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► To cite this version:

Florian Lasgorceux, Julien Papaix, Yoann Bunz, Damien Combrisson, Thomas Opitz. Space-time species distribution modeling for opportunistic presence-only data: a case study of passerines in a protected area. 2024. hal-04616332v1

HAL Id: hal-04616332

<https://hal.science/hal-04616332v1>

Preprint submitted on 18 Jun 2024 (v1), last revised 1 Jul 2024 (v2)

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Space-time species distribution modeling for opportunistic presence-only data: a case study of passerines in a protected area

Florian Lasgorceux¹, Julien Papaix¹, Yoann Bunz²,
Damien Combrisson², and Thomas Opitz¹

<https://doi.org/10.5802/fake.doi>

Abstract

In recent decades, Europe has experienced a significant decline in common bird species, particularly farmland species, due to anthropic pressures like agricultural intensification. Protected areas, such as the Écrins National Park in France, play a crucial role in mitigating these impacts. In this study, we utilized an opportunistic presence-only dataset of passerine occurrences to evaluate the impact of protected areas on passerine trends. The data, gathered by skilled rangers from Écrins National Park, were used for spatio-temporal modeling to assess the target-group relative abundance of 76 passerine species across a regular grid, with aggregated occurrences per spatio-temporal cell serving as a proxy for sampling effort. The model demonstrated good calibration for most species, with AUC values from cross-validation scenarios exceeding 0.8 in most cases. The model also effectively distinguished habitat preferences and migratory status. Additionally, we compared trends in target-group relative abundance over 2001–2019 in the Écrins National Park with those across France using the French Breeding Bird Survey (STOC program) for 59 common species. Our analysis revealed that forest specialist species benefited the most from protected areas, farmland species decreased more slowly, and high-elevation specialist species generally decreased. Though, some results should be interpreted with care since our assumption of a homogeneous reporting rate across target-group species may be too strong for some very common species. Our findings illustrate that the extensive spatio-temporal resolution provided by opportunistic presence-only data offers valuable insights into biological phenomena and their trends, while reducing the need for other data sources to determine sampling effort proxies. Similar datasets from various protected areas could serve as powerful tools for assessing the effectiveness of conservation policies.

Keywords: Écrins National Park, INLA, habitat preference, migratory status, Poisson process, opportunistic presence-only data, relative abundance, sampling effort, spatio-temporal model, STOC program, target-group

¹Biostatistics and Spatial Processes, INRAE, Avignon, France, ²Parc national des Écrins, Domaine de Charance, Gap, France

Correspondence

florian.lasgorceux@proton.me

Introduction

2

3 In recent decades, Europe has seen a significant decline in the populations of common bird
4 species (Inger et al., 2015), particularly those inhabiting agricultural landscapes (Donald et al.,
5 2001). This sharp decline in farmland bird species has prompted extensive research, leading to
6 numerous country-specific studies (Heldbjerg et al., 2018; Kamp et al., 2021; Newton, 2004;
7 Reif et al., 2008b; Sanderson et al., 2013; Traba and Morales, 2019; Wretenberg et al., 2006). A
8 large-scale study in Europe by Rigal et al., 2023 recently quantified the anthropic pressures im-
9 pacting common bird abundance. They identified agricultural intensification, particularly the use
10 of pesticides and fertilizers, as the primary factor contributing to the general decline, especially
11 among invertebrate feeders. In contrast, responses to changes in forest cover, urbanization, and
12 temperature showed greater variation among different species.

13 The conclusions regarding the health status of forest species in Europe are less consistent.
14 Gregory et al., 2007 estimated that, on average, common forest birds declined by 13% and com-
15 mon forest specialists by 18% from 1980 to 2003. In contrast, by considering a different indicator
16 over the period 1980-2015, Gregory et al., 2019 found a relative stability in common European
17 forest bird populations. A possible explanation for these differences could be the migratory sta-
18 tus of the species. Schulze et al., 2019 demonstrated that non-migratory forest bird species in
19 Central Europe have shown significant positive population trends due to beneficial changes in
20 forest management and environmental conditions. In contrast, birds migrating across continents
21 have declined in recent decades, suggesting significant, contrasting changes in bird populations
22 in Europe. Additionally, habitat preference plays a critical role. Reif et al., 2008a concluded that
23 species closely associated with lowland broad-leaved forests have experienced more positive
24 population trends, whereas those associated with montane and coniferous forests have shown
25 more negative trends.

26 Finally, mountain bird species are particularly vulnerable, experiencing an average decline of
27 10% in Europe (Lehikoinen et al., 2019). This decline is driven by climate and land use changes,
28 such as grazing pressure and afforestation, which have led to distribution shifts towards moun-
29 taintops. Studies by Flousek et al., 2015 and (Zamora and Barea-Azcón, 2015) support this, in-
30 dicating that species breeding at higher altitudes are experiencing more negative population
31 trends, with long-distance migrants being particularly affected.

32 Protected areas and conservation efforts play a crucial role in mitigating the decline of bird
33 populations across Europe. According to the IPBES, 2019, conservation investments from 1996
34 to 2008 have resulted in an average reduction of 29% in the extinction risk for mammals and
35 birds across 109 countries. Focusing on birds across Europe, the EU's Natura 2000 protected
36 area network, while not preventing country-wide population declines in some threatened grass-
37 land bird species (Silva et al., 2018), has been effective for bird conservation, notably for threat-
38 ened species (Duckworth and Altwegg, 2018). Studies by Barnes et al., 2023 also indicate posi-
39 tive associations between protected areas and bird abundance, particularly benefiting rare and
40 declining species. Timmers et al., 2022 conducted a comprehensive meta-analysis and demon-
41 strated a strong association between strict protection measures (International Union for Conser-
42 vation of Nature [IUCN] categories I-IV) and higher bird occurrence in larger forest fragments.

43 In France, a National Park is formed of two zones with different regulatory statuses: the core
44 (regulated area) - the national Park guarantees the protection of this area, as per its decrees, and
45 manages any human activities carried out there, in line with its management objectives - and the

46 surrounding area (projects) - a space designed to achieve ecological consistency and solidarity
47 with the National Park core. In this area, the National Park plays an advisory role and can act as
48 a partner in projects to preserve and promote the natural, historic, cultural and landscape her-
49 itage -. The Écrins National Park is one of those protected areas. The park's geographic features
50 include significant elevation changes, with several peaks over 4000 meters, extensive conifer-
51 ous forests (especially larch), and numerous alpine pastures. The park is responsible for multiple
52 biodiversity monitoring programs within its territory (Bunz, 2022), which have led to extensive
53 synthesis and research works (Noël et al., 2023).

54 In addition to data from monitoring programs, the Écrins National Park possesses a large
55 dataset of presence-only records collected opportunistically by rangers. The primary use of these
56 data is to ensure ecological surveillance with broad spatio-temporal resolution and to serve as
57 a basis for knowledge-sharing within the context of development projects. Using these data in
58 statistical modeling presents a challenge due to sampling variability, which occurs in space and
59 time, and between species and observers because of their opportunistic nature (Van Strien et al.,
60 2013). This sampling variability translates into biases in species distribution models that do not
61 account for it. In this study, we propose to harness this extensive dataset for modeling species
62 habitat preferences, classifying species migratory status, and studying time variations in target-
63 group relative abundance, meaning the relative abundance of a species against a pool of species
64 constituting the so-called target-group of species.

65 Various estimation frameworks and algorithms exist for constructing species distribution
66 models and calibrating their parameters from presence-only data. Widely used methods include
67 Maxent, based on the maximum-entropy principle (Phillips et al., 2006), and various statistical
68 regression modeling frameworks (Valavi et al., 2022). These methods are often based on point-
69 process representations of data (Renner et al., 2015; Warton and Shepherd, 2010), where each
70 observed occurrence of a species is viewed as a point in a cloud of points located in space and
71 time. In this context, models such as Maxent and logistic regression are equivalent to a special
72 case of the point-process setting (Fithian and Hastie, 2013; Renner and Warton, 2013). Due to
73 the uncertainty in reported positions in the Écrins National Park dataset, we rather implement a
74 degraded version of these point process models by aggregating occurrences into spatio-temporal
75 cells, which leads to the use of a generalized additive regression model.

76 Random-effect modeling are often used to capture the complex spatio-temporal structures
77 in data and ecological processes, accurately assessing various sources of uncertainty. This has
78 led to the widespread adoption of Bayesian inference techniques such as Markov Chain Monte
79 Carlo (MCMC, (Gilks et al., 1995; Link et al., 2002)) or Integrated Nested Laplace Approximations
80 (INLA, Illian et al., 2013). We apply the INLA approach to perform complex Bayesian spatio-
81 temporal inferences with relatively large datasets by combining generalized additive regression
82 models with the Stochastic Partial Differential Equation (SPDE) approach, the latter used to rep-
83 resent spatial random effects (Lindgren et al., 2011). The construction and estimation of complex
84 spatio-temporal ecological models are still recent developments (Belmont et al., 2024; Soriano-
85 Redondo et al., 2019), and as far as we know, our study represents the first attempt to evaluate
86 management policies of protected areas using solely opportunistic presence-only data for this
87 type of model.

Material and methods

88

89 Data

90 *Passerines presence-only data.* The dataset of interest comprises 102,513 opportunistically re-
91 ported events of passerine detections between 1994 and 2021, recorded by rangers of the Écrins
92 National Park with professional skills in naturalistic expertise. We chose to focus our study on
93 the *Passeriformes* because it is a taxon generally understood by all rangers, ensuring consistent re-
94 porting rates, unlike more specific taxa. Additionally, we have excluded three species – Common
95 Raven (*Corvus corax*), Red-billed Chough (*Pyrrhonorax pyrrhonorax*), and Alpine Chough (*Pyrrho-
96 corax graculus*) – due to the high uncertainty associated with their reported positions compared
97 to the rest of the passerines. We narrowed the temporal window to the 1994–2021 period to
98 ensure a minimum of 2000 reported events per year (see Appendix 1 for details).

99 The data were collected opportunistically, by sight and/or ear, without a predefined survey
100 methodology, meaning that observation and reporting of observed individuals rely on the mo-
101 tivation of the rangers. Each row of the dataset contains a position, a date, the name of the
102 reported species, the ID of the observer(s), and the number of individuals. However, we choose
103 not to consider the number of individuals because it can vary greatly due to species behavior,
104 particularly in gregarious species, and differences in observers' methods since some observers
105 report species abundance, while others only note presence (see the eBird example in Horns et al.,
106 2018). Thus, we consider one reported event as the presence of at least one reported individual,
107 resulting in a total of 102,513 passerine occurrences.

108 Based on interviews with various rangers, we have gained insight that the reported posi-
109 tion could be i) an approximation of the reported individual's position at detection time, ii) the
110 observer's position at detection time, or iii) another, different position where the observer gath-
111 ered several occurrences before adding them jointly to the data records. Though, when multiple
112 occurrences are gathered at a station position, rangers ensure that the environment is consis-
113 tent between the station position and the bird's individual position at detection time and that
114 the distance between these two positions does not exceed 250m. This distance of 250m is ob-
115 tained by considering at most 100m for the difference between the positions of the detected
116 individual and the observer by sound recognition (Hauptert et al., 2023), plus an additional 150m
117 for the distance between the position at detection time and the station position. To account for
118 this uncertainty surrounding the reported position, we aggregated the data by assigning each
119 reported position to the center of a regular spatial grid with 500m resolution covering the Écrins
120 National Park. We excluded boundary cells with an area smaller than 25m², which corresponds
121 to the resolution of the environmental covariates we use for characterizing the spatial habitat
122 preferences. This discretization results in dividing the Écrins National Park domain into 11,260
123 spatial cells.

124 Our objective is not only to infer species habitat preferences but also to analyze temporal
125 trend variations in relative abundance. Therefore, we divided the 28 years of data into seven pe-
126 riods of 4 years each to capture long-term changes between such periods. Additionally, in order
127 to take into account that some studied species are migratory, we further subdivided the data
128 temporally by month to investigate intra-annual variations. This spatio-temporal discretization
129 scheme results in a total of $7 \times 12 \times 11,260 = 945,840$ spatio-temporal cells.

130 *Passerine population trends synthesis in France.* To compare the local and national trends in rela-
131 tive abundance variations, we also utilized the French Breeding Bird Survey synthesis, known as
132 the STOC program, for the period 2001–2019 (Fontaine et al., 2020; Jiguet et al., 2012). These
133 data present the long-term abundance variation percentages of common birds in France dur-
134 ing this period. Comparing trends from opportunistic data and STOC data serves three main
135 purposes: (i) assessing the consistency of modeling assumptions, (ii) comparing local indicators
136 within a protected area to global indicators across the territory of the entire country, and (iii) pro-
137 viding insights into space-time population trends for species specialized in mountainous habitats,
138 for which surveys such as STOC are quite limited in terms of spatio-temporal coverage.

139 *Environmental Data.* The Écrins National Park is a high-mountain park where the terrain struc-
140 ture plays a predominant role in the ecosystems. We utilized the Digital Elevation Model data
141 from RGE (IGN, 2018) to extract the elevation (McVicar and Körner, 2013) on a 5m regular grid.
142 Subsequently, we calculated the slope at the same resolution using the ‘terrain’ function from
143 the R package *terra* (Hijmans, 2024). Ultimately, we derived two spatial covariates: the mean
144 elevation and the mean slope values per spatial cell at 500m resolution.

145 Regarding the land cover and land use data, we make use of the OSO dataset (Inglada et
146 al., 2018). Originally at a resolution of 10/20m, we applied the nearest neighbor strategy to
147 downscale the values to a 5m resolution, for alignment with the RGE data resolution. To avoid
148 statistical issues due to uncommon land cover and land use types in the Écrins National Park,
149 we aggregated data towards 10 representative categories: Urban, Crops, Meadows, Deciduous
150 forest, Coniferous forest, Grasslands, Woody Heaths, Mineral Surfaces, Glaciers and snow, and
151 Water (see Appendix 2 for further details). We then calculated the percentage of coverage of
152 each category in each spatial cell at 500m resolution.

