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1 **Reassessment of French breeding bird**
2 **population sizes using citizen science and**
3 **accounting for species detectability**

4
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23 **ABSTRACT**

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

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

58 Worldwide bird populations are nowadays caught in the midst of a global, man-driven erosion of
59 biodiversity caused by the synergistic effects of habitat destruction and fragmentation, resource
60 overexploitation, climate change, pollution, pesticide use as well as the global spread of invasive species
61 (Ceballos et al., 2015; Johnson et al., 2017). In Europe, the intensification of agriculture crystallises this
62 phenomenon because the ever-increased use of pesticides and fertilisers has been pointed out as the
63 main driver of current bird population declines (Rigal et al., 2023). Recent researches have pointed out
64 how important species-specific life attributes (e.g., species range and density) and functional traits (e.g.,
65 body mass, diet or dispersal) explain long-term bird trends and responses to global changes (Hong et al.,
66 2023; Santini et al., 2023; Germain et al., 2023). Monitoring long-term as well as shorter-term trends
67 have been historically possible through standardised biodiversity - including bird - surveys at a national
68 scale and aggregated at the continental one (Jiguet et al., 2012; Pilotto et al., 2020; Brlík et al., 2021). This
69 monitoring produces comprehensive distribution atlases pointing out current ranges and their historical
70 changes (Keller et al., 2020), as well as long-term population trends (Brlík et al., 2021). Identifying
71 common species declines in the long-term should be accounted for in agricultural and planning policies
72 (Gaston & Fuller, 2008; Rigal et al., 2023) to help reconciling society's needs with the safeguarding of
73 ordinary biodiversity (Couvet & Ducarme, 2014).

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

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

93 by subsequent in 1995 (Yeatman-Berthelot & Jarry, 1995) and 2015 (Issa & Muller, 2015). Each iteration
94 was marked by a significant increase in participating citizen birders, ranging from 500 to 2400 to 10,000.
95 However, while the ultimate aim of bird atlases is to acquire even knowledge across multiple species for
96 a given geographical area (typically national-wide inquiries), it is essential to note that rare and
97 threatened species benefit from more in-depth population monitoring than more frequent and abundant
98 ones (Ingram et al., 2021). Such exhaustive knowledge of rare species populations is due to interest risen
99 by high extinction risk (IUCN, 2001), the need for recovery plans (Farrier et al., 2007) and narrow
100 distributions allowing exhaustive counts (Quaintenne et al., 2020). In contrast, common species (being
101 altogether abundant, widespread; Rabinowitz, 1981) are considered Least Concern (LC). They
102 consequently tend to receive lesser attention than rarer species (Neeson et al., 2018) despite being key
103 components of global avian biomass changes (Gaston & Fuller, 2008; Inger et al., 2015; Whelan et al.,
104 2015; Rigal et al., 2023).

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

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

129 affect the estimation of long-term trends due to its unaddressed variation (Schmidt et al., 2013; Sanz-
130 Pérez et al., 2020).

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

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

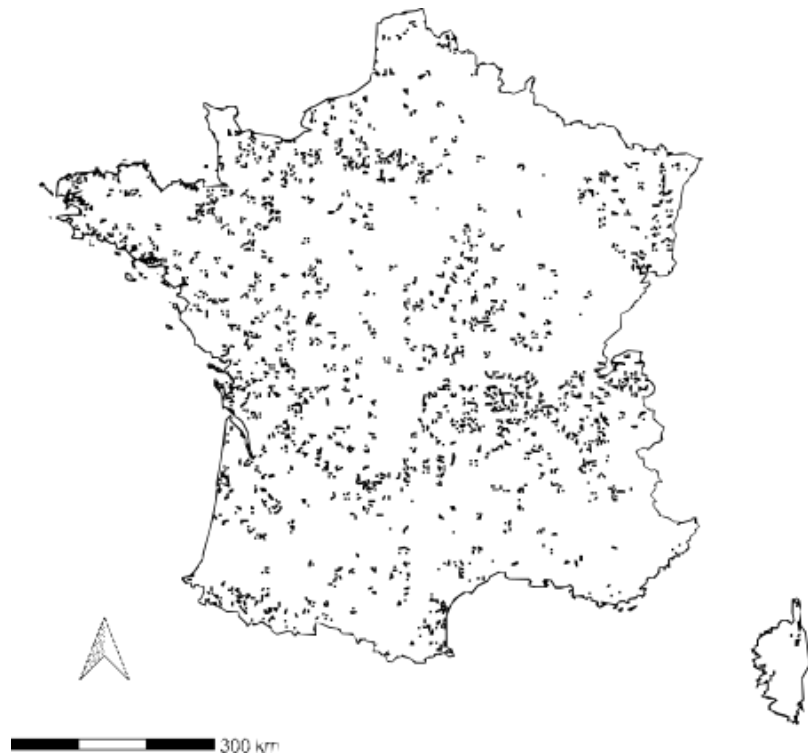
143 **Materials and methods**

144 **Sampling protocol**

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

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

164 opinion to capture the breeding phenology of each targeted species and exclude possible early or late
165 migrants from population size estimates (see Appendix S2.1).



