_δ^2 and σ_ϵ^2 are unique parameters common to all species.
234 From estimates of σ_δ^2 and σ_ϵ^2 , we calculate a between-species intra-class correlation (ICC) of
235 temporal variation to quantify national-level, between-year synchrony in adult survival across
236 species, on the logit scale, defined as $ICC = \frac{\sigma_\delta^2}{\sigma_\delta^2 + \sigma_\epsilon^2}$. The model description up until now defines
237 model 1.

238 The approach used for model 1 differs from Lahoz-Monfort et al. (2011) in that we define σ_ϵ^2
239 and ICC common to all species, while Lahoz-Monfort et al. (2011) estimated species-specific

240 parameters, $\sigma_{\epsilon_{species}}^2$ and $ICC_{species} = \frac{\sigma_{\delta}^2}{\sigma_{\delta}^2 + \sigma_{\epsilon_{species}}^2}$. We also fitted the model corresponding to Lahoz-
241 Monfort et al. (2011) and name it model 2. From model 2, we calculated the average of the 16
242 $ICC_{species}$ point estimates to compare it to the global ICC calculated from model 1. We now
243 explain the pros and cons of model 1 and model 2.

244 Our main goal was to quantify synchrony across species as a single value. A single value for
245 synchrony corresponds directly to the parameterization of model 1 where synchrony is captured
246 by a single ICC . In contrast, in model 2, to obtain the overall measure of synchrony, we need to
247 average 16 species-specific $ICC_{species}$, which is conceptually similar to our question of synchrony
248 across species, but less direct. Further, we rely on sparse, hard to collect, mark-recapture data, and
249 sample size limits the precision of estimates. In model 1, the ICC is estimated from all the data,
250 while in model 2 the $ICC_{species}$ are each estimated from a fraction of the data only and therefore
251 less precisely. The lack of data to estimate some $ICC_{species}$ may be a special concern in the
252 Bayesian framework since the prior may influence estimation of parameters informed by fewer
253 data points. Finally, model 2 has more variance parameters than model 1, which makes estimation
254 more difficult algorithmically, although these extra parameters are not of direct interest for the
255 estimation of synchrony. We observed that extensions of model 2 exploring factors contributing to
256 synchrony (see below models 3-5) had difficulties converging, while the same extensions of
257 model 1 converged.

258 On the other hand, model 1 assumes that species-specific time deviations came from a single
259 distribution, with a variance common to all species. However, this assumption may lead to a poor
260 fit to the data and may bias estimates when sample sizes vary among species. Model 2 relaxes the
261 assumption and provides a sanity check: if the estimation of synchrony in model 1 is robust to the

262 assumption of common distribution, then most species-specific $ICC_{species}$ in model 2 should be in
263 the range of values, and the average of $ICC_{species}$ should be similar to the ICC estimated in model
264 1.

265 In summary, model 2 is useful to illustrate the variability, or lack of variability in ICC across
266 species, and to check the statistical robustness to the imbalance of species sample sizes.
267 Nevertheless, we favor model 1 as it provides a more direct measure of synchrony and, given
268 sparse data as available here, allows a more powerful estimation of synchrony and test of the
269 factors contributing to synchrony. Below we describe how, building on model 1, we were able to
270 assess specific hypotheses about the contributions of weather and migratory type.

271 *Yearly weather covariates (models 3 and 4)*

272 Spring – early summer weather conditions were characterized for each site and year by daily
273 mean temperature and daily sum precipitation (as in Grosbois et al. 2006, Eglington et al. 2015,
274 Gaüzère et al. 2015, Dubos et al. 2018) from the E-OBS meteorological dataset (available at
275 <https://www.ecad.eu/>) during the breeding period (from April to July), with a 0.25° pixel
276 (approximately 20Km by 28Km) resolution using the R-package climateExtract (available at
277 <https://github.com/RetoSchmucki>). Since organisms are expected to be adapted to average local
278 conditions (e.g. Dubos et al. 2019), we tested for an effect of departure from local average
279 weather conditions, i.e. local spring weather anomalies. Anomalies were computed for each
280 variable, site and year, as the difference between the local value for a given spring and the mean
281 over the 2001–2016 period (as in Dubos et al. 2018). For the effect sizes for temperature and
282 precipitation to be comparable, anomalies were standardized (i.e. divided by the standard
283 deviation across all sites and years). However, we then used the yearly averages of anomalies
284 across all sites to capture the synchronizing effect of weather variables (Appendix S8 Fig. S1).

