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Reassessment of French breeding bird population sizes using citizen science and accounting for species detectability

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24 **ABSTRACT**

25 Higher efficiency in large-scale and long-term biodiversity monitoring can be obtained
26 through the use of Essential Biodiversity Variables, among which species population sizes
27 provide key data for conservation programs. Relevant estimations and assessment of actual
28 population sizes are critical for species conservation, especially in the current context of
29 global biodiversity erosion. However, knowledge on population size varies greatly,
30 depending on species conservation status and ranges. While the most threatened or
31 restricted-range species generally benefit from exhaustive counts and surveys, monitoring
32 common and widespread species population size tends to be neglected or is simply more
33 challenging to achieve. In such a context, citizen science (CS) is a powerful tool for the long-
34 term monitoring of common species through the engagement of various volunteers,
35 permitting data acquisition on the long term and over large spatial scales. Despite this
36 substantially increased sampling effort, detectability issues imply that even common
37 species may remain unnoticed at suitable sites. The use of structured CS schemes, including
38 repeated visits, enables to model the detection process, permitting reliable inferences of
39 population size estimates. Here, we relied on a large French structured CS scheme (EPOC-
40 ODF) comprising 27 156 complete checklists over 3 873 sites collected during the 2021-2023
41 breeding seasons to estimate the population size of 63 common bird species using
42 Hierarchical Distance Sampling (HDS). These population size estimates were compared to
43 the previous expert-based French breeding bird atlas estimations, which did not account
44 for detectability issues. We found that population size estimates from the former French
45 breeding bird atlas were lower than those estimated using HDS for 65% of species. Such a
46 prevalence of lower estimations is likely due to more conservative estimates inferred from
47 semi-quantitative expert-based assessments used for the previous atlas. We also found
48 that species with long-range songs such as the Common Cuckoo (*Cuculus canorus*), Eurasian
49 Hoopoe (*Upupa epops*) or the Eurasian Blackbird (*Turdus merula*) had, in contrast, higher
50 estimated population sizes in the previous atlas than in our HDS models. Our study
51 highlights the need to rely on sound statistical methodology to ensure reliable ecological
52 inferences with adequate uncertainty estimation and advocates for a higher reliance on
53 structured CS in support of long-term biodiversity monitoring.

54
55 **Keywords:** Bird atlases ; Biogeography ; Breeding Bird Surveys ; Citizen Science ;
56 Detectability ; Hierarchical Distance Sampling

Worldwide bird populations are nowadays caught in the midst of a global, man-driven erosion of biodiversity caused by the synergistic effects of habitat destruction and fragmentation, resource overexploitation, climate change, pollution, pesticide use as well as the global spread of invasive species (Ceballos et al., 2015; Johnson et al., 2017). In Europe, the intensification of agriculture crystallises this phenomenon because the ever-increased use of pesticides and fertilisers has been pointed out as the main driver of current bird population declines (Rigal et al., 2023). Recent researches have pointed out how important species-specific life attributes (e.g., species range and density) and functional traits (e.g., body mass, diet or dispersal) explain long-term bird trends and responses to global changes (Hong et al., 2023; Santini et al., 2023; Germain et al., 2023). Monitoring long-term as well as shorter-term trends have been historically possible through standardised biodiversity - including bird - surveys at a national scale and aggregated at the continental one (Jiguet et al., 2012; Pilotto et al., 2020; Brlík et al., 2021). This monitoring produces comprehensive distribution atlases pointing out current ranges and their historical changes (Keller et al., 2020), as well as long-term population trends (Brlík et al., 2021). Identifying common species declines in the long-term should be accounted for in agricultural and planning policies (Gaston & Fuller, 2008; Rigal et al., 2023) to help reconciling society's needs with the safeguarding of ordinary biodiversity (Couvét & Ducarme, 2014).

Monitoring the success of the implementation of such policies is possible through the measurement of Essential Biodiversity Variables (Jetz et al., 2019; Navarro et al., 2017; Pereira et al., 2013), including the assessment of species distribution range and population abundance or density (Santini et al., 2023). Global monitoring capabilities of species populations have increased over the past few decades as citizen science (CS) has gained prominence across various domains, particularly in ecology (Kullenberg & Kasperowski, 2016). This participatory approach has provided the public with unprecedented opportunities to contribute to biodiversity monitoring through data collection and indirectly through their engagement in policy evaluation (McKinley et al., 2017). The development of CS can be related to the emergence of multiple online databases (Newman et al., 2012) capable of gathering comprehensive datasets across large spatial scales and multiple taxa such as iNaturalist (www.inaturalist.org) and BioloVision (data.bioloVISION.net) or taxa-centred, for instance, eBird (www.ebird.org). The emergence of CS databases has thus resulted in an exponential increase in biodiversity monitoring capabilities, ranging from phenological shifts (Hurlbert & Liang, 2012), species distribution (Suzuki-Ohno et al., 2017; Matutini et al., 2021) and abundance estimation (Callaghan et al., 2021).

Traditionally, species autecology was recensed in atlases providing temporal snapshots of known distribution and population size estimates using discontinuously gathered data collected during a short period (Donald and Fuller, 1998) and allowing long-term changes assessment when repeated over decades (Keller et al., 2020). The first attempt of French avifauna compilation dates back to 1936 (Mayaud et al., 1936) while the first national atlas was published in 1976 (Yeatman et al., 1976) followed by subsequent in

93 1995 (Yeatman-Berthelot & Jarry, 1995) and 2015 (Issa & Muller, 2015). Each iteration was marked by a
94 significant increase in participating citizen birders, ranging from 500 to 2400 to 10,000. However, while the
95 ultimate aim of bird atlases is to acquire even knowledge across multiple species for a given geographical
96 area (typically national-wide inquiries), it is essential to note that rare and threatened species benefit from
97 more in-depth population monitoring than more frequent and abundant ones (Ingram et al., 2021). Such
98 exhaustive knowledge of rare species populations is due to interest risen by high extinction risk (IUCN,
99 2001), the need for recovery plans (Farrier et al., 2007) and narrow distributions allowing exhaustive counts
100 (Quaintenne et al., 2020). In contrast, common species (being altogether abundant, widespread;
101 Rabinowitz, 1981) are considered Least Concern (LC). They consequently tend to receive lesser attention
102 than rarer species (Neeson et al., 2018) despite being key components of global avian biomass changes
103 (Gaston & Fuller, 2008; Inger et al., 2015; Whelan et al., 2015; Rigal et al., 2023).

104 The principal cause of low quantitative coverage of common birds can be tied to the lack of specific
105 funding stemming from a conservation prioritisation approach (Brooks et al., 2006; Meine et al., 2006) and
106 the trade-off between data quality and data acquisition over large spatial scales (Devictor et al., 2010;
107 Kamp et al., 2016). In France, this incomplete knowledge translates into a significant drop in quality for
108 population size estimates of most common bird species, where 60% of breeding species population
109 estimates are qualified as medium (*i.e.* state of knowledge of species abundance considered more or less
110 satisfying, but semi-quantitative data are either lacking or outdated, see Comolet-Tirman et al., 2015) while
111 for rare and localised species (24% of species), estimates are considered as highly reliable (Comolet-Tirman
112 et al., 2022). To account for this discrepancy, a semi-quantitative estimation method was used for the last
113 atlas survey, with population sizes simply inferred from the average number of breeding pairs measured
114 over 10x10km grid cells using abundance classes of 1-9, 10-99, 100-999, 1000-6666 (the last upper limit
115 could vary according to knowledge about species densities) multiplied by the number of grid cells known
116 for nesting. Population sizes estimated using this method correspond to lower and upper limits. Lower
117 limits were obtained by calculating the geometric mean of the abundance classes weighted by the number
118 of 10x10 grid cells belonging to these abundance classes while upper limits were obtained by using the
119 arithmetic means (see Roché et al., 2013 method referred further as *ArGeom*).

120 However, similarly to other studies (Kellner & Swihart, 2014), this approach fails to account for species
121 detectability p defined as the probability of detecting at least one individual of a given species in a particular
122 sampling effort, given that individuals of that species are present in the area of interest during the sampling
123 session (Boulinier et al., 1998). Numerous studies have previously shown that p varies with time of day and
124 season (Skirvin, 1981), observers (Quinn et al., 2011) and year-specific factors (Kéry & Schmid, 2004).
125 Omitting species detectability by assuming perfect or constant p across sampling schemes, observers and
126 habitat types can lead to biased inferences (Nichols et al., 2009; Kéry, 2011) and affect the estimation of
127 long-term trends due to its unaddressed variation (Schmidt et al., 2013; Sanz-Pérez et al., 2020).