166

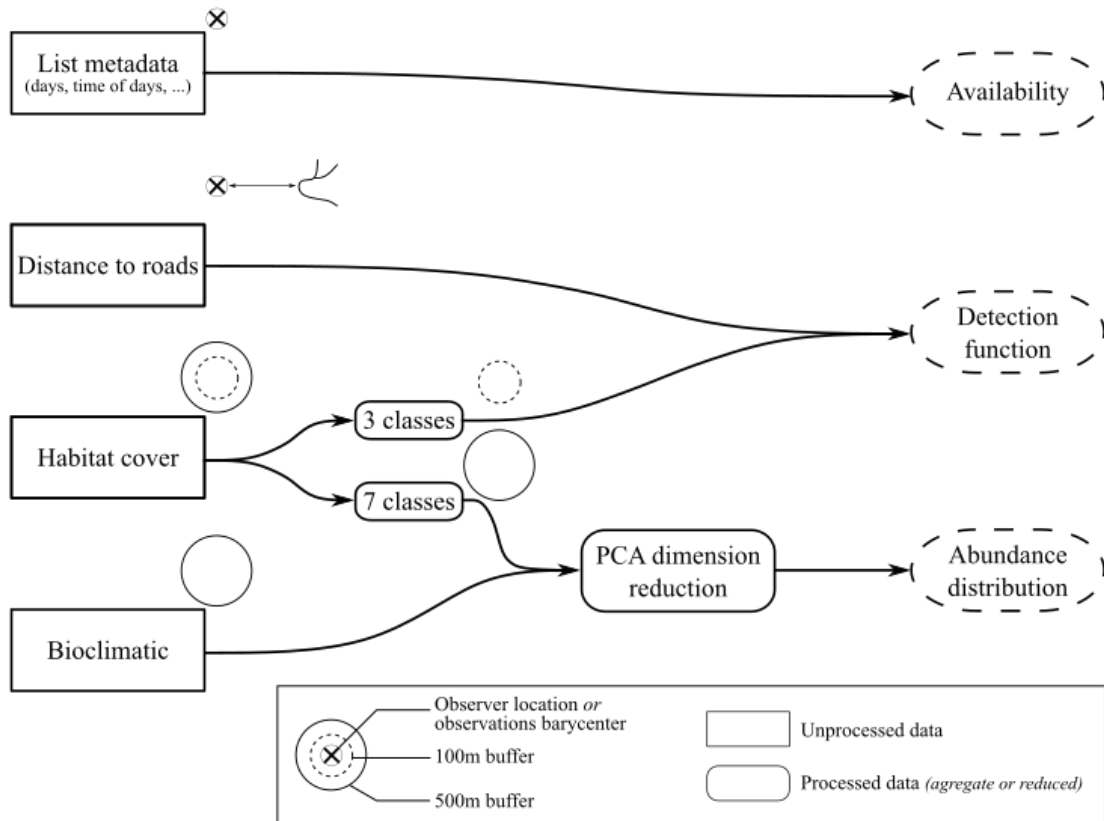
167 **Figure 1** - Spatial distribution of surveyed EPOC-ODF locations (n = 3 505) over 2021-2023 breeding
168 seasons.

169 **PCA reduction of environmental covariates**

170 For bioclimatic data, we used 19 variables from WorldClim at 1km resolution (Fick & Hijmans, 2017),
171 on which we applied a Principal Component Analysis (PCA), keeping the first three axes (82.3% of
172 explained variance), to limit multicollinearity through orthogonal transformation (Cruz-Cárdenas et al.,
173 2014).

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

186 was unavailable, we used the centroid of sightings as a proxy for observer location (Appendix S4). We
 187 used environmental data collected from a prediction grid covering France at a resolution of 2x2km for
 188 PCA dimension reduction. Outcomes from this initial PCA were used to transform environmental data
 189 collected from surveyed locations through PCA projections.



