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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Abstract

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

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

INTRODUCTION

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

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

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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).

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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

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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

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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.

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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 six $\pm$ four 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 $ICC = \dfrac{\sigma_\delta^2}{\sigma_\delta^2 + \sigma_\varepsilon^2}$. 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, $\sigma^2_{\varepsilon species}$ and $ICC_{species} = \dfrac{\sigma^2_\delta}{\sigma^2_\delta + \sigma^2_{\varepsilon species}}$. 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

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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).

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

298   the parameter estimate for the effect of h, and $\underline{x}_{ht}$ is the mean value of the weather variable h on

299   year t (across all sites). By definition σ^2_{sw} captures only synchronous variation. Therefore we

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

301   new $ICC = \dfrac{\sigma^2_{sw} + \sigma^2_\delta}{\sigma^2_{sw} + \sigma^2_\delta + \sigma^2_\varepsilon}$. 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

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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^2_{ww}) as the

316   variance in partial model predictions from the linear and quadratic effects of wNAO and sSR,

317   $\sigma^2_{ww} = var\left(p\left(\beta_{sSR}\,sSR + \beta_{sSR2}\,sSR^2\right) + \left(1-p\right)\left(\beta_{wNAO}\,wNAO + \beta_{wNAO2}\,wNAO^2\right)\right)$ 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 $\dfrac{\sigma^2_{ww}}{\sigma^2_{\delta} + \sigma^2_{sw}}$, and the $ICC = \dfrac{\sigma^2_{ww} + \sigma^2_{\delta}}{\sigma^2_{ww} + \sigma^2_{\delta} + \sigma^2_{\varepsilon}}$.

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

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329   modeled a Migratory-class-by-Year variance σ^2_m, while σ^2_δ remained the Year-variance common

330   to migratory classes and species, and $\sigma^2_{\varepsilon w}$ 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 $\dfrac{\sigma^2_m}{\sigma^2_m + \sigma^2_{\varepsilon w}}$. This index will

333   approach 1 if migratory strategy explains most of the asynchronous variation. The synchrony

334   within migratory-class was estimated as $\dfrac{\sigma^2_\delta}{\sigma^2_\delta + \sigma^2_{\varepsilon w}}$. 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).

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 (Morrisson 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.

39

40

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°)

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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Table

TABLE 1. Variance component estimates for survival probability under different assumptions

(models). Model 1 is the base model and captures all of the synchrony in the Year variance

parameter. Other models include various effects that may or may not explain some of the

synchrony, thus leaving a corrected synchrony as the Year variance parameter. Estimates are

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]