153 We also used the Historical Monthly Weather Data from WorldClim (CRU-TS 4.06 (Harris
154 et al., 2020) downscaled with WorldClim 2.1 (Fick and Hijmans, 2017)) at 2.5 minutes spatial
155 resolution (roughly 5km) between the years 1994 and 2021. The available variables were aver-
156 age minimum temperature (°C), average maximum temperature (°C), and total precipitation (mm).
157 We extracted the corresponding values in each spatial cell, for each month, and each year. Since
158 the inter-annual resolution of our spatio-temporal cells consists of periods of 4 years, we com-
159 puted the mean of the extracted values of the 4 corresponding years for a given spatial cell and
160 a given month. Finally, we removed the average minimum temperature covariate from our study
161 due to its high correlation with the average maximum temperature (Pearson’s $R > 0.99$).

162 *Preprocessing of model covariates.* Elevation shows strong variability in the Écrins National Park
163 with certain climate and land cover configurations arising predominantly within specific eleva-
164 tion ranges. As a result, both land cover and climatic variables are correlated.

165 Hence, we began by decomposing the climatic variables into their spatial means and spatio-
166 temporal anomalies with respect to their means. We then performed a Principal Component
167 Analysis (PCA, Janžekovič and Novak, 2012) using the R package *ade4* (Dray and Dufour, 2007).
168 The input variables were: the mean elevation, the mean slope, the percentages of coverage com-
169 puted for each of the ten representative categories derived from the OSO classification, as well
170 as the spatial means of average maximum temperature and total precipitation. The first 6 axes
171 of the PCA, accounting for 75% of the information, allow for useful interpretation and have

172 therefore been incorporated into the species distribution models (Appendix 3). The first princi-
 173 pal component axis explains a significant 31.1% of the variation in habitat types, primarily driven
 174 by high-elevation environments, especially in steep areas. The third axis is influenced by grass-
 175 lands, and the fourth axis is primarily driven by wetlands and glaciers. However, since we observe
 176 a significant predominance of bird occurrences in “Water” habitats within urbanized valleys (Fig-
 177 ure 13 in Appendix 3) compared to “Glaciers and snow” habitats (751 occurrences versus 80),
 178 we interpret the fourth axis as ‘urban wetlands’. The interpretation of the fifth axis is also asso-
 179 ciated with high-altitude vegetation, as it is primarily driven by dense, low-growing shrubs and
 180 small trees; henceforth, we will refer to these environments as “woody heaths”. The sixth axis is
 181 driven by low-elevation deciduous forests.

182 This results in the implementation of eight covariates in our statistical model: six spatial
 183 covariates from the PCA analysis replicated for each month and each period, and two spatio-
 184 temporal covariates defined as the anomalies of average maximum temperature and anomalies
 185 of total precipitation.

186 Statistical modeling

187 We applied the same Bayesian hierarchical model (Wikle, 2003) to each species with more than
 188 100 occurrences over the period from 1994 to 2021, excluding *Bombycilla garrulus* where 90%
 189 of its 146 occurrences were reported in 2005, due to a brief invasion event of this species within
 190 the Écrins National Park that year. This resulted in a total of 76 species being analyzed.

191 *Data model.* We denote by s a spatial cell, by m a month, and by p a temporal period of 4 years,
 192 with (s, m, p) representing the corresponding space-time cell. The response variable, denoted as
 193 $Y_i(s, m, p)$, is the number of reported occurrences of species i from the opportunistic presence-
 194 only dataset. We model $Y_i(s, m, p)$ with a hierarchical generative additive mixed model (Knappe,
 195 2016; Pedersen et al., 2019) using a Poisson distribution:

$$(1) \quad Y_i(s, m, p) \mid \mu_i(s, m, p) \sim \text{Poisson}(\mu_i(s, m, p)),$$

196 where $\mu_i(s, m, p)$ is the average number of reported occurrences of species i in the cell (s, m, p) .

197 We assume that $\mu_i(s, m, p)$ is obtained through the combination of two factors: (i) the abun-
 198 dance of species i in the cell (s, m, p) , denoted by $\Lambda_i(s, m, p)$, and (ii) the sampling effort in cell
 199 (s, m, p) for species i , denoted by $E_i(s, m, p)$, which we assume to both act in a multiplicative
 200 way on $\mu_i(s, m, p)$ (Giraud et al., 2016). These relationships lead us to formulate the following
 201 equation:

$$(2) \quad \mu_i(s, m, p) = \Lambda_i(s, m, p) \times E_i(s, m, p)$$

202 *Sampling effort.* A major challenge is now to quantify or eliminate the term representing the sam-
 203 pling effort. When working with passerine bird survey data, parameters such as the number of
 204 listening points, the duration of time spent at each point, distances, study areas, etc., are pre-
 205 defined and meticulously recorded. This ensures that data sampling remains consistent across
 206 different zones or years. With opportunistic data, this is not the case. Worse, sampling methods
 207 differ among observers, causing variations in the frequency of species reporting. This occurs
 208 because observers have the freedom to report sightings as they wish, resulting in significant
 209 differences in detection rates between observers and species. If not taken into account in the
 210 statistical modeling, this heterogeneous sampling will result in bias and wrong conclusions.

211 Within our spatio-temporal discretized framework, the first step is to obtain information
 212 about where and when no observations occurred. This helps distinguish between cells with zero
 213 occurrences due to the absence of observer presence and those with zero occurrences due to
 214 the absence of the species. The strategy involves utilizing the extensive opportunistic presence-
 215 only dataset, using reported occurrences of certain species as indicators of observer presence,
 216 as proposed by Botella et al., 2020. However, it is necessary to assume that these species are
 217 uniformly sampled by all the observers, corresponding to homogeneity in reporting rates across
 218 the species pool, as well as in the probability of detection. This explains one of our reasons to
 219 primarily restrict our study to passerines (see the Subsection *Passerines data*). Following existing
 220 literature, we refer to this set of chosen species with homogeneous sampling conditions as the
 221 target-group (TG) of species. Therefore, we denote the sampling effort term as E instead of E_i ,
 222 and we write $\Lambda_{TG}(s, m, p)$ for the cumulative abundance of all species in the target-group in cell
 223 (s, m, p) . We can then reformulate the average number of occurrences in terms of the abundance
 224 of species i compared to the cumulated abundance of the target-group, and the product of the
 225 sampling effort by the cumulated abundance of the target-group (Equation 4).

$$(3) \quad \mu_i(s, m, p) = \Lambda_i(s, m, p) \times E(s, m, p)$$

$$(4) \quad = \frac{\Lambda_i(s, m, p)}{\Lambda_{TG}(s, m, p)} \times \Lambda_{TG}(s, m, p) E(s, m, p).$$

226 To be able to statistically identify the first term that informs us about target-group relative
 227 abundance of species i , we now need a proxy of the second term $\Lambda_{TG}(s, m, p)E(s, m, p)$. The
 228 most natural approach is to use the number of reported occurrences of the target-group oc-
 229 currences, denoted as $y_{TG}(s, m, p)$. We chose to use the combined occurrences of all passerine
 230 species, which was consistent with algorithms similar to that of Botella et al., 2020 since they
 231 were all selected except for 4 species observed only once [à modifier : (DOI, Data, scripts, code,
 232 supplementary materials).] We kept only the cells with at least one occurrence of the target
 233 group, reducing the number of studied cells to 32,486.

234 *Target-group relative abundance.* Employing a spatio-temporal distribution model enables the im-
 235 plementation of numerous spatio-temporally structured latent fixed or random effects within the
 236 linear structure that we will assume for the predictor $\log(\mu_i(s, m, p))$. We opted to use only one
 237 generic model for each of the 76 species to automate model fitting and facilitate inter-species
 238 comparisons. In Poisson models, it is common practice to distribute the Poisson intensity, de-
 239 noted here as $\mu_i(s, m, p)$, using a log-link function to ensure that $\mu_i(s, m, p)$ remains positive.
 240 Focusing on the parameter of interest, the target-group relative abundance $\frac{\Lambda_i(s, m, p)}{\Lambda_{TG}(s, m, p)}$, we con-
 241 structed our linear regressor by incorporating the proxy of the sampling effort, $y_{TG}(s, m, p)$, as
 242 an offset (Equation 5).

243 By studying the abundance of a passerine compared to all others, we compare species with
 244 different biological characteristics, such as habitats and migration status, which need to be taken
 245 into account in the linear regression. We denoted α_i as the intercept. We examined a linear ef-
 246 fect of the spatial covariates $\mathbf{X}^{(PCA)}(s)$ (PCA components) and the spatio-temporal covariates
 247 $\mathbf{X}^{(anomalies)}(s, m, p)$ (anomalies of climatic covariates) to estimate habitat preferences of species i ,
 248 relative to other passerines. The term $W_i^{(m)}(s)$, $m = 1, \dots, 12$, represents a monthly latent spatio-
 249 temporal Gaussian field. Concretely, this field aims to model intra-annual spatial variations not

250 captured by the covariates, typically variations in target-group relative abundance due to the mi-
 251 gration of certain passerines within the territory of the Écrins National Park. Lastly, we denote
 252 by $f_i(p)$ a non-spatialized inter-annual effect, aiming to capture the variations in target-group
 253 relative abundance across each period p of 4 years.

$$(5) \quad \log(\mu_i(s, m, p)) = \log(y_{TG}(s, m, p)) + \log\left(\frac{\Lambda_i(s, m, p)}{\Lambda_{TG}(s, m, p)}\right)$$

$$(6) \quad = \log(y_{TG}(s, m, p)) + \alpha_i + \mathbf{X}^{(PCA)}(s)\beta_i + \mathbf{X}^{(anomalies)}(s, m, p)\gamma_i + W_i^{(m)}(s) + f_i(p).$$

254 *Statistical inference.* We employed the INLA package for the statistical inference of our models
 255 (Rue et al., 2009). INLA is a fast but accurate estimation method based on deterministic Laplace
 256 approximations –by contrast with approaches based on stochastic simulation, such as MCMC–
 257 and requires that the latent layer ($\log(\mu_i(s, m, p))$ in our model) follows a multivariate Gaussian
 258 distribution, possibly in very high dimension. In this setting, INLA enables the implementation
 259 of a wide range of Gaussian random effects, including spatial fields implemented through the
 260 SPDE approach, which provides a numerically convenient representation of the Matérn covari-
 261 ance function used routinely in spatial statistics (Lindgren et al., 2011), and of priors for hyperpa-
 262 rameters such as variances or correlation ranges. In Appendix 4, we precisely describe the prior
 263 distributions of all parts of $\log(\mu_i(s, m, p))$, i.e., the structure of the model components before
 264 updating them with information from observation data to obtain their posterior distributions.

265 Validation and post-processing

266 The model presented previously is quite comprehensive, allowing for a thorough examination
 267 of information on a species-by-species basis. In the following sections, we delineate the post-
 268 processing phase undertaken to synthesize this information. We address questions pertaining
 269 to the model’s validation and also delve into the three components of the linear predictor (Equa-
 270 tion 6): those concerning the fixed effects – specifically, habitat preferences compared to the
 271 target-group denoted by β_i and γ_i ; the spatial intra-annual component, characterized by the
 272 month-dependent Gaussian field W_i^m , which is associated with migratory status; and the inter-
 273 annual component, represented by the random i.i.d. Gaussian effect $f_i(p)$, which captures long-
 274 term trends in target-group relative abundance.

275 *Computational cost.* For each species, the model comprises 32,486 space-time cells with obser-
 276 vations, and a total of 7,676 latent variables to estimate across the prediction cells. We con-
 277 ducted analyses using the R programming language (R Core Team, 2024) and utilized version
 278 24.02.09 of INLA (Rue et al., 2009), leveraging the PARDISO 8.2 library to accelerate compu-
 279 tations (Eftekhari et al., 2021; Gaedke-Merzhäuser et al., 2023; Pasadakis et al., 2023). This
 280 configuration typically yields computation times averaging around one minute for each model
 281 fit on an 11th Gen Intel(R) Core(TM) i7-1165G7 @ 2.80GHz processor.

282 *Validation.* We evaluated whether our model effectively extracted meaningful insights from the
 283 opportunistic data by comparing its predictive performance against a baseline that considered
 284 only sampling effort. We focus on the prediction of the binary event of presence or absence of a
 285 species in a given cell and month and compute the Area-Under-the-Curve (AUC, Fawcett, 2006;
 286 Jin Huang and Ling, 2005) (where the curve is the so-called Receiver Operating Characteristic
 287 curve) as a simple scalar prediction score for each species using two predictors: (i) the sampling
 288 effort proxy offset and (ii) the full linear predictor (Equation 6). Next, we assessed the model’s

289 generalization ability for predicting new data using k-fold, spatial, and temporal cross-validation
290 scenarios. In k-fold cross-validation, the dataset is divided into k equal parts, with one part used
291 for validation while the rest is used for training (Jung, 2018). This approach yields $k + 1$ AUC
292 scores per species: k scores from predicting each part separately, and one from predicting the
293 entire dataset. We selected $k = 10$ to ensure comparability with temporal and spatial scenarios,
294 where the training data represented between 3.9% and 13.7% of the total volume. This choice
295 aimed to maintain consistency in the quantity of test data across scenarios, ensuring equitable
296 evaluation conditions. In the spatial scenario, we assessed model robustness by alternately re-
297 moving all spatio-temporal cells within a given municipality of the Écrins National Park. Seven
298 municipalities were selected based on geographic zones and data availability, resulting in seven
299 AUC scores per species. For the temporal scenario, we alternately randomly removed half of the
300 data for a given period, resulting in seven AUC scores per species. Further details on the size of
301 the training datasets are given in Appendix 5.