190

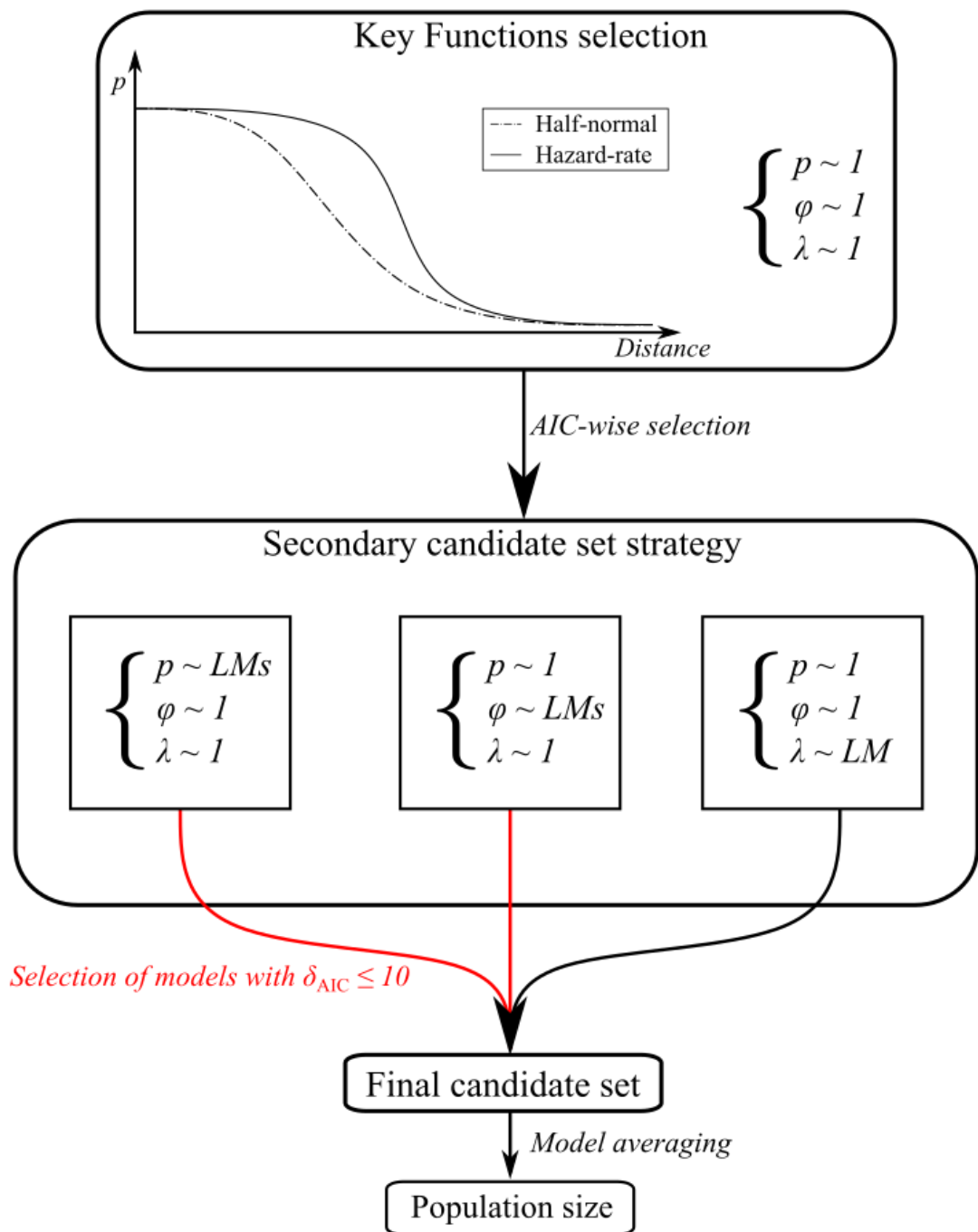
191 **Figure 2** - Global overview of covariates acquisition, treatments and usage workflow. Data are retrieved
 192 over observers' GPS location or approximated using observations barycenter, when unavailable, over two
 193 resolutions, 100m buffer (dotted circles) and 500m buffer radii (solid circles).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

198 **Modelling framework**

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

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

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



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

224

225 **Table 1** - Ensemble of sub-models tested in the secondary candidate set approach (Morin et al.,
 226 2020). (*) For the hour effort covariate, we used minutes from sunrise estimated from site
 227 longitude, 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

