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Synchrony in adult survival is remarkably strong among common 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.

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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;

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

Disentangling these three causes of synchrony is a notoriously complex topic in ecology. Cross-specific synchrony (or “interspecific synchrony”, Liebhold et al. 2004). Evidence accumulates that a few taxa can show a strong degree of synchrony over wide areas, even when they are ecologically, functionally and phylogenetically divergent (Post and Forchhammer 2004, Hansen et al. 2013, Black et al. 2018). Interspecific synchrony has been mainly revealed in two systems that are subject to trivial environmental forcing: species thriving in cold-driven environments (Post and Forchhammer 2004, Jones et al. 2003, Hansen et al. 2013, Koenig and Liebhold 2016, with cyclic dynamics, e.g. Huitu et al. 2004, Liebhold et al. 2004), and predatory marine seabirds that aggregate at a few colonies surrounding shared areas of high oceanic productivity (Lahoz-Monfort et al. 2011, 2013, 2017, Robinson et al. 2013). Evidence of cross-specific synchronous demography across a wide range of species are very few, and come from large-scale census of common wintering birds (6 species from UK, Swallow et al. 2016; 49 species from North-America, Koenig and Liebhold 2016), or very recently from broad-scale bird banding schemes (26 species from Europe, Morrisson et al. 2022).

Population size fluctuations can be asynchronous despite synchrony in some vital rates. Indeed, vital rates taken separately are expected to be more commonly synchronized than population sizes, due to life-history trade-offs (e.g. increased fecundity may decrease survival due to the cost of reproduction) and to demographic buffering, when the synchronous vital rate has a limited contribution to the population growth rate (Schaub et al. 2015, Saether et al. 2016). Dispersal can also desynchronize population sizes (Tavecchia et al. 2016). Identifying synchrony in some vital rates, rather than in population size, is nonetheless important because it points towards a demographic weakness: if the compensatory mechanism was to fail, then synchrony may scale-up to population size, increasing the risk of extinction (Sanz-Aguilar et al. 2016).

To the best of our knowledge, until recently, cross-species synchrony in vital rates had been studied only for a small number of species (2 to 6) at a single site or region : one on two duck species (Péron and Koons 2012), two on two salmon species (Malick and Cox 2016, Malick et al. 2017), all others on marine predatory birds (Lahoz-Monfort et al. 2011, 2013, 2017, Robinson et al. 2013). The reduced taxonomic coverage in those studies may have facilitated the detection of cross-species synchrony. Recently, Telensky et al. (2020) estimated the synchronizing effect of weather variables on breeding sites and winter sites for migrants for the survival of 16 songbird species and 42 sites located in the Czech Republic during 2004–2014, without explicitly estimating synchrony. In addition, Morrisson et al. (2022), studied patterns of spatial and temporal variation in productivity and survival using 26 songbird species across 10 areas comprising 336 European sites, estimating species-specific measures of synchrony (but not global synchrony across species). The lack of research on cross-species synchrony of vital rates likely results from (i) the lack of theories and methods to root (meta)community dynamics in processes operating at individual level (but see Lahoz-Monfort et al. 2017), and (ii) the complexity and computational intensiveness of pioneer methods to analyze multi-species, multi-site, long-term vital rate dataset (Grosbois et al. 2009, Lahoz-Monfort et al. 2011, 2013, 2017, Swallow et al. 2016). The reward for by-passing these limits is that evidencing cross-specific demographic processes reveal regulating mechanisms of overarching importance.