302 *Fixed effects.* We estimated the *a posteriori* distribution of coefficients β_i and γ_i separately for
303 each species i (Equation 6). The posterior mean of each parameter and its sign quantify the
304 importance of the covariates in explaining occurrences of species i relative to the occurrences
305 of all the passerines taken together. The credibility interval of each parameter helps determine
306 how strongly the corresponding covariate influences the species; if the interval does not contain
307 zero, we can consider the covariate as being “significant” (by analogy with the frequentist notion
308 of significance). To synthesize the estimated mean coefficients and assess parameter similarities
309 across species occupying comparable ecological habitats, we conducted Principal Component
310 Analysis (PCA) on estimated parameters followed by species clustering based on the estimated
311 mean effects. This clustering was performed using a hierarchical agglomerative clustering (HAC)
312 algorithm implemented through the *hclust* function, employing the *ward.D2* method (Murtagh
313 and Legendre, 2014).

314 *Month-based spatio-temporal Gaussian field.* The month-based spatio-temporal Gaussian field
315 $W_i^{(m)}$ adds flexibility to the model but is challenging to summarize graphically since we have
316 12 maps per species. Therefore, we opted to reduce dimensionality by spatially averaging each
317 field. For each species, this yields a curve of 12 points depicting the intra-annual variations in
318 occurrences relative to the target-group. Instead of plotting all 76 curves on a single graph, we
319 conducted a Functional Principal Component Analysis (FPCA, Ramsay and Silverman, 2005). The
320 mechanism of the approach is analogous to PCA but adapted to functions instead of vectors. In
321 our case, FPCA decomposes the intra-annual mean effect of a given species into (i) the mean
322 intra-annual effect across all species plus (ii) the remaining signal represented by scores associ-
323 ated with empirically identified harmonics. In a functional principal component analysis (FPCA),
324 harmonics represent the most significant modes of variation in the observed functions. These
325 harmonics are akin to principal components in traditional PCA but are applied to functions rather
326 than conventional variables, where the difference is that functions are represented as vectors
327 with a very large number of components (larger than the sample size of functions), and typically
328 show correlation for components at near positions within the vector. We utilized the *fda* package
329 to conduct these analyses (Ramsay et al., 2009).

330 *Inter-annual effects.* Our motivation for introducing the inter-annual effect in the linear predictor
331 (Equation 6) lies in comparing the target-group relative abundance trends of passerines in the

332 Écrins National Park with the relative abundance trends of common birds in the STOC. If we
 333 denote $\lambda_i^{(STOC)}(y)$ as the estimated abundance of species i in year y by the STOC, then the per-
 334 centage variation in abundance computed by the STOC (Fontaine et al., 2020) can be expressed
 335 as:

$$\left(\hat{\lambda}_i^{(STOC)}(2019) - \hat{\lambda}_i^{(STOC)}(2001)\right) \times \frac{100}{\hat{\lambda}_i^{(STOC)}(2001)}.$$

336 In the model presented in Equation 6, the term capturing the effect of the period p on the
 337 target-group relative abundance of species i is $\exp(f_i(p))$. The INLA method allows us to estimate
 338 a posterior distribution of each $\exp(f_i(p))$. To mimic the STOC period of study, we assume the
 339 target-group relative abundance to be constant in each period p . This allows us to attribute an
 340 estimated relative effect $f_i(y)$ to each year y between 2001 and 2019. We then calculated a
 341 regression line using a linear model with the $f_i(y)$ as the response variable and y the explanatory
 342 variable. If we denote $\hat{f}_i^{(ENP)}(y)$ the fitted value of this linear regression, we could calculate the
 343 percentage variations in target-group relative abundance of species i as

$$\left(\hat{f}_i^{(ENP)}(2019) - \hat{f}_i^{(ENP)}(2001)\right) \times \frac{100}{\hat{f}_i^{(ENP)}(2001)}.$$

344 To enhance robustness and take into account statistical uncertainty, we generated 1000 pos-
 345 terior distributions for each target-group relative abundance trend parameter and repeated this
 346 procedure. Then, we used the median percentage variation in target-group relative abundance
 347 as a reference for each species and compared it to the STOC.

348 Results

349 Validation

350 Figure 1 displays the boxplots of AUC values computed species by species as described in sec-
 351 tion *Validation and post-processing*. We notice a clear improvement in AUC when using the full
 352 linear predictor compared to using only the sampling-effort proxy as offset. This confirms that
 353 opportunistic data are not solely constrained by sampling methods and that valuable information
 354 can be extracted from them.

355 Regarding the boxplots of AUC values obtained using cross-validation (with one value for
 356 each hold-out dataset), we observe a few outliers among the species, some of which occur in all
 357 scenarios, as it is the case for *Cinclus cinclus* and *Motacilla cinerea*. These two species with poor
 358 AUC values relative to others are stream specialist species, for which covariates do not capture
 359 the habitat well. It is worth noting that a species appearing multiple times as an outlier within
 360 the same scenario is listed only once for readability.

361 The AUC values of models with cross-validation are typically slightly lower than those with-
 362 out cross-validation, as expected due to the reduction in the amount of training data and the
 363 more challenging prediction setting with new data not used during training. However, they re-
 364 main generally stable, suggesting that the model does not overfit. Furthermore, despite this re-
 365 lative decrease, the AUC values generally remain high, with approximately 75% of AUC values
 366 above 0.8 across all scenarios. Consequently, we conclude that the model demonstrates a very
 367 good fit to the data, except for two species: *Cinclus cinclus* and *Motacilla cinerea*, which we have
 368 excluded from further analysis.

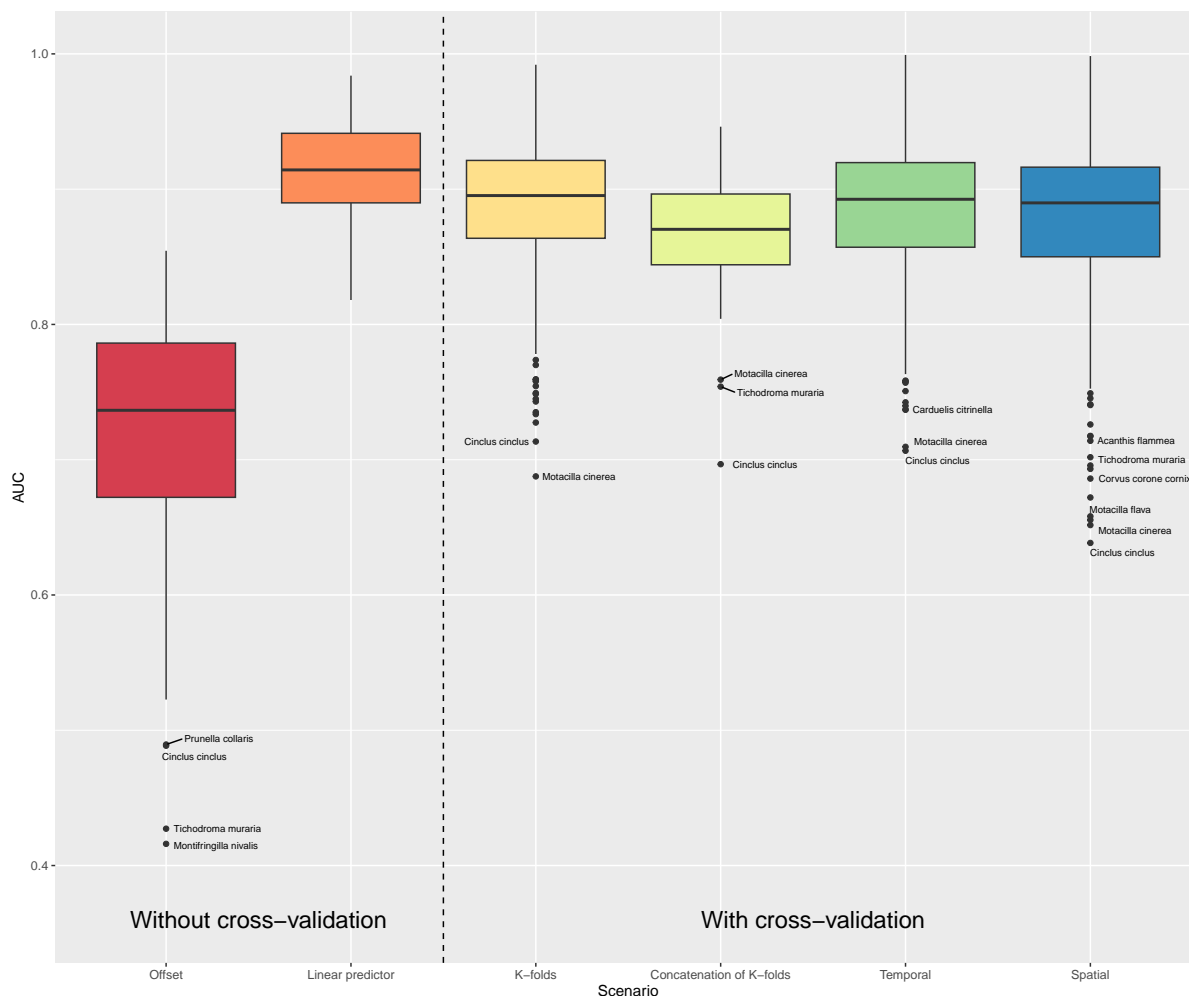


Figure 1 – AUC values calculated based on various linear-predictor and cross-validation scenarios. Boxplots summarize the set of AUC values for all species, and in the case of cross-validation for each combination of species and hold-out dataset. Notations are as follows: “Offset” – model where linear predictor contains only the offset; “Linear predictor” – model with full linear predictor; “K-folds” – model fitted by randomly removing 10% of the cells, ten times; “Concatenation of K-folds” – AUC values computed by concatenating the predictions of the K-folds scenarios; “Temporal” – model fitted by randomly removing half of the data in a given time period, for each time period; “Spatial” – model fitted by removing all the data which occurred in a given city, for seven cities. The species with multiple outlier AUC values in “K-folds”, “Temporal” and “Spatial” scenarios are only noted once. Details on the four cross-validation scenarios (where models always have the full linear predictor) can be found in the “Post-processing and Validation - Validation” section.

369 **Fixed Effects**

370 The mean estimated effects of each covariate and their significance are detailed in Tables 5-7
 371 in Appendix 6. To summarize the information on habitat spatial covariates, we provide a classi-
 372 fication into three clusters based on Principal Component Analysis conducted on the estimated
 373 mean coefficients for each habitat spatial covariate (see subsections “Data - Covariates” and
 374 “Validation and Post-processing - Fixed Effects”). We did not include any species with less than
 375 two significant covariates since we consider that the model does not provide enough informa-
 376 tion on them. These species are generally those, with very few occurrences, as 10 out of these

377 11 species have fewer than 551 occurrences over the 28 years of data, where the value 551 is
 378 below the 25th-percentile of species occurrences. The list of removed species is given in Table 8
 379 in Appendix 6. The PCA reveals two principal axes explaining 62.2% of the classification: the
 380 first axis distinguishes vegetated habitat (coniferous and deciduous forests VS urban wetlands),
 381 while the second axis highlights an altitudinal gradient.

382 The three clusters are presented in Figure 2. We interpret them as follows. Cluster 1: Species
 383 mostly found in closed habitats such as coniferous and deciduous forests (green); Cluster 2:
 384 Species mostly found in high-elevation environments (orange); Cluster 3: Species mostly found
 385 in open habitats and valleys (violet). These results are coherent when comparing a map of eleva-
 386 tion with a map of clusters with the highest occurrences on a 500m×500m regular grid in the
 387 Écrins National Park (see Figure 14 in Appendix 6).

388 The ellipse associated with forest species represents an altitudinal gradient, with species
 389 found in low-elevation forests (*Pyrrhula pyrrhula*), to medium (*Anthus trivialis*) and high-elevation
 390 forests (*Turdus torquatus*). We also observe this altitudinal gradient in the cluster associated with
 391 species from open habitats and valleys, with rocky habitat species such as *Tichodroma muraria*
 392 and *Phoenicurus ochruros*, at the boundary of the high-altitude species cluster. The cluster associ-
 393 ated with species specialized to high-elevation habitats is smaller but well-defined, with typical
 394 species such as *Prunella collaris* and *Montifringilla nivalis*.

395 To address the spatio-temporal covariates, we began by examining their impact on the linear
 396 predictor across all species. We computed the standard deviation of each covariate $X_j \in \mathbf{X}^{(PCA)}$
 397 (and $\mathbf{X}^{(anomalies)}$), multiplied by the mean estimated associated parameter $\beta_{i,j}$ (or $\gamma_{i,j}$) for each
 398 species, and then averaged these values. Our analysis revealed that the precipitation anomalies
 399 covariate had the smallest impact on the linear predictor, with a Mean(SD) of 0.09. This finding
 400 was further supported by only 12 species exhibiting a significant parameter associated with pre-
 401 cipitation anomalies. In contrast, the temperature anomalies covariate had a substantial effect on
 402 the linear predictor, with a Mean(SD) of 0.52, which is significant when compared to the elevation
 403 PCA axis (Mean(SD) = 0.79). Notably, 45 species demonstrated a significant parameter associ-
 404 ated with maximum temperature anomalies. Among these, we identified species with positive
 405 parameters—indicating they tend to be more prevalent when deviations in maximum tempera-
 406 tures from the mean are positive—such as *Emberiza hortulana* and *Lanius collurio*. Conversely, we
 407 also identified species with negative parameters—indicating they are more frequently observed
 408 when deviations in maximum temperatures from the mean are negative—such as *Coccothraustes*
 409 *coccothraustes* and *Fringilla montifringilla*. These results align with the ecological characteristics
 410 of these species, confirming that thermophilic species thrive in warmer conditions, while cold-
 411 resistant species are more abundant in cooler conditions.