228

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

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

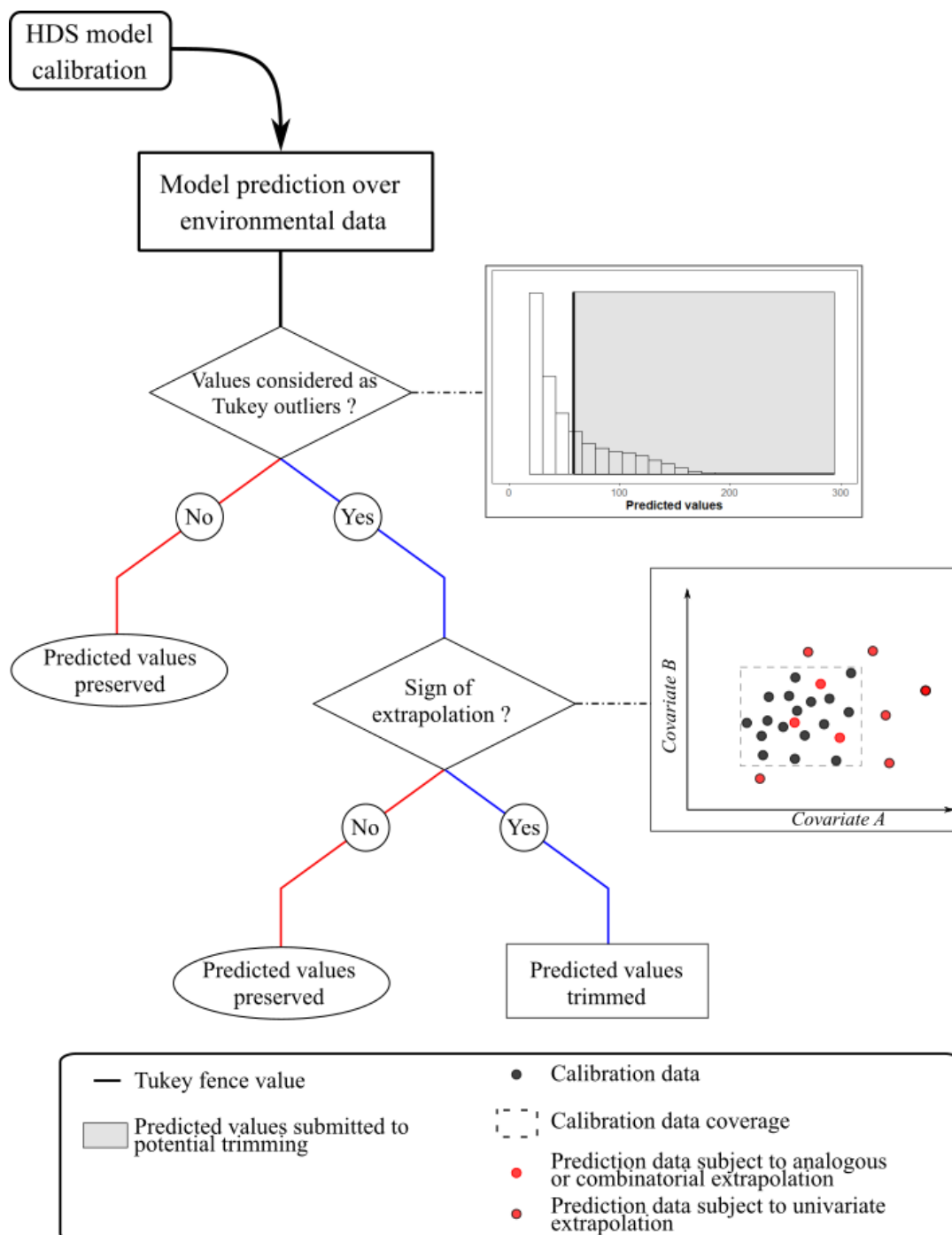
245 We assessed the robustness of our estimations to the exclusion of one year of data, corresponding to
246 a third of the global dataset. We compared population size estimates from EPOC-ODF data collected over
247 2021-2023 to estimates obtained from EPOC-ODF data collected over 2021-2022. Using the 2021-2022
248 subset, we estimated the population sizes of 30 species, detected in at least 150 distinct sites. From these
249 30 species, seven mean population sizes estimated using 2021 to 2023 data were outside the confidence
250 intervals estimated from 2021 to 2022 data, with a slightly smaller population size estimated (Table S2.2)
251 overall highlighting robust estimations.

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

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

261 We trimmed predicted values (Fig 4) over prediction grid cells showing signs of NT1 extrapolation, to
262 a threshold value determined using a Tukey fence (Tukey, 1977), estimated from the distribution of
263 predicted values with $k=1.5$. Extrapolation assessments were done using *dsmextra* 1.1.5 R package

264 (Bouchet et al., 2020). We used this post-prediction treatment to assess population size estimates
 265 stability. We measured the coefficient of variation, corresponding to the ratio between the standard
 266 deviation and the mean of the “untrimmed” and “outlier-trimmed” estimated range uncertainty. Large
 267 coefficients of variation imply great discrepancies in confidence intervals of untrimmed and outlier-
 268 trimmed estimated uncertainty intervals. This is mainly caused by the spatial filtering from the
 269 extrapolation assessment highlighting smaller geographic regions with similar environmental conditions
 270 from sampled ones and the trimming of predicted abundance outliers. Species with a coefficient of
 271 variation exceeding 30% were removed from the comparison of *ArGeom* and HDS population size
 272 estimates (Table S2.3).