128 Here, we propose an estimation method enabling a more robust approach of population size
129 estimations. We provide associated uncertainty intervals built upon a revised structured sampling scheme,
130 ensuring data traceability and allowing inferences in the spatial variation of species abundance by formally
131 including the detection process within the modelling framework.

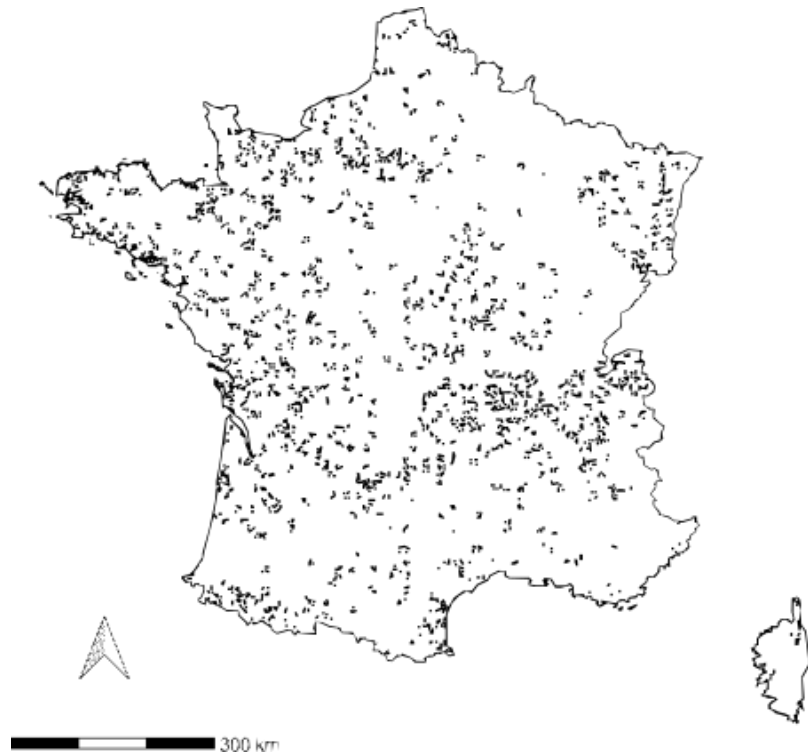
132 In this study, we aimed at testing whether applying this modelling framework on an unprecedentedly
133 large citizen-based dataset collected over France would (i) provide a new quantitative evaluation of French
134 breeding bird populations and (ii) allow a comparison of population sizes inferred through Hierarchical
135 Distance sampling from those inferred using the previous atlas methodology *ArGeom* across a large part of
136 French avifauna. In particular, we expect that quantifying the influence of species detectability would allow
137 more relevant ecological inferences (e.g., including environmental and sampling effort covariates to the
138 models) to approach closer to a realistic estimation of breeding bird population size at a national level than
139 previously used methodologies.

140 **Materials and methods**

141 **Sampling protocol**

142 EPOC-ODF (French structured estimation of breeding bird population size) is a French CS monitoring
143 scheme based upon 5-minute point counts, where observers are tasked to point locations of recorded
144 individuals, either through visual or auditory detection. Birders can register their field observations directly
145 using the NaturaList smartphone application or transcript later on the data portal Faune-France
146 (www.faune-france.org). The survey locations corresponded to the centroids of a 2x2km grid, selected
147 from a random sampling. Each location has to be visited three times during the breeding season, from
148 March to June, each consisting of three successive 5-minute point counts, to limit chances of duplicated
149 counts while being less demanding in observation effort (Fuller & Langslow, 1984). After completion, *i.e.*
150 nine visits during a breeding season, surveyed sites are removed from the sampling pool for the subsequent
151 year, to maximise the number of sites surveyed. See Appendix S1 for more details about the sampling
152 design.

153 Over the 2021 and 2023 breeding seasons, 276 distinct species were encountered over 27 156 complete
154 checklists collected over 3 873 pre-selected locations (Fig 1) by 520 observers. Sampling effort is monitored
155 through local associations tasked to recruit volunteers. The primary focus of the scheme being the
156 monitoring of common breeding bird species, we decided to constrain the number of species considered
157 viable targets of this scheme to 103 out of the 276 species contacted. We narrowed our study to 63 species
158 out of the initial set of 103, comprising only those recorded at a minimum of 150 distinct locations (3.9%
159 of total locations), to have a sample size allowing to reach model convergence. We also applied a temporal
160 filter that considered both observed activity during the breeding season and expert opinion to capture the
161 breeding phenology of each targeted species and exclude possible early or late migrants from population
162 size estimates (see Appendix S2.1).



163

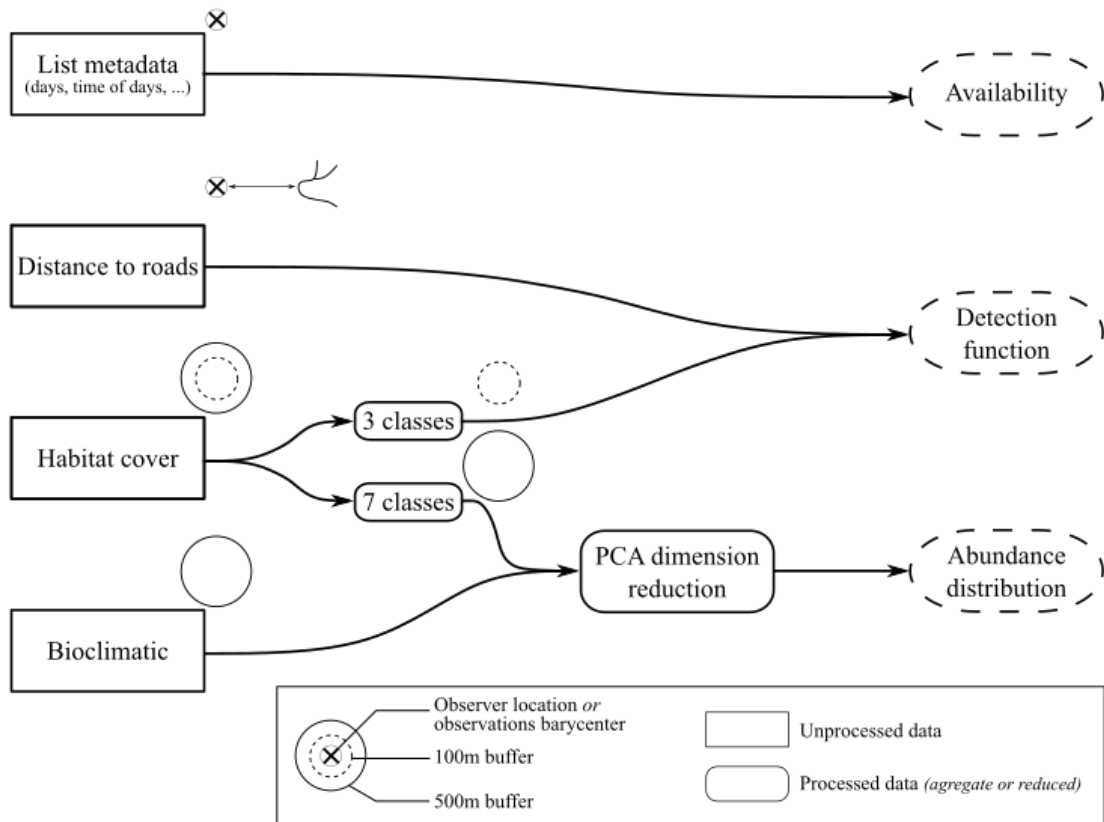
164 **Figure 1** - Spatial distribution of surveyed EPOC-ODF locations (n = 3 505) over 2021-2023 breeding seasons.

165 **PCA reduction of environmental covariates**

166 For bioclimatic data, we used 19 variables from WorldClim at 1km resolution (Fick & Hijmans, 2017),
 167 on which we applied a Principal Component Analysis (PCA), keeping the first three axes (82.3% of explained
 168 variance), to limit multicollinearity through orthogonal transformation (Cruz-Cárdenas et al., 2014).