412 Intra-annual effect

413 The first two extracted harmonics encompass a significant portion of the intra-annual variability,
 414 explaining 83% of the variance. While the primary harmonic exhibits a greater positive effect
 415 during winter months compared to summer months, the second harmonic shows a positive ef-
 416 fect in summer months and a negative effect in winter months (see Figure 15 in Appendix 7).
 417 Consequently, species with positive scores on the first harmonic tend to be overrepresented in
 418 winter, whereas species with positive scores on the second harmonic are more likely to be over-
 419 represented in spring and summer, which hints at a potential link with the migratory status of
 420 species.

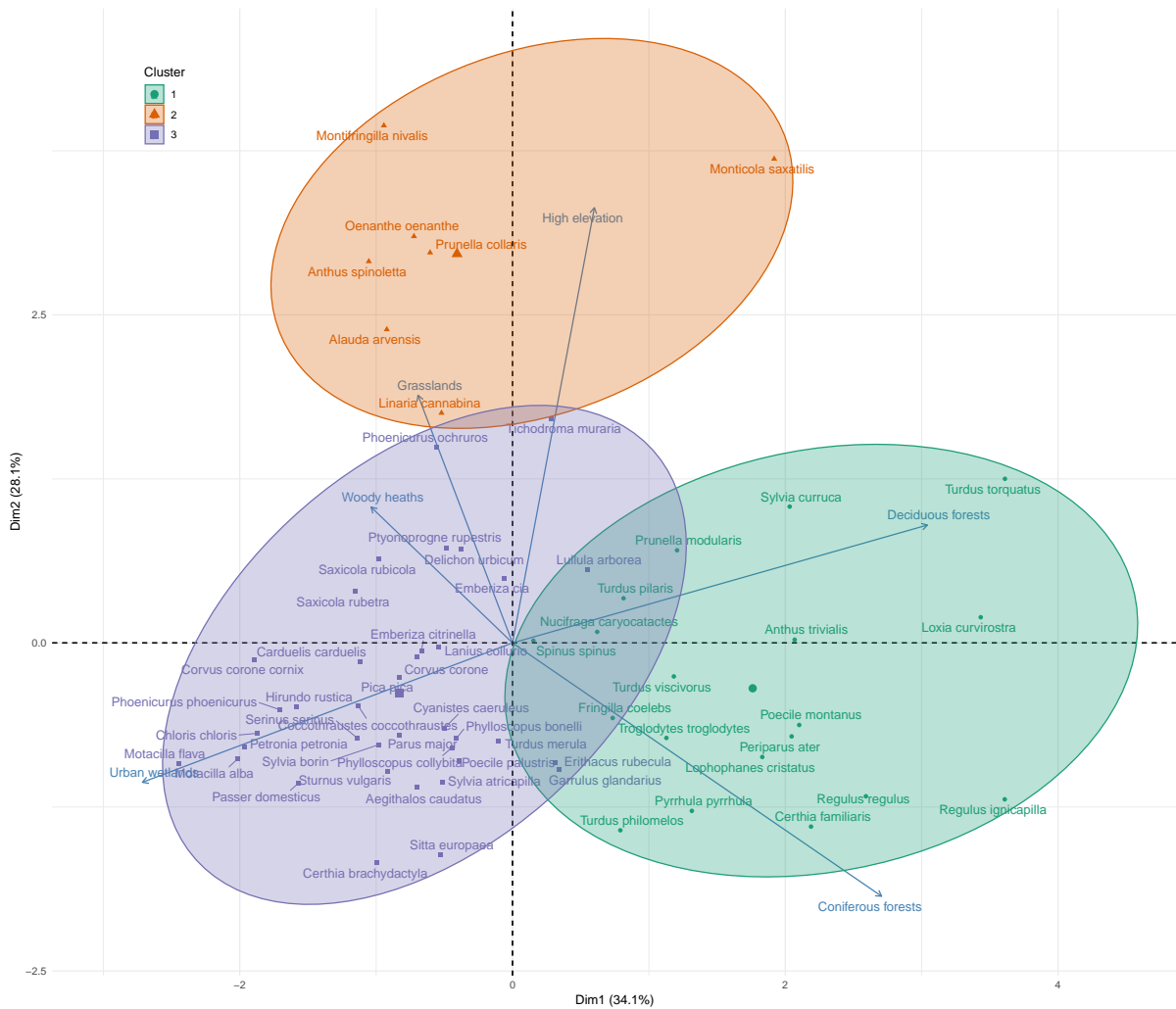


Figure 2 – Classification of 63 species in three clusters based on the estimated mean effects of spatial covariates. A Principal Component Analysis was conducted on the species with at least two credibility intervals that do not include 0. The two main axes explain 62.2% of the variance. Cluster 1: Species mostly found in closed habitats such as coniferous and deciduous forests (green); Cluster 2: Species mostly found in high-elevation environments (orange); Cluster 3: Species mostly found in open habitats and valleys (violet).

421 Figure 3 illustrates the scores associated with the two first harmonic for each species, cat-
 422 egorized by migratory status within the territory of the Écrins National Park, as provided by
 423 experts from the park. Colored ellipses are provided for readability. This analysis confirms that
 424 species overrepresented in winter and underrepresented in spring and summer primarily consist
 425 of sedentary species, while those underrepresented in winter and overrepresented in spring and
 426 summer correspond to migratory species. The details of the scores for each species are given in
 427 Table 9 in Appendix 7. These harmonics effectively distinguish between sedentary and migratory
 428 species within the Écrins National Park, affirming that the month-based spatio-temporal Gauss-
 429 ian field $W_i^{(m)}$ adequately accounts for spatial and intra-annual species variations not explained
 430 by the physical covariates across the territory.

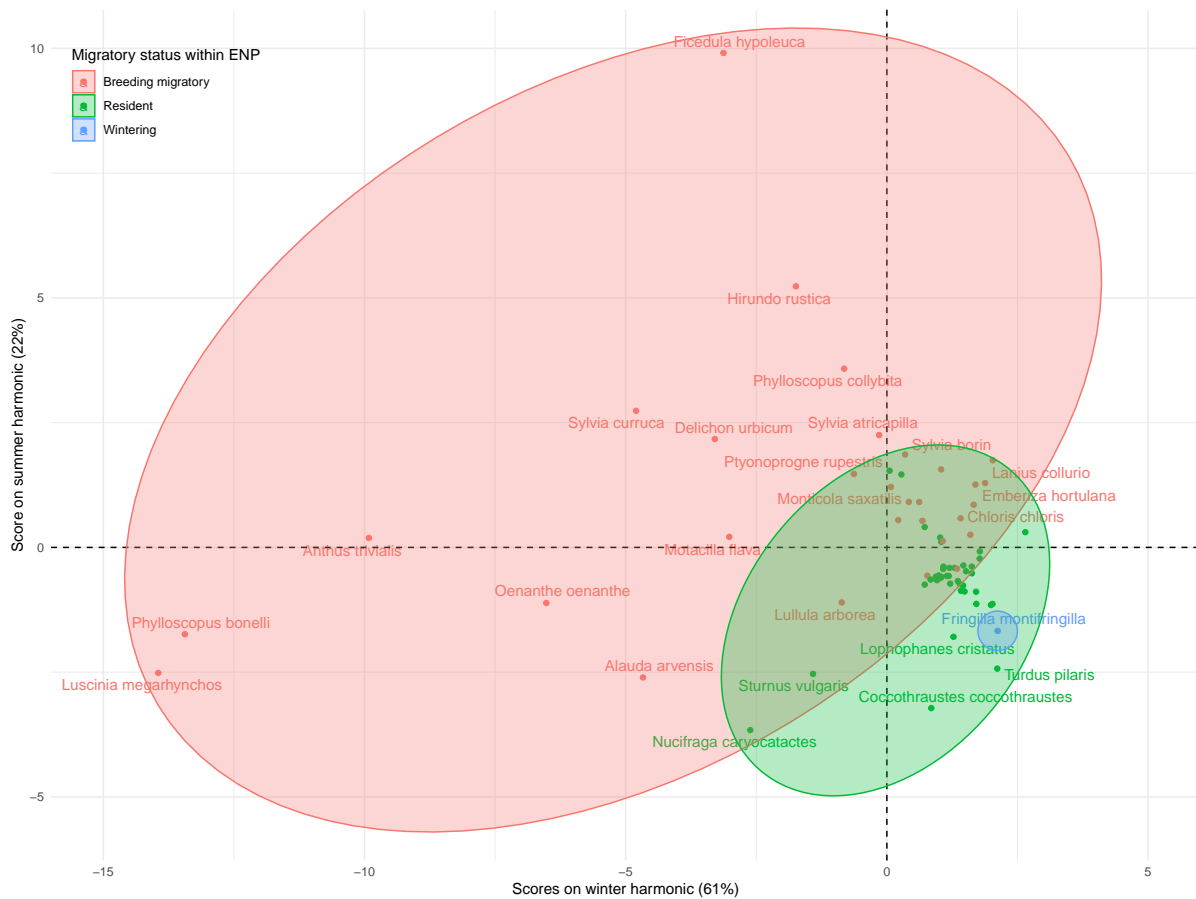


Figure 3 – Point plot of scores associated with the first two harmonics of the FPCA computed on the month-based spatio-temporal Gaussian field $W_i^{(m)}$ estimated for each species. The two first harmonics explain 83% of the variance. The species are categorized by their main migratory status within the territory of the Écrins National Park (ENP), as provided by experts from the park: breeding migratory (red); resident (green); wintering (blue).

431 Inter-annual variability and STOC comparison

432 The estimated percentage variations in target-group relative abundance in the Écrins National
 433 Park between 2001 and 2019, based on 1000 *a posteriori* samples, are illustrated in Figure 4.
 434 Species associated with high-elevation habitats exhibit a mean decline of -16.5% in target-
 435 group relative abundance during 2001–2019. This is mainly due to the strong decrease of three
 436 species: *Monticola saxatilis* (-53.5%), *Prunella collaris* (-26.4%) and *Montifringilla nivalis* (-23.4%).
 437 Conversely, species affiliated with the forest cluster experienced a growth of 12.4% over the
 438 same period.

439 Figure 4 shows that, out of the 19 forest species, 6 exhibited a positive trend while only 2
 440 showed a negative trend based on the 95% credibility interval. For comparison, it is noteworthy
 441 that the STOC reported a decrease of 9.7% in abundance for specialist forest species in France.
 442 When focusing specifically on passerines considered forest specialists by the STOC, the differ-
 443 ence becomes even more pronounced, with a growth of 23.2% in the Écrins National Park, while
 444 the STOC observed a growth of 2% for these species during the same period in France. It is im-
 445 portant to note that this percentage is nevertheless skewed by *Regulus ignicapilla*, which shows
 446 a growth of 168% in relative abundance over the period.

447 Species linked to the valleys cluster experienced a mean decrease of -3.2% in target-group relative
 448 abundance. However, comparing this figure with STOC trends is challenging due to the mix
 449 of generalist species with specialists of built and agricultural environments within this cluster. To
 450 address this, we compare below the trends of passerines in the Écrins National Park, classified by
 451 the STOC as generalist species or species specialized in built and agricultural environments, with
 452 our estimated trends in target-group relative abundance. Built-environment passerines demon-
 453 strate stability in the Écrins National Park (0.26%) compared to a slight decrease in France (-
 454 5.68%). Generalist passerines show an increase of 7.4% in target-group relative abundance in
 455 the park, aligning with the 7% growth reported by the STOC for these species (and 19.4% for
 456 generalist common birds, not only passerines). For farmland species, both show a decrease, but
 457 at a slower rate of -16.5% compared to -22.6% (and 29.5% for farmland common birds, not only
 458 passerines).

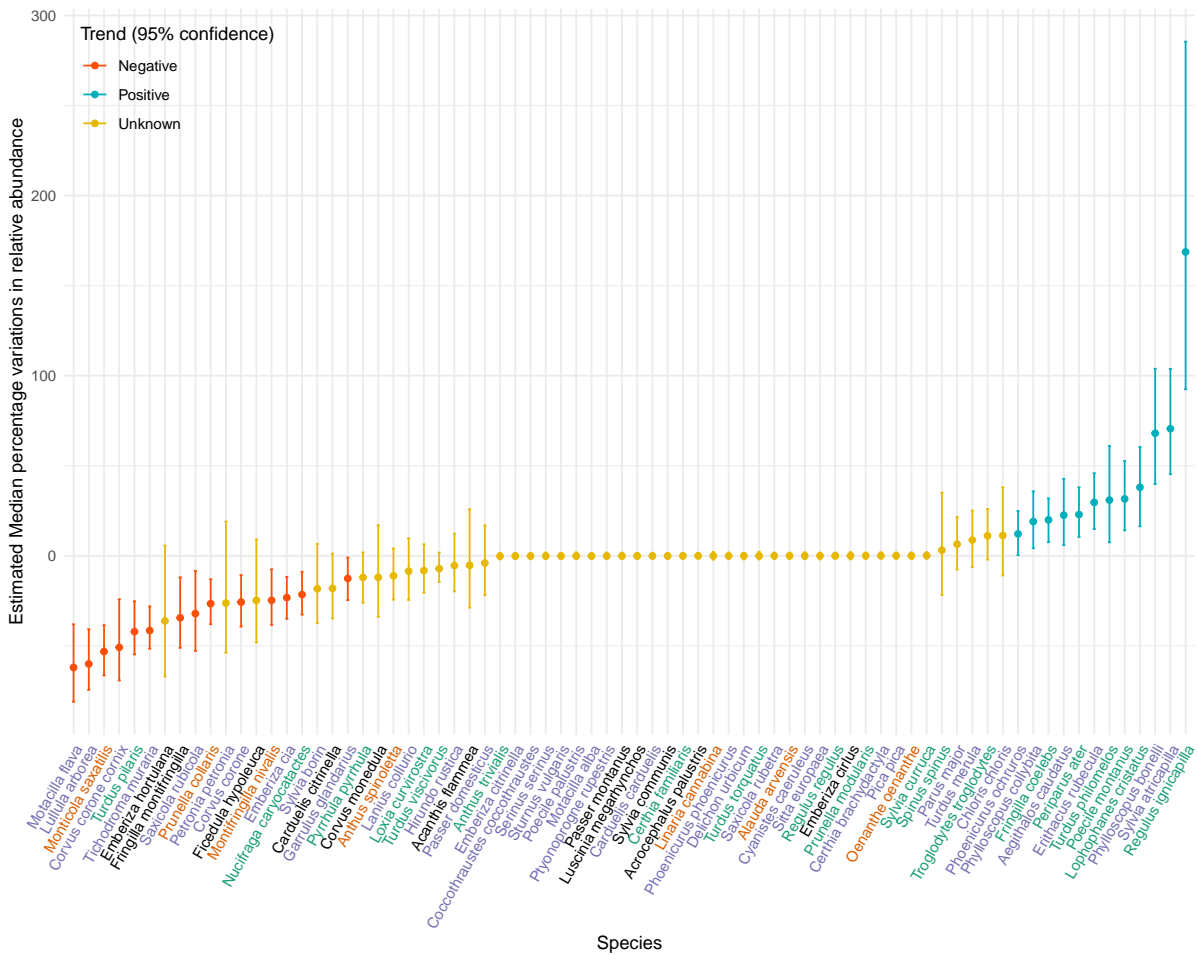


Figure 4 – Illustration of the estimated median percentage variations in target-group relative abundance and credibility intervals for 74 retained species in the Écrins National Park spanning the period 2001–2019. These trends are derived from 1000 samples of the *a posteriori* distribution of the inter-annual effect $\exp(f_i(p))$. Details can be found in the “Post-processing and Validation - Inter-annual effects” section. Credibility intervals shown in red (respectively blue) correspond to intervals below (respectively above) zero, while yellow intervals include zero. Species names are color-coded according to their cluster affiliation in Figure 2. Species with fewer than two significant covariates were not classified and are shown in black.