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

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

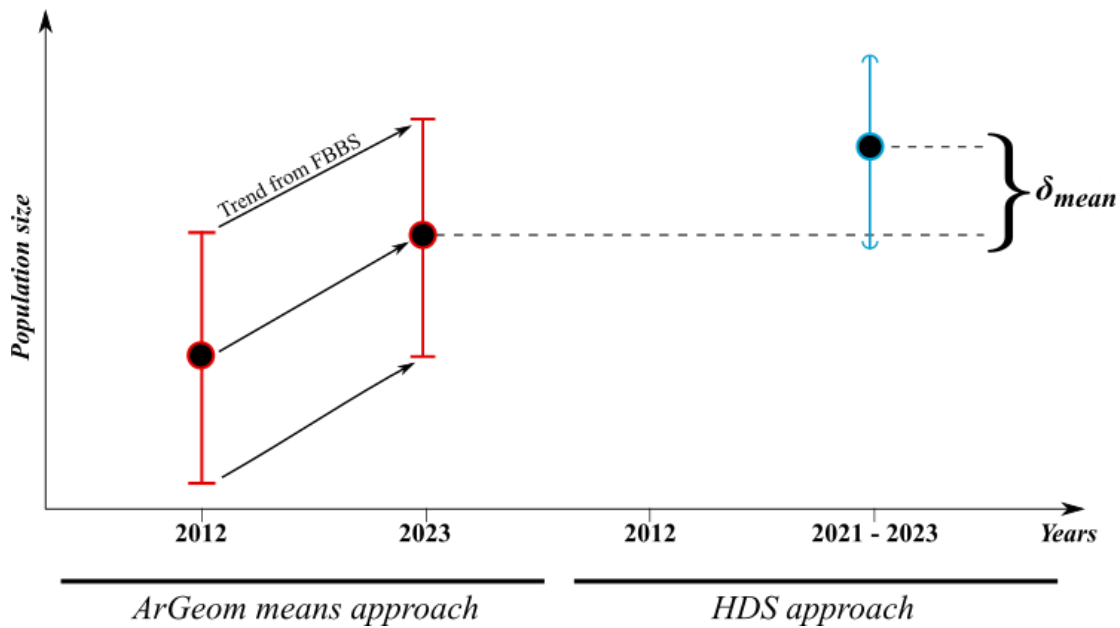
281 For comparable estimates between *ArGeom* and HDS approaches, we restricted the prediction grid
282 area species-wise for HDS estimation according to the distribution of their known breeding locations,
283 collected over a 10x10km grid during the previous French atlas (Issa & Muller, 2015). To estimate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

287 As the *ArGeom* approach estimated species bird population sizes as a number of breeding pairs
288 (Roché et al., 2013), for species where male identification in the field was impossible (no sexual
289 dimorphism), we used all available data, after applying the phenological filter, and divided HDS estimates
290 by two for comparable estimates with *ArGeom* population sizes. After retrieval of *ArGeom* estimates
291 from the previous atlas (Issa & Muller, 2015), we updated these estimates using recent population trend
292 estimates derived from the French breeding bird survey (FBBS; Jiguet et al., 2012) data spanning 2012-
293 2023 (Table S2.1). Given the absence of a mean estimate in the *ArGeom* approach, we approximated it
294 using the midpoint between the maximum and minimum estimated (Fig 5).

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

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

297



298

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

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

305 As species detectability stems from physical traits and vocalisations, phylogenetic related species
 306 tend to have the same detectability (Johnston et al., 2014; Sólymos et al., 2018). We calibrated a
 307 Phylogenetic Generalised Linear Mixed Model (PGLMM) using the phyloglmm 1.0 (Li & Bolker, 2019) R
 308 package. We study δ_{mean} variations across species while implementing a random effect covariance
 309 structured based on phylogenetic relatedness using phylogenetic distances retrieved from Burleigh et al.,
 310 (2015). The PGLMM model was calibrated using (i) extracted detection probabilities from the availability
 311 state estimated through HDS (fig 3 and appendix S5) after model averaging of the final candidate sets
 312 models in regards to AICc scores, and (ii) *ArGeom* uncertainty as fixed variables. For *ArGeom* uncertainty,
 313 corresponding to the difference between maximal and minimal estimated values, we relied on the
 314 decimal logarithm to limit variation in δ_{mean} solely due to different population size magnitudes.