169 We used habitat cover data from Theia OSO at 10m resolution (Thierion et al., 2022) and aggregated it
 170 according to two different scales: (1) a seven-class corresponding to habitat type (Urban, Annual crops,
 171 Perennial crops, Pastures, Grasslands, Forests, Water body/Mineral surfaces) and (2) three-class (Open,
 172 Forests, and Artificial) in regards to overall effect on detectability (fig 2). Additionally, we conducted PCA
 173 dimension reduction on the seven-class aggregation, retaining three of the six PCA (54.71% of explained
 174 variance) axes depicting environmental gradients for (i) forest-to-open-field cultures; (ii) open-field
 175 cultures-to-pastures and (iii) perennial crop-to-urban Appendix S3 for the workflow pipeline and habitat
 176 cover aggregation. Distances to roads were measured from ROUTE 500 (Cote et al., 2021). Environmental
 177 covariates were extracted over a 500m buffer radii upon registered observer location (fig 2). These
 178 distances were chosen according to mean dispersal distances and home range sizes in common European
 179 birds (Paradis et al., 1998). The three-class habitat covers were collected upon 100m circles radii to assess
 180 immediate habitat types that could hinder species detection. Whenever the exact location was unavailable,
 181 we used the centroid of sightings as a proxy for observer location (Appendix S4). We used environmental
 182 data collected from a prediction grid covering France at a resolution of 2x2km for PCA dimension reduction.

183 Outcomes from this initial PCA were used to transform environmental data collected from surveyed
 184 locations through PCA projections.



185

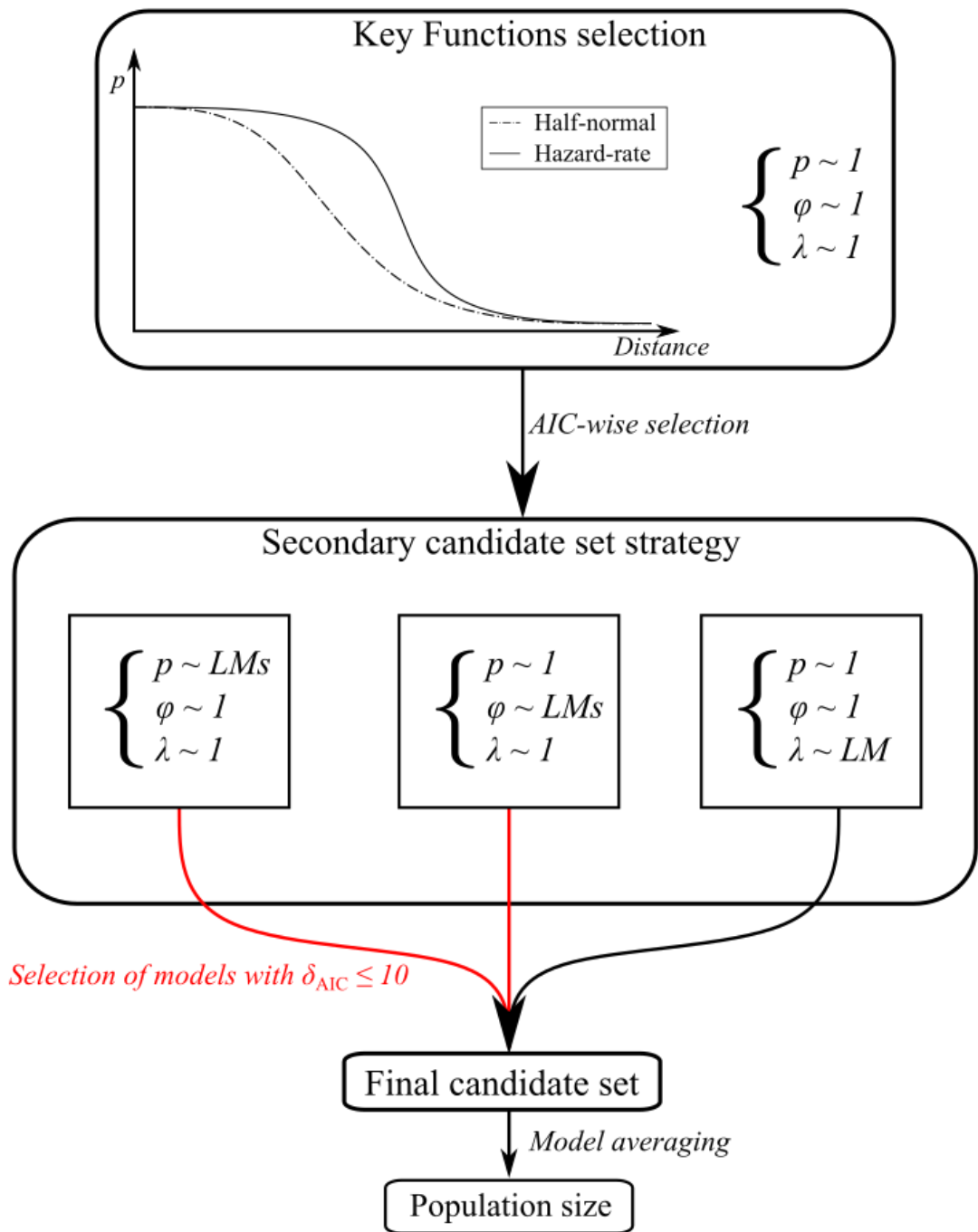
186 **Figure 2** - Global overview of covariates acquisition, treatments and usage workflow. Data are retrieved over
 187 observers' GPS location or approximated using observations barycenter, when unavailable, over two
 188 resolutions, 100m buffer (dotted circles) and 500m buffer radii (solid circles). Distance to roads is
 189 determined by measuring the distance between the nearest road to the observer location or observation
 190 barycenter. Habitat cover, in percentage, is aggregate over seven and three classes (see Table S3.1). Seven-
 191 class habitat cover and bioclimatic are reduced from PCA keeping the first three dimensions for bioclimatic
 192 data and three selected for the seven-class habitat cover.

193 **Modelling framework**

194 We used Hierarchical Distance Sampling (HDS) models to estimate the abundance of the target species
 195 while accounting for uncertainty arising from the observation process (Chandler et al., 2011; Kéry & Royle,
 196 2015). We applied a right-side truncation of 5%, removing observation distances above the 95% quantile,
 197 for each targeted species to remove extreme distance values for model robustness (Buckland et al., 2001).
 198 Then, we divided observation distances into five proportional bin classes based on the maximal observed
 199 distance. Models calibration and assessment were done using unmarked 1.2.5 R package (Fiske & Chandler,
 200 2011). Effort covariates were accounted for by incorporating the Julian date and the hours of list realisation
 201 (as minutes from sunrise), see Table 1.

202 Distance sampling key functions, depicting detection probabilities fall-off given distance of observation
 203 (Buckland et al., 2001), were chosen between half-normal and hazard-rate based on AIC (Akaike
 204 Information Criterion, Akaike, 1974), with other states kept constant.

205 We based our modelling framework on a secondary candidate set strategy (fig 3), where the detection
 206 and availability states of our HDS were fit according to the set of the first candidates while others were
 207 kept constant (Morin et al., 2020). For the Poisson process underlying abundance distribution, we used a
 208 single model consisting of retained covariate PCAs axes (Table 1). See Appendix Table S5.1 for the number
 209 of times where each sub-process was included in the final candidate sets.



211 **Figure 3** - Methodological framework for population size estimation. At first, a key function is determined
 212 AIC-wise between half-normal and hazard-rate with other components of the HDS kept constant. The
 213 selected key function is then used during the secondary candidate set strategy (Morin et al., 2020), fitting
 214 multiple sub-models (Table 1) for each state separately holding others constant. Sub-models with greatest
 215 support, $AIC \leq 10$ are then selected in a final candidate set consisting of multiple HDS through combinatorial
 216 association (Morin et al., 2020). At this stage, we used sub-models estimated coefficients as starting values
 217 to help model convergence. Population size estimates are obtained through model averaging of the final
 218 candidate set. *LM* : *Linear Model*

219

220 **Table 1** - Ensemble of sub-models tested in the secondary candidate set approach (Morin et al.,
 221 2020). (*) For the hour effort covariate, we used minutes from sunrise estimated from site longitude,
 222 latitude and date of list completion.