285 To explain between-species synchrony in annual survival variations that could be attributed to
 286 large-scale fluctuations in spring weather conditions, we fitted Model 3, identical to Model 1 but
 287 including fixed effects for the linear and quadratic effect of spring temperatures and precipitation,
 288 as well as the four pairwise interactions. Here we fitted multiple weather covariates known to
 289 explain variation in passerine vital rates, allowing non-linear and interactive effects as such non-
 290 additive effects are known to explain bird survival (Boyles et al. 2011, Pomara & Zuckerberg
 291 2017). This approach should be seen as an attempt to estimate the variance, and synchrony,
 292 related to weather, rather than an attempt to test the potential causal effects of weather presented
 293 in introduction.

294 Following Nakagawa and Schielzeth (2013) we estimated the synchronous variance explained
 295 by spring weather (σ_{sw}^2) as the variance in partial model predictions (that is, the linear
 296 combination of the products of each parameter estimate by the corresponding weather variable):

297
$$\sigma_{sw}^2 = \text{var} \left(\sum_{h=1}^8 \beta_h \bar{x}_{ht} \right)$$
 where h indexes the eight model parameters related to spring weather, β_h is

298 the parameter estimate for the effect of h , and \bar{x}_{ht} is the mean value of the weather variable h on
 299 year t (across all sites). By definition σ_{sw}^2 captures only synchronous variation. Therefore we

300 calculated the proportion of synchronous variation related by spring weather as $\frac{\sigma_{sw}^2}{\sigma_{\delta}^2 + \sigma_{sw}^2}$, and the

301 new $ICC = \frac{\sigma_{sw}^2 + \sigma_{\delta}^2}{\sigma_{sw}^2 + \sigma_{\delta}^2 + \sigma_{\epsilon}^2}$. As always, calculations were integrated over the model posterior

302 distribution to propagate uncertainty.

303 In Model 4, we added covariates related to winter weather to Model 1. For resident and short-
 304 distance migrants, that winter in western Europe or North-Africa, we used the North Atlantic
 305 Oscillation during winter (wNAO, averaged from December to March, available at

306 <http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm>). The wNAO captures broad scale weather
307 variation in Western Europe and North Africa (Forchhammer & Post 2004), which explains
308 variations in over-winter survival in several European bird species (Robinson et al. 2007,
309 Salewski et al. 2013). For long-distance migrants that winter in Western Africa, we used the
310 Sahel Rainfall during summer (sSR, averaged from July to September, available at
311 http://research.jisao.washington.edu/data_sets/sahel/). The sSR is often used as an proxy of
312 winter Sahel suitability for wintering songbirds, considering that habitat quality in December–
313 February is driven by rainfall during the previous summer (Robinson et al. 2007, Salewski et al.
314 2013). As done for spring weather covariates, we fitted linear and quadratic effects for wNAO
315 and sSR. We estimated the synchronous variance explained by winter weather (σ_{ww}^2) as the
316 variance in partial model predictions from the linear and quadratic effects of wNAO and sSR,
317 $\sigma_{ww}^2 = \text{var} \left(p \left(\beta_{sSR} sSR + \beta_{sSR2} sSR^2 \right) + (1 - p) \left(\beta_{wNAO} wNAO + \beta_{wNAO2} wNAO^2 \right) \right)$ where p is the
318 proportion of long-distance migratory species. This variance captures the weighed synchronous
319 variance among migratory species due to sSR, added to the weighed synchronous variance
320 among resident species due to wNAO, minus the asynchronous variance due to the small negative
321 covariance between sSR and wNAO (the two indices are expected to be independent, but the
322 empirical correlation was -0.12 [-0.58;0.40], p-value=0.66). The proportion of synchronous
323 variance related to winter weather was calculated as $\frac{\sigma_{ww}^2}{\sigma_{\delta}^2 + \sigma_{sw}^2}$, and the $ICC = \frac{\sigma_{ww}^2 + \sigma_{\delta}^2}{\sigma_{ww}^2 + \sigma_{\delta}^2 + \sigma_{\epsilon}^2}$.

324 *Migratory strategy (model 5)*

325 Because of shared wintering conditions among species, migratory strategy could reduce the
326 overall synchrony in annual survival. To quantify the importance of this effect, we fitted Model
327 5, a variation of Model 1 with a random effect for the interaction Year-by-Migratory behavior
328 (sixteen times two levels, resident or short-distance migrants vs. long-distance migrants). We thus

329 modeled a Migratory-class-by-Year variance σ_m^2 , while σ_δ^2 remained the Year-variance common
330 to migratory classes and species, and $\sigma_{\epsilon w}^2$ was the within migratory-class species-specific year
331 variance. The proportion of species-specific variance that depended on migratory-class (i.e.
332 asynchrony between migratory class among species) was estimated as $\frac{\sigma_m^2}{\sigma_m^2 + \sigma_{\epsilon w}^2}$. This index will
333 approach 1 if migratory strategy explains most of the asynchronous variation. The synchrony
334 within migratory-class was estimated as $\frac{\sigma_\delta^2}{\sigma_\delta^2 + \sigma_{\epsilon w}^2}$. If migratory strategy explains most of the
335 asynchronous variation, this index will approach 1, whereas if migratory strategy explains no
336 asynchronous variation, this index will approach the ICC value calculated from model 1.