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

318

Results

319 **Species trends over 2012-2023**

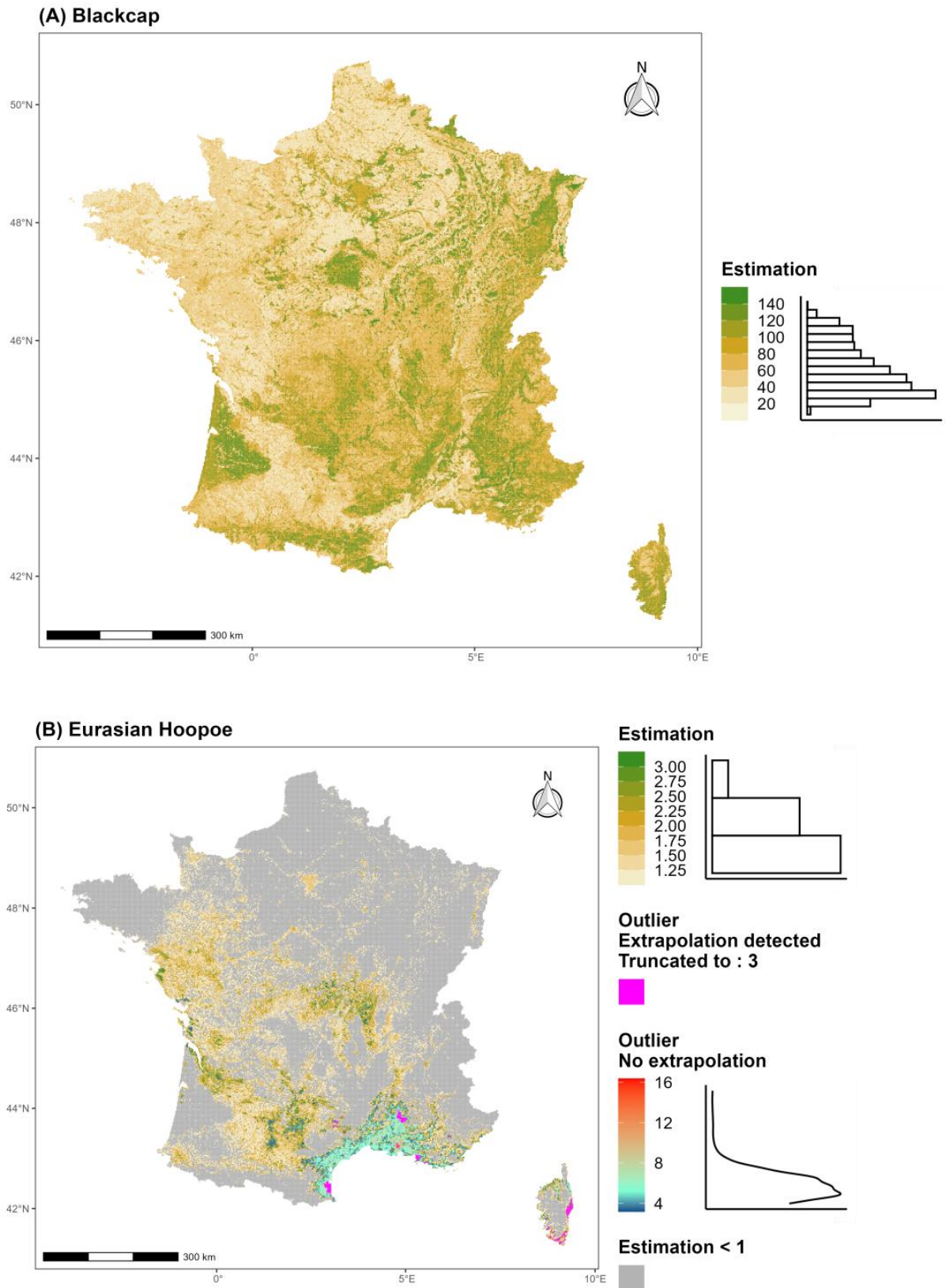
320 From 2012 to 2023, out of 63 bird species, 15 showed a significant decrease ($x = -22.79\% \pm 14.84$) in
321 total population size, while 16 showed a significant increase ($x = 28.02\% \pm 22.52$; see appendix S2 for
322 species-related FBBS trends).

323

324 **HDS population size estimations**

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

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



332

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

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

342

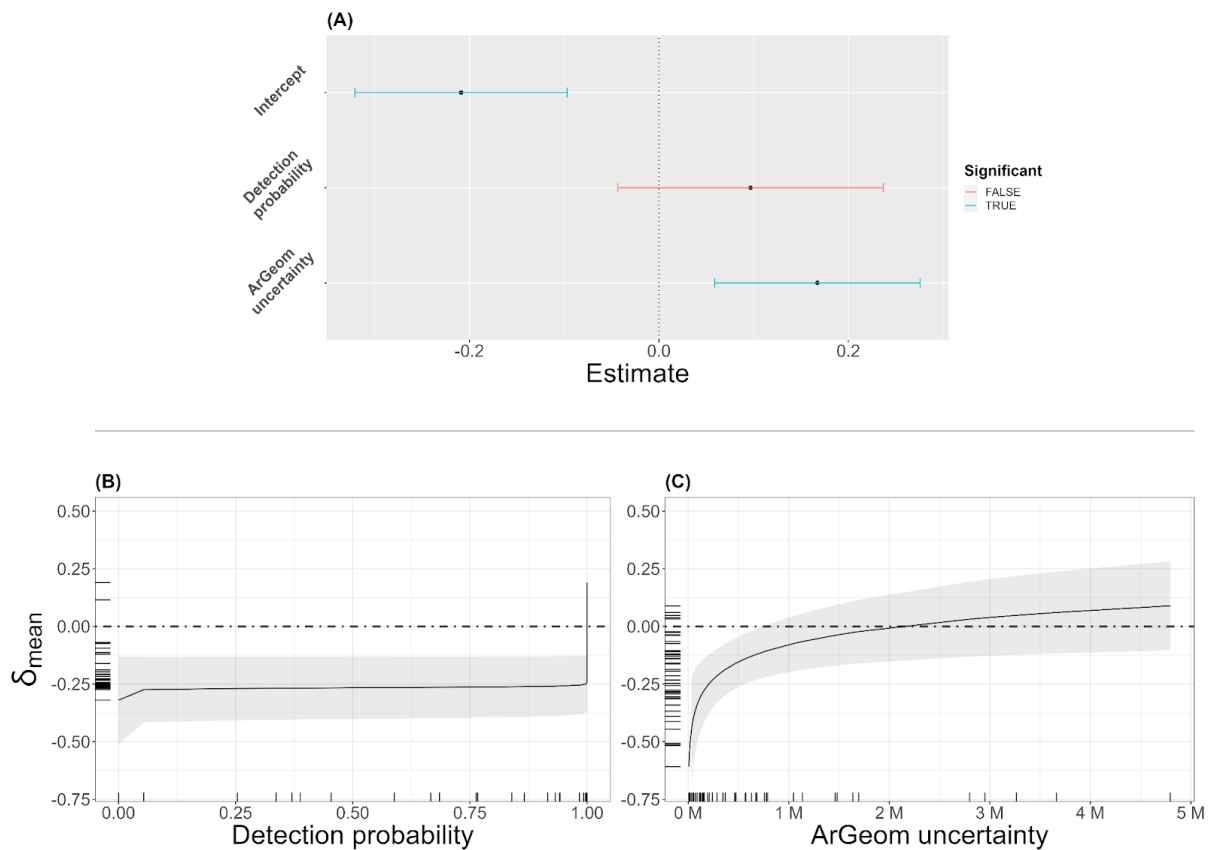
343 **Population size comparison between *ArGeom* and HDS**