States	Sub-models
Detection	~ Distance to roads
	~ Distance to roads + Proportion of artificial lands (100m)
	~ Distance to roads + Proportion of open lands (100m)
	~ Distance to roads + Proportion of forests (100m)
Availability	~ Julian date
	~ Julian date + Julian date ²
	~ Hour (*)
	~ Hour + Hour ²
	~ Julian date + Hour
	~ Julian date + Julian date ² + Hour
	~ Julian date + Hour + Hour ²
	~ Julian date + Julian date ² + Hour + Hour ²
Abundance	~ 3 Bioclimatics PCA axis + 3 Habitat cover PCA axis

223

224 HDS population size estimates were obtained by averaging retained secondary candidate sets models,
225 based on their relative model performance using AICc (Fig 3). We excluded the Eurasian Sparrowhawk
226 (*Accipiter nisus*), the Meadow Pipit (*Anthus pratensis*) and the Coal tit (*Periparus ater*), from model
227 averaging and exclusively relied upon prediction from best final models owing to substantial differences
228 observed among their secondary candidate sets models.

229 Model goodness-of-fit was assessed using an overdispersion coefficient metric (\hat{C} ; Johnson et al., 2010).
230 We used the chi-square metric as the discrepancy measure between observed and expected counts.
231 Computed \hat{C} corresponds to the ratio between the chi-square obtained from the fitted model to the mean
232 of bootstrapped chi-squares obtained from simulated datasets based upon estimated parameters (Kéry &
233 Royle, 2015). All models were fit according to a Poisson (P) distribution after top model assessment and
234 calculation of \hat{C} , secondary candidate sets with \hat{C} top models exceeding 1.2 were calibrated using a
235 Negative binomial (NB) distribution (Payne et al., 2018). For a global overview of our modelling approach,
236 see Appendix S5. Out of 63 species, we excluded nine species from the analysis; three exhibited signs of
237 underdispersion with \hat{C} values less than 0.9 while six had \hat{C} values exceeding 1.5 (Payne et al., 2018),
238 showing signs of overdispersion, despite being calibrated using a negative binomial distribution, see table
239 S2.1 for more details.

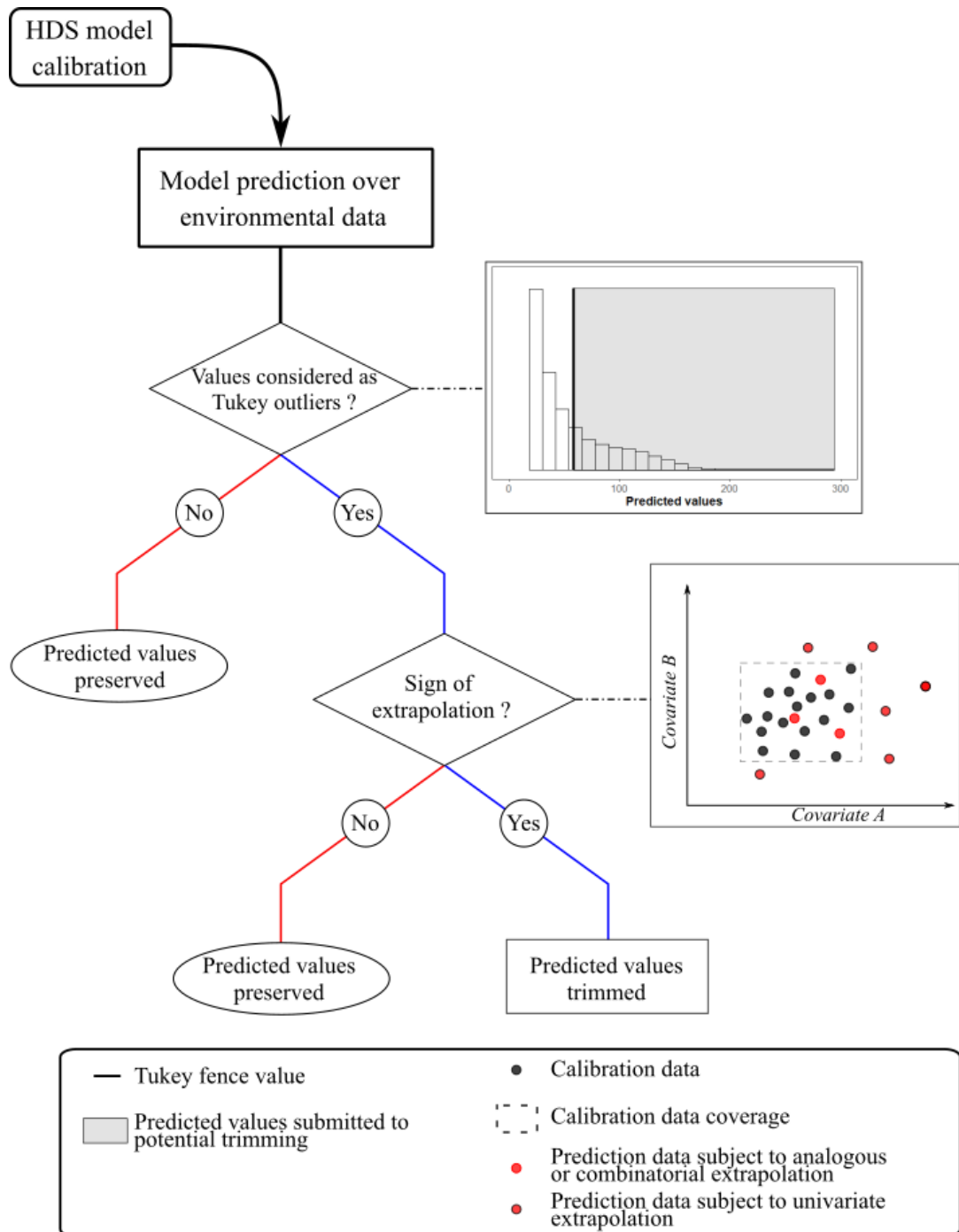
240 We assessed the robustness of our estimations to the exclusion of one year of data, corresponding to
241 a third of the global dataset. We compared population size estimates from EPOC-ODF data collected over
242 2021-2023 to estimates obtained from EPOC-ODF data collected over 2021-2022. Using the 2021-2022
243 subset, we estimated the population sizes of 30 species, detected in at least 150 distinct sites. From these
244 30 species, seven mean population sizes estimated using 2021 to 2023 data were outside the confidence
245 intervals estimated from 2021 to 2022 data, with a slightly smaller population size estimated (Table S2.2)
246 overall highlighting robust estimations.

247 **Trimming of HDS population size estimate: assessment of model extrapolation**

248 Population sizes were obtained by summing predicted values over the prediction grid. As we intend to
249 predict over a large surface, novel environmental conditions may arise, leading to possible dissimilarities
250 between the environmental gradient collected at survey sites and the environmental gradient over novel
251 conditions (Elith & Leathwick, 2009). Mesgaran et al., 2014 described two types of extrapolation; (i) Novelty
252 type I (NT1) where projected points (*i.e* prediction grid) are outside the range of individual covariates
253 collected by the sampling scheme and (ii) Novelty type II (NT2) depicting the case when projected points
254 are within univariate range but constitute novel combinations between covariates.

255 We trimmed predicted values (Fig 4) over prediction grid cells showing signs of NT1 extrapolation, to a
256 threshold value determined using a Tukey fence (Tukey, 1977), estimated from the distribution of
257 predicted values with $k=1.5$. Extrapolation assessments were done using *dsmextra* 1.1.5 R package
258 (Bouchet et al., 2020). We used this post-prediction treatment to assess population size estimates stability.

259 We measured the coefficient of variation, corresponding to the ratio between the standard deviation and
 260 the mean of the “untrimmed” and “outlier-trimmed” estimated range uncertainty. Large coefficients of
 261 variation imply great discrepancies in confidence intervals of untrimmed and outlier-trimmed estimated
 262 uncertainty intervals. This is mainly caused by the spatial filtering from the extrapolation assessment
 263 highlighting smaller geographic regions with similar environmental conditions from sampled ones and the
 264 trimming of predicted abundance outliers. Species with a coefficient of variation exceeding 30% were
 265 removed from the comparison of *ArGeom* and HDS population size estimates (Table S2.3).



267 **Figure 4** - Decision tree of the post-prediction treatment. First, we analysed the distribution of predicted
268 abundance values across the prediction grid and detected outliers, using a hinge of $k = 1.5$ (Tukey, 1977).
269 We compared each environmental condition of the prediction grid cell with the environmental condition
270 collected by the sampling scheme and used for model calibration. When a prediction cell depicted signs of
271 NT1 extrapolation and its estimated abundance was considered as an outlier, we trimmed the predicted
272 grid cell abundance to the Tukey fences value.