337 All parameter estimates for all models are provided in Appendix S11.

338

339 **RESULTS**

340 *Cross-species temporal synchrony of annual adult local survival*

341 Inter-annual variation in adult local survival probabilities was largely synchronous across the
342 16 studies species (Fig. 2). The ICC of 73% [47–94], indicates that most of the temporal variance
343 in apparent survival probability (at national scale) was common to all species (Table 1: Model 1).
344 Conversely, this implies that only 27% [6–53] of temporal fluctuations of survival probabilities
345 were species-specific.

346 Species showed considerable variation in $ICC_{species}$ (Fig. 3), although estimates came with
347 broad credible intervals. Using linear regression integrated over the posterior distribution of
348 $ICC_{species}$, there was no significant association between the value of $ICC_{species}$ and migratory type
349 (Fig. 3; pMCMC=0.48) nor with species sample size (pMCMC=0.31). More qualitatively, we also

350 did not see any pattern linking the values of $ICC_{species}$ and the species characteristics. The mean of
351 the 16 point estimates for $ICC_{species}$ was 76%.

352 This strong synchrony was robust to (i) the uneven contributions of species to the mark-
353 recapture dataset ($ICC = 65\%$ [28–90], Appendix S4), (ii) the removal of the part of synchrony
354 due to a potential linear trend in survival probability ($ICC = 56\%$ [23–86], Appendix S5; note
355 that this calculation necessarily excludes some true synchrony), (iii) prior distribution (Appendix
356 S6), and (iii) the effects of weather and migratory behavior presented here below.

357 Graphically (Fig. 2), some years seemed to deviate more from the mean survival probability,
358 and may have contributed more to synchrony: estimates of survival probability between the years
359 2001–2002, 2002–2003 were larger than average while estimates for the years 2005–2006 and
360 2008–2009 were particularly low (Appendix S7: Fig. S2). However, our *ad hoc* approach using
361 model estimates (Appendix S7) failed at identifying statistical support for variability in yearly
362 contributions to synchrony.

363 *Contributions of weather effects to survival probability synchrony*

364 According to Model 3, spring weather variables taken together explained only 1.4% [0.01–5.5]
365 of synchrony, whereas according to Model 4, the winter weather variables explained 12% [0.3–
366 37] of the synchrony. Assuming independence of spring and winter weather variables, they
367 explain 13% [0.8–39] of synchrony together (and explain 10% [0.6–23] of the total temporal
368 variance, Table 1). There was no clear evidence for an effect of any of the weather-related
369 parameters on survival probability with all credible intervals overlapping zero (across all species,
370 i.e. additive effects; Appendix S8: Table S1). Higher spring precipitation and more extreme
371 spring temperatures tended to increase survival probability (Appendix S8: Fig. S1). For winter
372 weather covariates, survival probability appeared a bit higher for high sSR values, while there

373 was no discernible effect of wNAO (across all species, i.e. additive effects; Appendix S8: Fig.
374 S2).

375 *Contributions of migratory strategy to survival probability synchrony*

376 The interaction between year and migratory strategy captured only a small amount of
377 asynchronous-variation in survival among species (9% [0–30], Table 1). The synchrony
378 estimated from model 4, after removing the species:year variation related to migratory type (i.e.,
379 synchrony corrected for migratory type) was 79% [42–97]. This approximate lack of dependence
380 of synchrony on migratory behavior is apparent in Fig. 2 and Fig. 3.