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

Figure legend

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
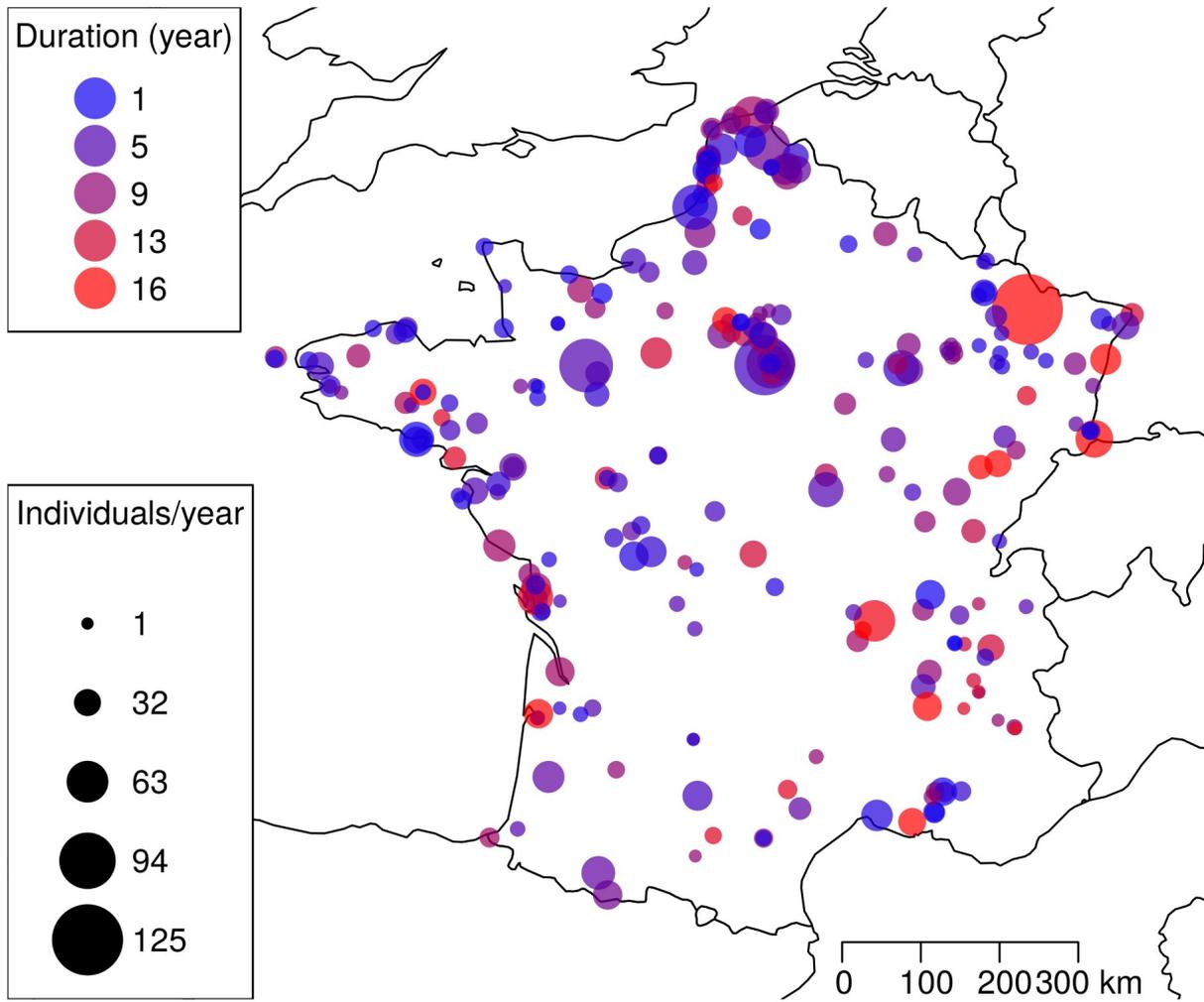
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763   Figure 2
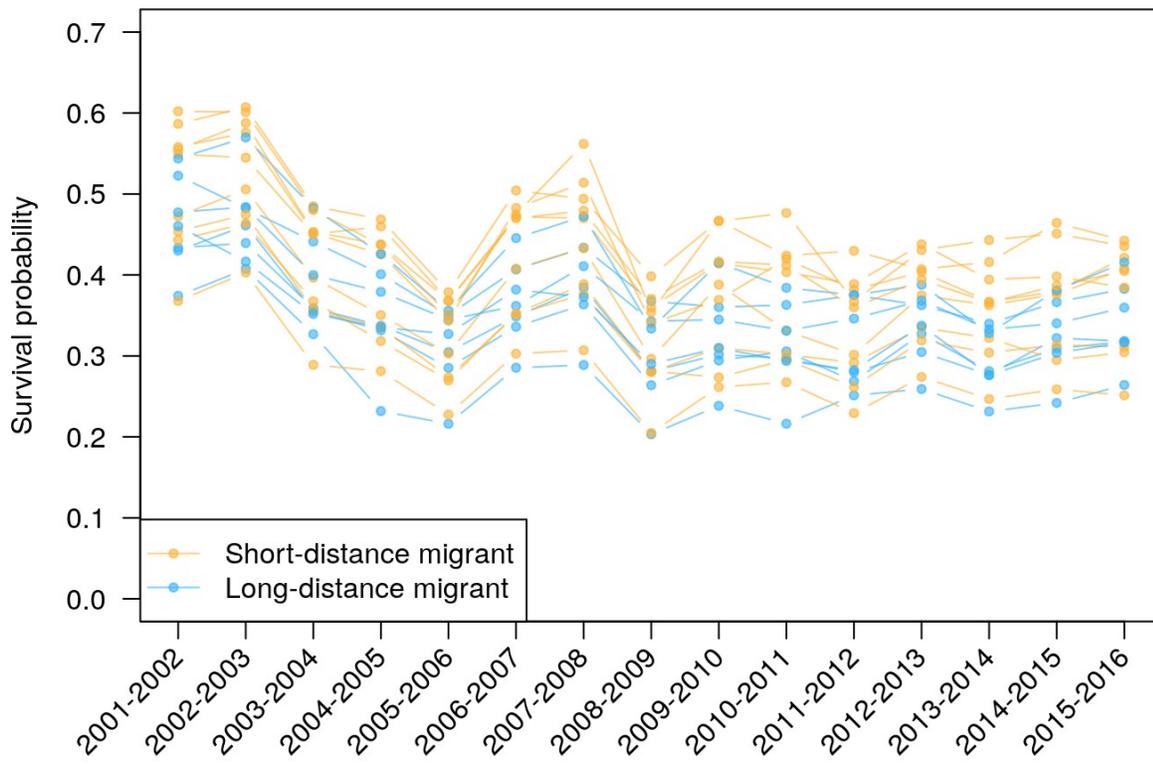
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771   Figure 3