273 **Comparison of *ArGeom* and HDS estimated population sizes**

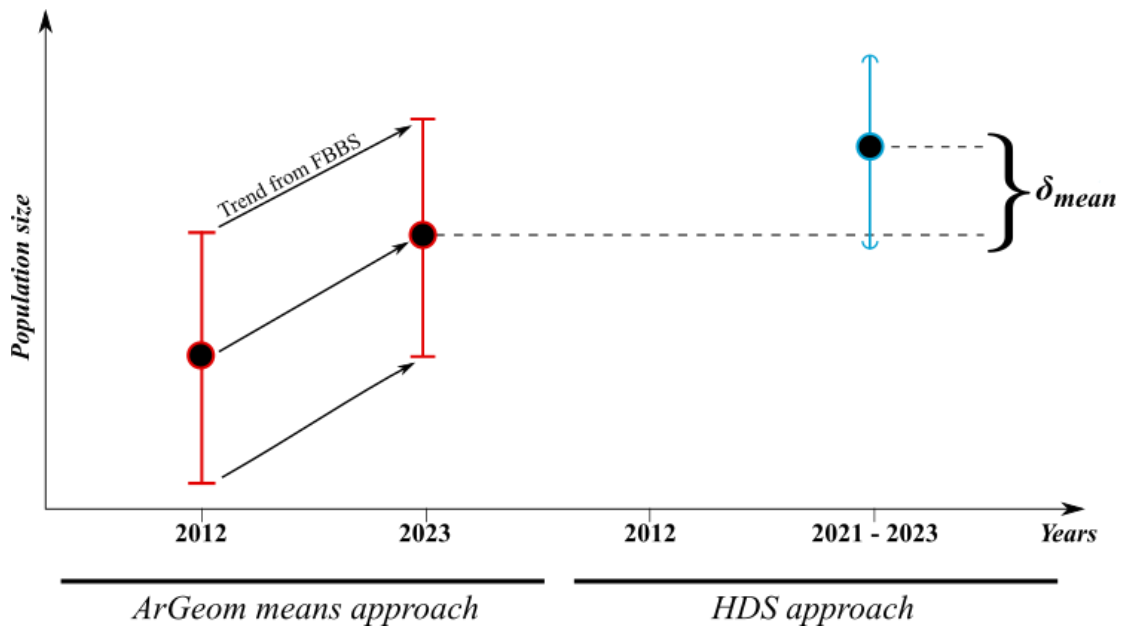
274 For comparable estimates between *ArGeom* and HDS approaches, we restricted the prediction grid
275 area species-wise for HDS estimation according to the distribution of their known breeding locations,
276 collected over a 10x10km grid during the previous French atlas (Issa & Muller, 2015). To estimate breeding
277 populations of species for which male identification was possible, either male vocalisations or visual
278 distinctions because of sexual dimorphism, an ad-hoc filter was applied (Table S2.1), resulting in HDS
279 estimates reflecting the male counts for those species.

280 As the *ArGeom* approach estimated species bird population sizes as a number of breeding pairs (Roché
281 et al., 2013), for species where male identification in the field was impossible (no sexual dimorphism), we
282 used all available data, after applying the phenological filter, and divided HDS estimates by two for
283 comparable estimates with *ArGeom* population sizes. After retrieval of *ArGeom* estimates from the
284 previous atlas (Issa & Muller, 2015), we updated these estimates using recent population trend estimates
285 derived from the French breeding bird survey (FBBS; Jiguet et al., 2012) data spanning 2012-2023 (Table
286 S2.1). Given the absence of a mean estimate in the *ArGeom* approach, we approximated it using the
287 midpoint between the maximum and minimum estimated (Fig 5).

288 To study the differences between the two approaches, we measured δ_{mean} corresponding to the
289 percentage of the difference between HDS and *ArGeom* estimates.

$$290 \quad \delta_{mean} = \frac{(Estimates_{ArGeom} - Estimates_{HDS})}{(Estimates_{ArGeom} + Estimates_{HDS})/2}$$

291



292

293 **Figure 5** - Population size estimates comparison methodology, *ArGeom* in red and HDS in blue. *ArGeom*
 294 estimates for 2012 were obtained through calculations using both arithmetic and geometric means (Roché
 295 et al., 2013) and were then updated to 2023 using specific mean trend estimates from FBBS (Table S2.1).
 296 Flat intervals signify min and max value estimates, while curved intervals signify confidence intervals.

297 **Study of variation of estimated population sizes between the two approaches**

298 As species detectability stems from physical traits and vocalisations, phylogenetic related species tend
 299 to have the same detectability (Johnston et al., 2014; Sólymos et al., 2018). We calibrated a Phylogenetic
 300 Generalised Linear Mixed Model (PGLMM) using the phyloglmm 1.0 (Li & Bolker, 2019) R package. We
 301 study δ_{mean} variations across species while implementing a random effect covariance structured based on
 302 phylogenetic relatedness using phylogenetic distances retrieved from Burleigh et al., (2015). The PGLMM
 303 model was calibrated using (i) extracted detection probabilities from the availability state estimated
 304 through HDS (fig 3 and appendix S5) after model averaging of the final candidate sets models in regards to
 305 AICc scores, and (ii) *ArGeom* uncertainty as fixed variables. For *ArGeom* uncertainty, corresponding to the
 306 difference between maximal and minimal estimated values, we relied on the decimal logarithm to limit
 307 variation in δ_{mean} solely due to different population size magnitudes.

308 Response weights consisted of normalised weights from the inverse of uncertainty around FBBS trends
 309 between 2012 and 2023 (Table S2.1), divided by the mean to limit excessive weight attribution and
 310 facilitate model convergence.

311

Results

312 **Species trends over 2012-2023**

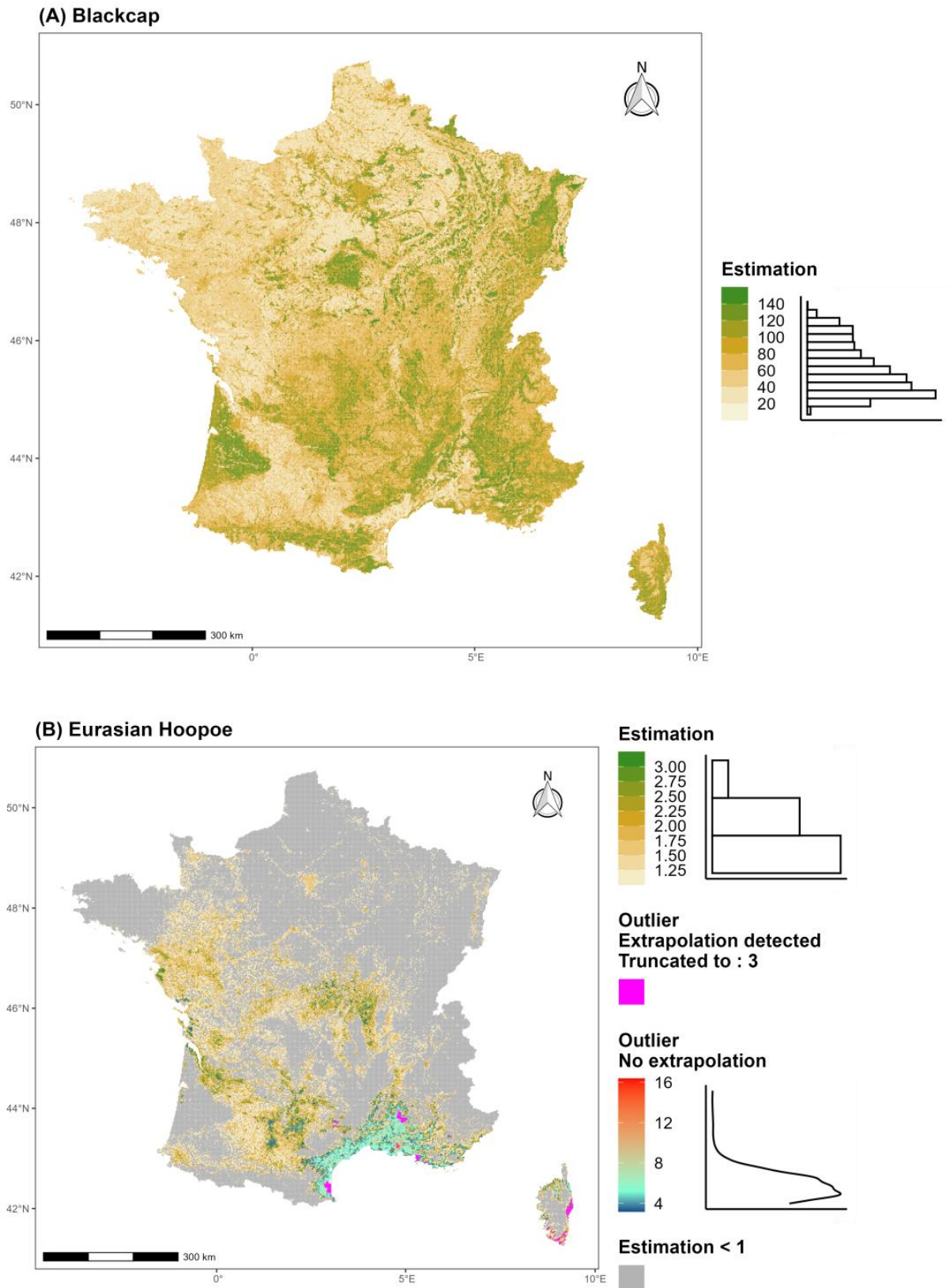
313 From 2012 to 2023, out of 63 bird species, 15 showed a significant decrease ($x = -22.79\% \pm 14.84$) in
314 total population size, while 16 showed a significant increase ($x = 28.02\% \pm 22.52$; see appendix S2 for
315 species-related FBBS trends).