381

382 **DISCUSSION**

383 Unexpectedly, annual fluctuations in adult local survival proved to be largely (and robustly,
384 Appendices S4, S5, S6) synchronous across the 16 songbird species that dominate bird
385 communities in France: 73% [47–94] of between-year variance in survival probability was
386 common to all species. This result is all the more remarkable given that these species differ in
387 various life-history traits that concern local survival: they cover the range of songbird migratory
388 behavior, body mass (8 to 88 g) and number of broods per year, and they partly differ in habitat
389 use (terrestrial and humid shrub lands) and specialization (Appendix S1). Moreover, our
390 estimates represent ‘minimal synchrony’ since they are not controlled for potentially
391 desynchronizing factors, like intra- and inter-specific negative density dependence, that is,
392 estimated synchrony should be higher if we could control for those factors (Péron and Koons
393 2012, Swallow et al. 2016). This value of synchrony is as high as for spatial synchrony in local
394 survival probability across populations of a same species (67% and 71% in two long-lived birds,

395 Jenouvrier et al. 2009, Grosbois et al. 2009), and higher than survival synchrony observed across
396 two syntopic ducks (49%, Péron and Koons 2012). Short-lived organisms (Appendix S1) are
397 under stronger environment-dependence than long-lived species (Saether et al. 2016), which may
398 contribute to the observed high inter-specific synchrony in the studied set of species. The species-
399 specific synchronies ($ICC_{species}$) varied from very high to low (Figure 4). This means that some
400 species (such as *Cettia cetti*) had considerable species-specific temporal variability in adult
401 survival, probably due to its high sensitivity to winter harshness (Moussus 2010), whereas in others
402 (such as *Sylvia atricapilla*) the temporal variability in adult survival corresponded almost entirely
403 to the average variability across the 16 species. We did not find clear patterns explaining
404 differences in synchrony among species (i.e., migration type, sample size, habitat), and species-
405 specific synchronies were estimated with broad confidence intervals. Therefore the determinants
406 of species synchrony with the rest of the community remain to be identified with a larger dataset,
407 involving more species (i.e. more diversity in life history traits) and more years. We can conclude
408 that, at a country scale, the drivers of annual variations of average adult apparent survival
409 probability are largely common to many species. Drivers that actually differ between species and
410 determine local population dynamics must occur and operate at site or regional level (Giraud et
411 al. 2013, Gaüzère et al. 2015, Cayuela et al. 2019, Morrison et al. 2013, 2021).

412 The presence of strong synchrony in adult survival among songbirds at the country scale
413 reveals a demographic risk for metapopulation and metacommunity (Liebhold et al. 2004, Koenig
414 and Liebhold 2016), but also offers an opportunity to identify key drivers of survival that are
415 common to many species and thereby inform conservation (Morrison et al. 2021, 2022). Below,
416 we discuss the potential mechanisms driving synchronous survival, and whether those
417 mechanisms are more likely to act during the breeding season or rather in winter on non-breeding
418 grounds.

419 Climate forcing could be responsible for cross-species synchronous events of high
420 mortality/survival, either through direct or indirect effects. The few former studies on common
421 songbirds concluded that climate forcing was responsible for (a part of) the observed cross-
422 species synchrony in abundances or vital rates (Jones et al. 2003, Grosbois et al. 2006, Koenig
423 and Liebhold 2016, Swallow et al. 2016, Telenský et al. 2020). However, within-species neither
424 broad scale climatic variables nor local weather variables explained synchronous survival
425 variation in blue tits populations (Bastianelli et al. 2021), and synchronous survival in little auk
426 populations was likely explained by trophic interactions rather than climate (Reiertsen et al.
427 2021). In the present study we failed to identify a statistically significant role for any climatic
428 variables and the spring and winter variables explained only 13% [0.8–39] of the synchrony
429 together (and 10% [0.6–23] of the total temporal variance). Nevertheless, we likely
430 underestimated the importance of climate. First, the variables we use do not explicitly consider
431 weather properties such as extreme temperature or precipitation events, or species-specific
432 periods of sensitivity to weather (van de Pol et al. 2016). Second, we used climatic variables
433 averaged either over spring or winter, which is unlikely to represent the cumulative effect of
434 climatic variations experienced throughout the year. Finally, our modeling investigated the direct
435 effects of weather whereas indirect or delayed effects may be more influential, particularly
436 weather-driven primary and secondary productivity and their effects on the cost of reproduction.

437 What other mechanisms than direct climate forcing could synchronize annual adult local
438 survival across species? First, environmentally-driven, community-level density-dependency of
439 adult survival probability could also generate cross-species synchrony. To rear their offspring,
440 common songbird species rely on very similar preys (larvae and soft invertebrates). The hotter
441 the year, the higher bird productivity (i.e. juvenile production per adult) for most of these same