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

On the other hand, if survival was to covary more synchronously and across migration strategies, it would point towards a role of conditions on the breeding grounds, and climate forcing during the breeding season would be a likely synchronizing process. In addition to factors that explain mortality during winter, climate forcing during the breeding season could synchronize species through its effect on primary and secondary productivity. During nestling rearing, all songbirds feed their chicks exclusively with invertebrates. High precipitations and mild to hot temperatures favor high invertebrate production (Eglington et al. 2015, Dubos et al. 2018, 2019), minimizing the foraging effort for chick rearing by breeding adults, and decreasing exposure to predators (Eglington et al. 2015). Aphids and Lepidoptera are subject to spatial synchronization of their abundance by climate forcing (Jones et al. 2003, Sheppard et al. 2015, Kahilainen et al. 2018). A remarkable food-supplementation experiment demonstrated that food availability during breeding has a direct effect on annual adult survival in a long-distance migratory species: simply increasing food availability during reproduction (i.e. over 4–5 months) increased survival by 5% (Seward et al. 2013). Moreover, in highly productive years, a higher proportion of adults engage in rearing a second brood (Visser et al. 2003), potentially at a supplementary cost in terms of survival (Woodworth et al. 2017a). If facultative multi-brooding species (62% of studied species; Appendix S1) are synchronous in their choice to lay a second brood, their adult survival could be synchronized by the cost of reproduction. Schaub et al. (2015) demonstrated that the probability of double brooding was actually the most synchronous vital rates across the 9 populations of an aerial insectivorous songbird, the Barn Swallow (*Hirundo rustica*). All these lines of evidence support that the environmental conditions during the short period of reproduction could have a major incidence on year-round survival in temperate songbirds.

To assess the respective role of climate forcing during the breeding (i.e. common to all species) *vs.* non-breeding seasons (i.e. common to species wintering in the same climatic region), we tested for the dependence of survival on local temperatures and precipitations at the breeding sites during the breeding season, and on global climate indices related to conditions on the wintering grounds during the non-breeding season (the winter North Atlantic Oscillation and the summer Sahel rainfalls, see Methods). We predicted that, if climate exerts forcing on adult mortality during the breeding season, survival probability variations should be synchronous to some extent across species. These synchronous peaks of mortality or high survival should depend on spring weather conditions. On the other hand, if climate forcing operates mainly during the ‘harsh’ season (winter), survival variations should be synchronous among species sharing the same migratory behavior (but not across all species), and should depend on yearly fluctuations in winter harshness indices.

METHODS

Study site and species

Mark-recapture data were collected by volunteer bird ringers under the French Constant-ringing-Effort-Site (CES) banding scheme (Julliard and Jiguet 2002) over the period 2001–2016, with the goal of estimating annual local survival and recapture probabilities. We consider “local survival”, rather than “true survival”, as our data cannot distinguish between mortality and permanent emigration. At each CES site, the local bird community is sampled 3.17 ± 1.06 SD times per breeding season (first session in May 21 ± 15 days) and July (last session in July 4 ± 12 days), with 14 ± 7 mist nets (12-m long), spread over an area of ~ 3 hectares (4 to 5 mist nets per hectare). A capture session typically starts at dawn, and lasts until midday. For every site, the number, dates and hours of capture sessions, as well as the mist net locations, are held constant across sessions and years. Sites are monitored for an average of six ± four years. Sites are typically located in low canopy habitats such as shrub lands, open woodlands and reed beds, where birds are easily trapped with 3.5-m high mist nets. Each captured bird is marked with a metal band bearing a unique identifier, identified at the species level, aged (juvenile or adult), sexed (Svensson 1992), and released at the point of capture. All recaptures of marked individuals are recorded. To secure minimal robustness of site-level estimates, we retained only those species with at least five individuals captured, on average, per year. Juvenile mortality is highly confounded with dispersal and was not considered (Johnston et al. 2016). Overall, our mark-recapture dataset consists of 20,912 adults from 16 species, including 5,198 individuals recaptured across years at least once (see Appendix S1) and 242 sites (Fig. 1 and Appendix S10 Fig. S1), over a period of 16 years (Dehorter and CRBPO 2017).

Bayesian survival data analysis

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

We built a Bayesian formulation of the CJS model applying a Markov Chain Monte Carlo (MCMC) sampling procedure (Lahoz-Monfort et al. 2011) implemented in JAGS (Plummer 2003) called from R version 3.5.1 (R Development Core Team 2015) using the R-package R2jags version 4.2.0 (Su and Yajima 2015). We chose weakly informative priors for all parameters (Appendix S3). Details on specification of prior distributions for the parameters and satisfactory convergence criteria are provided in Appendix S3. All models accounted for the variation of local survival and recapture probabilities between sexes (effect common to all species), species and sites (see Appendix S3). We addressed only synchrony across all sites, ignoring the spatio-temporal (i.e. Site:Year random variance) and the species-specific spatio-temporal variances (i.e. Species:Site:Year random variance) in local adult survival probability. Such a full, hierarchical partitioning of variance was not achievable with the amount of mark-recapture data available within year-site-species. We report posterior modes as point estimates and 95% highest posterior density credible intervals to show estimation uncertainty.