316

317 **HDS population size estimations**

318 Out of the 54 species with acceptable values of overdispersion (\hat{C}) using the *HDS* approach, we excluded
319 eight species showing large discrepancies in population size estimates (Appendix S2, Table S2.3) between
320 pre- and post-prediction treatment (Fig. 2.).

321 Out of the remaining 46 species used for comparison between *ArGeom* and *HDS* estimates, *HDS* models
322 showed acceptable values of overdispersion (\hat{C}) ranging from 0.94 to 1.2 ($\bar{x} = 1.07 \pm 0.06$) for 38 species
323 calibrated using a Poisson distribution and 1.09 to 1.47 ($\bar{x} = 1.27 \pm 0.13$) for eight species calibrated using
324 a Negative binomial distribution.



325

326 **Figure 6** - Examples of resulting abundance maps for the (A) Blackcap (*Sylvia atricapilla*), and (B) Eurasian
 327 Hoopoe (*Upupa epops*). Estimations correspond to the number of male, or potential pairs (see Table S2.3)
 328 over a 4 km-squared area. Grid cell predictions are categorised into three groups: (1) those with estimated

329 abundance not considered as outliers depicted with a green colour step gradient and its distribution
330 histogram ; (2) those with estimated abundance considered as outliers and not subject to NT1
331 extrapolation, displayed in a blue-to-red gradient, along with their distribution density; and (3) those with
332 estimated abundance considered as outliers with novel environmental conditions subject to NT1
333 extrapolation highlighted in pink with the Tukey value used for trimming in the post-prediction treatment.

334

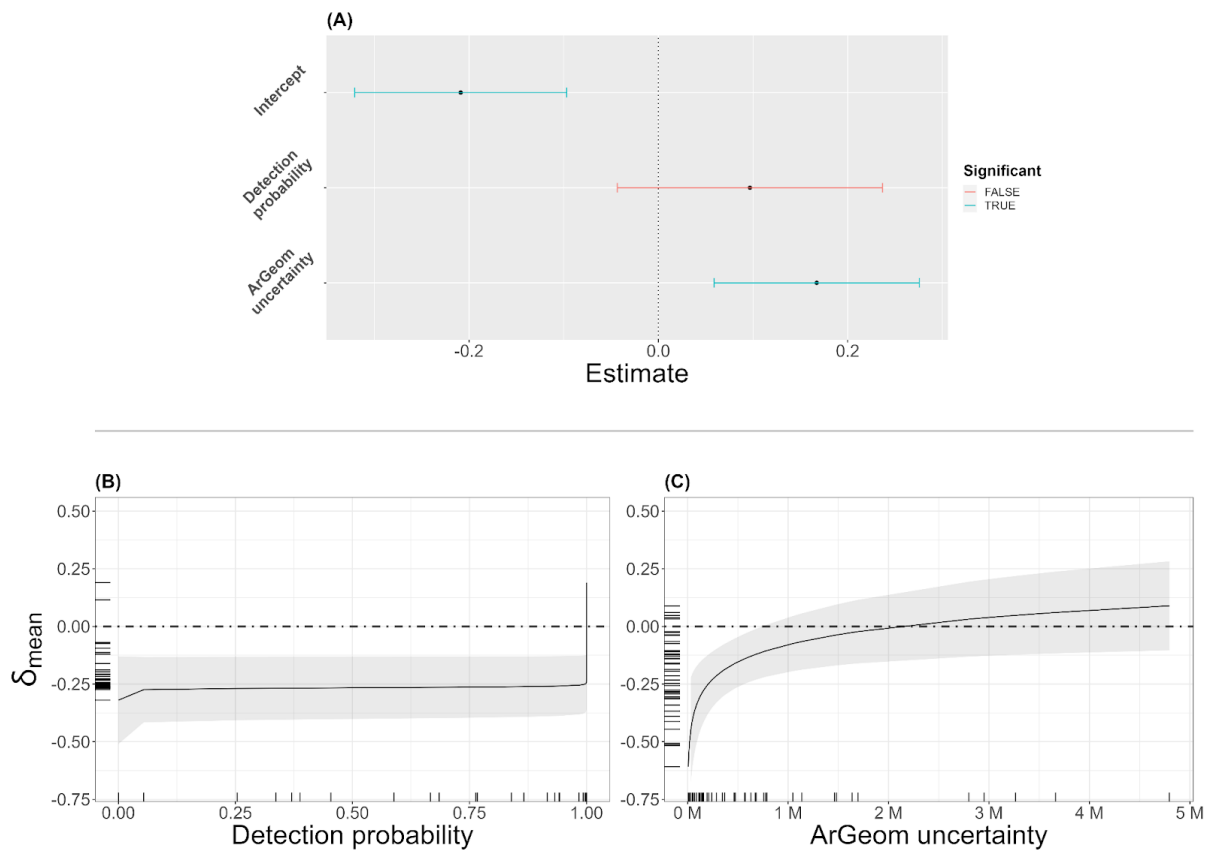
335 **Population size comparison between *ArGeom* and HDS**

336 Across all species, estimated mean density ranges from 0.09 to 27.51 individuals per square kilometre,
337 while *ArGeom* range uncertainty varies from 3.9 to 6.69 on the decimal logarithm scale corresponding to
338 variations from 7,920 to 4,850,000 in estimated number of pairs. See Table S6.1-3 for more details about
339 species estimated population size according to *ArGeom* and HDS approaches.

340 A comparison between updated *ArGeom* and HDS estimated population sizes showed that HDS
341 estimates were higher than *ArGeom* for 30 of the 46 species tested (Table S6.1). Our results suggest lower
342 estimates from *ArGeom* ($\delta_{mean} < -0.2$), either for open habitat specialists such as European Stonechat
343 (*Saxicola rubicola*), European Goldfinch (*Carduelis carduelis*) or Eurasian Linnet (*Carduelis cannabina*) than
344 for forest generalists such as Great Spotted Woodpecker (*Dendrocopos major*), Blue Tit (*Cyanistes*
345 *caeruleus*) or Eurasian Blackcap (Fig 6.A) with $\delta_{mean} = -0.629 \pm 0.4$, over 22 species. Species whose
346 estimations were similar ($\delta_{mean} \in [-0.2; 0.2]$, with on average $\delta_{mean} = -0.006 \pm 0.096$, over 17 species)
347 between *ArGeom* and HDS included species such as Eurasian Wren (*Troglodytes troglodytes*), Great Tit
348 (*Parus major*), European Robin (*Erithacus rubecula*) and European Nuthatch (*Sitta europea*). Fewer species,
349 mainly characterised by greater maximal observation distances, such as Common Cuckoo (*Cuculus*
350 *canorus*), Eurasian Hoopoe (Fig 6.B) and European Blackbird (*Turdus merula*) had higher population sizes
351 estimated by *ArGeom* approach compared to HDS ($\delta_{mean} > 0.2$, with on average $\delta_{mean} = 0.41 \pm 0.148$,
352 over 7 species; see Appendix S6 for population size comparison table).