442 species (Eglington et al. 2015, Dubos et al. 2019). Hence, intra- and interspecific competition for
443 shared resources is likely to operate at local community-level in common songbirds, potentially
444 resulting in large-scale, weather-driven density-dependent regulations of adult survival. But
445 intraspecific density-dependence can also be a source of asynchrony across species (Péron and
446 Koons 2012, Martin et al. 2017). The actual role of community-level density-dependence at
447 synchronizing adult survival probability across species remains to be properly investigated
448 (Swallow et al. 2016). Second, breeding dispersal could contribute to cross-species synchrony in
449 adult local survival (also named apparent survival). Local survival results from survival and
450 residency (i.e. absence of dispersal, Saracco et al. 2010) at the scale of study sites. If individuals
451 of different species tend to synchronously disperse more in some years than in others, then
452 dispersal-induced fluctuations in adult local survival would be synchronous across species at
453 national level. Following bad reproductive experience at one location (e.g., weather-driven early
454 reproductive failure), a higher proportion of adults settle away in the following year (e.g., Arlt &
455 Part 2008). However, synchronous breeding dispersal seems unlikely to induce such a high
456 synchrony in adult local survival because adults are typically reported to disperse in low
457 proportion (1–10% order of magnitude) between breeding events, even in long-distance migrants
458 (Greenwood and Harvey 1982). Moreover, males, the sex that dominates in our dataset (64%),
459 are the most resident sex in birds (Amrhein et al. 2012).

460 Could conditions during the non-breeding season explain the high synchrony in adult
461 survival across songbirds in France? Across both long-distance migrants, short-distance migrants
462 and residents, we found that winter conditions explained 9% [0.2-27] of the variation in annual
463 survival (12% [0.3–37] of the synchrony). This proportion is relatively weak, but potentially
464 significant biologically, and as already explained it is likely that we underestimate the

465 synchronizing importance of weather. Winter harshness is commonly proposed to explain a large
466 proportion of year-round mortality in small organisms like songbirds (Grosbois et al. 2006,
467 Robinson et al. 2007, Salewski et al. 2013, Johnston et al. 2016, Saether et al. 2016), including in
468 migratory songbirds (Robinson et al. 2007, Woodworth et al. 2017b). Recent studies on
469 multispecies population synchrony have also emphasized a major role of winter climate forcing,
470 but these few studies were biased towards cold-driven ecosystems, like high latitude ($>45^\circ$)
471 populations that are subject to extreme winter events (Post & Forchhammer 2004, Jones *et al.*
472 2003, rain-on-snow icing events in Hansen et al. 2013, Pomara & Zuckerberg 2017). Restricting
473 the analysis to long-distance migrant species only, Telenský et al (2020) found that water
474 availability on the wintering grounds explained 15% of the variation in temporal survival but the
475 result was statistically non-significant. Overall, it seems likely that conditions on the non-
476 breeding grounds, especially climate, contribute somewhat to the synchrony in adult survival,
477 even though the 16 studied species spread from France to Central Africa during the winter. This
478 conclusion has profound implications for conservation planning for common habitats: breeding
479 habitat degradation is a major cause of ongoing massive, synchronous population declines
480 (Eglington and Pearce-Higgins 2012, including in migratory species (Morrison et al. 2013).
481 Ecosystem functionality over breeding areas should be the primary focus of conservation in
482 western countries with highly degraded habitats (Morrison et al. 2013), not waiting for other
483 countries along the migratory flyways or at wintering grounds to take actions to improve
484 environmental conditions for migratory birds (Morrison et al. 2013).

485 Differences in migratory strategy explained very little temporal variation in survival
486 probability. Instead, synchrony within migratory strategy was similar to synchrony across
487 migratory strategies (Table 1: Model 5). Although they did not explicitly quantify synchrony, this

488 result is qualitatively supported by Morrisson et al. (2021) who found a positive covariation
489 between the survival of resident species and that of long-distance migrant species, at least those
490 spending winter in humid areas. Resident and long-distance migrants winter on two different
491 continents (at a distance of 2000–3000 km and 35–45° apart in latitude) in which variation in
492 environmental conditions are unlikely to be correlated.

493 At least graphically (Fig. 2), environmental forcing seems to be stronger in some years,
494 and much weaker in later years (from 2009 and after). Synchrony is actually expected to be
495 heterogeneous across years, or even transitory (Klapwijk et al. 2018), and to be largely
496 attributable to the occurrence of environmental disturbances in some years (Cattadori et al. 2005,
497 Keitt 2008). For instance, Jenouvrier et al. (2009) showed that the high synchrony (71%) in
498 Scopoli’s shearwater adult local survival was attributed to only two ‘low’ years out of 8. In
499 ‘normal’ years, species specificities (e.g. ecological niche differentiation) would dominate
500 (Liebhold et al. 2004, Robinson et al. 2013). As climate warms and increasingly fluctuates
501 through time and space with stronger and more frequent out-of-norm weather events, spatial and
502 cross-species synchrony is likely to increase in strength (Post and Forchhammer 2004, Hansen et
503 al. 2013, Koenig and Liebhold 2016, Hansen et al. 2020) over wider spatial scales (Black et al.
504 2018). To properly assess the yearly contributions to synchrony (and trends) requires longer time
505 series than the present dataset. Analytical methods are also not yet readily implementable to such
506 multi-year, multi-site, multi-species mark-recapture dataset (Cattadori et al. 2005, Lahoz-Monfort
507 et al. 2017). Our conclusions on cross-species synchrony in adult local survival now need to be
508 up-scaled to population and community levels, to understand compensatory intra- and inter-
509 specific demographic processes (Péron and Koons 2012, Tavecchia et al. 2016, Lahoz-Monfort et