Temporal synchrony in survival across species

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

The approach used for model 1 differs from Lahoz-Monfort et al. (2011) in that we define σ_{ε}^{2} and *ICC* common to all species, while Lahoz-Monfort et al. (2011) estimated species-specific parameters, $\sigma^2_{\varepsilon species}$ and $ICC_{species}=\frac{\sigma^2_{\delta}}{\sigma^2_{\delta}+\sigma^2_{\varepsilon species}}$. We also fitted the model corresponding to Lahoz-Monfort et al. (2011) and name it model 2. From model 2, we calculated the average of the 16 $ICC_{species}$ point estimates to compare it to the global ICC calculated from model 1. We now explain the pros and cons of model 1 and model 2.

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

On the other hand, model 1 assumes that species-specific time deviations came from a single distribution, with a variance common to all species. However, this assumption may lead to a poor fit to the data and may bias estimates when sample sizes vary among species. Model 2 relaxes the assumption and provides a sanity check: if the estimation of synchrony in model 1 is robust to the assumption of common distribution, then most species-specific $ICC_{species}$ in model 2 should be in the range of values, and the average of $ICC_{species}$ should be similar to the ICC estimated in model 1.

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

Yearly weather covariates (models 3 and 4)

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

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

Following Nakagawa and Schielzeth (2013) we estimated the synchronous variance explained by spring weather (σ^2_{sw}) as the variance in partial model predictions (that is, the linear combination of the products of each parameter estimate by the corresponding weather variable): $\sigma^2_{sw} = var\left(\sum_{h=1}^{8} \beta_h \bar{x}_{ht}\right)$where *h* indexes the eight model parameters related to spring weather, β_h is the parameter estimate for the effect of *h*, and $\underline{x}_{ht}$ is the mean value of the weather variable *h* on year *t* (across all sites). By definition σ^2_{sw}captures only synchronous variation. Therefore we calculated the proportion of synchronous variation related by spring weather as $\frac{\sigma^2_{sw}}{\sigma^2_{\delta} + \sigma^2_{sw}}$, and the new $ICC = \frac{\sigma^2_{sw} + \sigma^2_{\delta}}{\sigma^2_{sw} + \sigma^2_{\delta} + \sigma^2_{\varepsilon}}$. As always, calculations were integrated over the model posterior distribution to propagate uncertainty.

In Model 4, we added covariates related to winter weather to Model 1. For resident and short-distance migrants, that winter in western Europe or North-Africa, we used the North Atlantic Oscillation during winter (wNAO, averaged from December to March, available at http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm). The wNAO captures broad scale weather variation in Western Europe and North Africa (Forchhammer & Post 2004), which explains variations in over-winter survival in several European bird species (Robinson et al. 2007, Salewski et al. 2013). For long-distance migrants that winter in Western Africa, we used the Sahel Rainfall during summer (sSR, averaged from July to September, available at http://research.jisao.washington.edu/data_sets/sahel/). The sSR is often used as an proxy of winter Sahel suitability for wintering songbirds,considering that habitat quality in December–February is driven by rainfall during the previous summer (Robinson et al. 2007, Salewski et al. 2013). As done for spring weather covariates, we fitted linear and quadratic effects for wNAO and sSR. We estimated the synchronous variance explained by winter weather (σ^2_{ww}) as the variance in partial model predictions from the linear and quadratic effects of wNAO and sSR, $\sigma^2_{ww}=var\left(p\left(\beta_{sSR}\,sSR+\beta_{sSR2}\,sSR^2\right)+\left(1-p\right)\left(\beta_{wNAO}\,wNAO+\beta_{wNAO2}\,wNAO^2\right)\right)$ where p is the proportion of long-distance migratory species. This variance captures the weighed synchronous variance among migratory species due to sSR, added to the weighed synchronous variance among resident species due to wNAO, minus the asynchronous variance due to the small negative covariance between sSR and wNAO (the two indices are expected to be independent, but the empirical correlation was -0.12 [-0.58;0.40], p-value=0.66). The proportion of synchronous variance related to winter weather was calculated as $\frac{\sigma^2_{ww}}{\sigma^2_{\delta}+\sigma^2_{sw}}$, and the $ICC=\frac{\sigma^2_{ww}+\sigma^2_{\delta}}{\sigma^2_{ww}+\sigma^2_{\delta}+\sigma^2_{\varepsilon}}$.