353 Results from the PGLMM (Fig 7.A) showed an overall significantly lower *ArGeom* population size
354 estimates (-0.209, with 95% CI : [-0.321;-0.097], Pval = 0.001), as well as a significant positive effect of
355 *ArGeom* range intervals (0.167, with 95% CI : [0.059;0.276], Pval = 0.003) on the differences between the
356 two approaches. Species detection probabilities had no significant effect (0.097, with 95% CI : [-
357 0.043;0.237], Pval = 0.176) on δ_{mean} variation.

358 Marginal effect plots from the PGLMM model showed that the mean response of δ_{mean} over species
359 detection probability was predominantly negative, ranging from -0.45 to -0.1 (Fig 6.B), for *ArGeom*
360 uncertainty. This showed that δ_{mean} tended towards the convergence of population size estimates (Fig
361 7.C) for species with larger estimated interval ranges. There were no signs of multicollinearity (VIF < 5;
362 James et al., 2013) between the two variables.



363

364 **Figure 7** - Results from the PGLMM. (A) Confidence intervals of the model coefficient, parameters,
 365 coefficients significantly different from 0 are represented in blue. Marginal effect plots of population size
 366 estimate differences (δ_{mean}) responses. δ_{mean} responses are predicted over gradients of focal terms,
 367 either species detection probabilities (B) or *ArGeom* reported uncertainties (C), while other covariates are
 368 held constant at their mean. Species detection probabilities and *ArGeom* uncertainty are represented on
 369 their natural scales, after inverse logit and inverse decimal logarithm transformation, respectively. Dot-
 370 dash line corresponds to a δ_{mean} of 0, signifying estimated population size convergence by the two
 371 approaches, negative and positive values of δ_{mean} reflect lower and higher population size estimates of
 372 *ArGeom* relative to those obtained using HDS.

373

Discussion

374 Our results showed that bird population size estimates from the previous *ArGeom* approach, not
 375 accounting for the observation process nor habitat affinity covariates, are predominantly lower than
 376 population sizes estimated from the HDS approach, up to 65% of species. While we found that the prior
 377 estimated uncertainty ranges from *ArGeom* had a positive effect on the convergence of population sizes
 378 estimated by the two methodological approaches (expert estimates based on atlas data vs predicted
 379 estimates from modelled citizen science data accounting for detection probabilities), we did not find a
 380 significant effect of species detection probabilities which could explain the differences between the two
 381 approaches. We show that *ArGeom* produces population sizes that are largely lower than those obtained
 382 by HDS ($\delta_{mean} < 0.2$) regardless of habitat specialisation or affinity. This is likely due to the methodology

383 used for *ArGeom* that did not account for the detection process nor for species-habitat relationships when
384 extrapolating locally known abundances to unsampled locations.

385 Despite the lack of significant evidence for the effect of species detection probabilities on population
386 size estimations, our results tend to corroborate previous studies where ignored detection processes had
387 likely biased ecological inferences, including species distribution models (Kéry et al., 2010), population
388 trends (Norvell et al., 2003; Schmidt et al., 2013) and population sizes (Kéry et al., 2005). This lack may be
389 especially true in a context of global change, where avian breeding phenology showed evidence of shifts
390 towards earlier breeding over the years (Parmesan, 2007; Devictor et al., 2012; Gaüzère & Devictor, 2021)
391 to synchronise with their food sources (Visser et al., 2006; Michel et al., 2016). Such shifts induce diverse
392 species-related seasonal and inter-annual changes in detectability that need to be accounted for,
393 particularly for schemes spanning over multiple species (Lehikoinen, 2013).

394 In France, the *ArGeom* approach was developed in the context of moderate semi-quantitative data
395 collection with an acknowledged uneven participation across the territory (Roché et al., 2013; Issa &
396 Muller, 2015). The semi-quantitative data collection was based on the estimation of the number of
397 breeding pairs over 10x10km grids derived from a mixture of count prospects and expert opinions collected
398 over 1953 out of 5879 10x10km grids (Issa & Muller 2015). As the primary goal of this approach was to give
399 a likely magnitude of population size across the territory (Roché et al., 2013), *ArGeom* intervals were
400 produced by the extrapolation from the initially prospected 10x10km grids to all metropolitan grid cells
401 considered suitable for breeding, after the detection of potential and confirmed breeding evidence.
402 Although proved useful and relevant to assess population sizes when large-scale quantitative data on
403 species occurrences are lacking or are unevenly distributed, such a methodology implies greater
404 uncertainty intervals for abundant and broadly distributed species and smaller intervals for scarce and
405 narrowly distributed species when not accounting for measurement uncertainty.

406 Contrary to generalist species, which have widespread distributions due to broader habitat niche
407 breadths, specialists are generally more localised (Clavel et al., 2011) and typically use a smaller range of
408 habitats (Julliard et al., 2006). Despite a growing interest in rare species-focused monitoring (Fontaine et
409 al., 2022), citizen sciences programs are mainly designed for large-scale multi-species surveys (Devictor et
410 al., 2010). Citizen science schemes balance between a trade-off among data quantity and data quality,
411 corresponding to either the acquisition of a great quantity of unstructured scheme, or the acquisition of
412 standardised data implying replicated visits over randomly sampled locations (Devictor et al., 2010). As
413 such, in the first case, citizen science schemes could be more prone to false-negative errors, resulting in
414 biased inferences over habitat cover relations due to omission of the detection process (Johnston et al.,
415 2022). In the second case, given the small habitat range of specialist species and the scale of the territory
416 sampled (e.g., here the metropolitan French territory), citizen science sampling schemes could be
417 representative of the entire territory sampled but with a higher risk of missing some key habitats and
418 associated specialist species.

419 **Potential consequences for community-level assessments**

420 A recent study about long-term effects of climate and land use changes on bird communities (Gaüzère
421 et al., 2020) showed that both generalist cold-dwelling species, such as the Common Chiffchaff
422 (*Phylloscopus collybita*) or the Eurasian Blackcap, and warm-dwelling species, such as the Common
423 Nightingale (*Luscinia megarhynchos*) had the most substantial negative and positive contributions to the
424 trend in Community Thermal Index (CTI), a community-weighted index representing the realised thermal
425 niche of a community based upon species relative abundance and species thermal indices (STI). In the
426 present study, these species tended to have lower population sizes estimated when the detection process
427 was omitted compared to estimates based on our modelling approach. As a result, this could affect the
428 estimations of their contribution to the calculation of community-weighted mean indices, such as CTI, and
429 therefore bias the estimation of the trend in community thermal response and subsequent studies of
430 aggregated indices, which are known to display large regional variation (Rigal & Knape, 2024). We,
431 therefore, suggest that considering the detection process in studies relying on community-weighted
432 indexes by species' relative abundances could be as important as it is for estimating population sizes.

433 Community indices such as species diversity (Ricotta, 2005) and functional diversity (Villéger et al.,
434 2008; Gaüzère et al., 2019) are commonly use species relative abundance as a basis, without taking into
435 account the detection process (Pillar & Duarte, 2010), despite multiple studies showing it could affect
436 community indices inference (Tingley & Beissinger, 2013; McNew & Handel, 2015; Jarzyna & Jetz, 2016;
437 Richter et al., 2021).

438 **Conservation implications**

439 Our study also suggested that lower or higher population sizes estimated from *ArGeom* were not
440 randomly distributed among species according to their conservation status. Out of the 46 species
441 estimations used in the comparison analysis, 10 had an unfavourable conservation status in France (*i.e.*
442 lower than Least Concern, LC; UICN France et al., 2016).