459 Figure 5 displays more precisely the percentage variations of target-group relative abundance
 460 in the Écrins National Park against the percentage variations of abundance in France computed
 461 by the STOC, between 2001 and 2019. More details on the trends are given in Table 10, Appen-
 462 dix 8. Each species lies in one of the four quadrants. Quadrants (ii) and (iii) correspond to species
 463 whose trends locally within the Écrins National Park align with those in France: increasing for
 464 quadrant (ii) and decreasing for quadrant (iii). Quadrant (i) corresponds to species trending up-
 465 ward nationally but downward in the Écrins, whereas quadrant (iv) represents species increasing
 466 in the Écrins but decreasing nationally. The number of species in each quadrant is as follows: 8
 467 for (i), 14 for (ii), 24 for (iii) and 14 for (iv). Quadrant (iv) is primarily composed of forest species,
 468 while quadrant (i) consists mainly of generalist species, particularly common ones.

469 Furthermore, while the national park status does not prevent the decline of certain species,
 470 it is noteworthy that for 38 species out of 60, trends are more favorable within the national
 471 park compared to national trends for all of France as represent by the $y = x$ slope in Figure 5.
 472 However, some species for which this is not the case are very common (quadrant (i)) and may be
 473 subject to reporting bias (see Discussion).

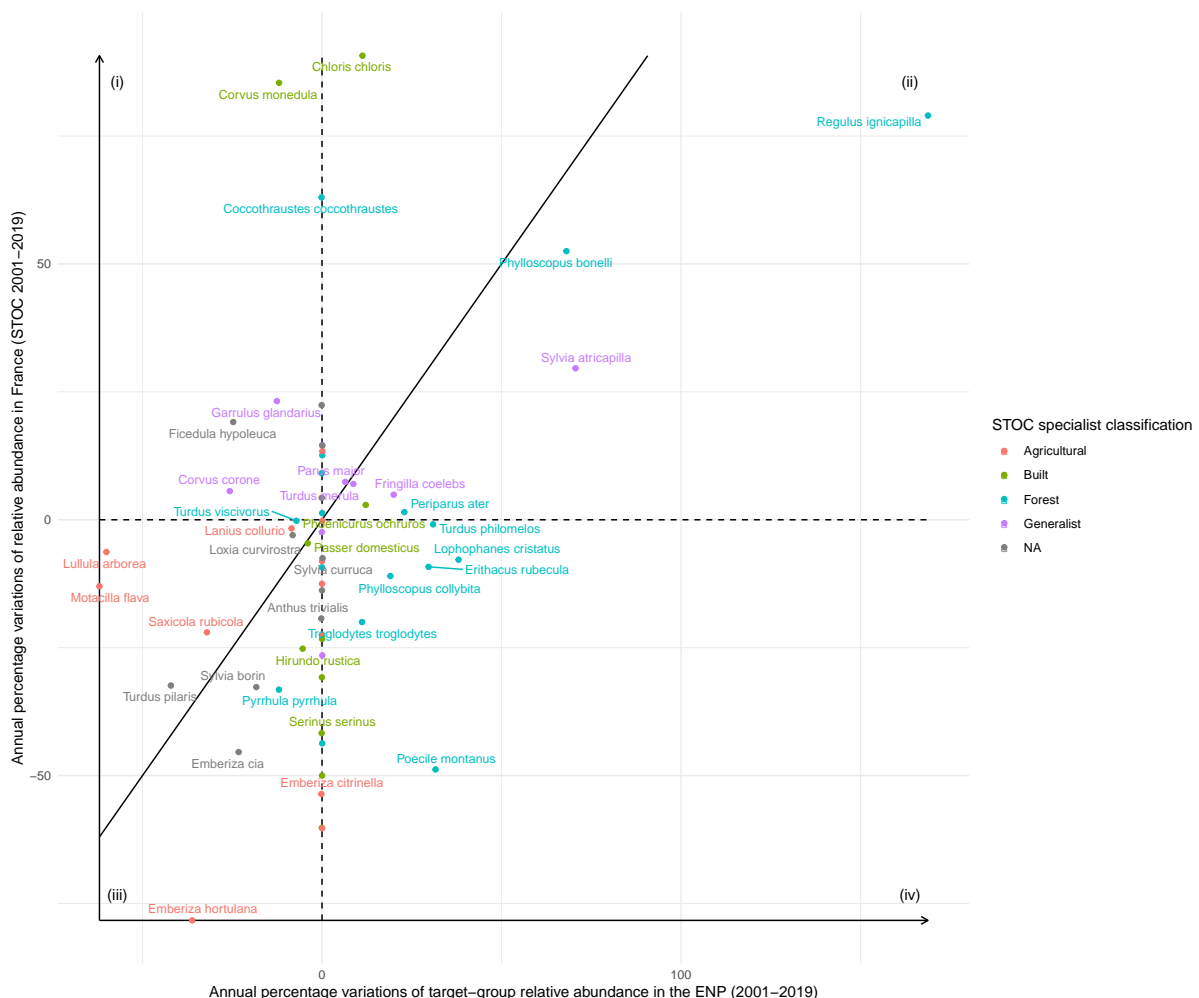


Figure 5 - Point plot of the estimated median percentage variations of target-group relative abundance in the Écrins National Park between 2001 and 2019, against the percentage variations of relative abundance in France between 2001 and 2019 computed by the STOC for 60 species. The names of species with less than 0.1% variation in target-group relative abundance are not plotted for readability.

Discussion

474

475 In our study, we demonstrated that under the assumption of sampling homogeneity across
476 species (but where sampling effort is still allowed to vary in space and time), opportunistic
477 presence-only data could be leveraged to estimate habitat preferences, migratory status, and
478 target-group relative abundance trends of passerine species. This finding is not novel *per se*,
479 as numerous studies have utilized such data to model species distributions or abundance trends
480 (Botella et al., 2020; Bradter et al., 2018; Kéry et al., 2010; Phillips et al., 2009; Valavi et al., 2022;
481 Van Strien et al., 2013). However, it is one of only a few approaches achieving this within a unique
482 spatio-temporal model. To our knowledge, the most similar work has been done by Giraud et al.,
483 2016 and Coron et al., 2018 modeling spatial relative abundance (abundance divided by the
484 abundance of an arbitrarily chosen cell) of passerines using a Poisson distribution. Their work
485 provides theoretical results regarding parameter identifiability, as well as scenarios for data simu-
486 lation and parameter estimation. However, the use of their models requires access to appropriate
487 survey data based on a standardized sampling protocol, whereas our study relied solely on a sin-
488 gle set of opportunistic data. We also found the inclusion of the month-based spatio-temporal
489 latent Gaussian field $W_i^{(m)}$ and the use of Functional Principal Component Analysis to be per-
490 tinent for assessing phenological effects when modeling target-group relative abundances of
491 species with different migratory statuses. Another potential application of such Gaussian fields
492 and FPCA could involve implementing a nonlinear additive predictor component for altitude to
493 study species' phenological changes as responses to climate: altitude ascents, migrations, etc.

494 The STOC has demonstrated the effectiveness of public policies on protected areas. Outside
495 of reserves, the average decline of 56 species between 2004 and 2018 was -6.6%, whereas
496 within reserves, an increase of 12.5% was observed (Fontaine et al., 2020). Additionally, our
497 study offers new insights into the role of protected areas in mitigating the decline of passerine
498 populations, though our trends should be interpreted with caution. Indeed, several very com-
499 mon species show a negative estimated target-group relative abundance in the park, while the
500 STOC indicates positive trends for these same species. Thus, we believe that our assumption of
501 homogeneous reporting is overly optimistic and partially inaccurate. Despite this issue affecting
502 7 out of 60 species, we can still draw meaningful conclusions.

503 Notably, we demonstrate that forest passerines benefit the most in the Écrins National Park.
504 While not reversing the trend, the decline of farmland passerines in the park is slower than in the
505 rest of France, consistent with findings from previous studies (Palacín and Alonso, 2018; Silva
506 et al., 2018). Furthermore, our study provides novel insights into high mountain species not pre-
507 viously investigated by the STOC. Our indicator, the target-group relative abundance, shows a
508 global decline for species specialist to high-elevation environments. This trend aligns with the
509 global decrease of mountain specialist species in Europe (-10% during 2002–2014) as reported
510 by Lehtikoinen et al., 2019. These findings will be valuable for comparison with upcoming anal-
511 yses of the STOM, a survey analogous to the STOC for mountain species, which has only been
512 operational since 2012, with its first results yet to be analyzed.

513 We identify three areas for future improvements in our modeling approach using solely op-
514 portunist data:

515 (i) The assumption of uniform sampling, which could be questionable due to differences in de-
516 tectability, species commonness/rarity (Snäll et al., 2011), or agent identification skills and re-
517 porting prevalence (Bradter et al., 2018), albeit reasonable in practice and lacking better options.

518 Heterogeneous detectability remains an issue without data based on standardized sampling pro-
519 tocols and seems difficult to correct except for trying to include prior expert knowledge into
520 models. Different reporting behavior due to species commonness/rarity can introduce bias in
521 estimated intercept terms, such as α_j in Equation 6, but would not have any impact on the other
522 terms varying in space and/or time, as long as this bias in reporting behavior is homogeneous
523 across space, time and physical predictors. Effects related to agent identification skills and re-
524 porting prevalence could potentially be identified by including random effects for the rangers
525 in the model. As a general recommendation to reduce biases and improve the exploitability of
526 opportunistic presence-only data, we suggest that when observers report a species, all species
527 of the same taxon should also be reported for better use of opportunistic presence-only data in
528 species distribution modeling.

529 (ii) The acquired information is relative to a target-group of species since we used the target-
530 group occurrences as a proxy for the sampling effort (Equation 4). This implies that the potential
531 for interpretations of results in terms of absolute abundance and its variation across covariates,
532 space, and time remains relatively limited.

533 (iii) There are multiple ways to define this target-group, which impacts the interpretation of
534 abundances relative to it. The composition of this target-group primarily relies on available data
535 sources, ranging from studies covering a single species (Farr et al., 2021) to those encompass-
536 ing thousands (Botella et al., 2021). Some studies focus exclusively on species within the same
537 taxonomic group (Van Strien et al., 2013), while others consider species across different taxa
538 (Escamilla Molgora et al., 2022). Botella et al., 2020 recommends choosing a set of species that
539 are consistently abundant across a broad range of environmental sub-regions, that we did in this
540 study.

541 We have recognized a pressing need for more comprehensive descriptions of what we refer
542 to as “sampling effort” when dealing with opportunistic presence-only data, and for method-
543 ologies to effectively incorporate it into modeling endeavors. Various strategies have been pro-
544 posed to address sampling efforts depending on the studied taxa, the available datasets and the
545 type of model. These include the utilization of random or target-group pseudo-absences with
546 Maxent (Phillips et al., 2006, 2009), target-group background occurrences (Botella et al., 2020),
547 integration of information from detection/nondetection data (Dorazio, 2014; Fithian et al., 2015;
548 Giraud et al., 2016), or questionnaires (Bradter et al., 2018). Additionally, consideration of proxy
549 variables such as road density or population density (Kervellec et al., 2023), and covariates rep-
550 resenting the accessibility of a site, such as distance to roads, cities, coastlines, and protected
551 areas (El-Gabbas and Dormann, 2018; Henckel et al., 2020; Moreira et al., 2024; Warton et al.,
552 2013) or refinements between these methods and the target-group approach (Chauvier et al.,
553 2021). Another commonly used proxy, especially in studies focusing on cetaceans and fish, is
554 the logbooks of vessels (Alglave et al., 2022; Ver Hoef et al., 2021).

555 Our findings suggest that, despite the statistical challenges arising from taking sampling bi-
556 ases into account, opportunistic presence-only data provide unparalleled spatio-temporal cov-
557 erage, allowing for the depiction of consistent biological indicators that would be challenging
558 to obtain using traditional methods. This includes monitoring trends in target-group relative
559 abundance over extended periods and developing species distribution models across vast ge-
560 ographical areas. Such information can serve as valuable quantitative indicators for assessing
561 the effectiveness of conservation policies in protected areas.