Migratory strategy (model 5)

Because of shared wintering conditions among species, migratory strategy could reduce the overall synchrony in annual survival. To quantify the importance of this effect, we fitted Model 5, a variation of Model 1 with a random effect for the interaction Year-by-Migratory behavior (sixteen times two levels, resident or short-distance migrants vs. long-distance migrants). We thus modeled a Migratory-class-by-Year variance σ_m^2, while σ_δ^2 remained the Year-variance common to migratory classes and species, and $\sigma_{\varepsilon w}^2$was the within migratory-class species-specific year variance. The proportion of species-specific variance that depended on migratory-class (i.e. asynchrony between migratory class among species) was estimated as $\frac{\sigma_m^2}{\sigma_m^2+\sigma_{\varepsilon w}^2}$. This index will approach 1 if migratory strategy explains most of the asynchronous variation. The synchrony within migratory-class was estimated as $\frac{\sigma_\delta^2}{\sigma_\delta^2+\sigma_{\varepsilon w}^2}$. If migratory strategy explains most of the asynchronous variation, this index will approach 1, whereas if migratory strategy explains no asynchronous variation, this index will approach the ICC value calculated from model 1.

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

RESULTS

Cross-species temporal synchrony of annual adult local survival

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

Species showed considerable variation in $ICC_{species}$ (Fig. 3), although estimates came with broad credible intervals. Using linear regression integrated over the posterior distribution of $ICC_{species}$, there was no significant association between the value of $ICC_{species}$ and migratory type (Fig. 3; pMCMC=0.48) nor with species sample size (pMCMC=0.31). More qualitatively, we also did not see any pattern linking the values of $ICC_{species}$ and the species characteristics. The mean of the 16 point estimates for $ICC_{species}$ was 76%.

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

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

Contributions of weather effects to survival probability synchrony

According to Model 3, spring weather variables taken together explained only 1.4% [0.01–5.5] of synchrony, whereas according to Model 4, the winter weather variables explained 12% [0.3–37] of the synchrony. Assuming independence of spring and winter weather variables, they explain 13% [0.8–39] of synchrony together (and explain 10% [0.6–23] of the total temporal variance, Table 1). There was no clear evidence for an effect of any of the weather-related parameters on survival probability with all credible intervals overlapping zero (across all species, i.e. additive effects; Appendix S8: Table S1). Higher spring precipitation and more extreme spring temperatures tended to increase survival probability (Appendix S8: Fig. S1). For winter weather covariates, survival probability appeared a bit higher for high sSR values, while there was no discernible effect of wNAO (across all species, i.e. additive effects; Appendix S8: Fig. S2).