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

348 A comparison between updated *ArGeom* and HDS estimated population sizes showed that HDS
349 estimates were higher than *ArGeom* for 30 of the 46 species tested (Table S6.1). Our results suggest
350 lower estimates from *ArGeom* ($\delta_{mean} < -0.2$), either for open habitat specialists such as European
351 Stonechat (*Saxicola rubicola*), European Goldfinch (*Carduelis carduelis*) or Eurasian Linnet (*Carduelis*
352 *cannabina*) than for forest generalists such as Great Spotted Woodpecker (*Dendrocopos major*), Blue Tit
353 (*Cyanistes caeruleus*) or Eurasian Blackcap (Fig 6.A) with $\delta_{mean} = -0.629 \pm 0.4$, over 22 species. Species
354 whose estimations were similar ($\delta_{mean} \in [-0.2;0.2]$, with on average $\delta_{mean} = -0.006 \pm 0.096$, over 17
355 species) between *ArGeom* and HDS included species such as Eurasian Wren (*Troglodytes troglodytes*),
356 Great Tit (*Parus major*), European Robin (*Erithacus rubecula*) and European Nuthatch (*Sitta europea*).
357 Fewer species, mainly characterised by greater maximal observation distances, such as Common Cuckoo
358 (*Cuculus canorus*), Eurasian Hoopoe (Fig 6.B) and European Blackbird (*Turdus merula*) had higher
359 population sizes estimated by *ArGeom* approach compared to HDS ($\delta_{mean} > 0.2$, with on average $\delta_{mean} =$
360 0.41 ± 0.148 , over 7 species; see Appendix S6 for population size comparison table).

361 Results from the PGLMM (Fig 7.A) showed an overall significantly lower *ArGeom* population size
362 estimates (-0.209, with 95% CI : [-0.321;-0.097], Pval = 0.001), as well as a significant positive effect of
363 *ArGeom* range intervals (0.167, with 95% CI : [0.059;0.276], Pval = 0.003) on the differences between the
364 two approaches. Species detection probabilities had no significant effect (0.097, with 95% CI : [-
365 0.043;0.237], Pval = 0.176) on δ_{mean} variation.

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



371

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

381

Discussion

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

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

393 Despite the lack of significant evidence for the effect of species detection probabilities on population
394 size estimations, our results tend to corroborate previous studies where ignored detection processes had
395 likely biased ecological inferences, including species distribution models (Kéry et al., 2010), population
396 trends (Norvell et al., 2003; Schmidt et al., 2013) and population sizes (Kéry et al., 2005). This lack may be
397 especially true in a context of global change, where avian breeding phenology showed evidence of shifts
398 towards earlier breeding over the years (Parmesan, 2007; Devictor et al., 2012; Gaüzère & Devictor,
399 2021) to synchronise with their food sources (Visser et al., 2006; Michel et al., 2016). Such shifts induce
400 diverse species-related seasonal and inter-annual changes in detectability that need to be accounted for,
401 particularly for schemes spanning over multiple species (Lehikoinen, 2013).

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

414 Contrary to generalist species, which have widespread distributions due to broader habitat niche
415 breadths, specialists are generally more localised (Clavel et al., 2011) and typically use a smaller range of
416 habitats (Julliard et al., 2006). Despite a growing interest in rare species-focused monitoring (Fontaine et
417 al., 2022), citizen sciences programs are mainly designed for large-scale multi-species surveys (Devictor et
418 al., 2010). Citizen science schemes balance between a trade-off among data quantity and data quality,
419 corresponding to either the acquisition of a great quantity of unstructured scheme, or the acquisition of
420 standardised data implying replicated visits over randomly sampled locations (Devictor et al., 2010). As
421 such, in the first case, citizen science schemes could be more prone to false-negative errors, resulting in
422 biased inferences over habitat cover relations due to omission of the detection process (Johnston et al.,
423 2022). In the second case, given the small habitat range of specialist species and the scale of the territory
424 sampled (e.g., here the metropolitan French territory), citizen science sampling schemes could be
425 representative of the entire territory sampled but with a higher risk of missing some key habitats and
426 associated specialist species.