562 In our case study, very large occurrence numbers were available for the target-group, such that
563 uncertainties about the target-group abundance can be expected to be relatively small. For mod-
564 eling more precisely the target-group abundance, for example in cases with smaller occurrence
565 numbers or when large areas of the study domain are only very weakly sampled, we could de-
566 velop an alternative approach wherein $Y_{TG}(s, m, p)$ could be initially modeled with a Poisson
567 distribution using a mean parameter $\mu_{TG}(s, m, p)$, fitted to the data to estimate $\mu_{TG}(s, m, p)$.
568 Subsequently, we would use the estimated Poisson mean as a proxy for $\Lambda_{TG}(s, m, p)E(s, m, p)$,
569 rather than the raw count. This modification could potentially enhance robustness and improve
570 the assessment of uncertainties inherent to our modeling approach.

571

Acknowledgements

572 The authors would like to thank all the staff of the Écrins National Park and its scientific team
573 for contributing to the dataset. They also appreciate advice of Denis Allard on using factorial
574 principal component analysis, and Loïc Houde for technical support with the high-performance
575 computing cluster used to implement the models of this case study.

576

Fundings

577 The authors declare that they have received no specific funding for this study.

578

Conflict of interest disclosure

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

581

Data, script, code, and supplementary information availability

582 Data are available online (<https://doi.org/10.24072/fake1>[Replace by the DOI of the
583 webpage hosting the data]; cite[Replace by the citation of the data])

584 Script and codes are available online (<https://doi.org/10.24072/fake2>[Replace by the DOI
585 of the webpage hosting the script and code]; cite[Replace by the citation of the script and code])

586 Supplementary information is available online (<https://doi.org/10.24072/fake3>[Replace by
587 the DOI of the webpage hosting the Supplementary information]; cite[Replace by the citation
588 of the Supplementary information])

589 The DOI hyperlinks should be active. They should also be present in the reference list and cited
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591 available). Do not forget to add the reference of the recommendation, the reference of the data,
592 scripts, code and supplementary material to your bib file, if appropriate.

593

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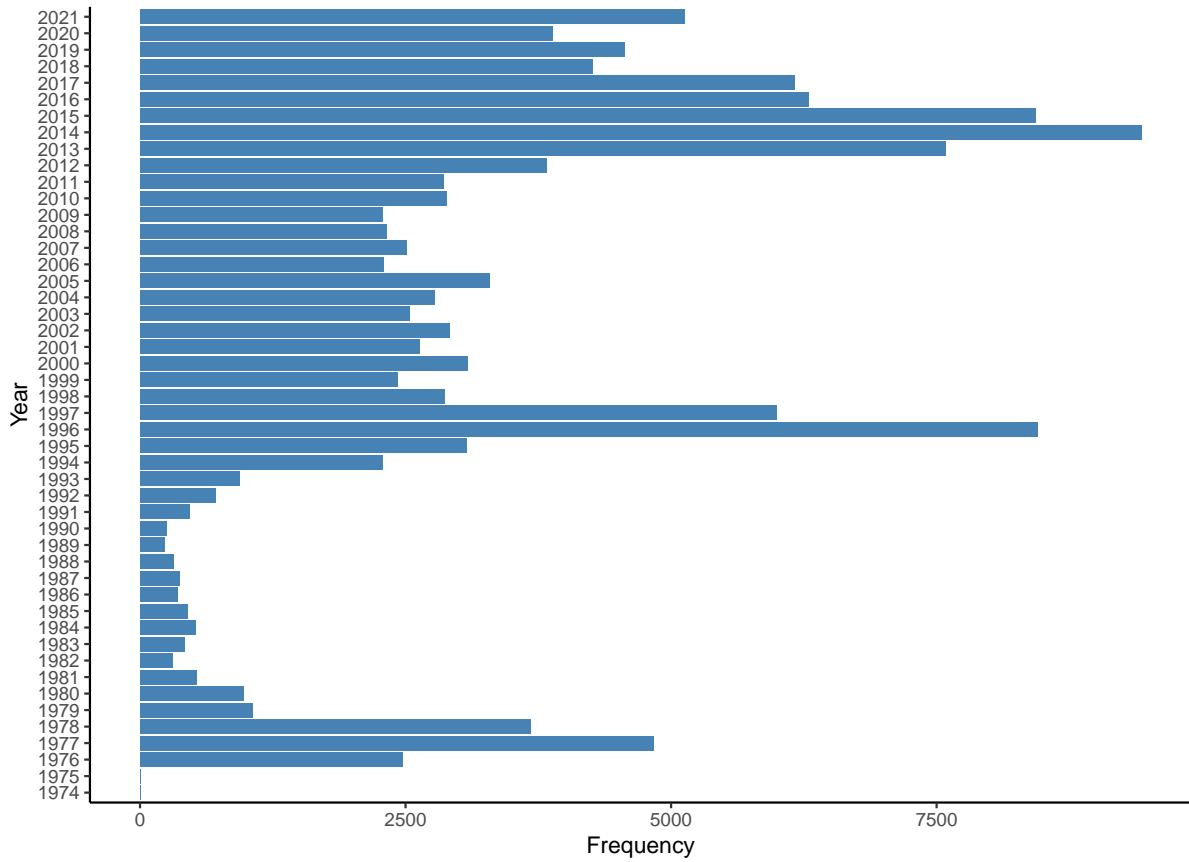
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1. Passerines data



Source: Écrins National Park

Figure 6 - Number of reported opportunistic passerine occurrences in the Écrins National Park between 1974 and 2021. Three passerines were excluded from the barplot: Common Raven (*Corvus corax*), Red-billed Chough (*Pyrrhonorax pyrrhonorax*), Alpine Chough (*Pyrrhonorax graculus*) for a total of 102,513 occurrences.

850

2. OSO covariates

851 The OSO data are raster data produced at 10m and 20m spatial resolution. These two outputs
 852 are provided because the Sentinel-2 spectral bands used in the production process are acquired
 853 at 10m (visible and near-infrared) and 20m (red-edge, near and medium infrared) (Inglada, 2018).
 854 The nomenclature includes 24 classes. We then apply the nearest neighbor strategy to adjust
 855 the values to a 5m resolution, aligning with the elevation data resolution used in this study (IGN,
 856 2018). We present in Table 1 the percentage of coverage for each OSO class in the Écrins Na-
 857 tional Park. The percentage of coverage for a chosen class is computed as the number of spatial
 858 cells of this class over the total number of spatial cells, based on a 5m regular grid of the Écrins
 859 National Park domain.

Table 1 – OSO data nomenclature including percentage coverage at a 5m resolution Écrins National Park. Classes with a percentage of coverage greater than 1% are in bold for easier readability.

Number	Nomenclature	Percentage
1	Dense buildings	<0.1%
2	Sparse buildings	0.6%
3	Industrial and commercial areas	0.3%
4	Road surfaces	<0.1%
5	Rapeseed	<0.1%
6	Cereal with straw	0.1%
7	Protein crops	<0.1%
8	Soybean	<0.1%
9	Sunflower	<0.1%
10	Corn	0.1%
11	Rice	<0.1%
12	Tubers/roots	<0.1%
13	Meadows	2.1%
14	Orchards	<0.1%
15	Vineyards	<0.1%
16	Deciduous forests	3.7%
17	Coniferous forests	16.0%
18	Grasslands	40.1%
19	Woody heaths	5.3%
20	Mineral surfaces	27.7%
21	Beaches and dunes	0.1%
22	Glaciers or snow	2.8%
23	Water	1.1%
0	Other	<0.1%

860 Some classes are nearly absent in the Écrins National Park. Hence, the first four classes: *Dense*
 861 *buildings*, *Sparse buildings*, *Industrial and commercial areas* and *Road surfaces* are gathered into
 862 the **Urban** terminology. The following classes: *Rapeseed*, *Cereal with straw*, *Legumes*, *Soybean*,
 863 *Sunflower*, *Corn*, *Rice*, *Tubers/roots*, *Orchards*, *Vineyards* are gathered into the **Crops** terminology.
 864 Due to their very low percentage of surface area, the classes *Beaches and dunes* and *Other* are
 865 excluded from the analysis.

866 Hence, the land cover land used classification used in the article is composed of 10 classes
 867 and is summarized in Table 2.

Table 2 – OSO data nomenclature adjusted for the Écrins National Park, including percentage coverage at a 5m resolution in the Écrins National Park.

Nomenclature	Percentage
Urban	0.9%
Crops	0.3%
Meadows	2.1%
Deciduous forests	3.7%
Coniferous forests	16.0%
Grasslands	40.1%
Woody heaths	5.3%
Mineral surfaces	27.7%
Glaciers or snow	2.8%
Water	1.1%

868 Using a spatial grid with a resolution of 500m, we calculated the coverage percentage of
 869 these 10 classes in each spatial cell to construct the OSO covariates, which formed the basis of
 870 the Principal Component Analysis.

871 **References**

- 872 Inglada, J, Vincent, A, & Thierion, V (2018). Theia OSO Land Cover Map 2018 [Data set]. Zenodo.
 873 <https://doi.org/10.5281/zenodo.3613415>
 874 IGN (2018). RGE ALTI®. Version 2.0.

875

3. PCA figures

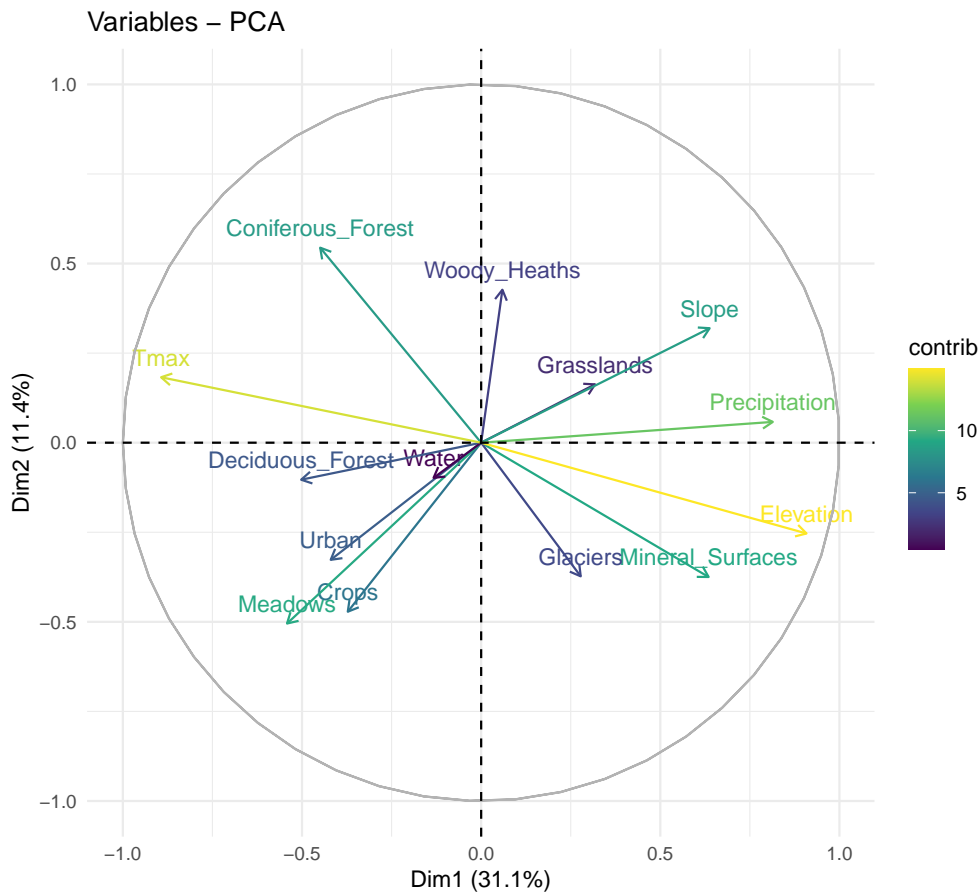


Figure 7 – Correlation circles of axis 1 and 2 of the PCA.

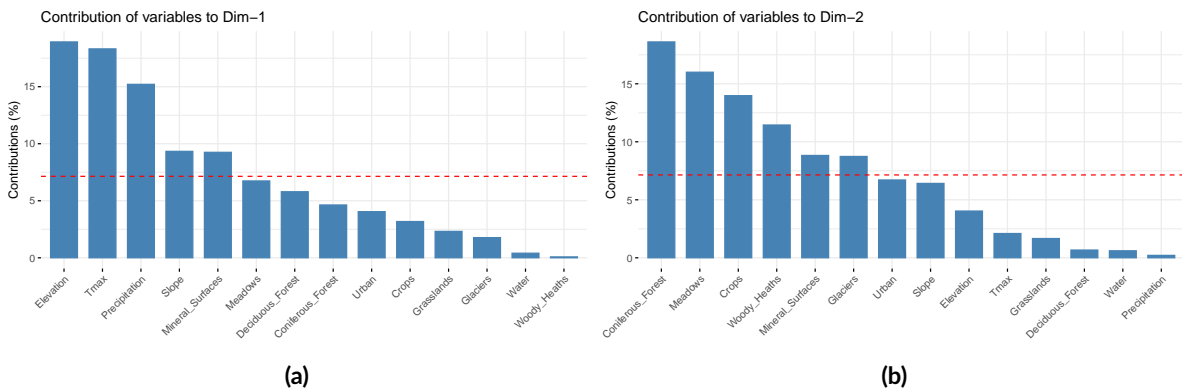


Figure 8 – Contribution of each spatial covariate to the axis 1 (a) and 2 (b) of the PCA.