510 al. 2017) that may regulate meta-communities and preserve them from extinction risks due to
511 synchronization.

512

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521

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727 **Table**

728 TABLE 1. Variance component estimates for survival probability under different assumptions
 729 (models). Model 1 is the base model and captures all of the synchrony in the Year variance
 730 parameter. Other models include various effects that may or may not explain some of the
 731 synchrony, thus leaving a corrected synchrony as the Year variance parameter. Estimates are
 732 posterior modes and 95% highest probability density credible intervals.

Variance component	Model 1 (base)	Model 2 (Species-specific Year:Species)	Model 3 (Spring weather)	Model 4 (Winter weather)	Model 5 (Migration:Year)
Year (synchrony)	0.098 [0.031–0.234]	0.090 [0.016–0.203]	0.091 [0.023–0.216]	0.092 [0.019–0.214]	0.091 [0.009–0.205]
Model-specific synchrony term	-	16 species specific variances	Spring weather ² 0.001 [<0.001–0.0029]	Winter weather ² 0.008 [<0.001–0.020]	-
Year:Species (asynchrony)	0.034 [0.012–0.068]	Mean across species 0.026	0.034 [0.007–0.062]	0.036 [0.010–0.066]	0.032 [0.007– 0.065]
Model-specific asynchrony term	-	-	-	-	Migration:Year 0.011 [0–0.036]
Site	0.155 [0.076–0.232]	0.157 [0.088–0.237]	0.156 [0.081–0.232]	0.152 [0.087–0.226]	0.152 [0.085–0.226]
Variance sum ³	0.287	-	0.287	0.286	0.286

ICC ¹	73% [47–94]	Mean 76%	72% [47-93]	68% [36-95]	79% [42–97]
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733 *Notes:* 1. Intra-class correlations (see Methods) are estimates of synchrony across species, i.e., the
734 proportion of Year variance over ‘total’ temporal variance, which varies across models. 2.
735 Weather variables were introduced as fixed effects and the variance they explain was computed
736 post-hoc, while all other variance components were directly estimated as random effects. 3. The
737 sum of the variances is expected to be constant, but may vary a bit due to rounding, and because
738 survival is not directly observed but predicted as a latent variable (i.e., survival does not have a
739 defined variance observable independently of a model).