Contributions of migratory strategy to survival probability synchrony

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

DISCUSSION

Unexpectedly, annual fluctuations in adult local survival proved to be largely (and robustly, Appendices S4, S5, S6) synchronous across the 16 songbird species that dominate bird communities in France: 73% [47–94] of between-year variance in survival probability was common to all species. This result is all the more remarkable given that these species differ in various life-history traits that concern local survival: they cover the range of songbird migratory behavior, body mass (8 to 88 g) and number of broods per year, and they partly differ in habitat use (terrestrial and humid shrub lands) and specialization (Appendix S1). Moreover, our estimates represent 'minimal synchrony' since they are not controlled for potentially desynchronizing factors, like intra- and inter-specific negative density dependence, that is, estimated synchrony should be higher if we could control for those factors (Péron and Koons 2012, Swallow et al. 2016). This value of synchrony is as high as for spatial synchrony in local survival probability across populations of a same species (67% and 71% in two long-lived birds, Jenouvrier et al. 2009, Grosbois et al. 2009), and higher than survival synchrony observed across two syntopic ducks (49%, Péron and Koons 2012). Short-lived organisms (Appendix S1) are under stronger environment-dependence than long-lived species (Saether et al. 2016), which may contribute to the observed high inter-specific synchrony in the studied set of species. The species-specific synchronies ($ICC_{species}$) varied from very high to low (Figure 4). This means that some species (such as *Cettia cetti*) had considerable species-specific temporal variability in adult survival, probably due to its high sensitivity to winter harshness (Moussus 2010), whereas in others (such as *Sylvia atricapilla*) the temporal variability in adult survival corresponded almost entirely to the average variability across the 16 species. Morrisson et al. 2022 also reported a wide range of species-specific synchronies, although our estimates were generally a bit higher, with no point estimate below 0.1 (vs. a minimu of 0.03), a majority of species above 0.5 (vs. 22 out of 26 species below 0.5) and several very close to 1 (vs. only 2 above 0.8). These differences may be explained by the broader geographic range of sites in Morrisson et al. 2022, spanning 8 European countries. We did not find clear patterns explaining differences in synchrony among species (i.e., migration type, sample size, habitat), and species-specific synchronies were estimated with broad confidence intervals. Therefore the determinants of species synchrony with the rest of the community remain to be identified with a larger dataset, involving more species (i.e. more diversity in life history traits) and more years. We can conclude that, at a country scale, the drivers of annual variations of average adult apparent survival probability are largely common to many species. Drivers that actually differ between species and determine local population dynamics must occur and operate at site or regional level (Giraud et al. 2013, Gaüzère et al. 2015, Cayuela et al. 2019, Morrison et al. 2013, 2021).

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

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

What other mechanisms than direct climate forcing could synchronize annual adult local survival across species? First, environmentally-driven, community-level density-dependency of adult survival probability could also generate cross-species synchrony. To rear their offspring, common songbird species rely on very similar preys (larvae and soft invertebrates). The hotter the year, the higher bird productivity (i.e. juvenile production per adult) for most of these same species (Eglington et al. 2015, Dubos et al. 2019). Hence, intra- and interspecific competition for shared resources is likely to operate at local community-level in common songbirds, potentially resulting in large-scale, weather-driven density-dependent regulations of adult survival. But intraspecific density-dependence can also be a source of asynchrony across species (Péron and Koons 2012, Martin et al. 2017). The actual role of community-level density-dependence at synchronizing adult survival probability across species remains to be properly investigated (Swallow et al. 2016). Second, breeding dispersal could contribute to cross-species synchrony in adult local survival (also named apparent survival). Local survival results from survival and residency (i.e. absence of dispersal, Saracco et al. 2010) at the scale of study sites. If individuals of different species tend to synchronously disperse more in some years than in others, then dispersal-induced fluctuations in adult local survival would be synchronous across species at national level. Following bad reproductive experience at one location (e.g., weather-driven early reproductive failure), a higher proportion of adults settle away in the following year (e.g., Arlt & Part 2008). However, synchronous breeding dispersal seems unlikely to induce such a high synchrony in adult local survival because adults are typically reported to disperse in low proportion (1–10% order of magnitude) between breeding events, even in long-distance migrants (Greenwood and Harvey 1982). Moreover, males, the sex that dominates in our dataset (64%), are the most resident sex in birds (Amrhein et al. 2012).