443 Among these species of conservation concern, two species, European Greenfinch (*Carduelis chloris*)
444 and European Turtle Dove (*Streptoptelia turtur*), showed no signs of difference in their population sizes. By
445 contrast, five species, European Stonechat, Barn Swallow (*Hirundo rustica*), Red-backed Shrike (*Lanius*
446 *collurio*), Eurasian Kestrel (*Falco tinnunculus*) and Willow Warbler (*Phylloscopus trochillus*) considered as
447 NT (Near Threatened) and three species, Eurasian Linnet, European Goldfinch and European Serin (*Serinus*
448 *serinus*) considered as VU (Vulnerable) had lower population sizes estimated from *ArGeom* than from HDS
449 approach (NT : $\bar{\delta}_{mean} = -0.608 \pm 0.217$ and VU : $\bar{\delta}_{mean} = -0.667 \pm 0.146$). Our results showed that these
450 species may need a reevaluation of their conservation status and highlight the need to rely on hierarchical
451 models taking account of the detection process in ecological inferences, given that potential
452 misclassification of population conservation status may arise from process noise and observation error
453 (Connors et al., 2014). As conservation policy decisions depend on uncertainty levels (Williams, 2003;

454 Freckleton, 2020), assessing measurement error through the integration of the detection process (Nichols
455 et al., 2011) could provide more reliable ecological inferences (Guillera-Arroita et al., 2014). CS schemes
456 are becoming more and more a reliable source of data to ensure biodiversity monitoring (Chandler et al.,
457 2017) and can, through standardisation (Buckland & Johnston, 2017; Johnston et al., 2019), contribute to
458 the calibration of data-hungry models such as hierarchical models for reliable ecological inferences (Isaac
459 et al., 2020; Kéry & Royle, 2021; Johnston et al., 2022).

460 **Comparison to other European countries**

461 Another way to assess the relevance of the two estimation approaches would be to compare their
462 population size estimates to the ones obtained from other European countries, using a ratio between
463 countries to produce comparable estimates. Such an approach should however be used with caution
464 because it would be limited by comparability in habitat repartitions or biogeographical considerations
465 among different European countries. To go further into inter-country comparisons, we relied on the
466 German population sizes estimated for the previous European Bird Directive (BirdLife International, 2021)
467 obtained from both point count and territory mapping methods (Gedeon et al., 2015). For abundant
468 species such as the Blackcap ($\delta_{mean} = -0.29$; German population size expressed in millions of pairs = [7.17
469 - 9.49]), both approaches led to similar results than German population estimates, while HDS estimates
470 were closer to German population sizes for the Firecrest (*Regulus ignicapilla*; $\delta_{mean} = -0.46$; [1.92 - 2.85])
471 and the Blue Tit ($\delta_{mean} = -0.42$; [5.01 - 7.41]). For species with higher population sizes estimated by *ArGeom*
472 than HDS ($\delta_{mean} > 0.2$), the Common Cuckoo ($\delta_{mean} = 0.25$; [0.58 - 0.95]) and the Corn Bunting (*Emberiza*
473 *calandra*; $\delta_{mean} = 0.6$; [0.25 - 0.44]) showed estimates of German populations closer to the HDS than the
474 *ArGeom* approach. Finally, for the Common Whitethroat (*Curruca communis*; $\delta_{mean} = 0.42$; [0.93 - 1.47]),
475 the German population size is closer to *ArGeom* estimates (see appendix S6.4 for additional information).

476 Regarding magnitudes, both approaches produced similar estimates compared to German ones.
477 However, due to different sampling and modelling methods used, these formal comparisons, although
478 informative, need to be more fully satisfying and highlight the discrepancies in sampling and analytical
479 methods across the European continent (Keller et al., 2020). Such differences could be accounted for,
480 either by (i) a global standardisation of schemes, as promoted by the PECBMS (Pan-European Common Bird
481 Monitoring Scheme; Brlík et al., 2021) for species trends, but also (ii) through the use of Integrated Models
482 (IM) capable of mobilising data from multiple and somewhat heterogeneous sources (Isaac et al., 2020;
483 Zipkin et al., 2021a).

484 **Study limitations**

485 Our approach relies on data collected from the EPOC-ODF structured CS schemes, providing data with
486 repeated visits. However, as is, the frequentist framework of *unmarked* R package (Kellner et al., 2023)
487 does not permit inferences on social species occurring in large flocks. Taking account of social species
488 during the breeding season (corresponding to 1/10th of the scheme targeted species) would therefore
489 require a Bayesian framework to include the effect of flock size on species detectability (Clement et al.,
490 2017).

491 Given the timeframe and the sampling design, i.e., all sites are not visited every year to maximise the
492 number of total surveyed locations, it is not possible to estimate species demographic parameters, such as
493 survival and recruitment (Sollmann et al., 2015; Schmidt & Rattenbury, 2018). We also assumed a sex ratio
494 of 1:1 for species without sexual dimorphism, during the breeding season, which could potentially bias
495 estimates for species deviating from this assumption. Taking account of species population structure
496 requires frameworks such as Integrated Population Models (IPM; Schaub & Ullrich, 2021) and specific data
497 collection (King, 2014), for instance, bagging or nest surveillance.

498 As obtaining relevant predictions of species abundance over unsampled environmental conditions was
499 one of our main methodological challenges, we used environmental data condensing habitat information
500 (Tredennick et al., 2021). To fit our statistical framework, we assumed that most bird species would interact
501 with their habitat following a linear relationship (see Fig. 3). We therefore used PCA reduction to
502 summarise species linear responses to national-scale habitat gradients including forest-to-open-field
503 cultures, open-field cultures-to-pastures and perennial crop-to-urban habitats (see appendix S3). PCA
504 reduction permits model convergence by condensing complex habitat structures to a small number of
505 environmental covariates, though it could bias estimates of species thriving in a specific habitat restricted
506 to the extreme edge of the sampled gradients. Other methods such as Spatially Varying Covariates models
507 (SVC; Gelfand et al., 2003) could be used to better account for habitat structure complexity across spatial
508 gradients (Thorson et al., 2023).

509 Previous studies have shown that unaccounted variations in species availability, considering a constant
510 detection probability or unmodelled variations, could lead to substantial bias in estimated abundance (Link
511 et al., 2018; Barker et al., 2018; Duarte et al., 2018). N-mixture biased estimations can be linked to non-
512 assessment of the sampled area, where a smaller or greater sampled effective area could lead to under-
513 or overestimation (Kéry & Royle, 2015). In our study, as we relied on distance sampling methods, we define
514 an effective sampled area, based upon collected observation distance, but we also assumed that
515 individuals considered exposed to the sampling (*i.e.* 'statistically' available for modelling) could still be
516 undetected due to small species home ranges or plot-specific habitat cover (Chandler et al., 2011; see Table
517 1 and Figure 2, for covariates used to model species detectability and appendix S5 for model formulation).
518 Despite such consideration, for the HDS model, we assumed that detected individuals were

519 homogeneously distributed over the sampled area. Violating this assumption could lead to within-sample
520 variation that needs to be accounted for, otherwise leading to biased estimates (Mizel et al., 2018).

521 Another potential drawback relies on the quantity of data collected through this structured CS scheme.
522 Over the same breeding season, the semistructured scheme EPOC without temporal replicates nor fixed
523 location requirements collected three times the amount of complete checklists as the structured EPOC-
524 ODF scheme, highlighting CS trade-off of scheme standardisation upon data collection over spatial and
525 temporal scales (Devictor et al., 2010). One way to address this trade-off would be to apply data integration
526 methods mobilising multiple data sources to be used for ecological inferences (Zipkin et al., 2019, 2021b),
527 either by estimating abundance of less recorded species through trait-based associations (Callaghan et al.,
528 2021, 2022; Robinson et al., 2022) or by constructing joint likelihood functions (Fithian et al., 2015; Fletcher
529 et al., 2019).

530 **Conclusion**

531 Our results suggested an overall lower population size estimate of French common breeding birds
532 obtained from the last French Breeding Bird atlas methodology than from the Hierarchical Distance
533 Sampling modelling used in the present work. Using large-scale datasets from citizen science obtained from
534 standard scheme initiatives allowed us to infer the variation in species abundance, while explicitly
535 modelling the detection process separately from the ecological one. Not accounting for the observation
536 process might have resulted in misleading expert-only estimations of population sizes in the previous atlas,
537 at least for some widespread species not benefitting from exhaustive surveys. In conclusion, our results
538 advocate for more reliance on the use of statistical tools accounting for the detection process, such as
539 hierarchical models, which, in association with large-scale citizen science data, could constitute a standard
540 methodology to estimate reliable abundance from breeding bird atlases or biodiversity surveys deployed
541 at national or geographically broader scales

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558

Conflict of interest disclosure

559 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in
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561

Data, scripts, code, and supplementary information availability

562 Data, scripts and code are available online: <https://doi.org/10.5281/zenodo.11402818> ; Nabias et al,
563 2024

564 Supplementary information is available online: <https://doi.org/10.5281/zenodo.11402818> ; Nabias et
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