740

741 **Figure legend**

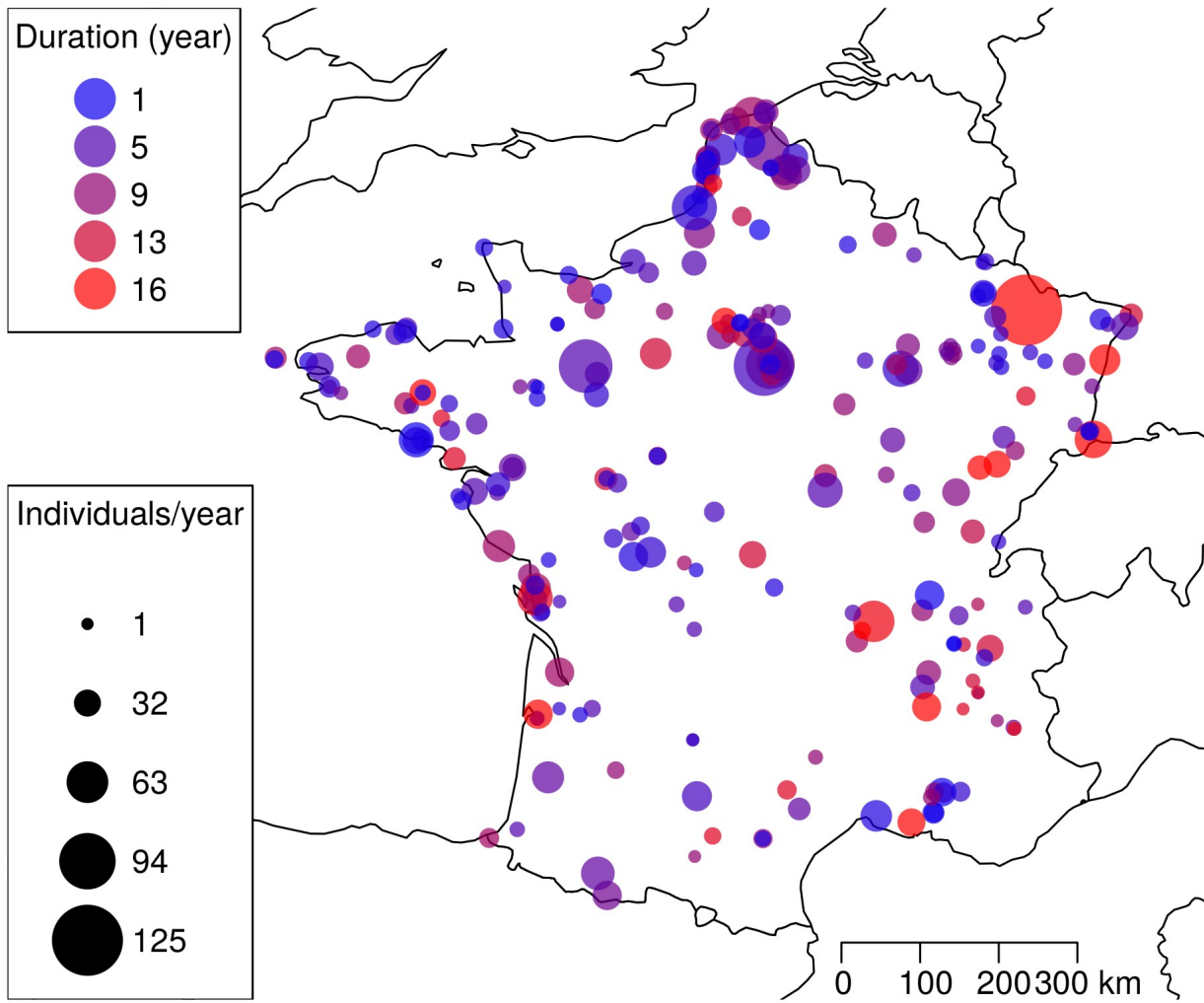
742 FIG. 1. Spatial distribution of the 242 sites across continental France used in this study. Color
743 indicates the duration of a site, in years, corresponds to the number of years for which we
744 estimated year survival in our models. The true duration of the monitoring of the site is always at
745 least one more year. Point size indicates the average number of individuals, used in analyses, per
746 year of monitoring for a given site.

747 FIG. 2. Inter-annual fluctuation of local survival probabilities by species for adult individuals.
748 Estimates were obtained independently for each species (with resident males as intercept) from a
749 model with fully Year-dependent survival and explicitly modelling an interaction between Year
750 and Migratory behavior (resident/short-distance migrants *versus* long-distance migrants, i.e.
751 model 5).

752 FIG. 3. Synchrony for each species and overall. Estimates of Intra-Class Correlations measuring
753 synchrony in adult survival, for each species separately (see appendix 1 for species details), and
754 across all species taken together. Lower species-specific synchrony means that mean survival
755 probability is more variable in that species. Species-specific estimates were obtained from model
756 2, while the overall estimate was obtained from model 1. Yellow lines represent short-distance
757 migrants, blue lines represent long-distance migrants. Filled circles represent posterior modes,
758 empty circles posterior means, thick lines 50% quantile CI and thin lines 95% HPD CI.