Could conditions during the non-breeding season explain the high synchrony in adult survival across songbirds in France? Across both long-distance migrants, short-distance migrants and residents, we found that winter conditions explained 9% [0.2-27] of the variation in annual survival (12% [0.3–37] of the synchrony). This proportion is relatively weak, but potentially significant biologically, and as already explained it is likely that we underestimate the synchronizing importance of weather. Winter harshness is commonly proposed to explain a large proportion of year-round mortality in small organisms like songbirds (Grosbois et al. 2006, Robinson et al. 2007, Salewski et al. 2013, Johnston et al. 2016, Saether et al. 2016), including in migratory songbirds (Robinson et al. 2007, Woodworth et al. 2017b). Recent studies on multispecies population synchrony have also emphasized a major role of winter climate forcing, but these few studies were biased towards cold-driven ecosystems, like high latitude (>45°) populations that are subject to extreme winter events (Post & Forchhammer 2004, Jones *et al.* 2003, rain-on-snow icing events in Hansen et al. 2013, Pomara & Zuckerberg 2017). Restricting the analysis to long-distance migrant species only, Telenský et al (2020) found that water availability on the wintering grounds explained 15% of the variation in temporal survival but the result was statistically non-significant. Overall, it seems likely that conditions on the non-breeding grounds, especially climate, contribute somewhat to the synchrony in adult survival, even though the 16 studied species spread from France to Central Africa during the winter. This conclusion has profound implications for conservation planning for common habitats: breeding habitat degradation is a major cause of ongoing massive, synchronous population declines (Eglington and Pearce-Higgins 2012, including in migratory species (Morrison et al. 2013). Ecosystem functionality over breeding areas should be the primary focus of conservation in western countries with highly degraded habitats (Morrison et al. 2013), not waiting for other countries along the migratory flyways or at wintering grounds to take actions to improve environmental conditions for migratory birds (Morrison et al. 2013).

Differences in migratory strategy explained very little temporal variation in survival probability. Instead, synchrony within migratory strategy was similar to synchrony across migratory strategies (Table 1: Model 5). Although they did not explicitly quantify synchrony, this result is qualitatively supported by Morrisson et al. (2021) who found a positive covariation between the survival of resident species and that of long-distance migrant species, at least those spending winter in humid areas. Resident and long-distance migrants winter on two different continents (at a distance of 2000–3000 km and 35–45° apart in latitude) in which variation in environmental conditions are unlikely to be correlated.

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

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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]

Notes: 1. Intra-class correlations (see Methods) are estimates of synchrony across species, i.e., the proportion of Year variance over ‘total’ temporal variance, which varies across models. 2. Weather variables were introduced as fixed effects and the variance they explain was computed post-hoc, while all other variance components were directly estimated as random effects. 3. The sum of the variances is expected to be constant, but may vary a bit due to rounding, and because survival is not directly observed but predicted as a latent variable (i.e., survival does not have a defined variance observable independently of a model).