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

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

441 Community indices such as species diversity (Ricotta, 2005) and functional diversity (Villéger et al.,
442 2008; Gaüzère et al., 2019) are commonly use species relative abundance as a basis, without taking into
443 account the detection process (Pillar & Duarte, 2010), despite multiple studies showing it could affect
444 community indices inference (Tingley & Beissinger, 2013; McNew & Handel, 2015; Jarzyna & Jetz, 2016;
445 Richter et al., 2021).

446 **Conservation implications**

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

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

462 Freckleton, 2020), assessing measurement error through the integration of the detection process
463 (Nichols et al., 2011) could provide more reliable ecological inferences (Guillera-Arroita et al., 2014). CS
464 schemes are becoming more and more a reliable source of data to ensure biodiversity monitoring
465 (Chandler et al., 2017) and can, through standardisation (Buckland & Johnston, 2017; Johnston et al.,
466 2019), contribute to the calibration of data-hungry models such as hierarchical models for reliable
467 ecological inferences (Isaac et al., 2020; Kéry & Royle, 2021; Johnston et al., 2022).

468 **Comparison to other European countries**

469 Another way to assess the relevance of the two estimation approaches would be to compare their
470 population size estimates to the ones obtained from other European countries, using a ratio between
471 countries to produce comparable estimates. Such an approach should however be used with caution
472 because it would be limited by comparability in habitat repartitions or biogeographical considerations
473 among different European countries. To go further into inter-country comparisons, we relied on the
474 German population sizes estimated for the previous European Bird Directive (BirdLife International, 2021)
475 obtained from both point count and territory mapping methods (Gedeon et al., 2015). For abundant
476 species such as the Blackcap ($\delta_{mean} = -0.29$; German population size expressed in millions of pairs = [7.17
477 - 9.49]), both approaches led to similar results than German population estimates, while HDS estimates
478 were closer to German population sizes for the Firecrest (*Regulus ignicapilla*; $\delta_{mean} = -0.46$; [1.92 - 2.85])
479 and the Blue Tit ($\delta_{mean} = -0.42$; [5.01 - 7.41]). For species with higher population sizes estimated by
480 *ArGeom* than HDS ($\delta_{mean} > 0.2$), the Common Cuckoo ($\delta_{mean} = 0.25$; [0.58 - 0.95]) and the Corn Bunting
481 (*Emberiza calandra*; $\delta_{mean} = 0.6$; [0.25 - 0.44]) showed estimates of German populations closer to the
482 HDS than the *ArGeom* approach. Finally, for the Common Whitethroat (*Curruca communis*; $\delta_{mean} = 0.42$;
483 [0.93 - 1.47]), the German population size is closer to *ArGeom* estimates (see appendix S6.4 for additional
484 information).

485 Regarding magnitudes, both approaches produced similar estimates compared to German ones.
486 However, due to different sampling and modelling methods used, these formal comparisons, although
487 informative, need to be more fully satisfying and highlight the discrepancies in sampling and analytical
488 methods across the European continent (Keller et al., 2020). Such differences could be accounted for,
489 either by (i) a global standardisation of schemes, as promoted by the PECBMS (Pan-European Common
490 Bird Monitoring Scheme; Brlík et al., 2021) for species trends, but also (ii) through the use of Integrated
491 Models (IM) capable of mobilising data from multiple and somewhat heterogeneous sources (Isaac et al.,
492 2020; Zipkin et al., 2021a).

493 **Study limitations**

494 Our approach relies on data collected from the EPOC-ODF structured CS schemes, providing data with
495 repeated visits. However, as is, the frequentist framework of *unmarked* R package (Kellner et al., 2023)
496 does not permit inferences on social species occurring in large flocks. Taking account of social species
497 during the breeding season (corresponding to 1/10th of the scheme targeted species) would therefore
498 require a Bayesian framework to include the effect of flock size on species detectability (Clement et al.,
499 2017).

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

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

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

529 could lead to within-sample variation that needs to be accounted for, otherwise leading to biased
530 estimates (Mizel et al., 2018).

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

540 **Conclusion**

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

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556 HDS models were calibrated on the SACADO MeSU platform at Sorbonne Université at Paris – France,
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568

569

Conflict of interest disclosure

570 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in
571 relation to the content of the article

572

573

Data, scripts, code, and supplementary information availability

574 Data, scripts and code are available online: <https://doi.org/10.5281/zenodo.11402818> ; Nabias et al,
575 2024

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