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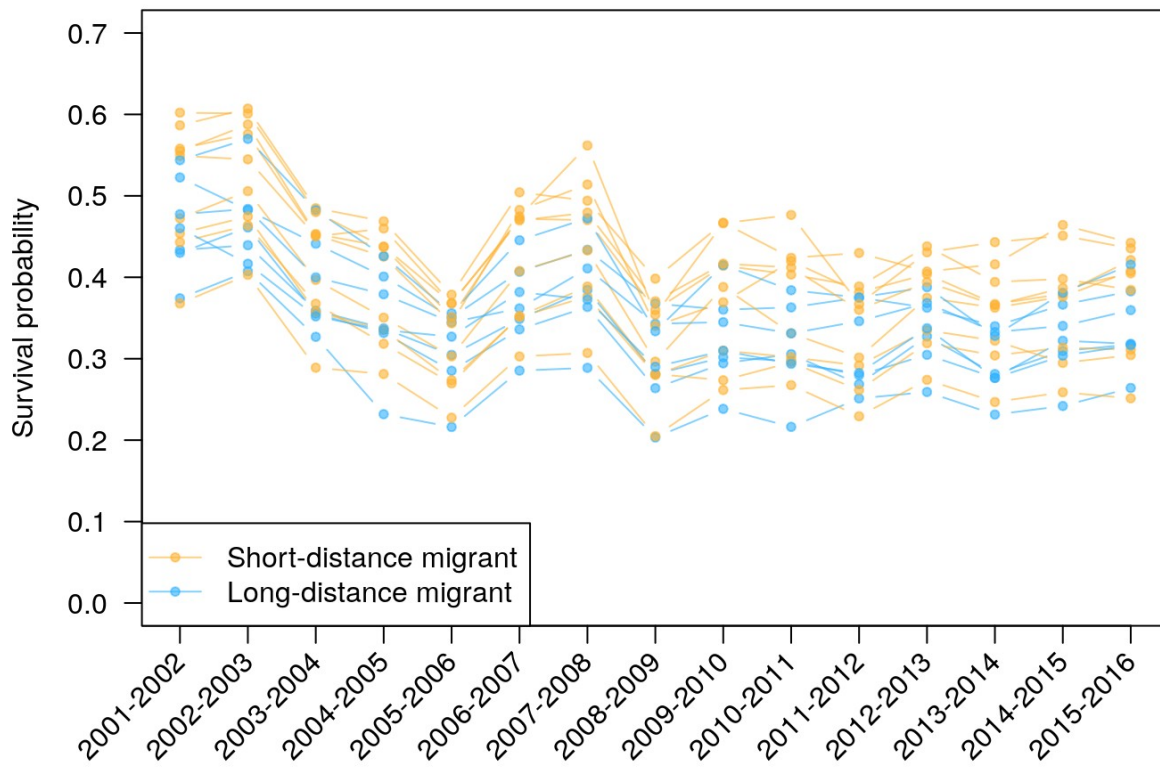
760 Figure 1



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763 Figure 2



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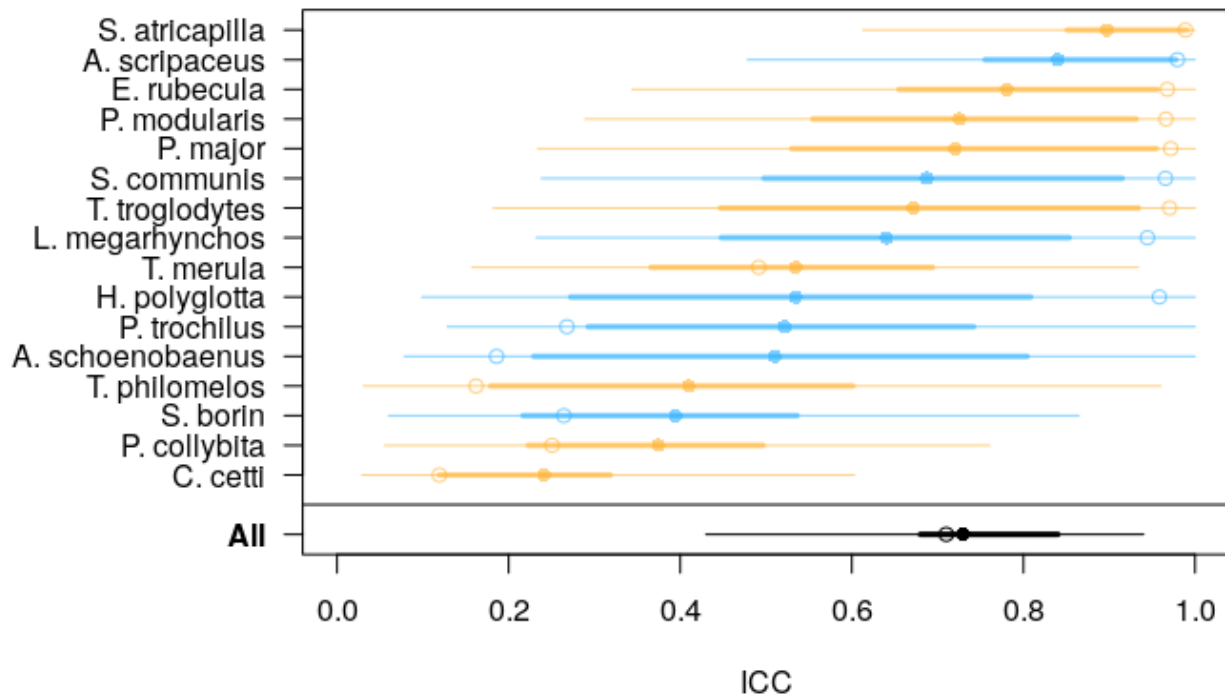
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771 Figure 3



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