Figure legend

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

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

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

Figure 1

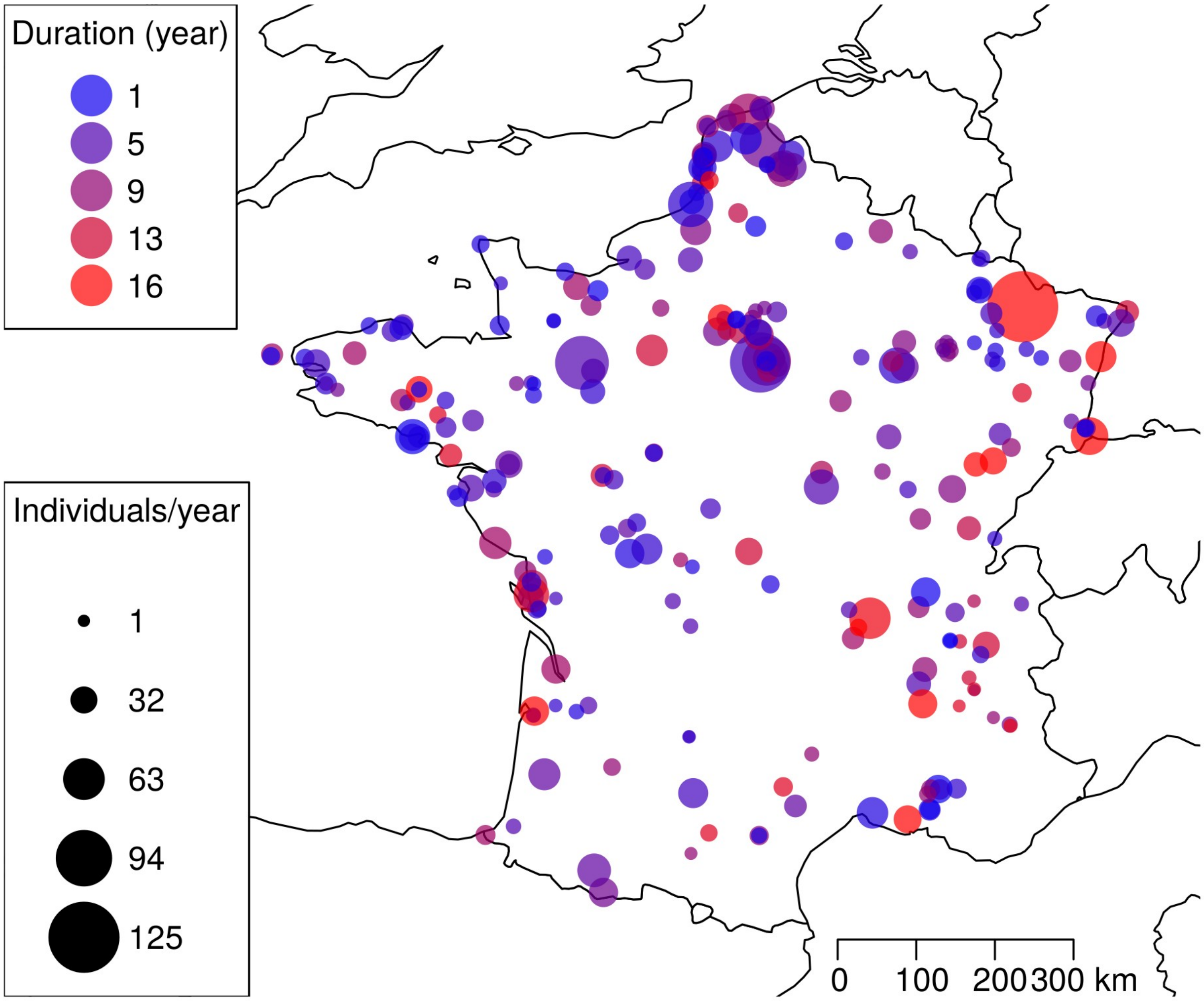

Duration (year)
1
5
9
13
16
Individuals/year
1
32
63
94
125
0
100
200
300 km

Figure 2