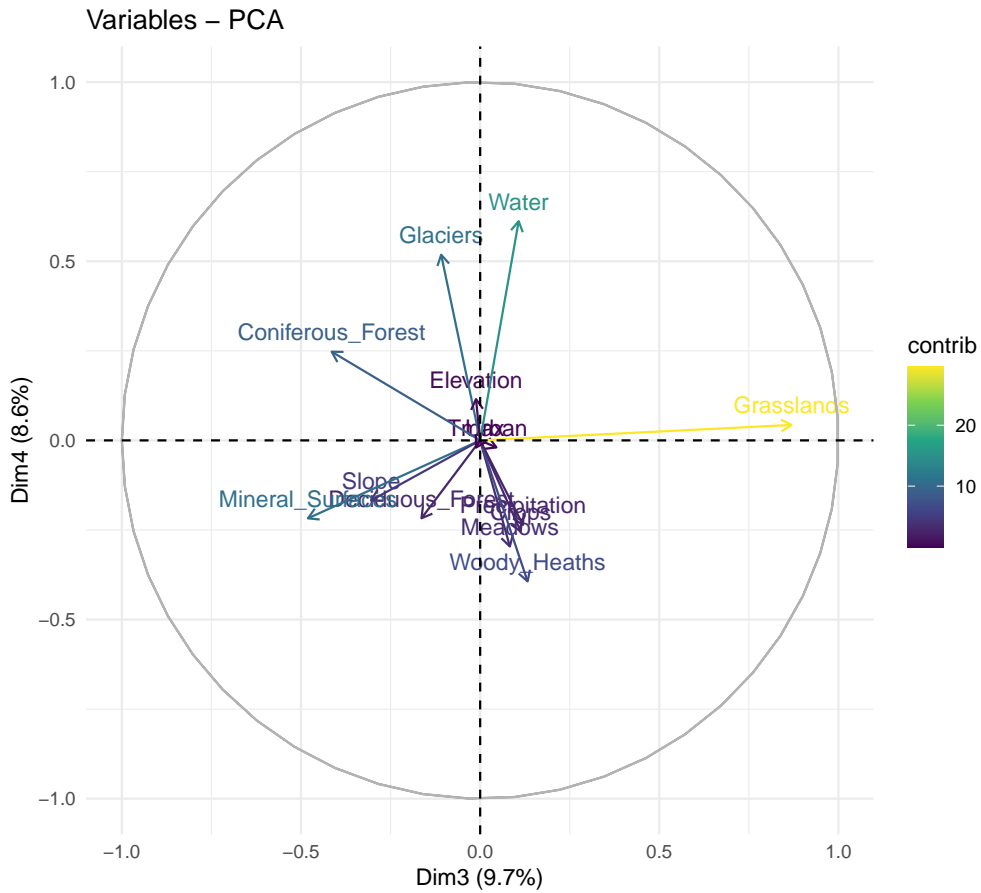


Figure 9 - Correlation circles of axis 3 and 4 of the PCA.

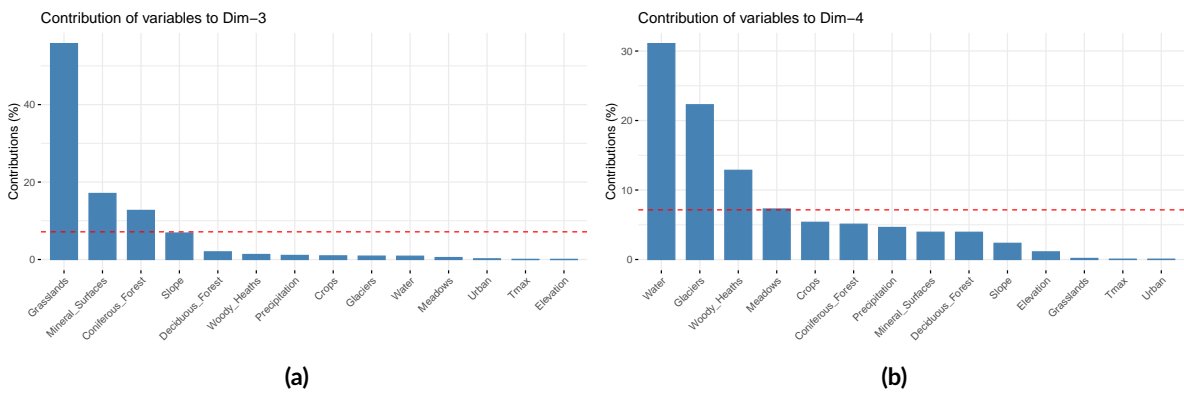


Figure 10 - Contribution of each spatial covariate to the axis 3 (a) and 4 (b) of the PCA.

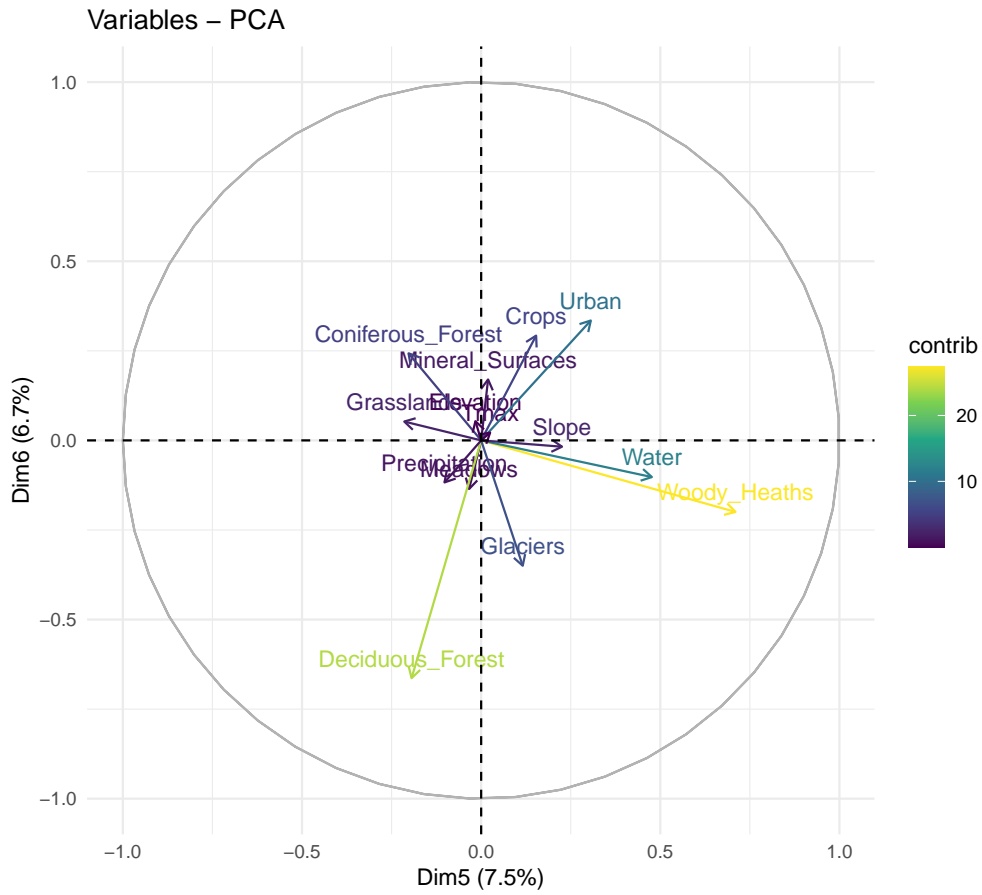


Figure 11 – Correlation circles of axis 5 and 6 of the PCA.

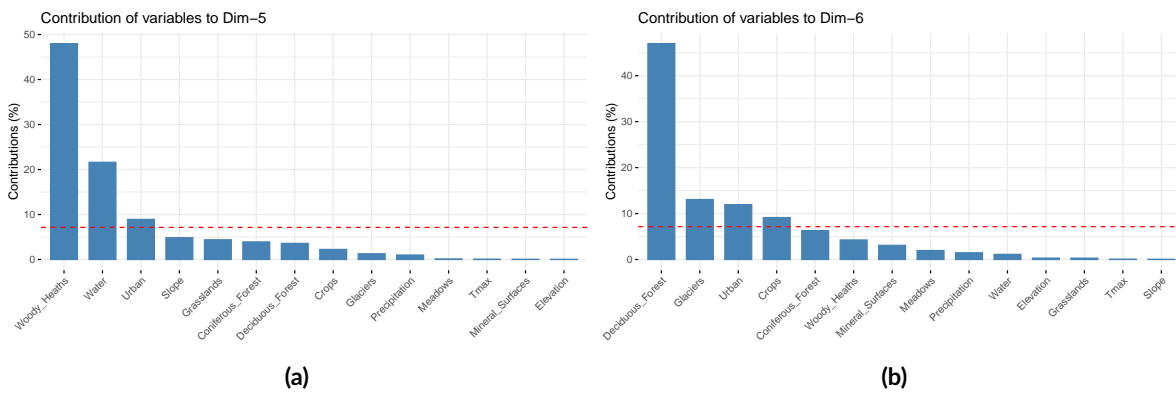


Figure 12 – Contribution of each spatial covariate to the axis 5 (a) and 6 (b) of the PCA.

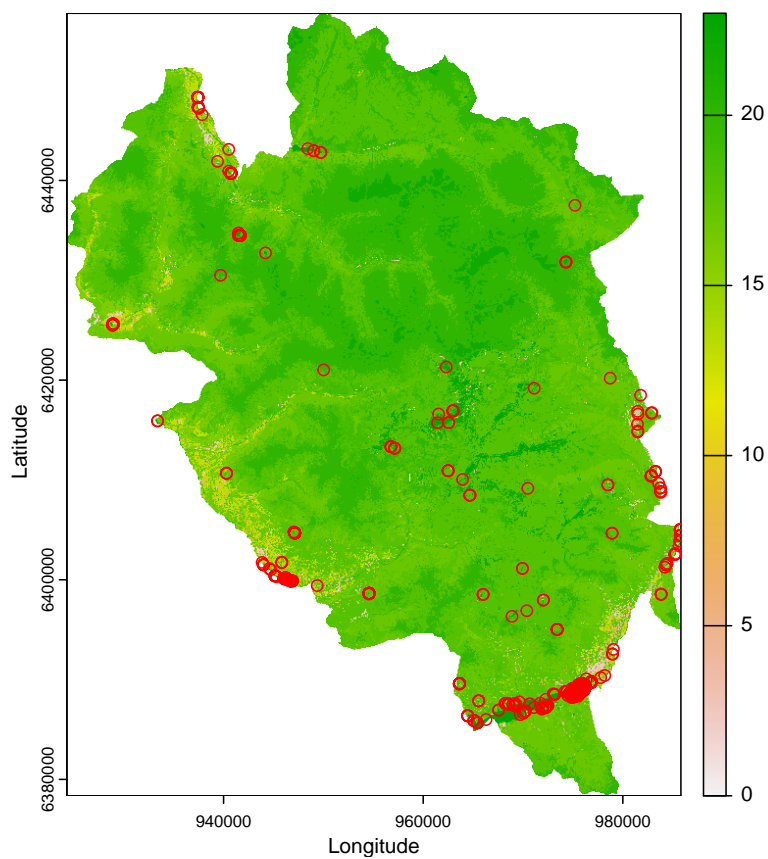


Figure 13 – Map of passerine occurrences in wetlands (red circles) on OSO land cover land used classification in the Écrins National Park . Each number correspond to a class described in Table 1. The observations mainly occur in urban wetlands in the valleys.

4. Parameter models – Priors

876

877 We will now describe each prior used, i.e., the structure of the model components before
878 updating them with information from observation data to obtain their posterior distributions.
879 Each of the parameters β_i or γ_i associated with the fixed covariate effects has a very weakly
880 informative Gaussian prior distribution centered at zero and with a precision hyperparameter
881 $\tau_\beta = 10^{-3}$. For each month m , the spatial field $W_i^{(m)}$ is *a priori* represented using a 2-dimensional
882 Gaussian random field based on the SPDE approach, where the Matérn covariance function has
883 a fixed shape parameter $\nu^{(m)} = 1$, while the effective range, $\rho_i^{(m)}$, and the standard deviation,
884 $\sigma_i^{(m)}$, are endowed with so-called penalized complexity priors (PC priors, Simpson et al., 2017): *a*
885 *priori*, the probability of having range less than $\rho_0^{(m)} = 1$ is set to $\alpha_\rho^{(m)} = 0.5$, and the probability
886 of having standard deviation larger than $\sigma_0^{(m)} = 1$ is set to $\alpha_\sigma^{(m)} = 0.5$. Since the spatial field $W_i^{(m)}$
887 is replicated month by month, a cyclic *AR*(1) correlation structure (Box et al., 2015) is applied
888 such that the value of $W_i^{(m)}$ is informed by the values of $W_i^{(m-1)}$ and $W_i^{(m+1)}$, where $m-1 = 12$
889 for $m = 1$ and $m+1 = 1$ for $m = 12$. Regarding each period p , the inter-annual random effects
890 $f_i(p)$ have independent and identically distributed Gaussian prior distributions with a precision
891 hyperparameter $\tau_f = 10^{-3}$.

892

References

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- 895 Simpson D., Rue H., Riebler A., Martins T.G., Sørbye S.H. (2017). Penalising Model Component
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5. Temporal and spatial cross-validation scenarios

Table 3 – Table of temporal cross-validation scenarios. The total number of space-time cells with at least one occurrence in the target-group is 32,486. For each scenario, half of these cells of the corresponding period of four years and their associated occurrences are removed.

Scenario	Period	Removed cells	Percentage
13	1994-1997	1782	5.5%
14	1998-2001	1274	3.9%
15	2002-2005	1512	4.7%
16	2006-2009	1525	4.7%
17	2010-2013	2670	8.2%
18	2014-2017	4477	13.8%
19	2018-2021	3001	9.2%

Table 4 – Table of spatial cross-validation scenarios. The total number of space-time cells with at least one occurrence in the target-group is 32,486. For each scenario, the cells of a given city and their associated occurrences are removed.