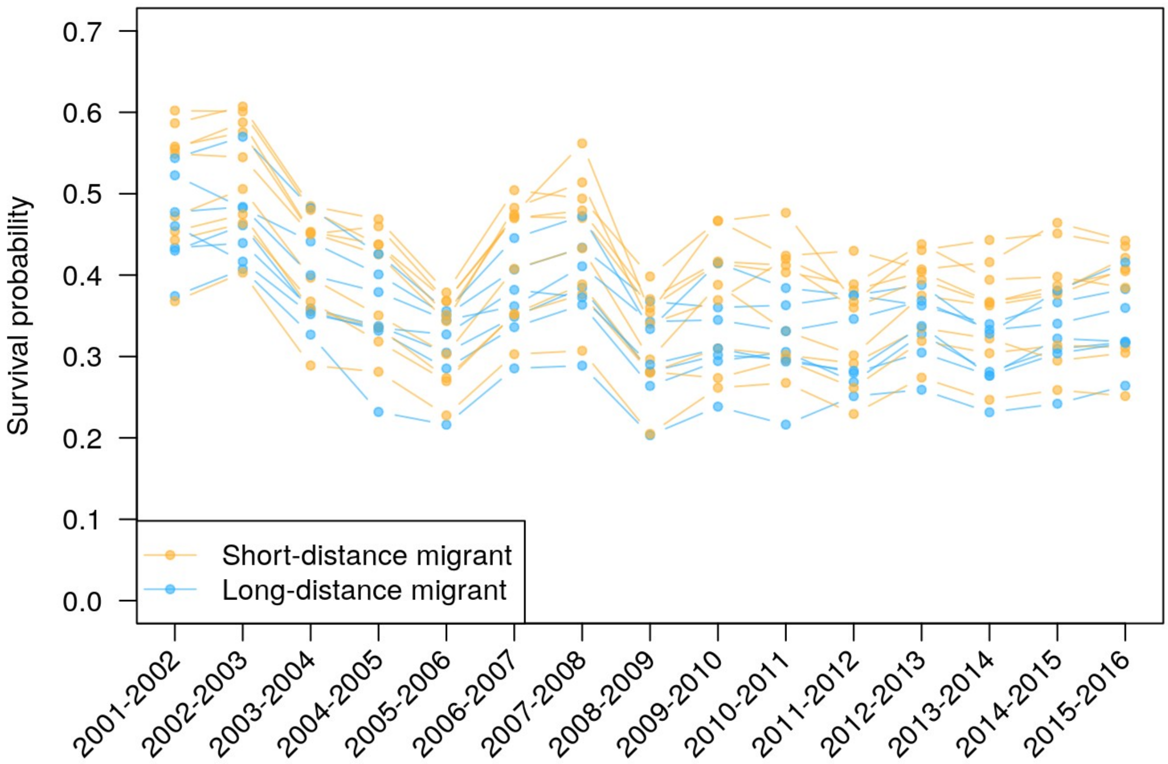
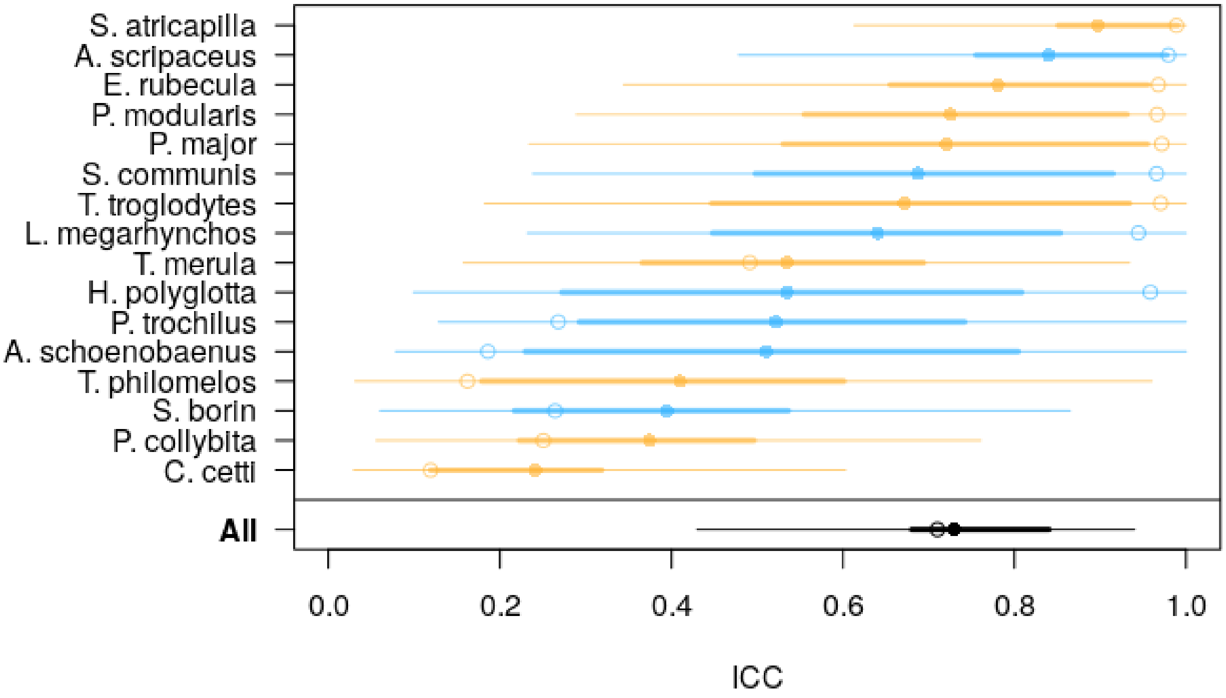


Figure 3


S. atricapilla
A. scripaceus
E. rubecula
P. modularis
P. major
S. communis
T. troglodytes
L. megarhynchos
T. merula
H. polyglotta
P. trochilus
A. schoenobaenus
T. philomelos
S. borin
P. collybita
C. cetti
All
0.0
0.2
0.4
0.6
0.8
1.0
ICC