Scenario	Period	Removed cells	Percentage
20	Saint-Christophe-en-Oisans	4407	13.6%
21	Valjouffrey	2473	7.6%
22	La Chapelle-en-Valgaudémar	2700	8.3%
23	Orcières	2167	6.7%
24	Châteauroux-les-Alpes	1839	5.7%
25	L'Argentière-la-Bessée	1345	4.1%
26	La Grave	2656	8.2%

6. Habitat preferences

Table 5 – Mean estimated parameters on spatial covariates : PCA Axis 1 to 3. Significant parameters based on the 95% interval of credibility are in bold.

Species (Occurrences)	High Elevation	Coniferous forests	Grasslands
<i>Acanthis flammea</i> (464)	0.03	0.1	0.39
<i>Acrocephalus palustris</i> (138)	-0.39	0.25	0.45
<i>Aegithalos caudatus</i> (1599)	-0.29	0.15	-0.29
<i>Alauda arvensis</i> (1068)	0.98	-0.54	0.73
<i>Anthus spinoletta</i> (1934)	1	-0.57	0.65
<i>Anthus trivialis</i> (1292)	-0.13	0.53	0.47
<i>Bombycilla garrulus</i> (146)	NA	NA	NA
<i>Carduelis carduelis</i> (1549)	-0.21	-0.12	0.24
<i>Carduelis citrinella</i> (730)	0.49	0.04	0.33
<i>Certhia brachydactyla</i> (449)	-0.62	0.07	-0.35
<i>Certhia familiaris</i> (984)	-0.09	0.71	-0.27
<i>Chloris chloris</i> (668)	-0.36	-0.4	-0.11
<i>Cinclus cinclus</i> (1887)	-0.67	0.11	-0.05
<i>Coccothraustes coccothraustes</i> (486)	-0.18	-0.18	-0.11
<i>Corvus corone</i> (1745)	-0.21	-0.04	0.24
<i>Corvus corone cornix</i> (187)	-0.66	0.08	1.02
<i>Corvus monedula</i> (152)	-0.43	-0.05	-0.71
<i>Cyanistes caeruleus</i> (1892)	-0.27	0.01	-0.17
<i>Delichon urbicum</i> (734)	0.21	-0.13	-0.04
<i>Emberiza cia</i> (1548)	0.1	0.01	0.05
<i>Emberiza cirrus</i> (202)	-0.69	0.16	0.11
<i>Emberiza citrinella</i> (1734)	-0.21	-0.07	0.39
<i>Emberiza hortulana</i> (134)	0.02	0.24	0.91
<i>Erithacus rubecula</i> (3354)	-0.35	0.26	-0.18
<i>Ficedula hypoleuca</i> (273)	-0.55	0.13	0.05
<i>Fringilla coelebs</i> (5447)	-0.26	0.3	0.03
<i>Fringilla montifringilla</i> (551)	-0.22	-0.01	0.04
<i>Garrulus glandarius</i> (2201)	-0.37	0.31	-0.13
<i>Hirundo rustica</i> (642)	-0.38	-0.11	0.38
<i>Lanius collurio</i> (834)	-0.24	-0.14	0.35
<i>Linaria cannabina</i> (1369)	0.47	-0.31	0.55
<i>Lophophanes cristatus</i> (2160)	-0.16	0.63	-0.17
<i>Loxia curvirostra</i> (1890)	0.22	0.83	0.34
<i>Lullula arborea</i> (321)	-0.15	0.48	0.94
<i>Luscinia megarhynchos</i> (376)	-0.46	0.12	0.29
<i>Monticola saxatilis</i> (566)	1.16	-0.35	0.47
<i>Montifringilla nivalis</i> (999)	1.48	-1.13	0.44
<i>Motacilla alba</i> (1088)	-0.55	-0.22	0.22
<i>Motacilla cinerea</i> (697)	-0.37	-0.05	-0.08

<i>Motacilla flava</i> (144)	-0.24	-0.59	0.37
<i>Nucifraga caryocatactes</i> (2275)	0.39	0.49	0.02
<i>Oenanthe oenanthe</i> (2263)	0.94	-0.68	0.66
<i>Parus major</i> (3165)	-0.31	0	-0.16
<i>Passer domesticus</i> (947)	-0.45	-0.44	-0.09
<i>Passer montanus</i> (209)	-0.9	0.22	0.8
<i>Periparus ater</i> (3595)	-0.18	0.45	-0.21
<i>Petronia petronia</i> (197)	-0.48	-0.42	0.24
<i>Phoenicurus ochruros</i> (4183)	0.48	-0.43	0.11
<i>Phoenicurus phoenicurus</i> (668)	-0.27	-0.24	0.07
<i>Phylloscopus bonelli</i> (1668)	-0.17	0.17	-0.28
<i>Phylloscopus collybita</i> (2944)	-0.27	0.3	-0.03
<i>Pica pica</i> (1061)	-0.32	-0.18	0.24
<i>Poecile montanus</i> (2433)	0.07	0.7	-0.01
<i>Poecile palustris</i> (774)	-0.35	0.09	-0.21
<i>Prunella collaris</i> (1775)	1.2	-0.78	0.05
<i>Prunella modularis</i> (1386)	0.2	0.29	0.24
<i>Ptyonoprogne rupestris</i> (1695)	0.26	-0.11	-0.12
<i>Pyrrhula pyrrhula</i> (1816)	-0.32	0.44	-0.29
<i>Regulus ignicapilla</i> (686)	-0.37	0.74	-0.33
<i>Regulus regulus</i> (1030)	-0.27	0.79	-0.22
<i>Saxicola rubetra</i> (944)	-0.2	-0.15	0.74
<i>Saxicola rubicola</i> (313)	-0.14	-0.13	0.75
<i>Serinus serinus</i> (736)	-0.46	-0.09	-0.01
<i>Sitta europaea</i> (1841)	-0.47	0.03	-0.51
<i>Spinus spinus</i> (848)	-0.07	0.18	0.17
<i>Sturnus vulgaris</i> (353)	-0.56	-0.29	0.46
<i>Sylvia atricapilla</i> (1904)	-0.46	0.13	-0.24
<i>Sylvia borin</i> (576)	-0.49	0.14	0.23
<i>Sylvia communis</i> (143)	-0.39	0.36	0.71
<i>Sylvia curruca</i> (753)	0.26	0.35	0.28
<i>Tichodroma muraria</i> (1318)	0.86	-0.27	-0.46
<i>Troglodytes troglodytes</i> (2903)	-0.27	0.47	0.01
<i>Turdus merula</i> (2938)	-0.39	0.18	-0.04
<i>Turdus philomelos</i> (1209)	-0.37	0.56	-0.06
<i>Turdus pilaris</i> (1270)	0.04	0.2	0.29
<i>Turdus torquatus</i> (1665)	0.51	0.64	0.36
<i>Turdus viscivorus</i> (2585)	-0.11	0.43	0.21

Table 6 – Mean estimated parameters on spatial covariates : PCA Axis 4 to 6. Significant parameters based on the 95% interval of credibility are in bold.

Species (Occurrences)	Urban wetlands	Woody Heaths	Deciduous forests
<i>Acanthis flammea</i> (464)	-0.26	-0.09	0.13
<i>Acrocephalus palustris</i> (138)	-0.24	-0.04	-0.25
<i>Aegithalos caudatus</i> (1599)	0	0.07	-0.2
<i>Alauda arvensis</i> (1068)	0.11	-0.34	-0.01
<i>Anthus spinoletta</i> (1934)	0.02	0.1	0.01
<i>Anthus trivialis</i> (1292)	-0.43	-0.37	0.14
<i>Bombycilla garrulus</i> (146)	NA	NA	NA
<i>Carduelis carduelis</i> (1549)	0.15	-0.01	-0.08
<i>Carduelis citrinella</i> (730)	-0.02	0.04	0.03
<i>Certhia brachydactyla</i> (449)	0.05	0.03	-0.22
<i>Certhia familiaris</i> (984)	-0.27	-0.56	0.08
<i>Chloris chloris</i> (668)	0.23	-0.01	-0.17
<i>Cinclus cinclus</i> (1887)	0.14	0.04	-0.16
<i>Coccothraustes coccothraustes</i> (486)	0.15	0	-0.1
<i>Corvus corone</i> (1745)	-0.02	-0.02	-0.11
<i>Corvus corone cornix</i> (187)	-0.09	0.08	-0.41
<i>Corvus monedula</i> (152)	-0.1	0.67	-0.23
<i>Cyanistes caeruleus</i> (1892)	-0.06	0.05	-0.12
<i>Delichon urbicum</i> (734)	-0.02	0.26	0.04
<i>Emberiza cia</i> (1548)	-0.2	0.16	-0.05
<i>Emberiza cirius</i> (202)	-0.19	0	-0.06
<i>Emberiza citrinella</i> (1734)	-0.11	-0.18	-0.18
<i>Emberiza hortulana</i> (134)	-0.29	0.09	-0.1
<i>Erithacus rubecula</i> (3354)	-0.1	0.01	-0.01
<i>Ficedula hypoleuca</i> (273)	0.09	0.09	-0.13
<i>Fringilla coelebs</i> (5447)	-0.12	-0.1	0.07
<i>Fringilla montifringilla</i> (551)	-0.09	-0.02	-0.08
<i>Garrulus glandarius</i> (2201)	-0.16	-0.03	-0.06
<i>Hirundo rustica</i> (642)	0.27	-0.07	-0.14
<i>Lanius collurio</i> (834)	-0.14	-0.2	-0.14
<i>Linaria cannabina</i> (1369)	0.08	0.04	0.12
<i>Lophophanes cristatus</i> (2160)	-0.11	-0.15	0.24
<i>Loxia curvirostra</i> (1890)	-0.23	-0.46	0.51
<i>Lullula arborea</i> (321)	-0.21	-0.05	0.01
<i>Luscinia megarhynchos</i> (376)	-0.14	-0.05	-0.11
<i>Monticola saxatilis</i> (566)	-0.61	0.09	0.35
<i>Montifringilla nivalis</i> (999)	-0.18	-0.09	0.01
<i>Motacilla alba</i> (1088)	0.34	-0.02	-0.16
<i>Motacilla cinerea</i> (697)	0.25	0.07	-0.2
<i>Motacilla flava</i> (144)	0.83	-0.72	-0.02
<i>Nucifraga caryocatactes</i> (2275)	0.15	-0.01	0.13

<i>Oenanthe oenanthe</i> (2263)	-0.15	0.06	0.03
<i>Parus major</i> (3165)	-0.03	0.11	-0.17
<i>Passer domesticus</i> (947)	0.38	-0.3	-0.05
<i>Passer montanus</i> (209)	0.07	-0.27	0
<i>Periparus ater</i> (3595)	-0.23	-0.24	0.26
<i>Petronia petronia</i> (197)	0.1	-0.32	-0.33
<i>Phoenicurus ochruros</i> (4183)	-0.15	0.11	-0.04
<i>Phoenicurus phoenicurus</i> (668)	0.25	0	-0.16
<i>Phylloscopus bonelli</i> (1668)	-0.06	0.14	-0.15
<i>Phylloscopus collybita</i> (2944)	0	0.1	-0.14
<i>Pica pica</i> (1061)	-0.02	-0.12	-0.12
<i>Poecile montanus</i> (2433)	-0.17	-0.37	0.19
<i>Poecile palustris</i> (774)	-0.05	0.05	-0.11
<i>Prunella collaris</i> (1775)	-0.08	0.18	0.09
<i>Prunella modularis</i> (1386)	-0.17	0.02	0.22
<i>Ptyonoprogne rupestris</i> (1695)	-0.07	0.32	-0.03
<i>Pyrrhula pyrrhula</i> (1816)	-0.1	-0.24	0.14
<i>Regulus ignicapilla</i> (686)	-0.56	-0.42	0.35
<i>Regulus regulus</i> (1030)	-0.22	-0.24	0.3
<i>Saxicola rubetra</i> (944)	-0.07	-0.17	-0.22
<i>Saxicola rubicola</i> (313)	-0.21	-0.1	-0.26
<i>Serinus serinus</i> (736)	0.14	0.11	-0.08
<i>Sitta europaea</i> (1841)	0	-0.08	-0.16
<i>Spinus spinus</i> (848)	0.09	0.04	0.13
<i>Sturnus vulgaris</i> (353)	0.32	-0.67	0.03
<i>Sylvia atricapilla</i> (1904)	0.01	0.16	-0.09
<i>Sylvia borin</i> (576)	0	0.06	-0.21
<i>Sylvia communis</i> (143)	-0.3	0.09	-0.1
<i>Sylvia curruca</i> (753)	-0.49	-0.03	0.2
<i>Tichodroma muraria</i> (1318)	-0.16	0.4	0.13
<i>Troglodytes troglodytes</i> (2903)	-0.23	-0.13	0.05
<i>Turdus merula</i> (2938)	-0.07	0.05	-0.05
<i>Turdus philomelos</i> (1209)	0.03	-0.26	0.05
<i>Turdus pilaris</i> (1270)	-0.23	-0.15	0.06
<i>Turdus torquatus</i> (1665)	-0.6	-0.3	0.41
<i>Turdus viscivorus</i> (2585)	-0.22	-0.19	0.08

Table 7 – Mean estimated parameters on spatio-temporal covariates : anomalies of maximum temperature and anomalies of precipitation. Significant parameters based on the 95% interval of credibility are in bold.

Species (Occurrences)	Anomalies of Tmax	Anomalies of Precipitation
<i>Acanthis flammea</i> (464)	-0.002	-0.0215
<i>Acrocephalus palustris</i> (138)	-0.0044	0.2126
<i>Aegithalos caudatus</i> (1599)	0.001	-0.0633
<i>Alauda arvensis</i> (1068)	0.003	0.1266
<i>Anthus spinoletta</i> (1934)	0.0026	0.0376
<i>Anthus trivialis</i> (1292)	0.0019	0.0237
<i>Bombycilla garrulus</i> (146)	NA	NA
<i>Carduelis carduelis</i> (1549)	6e-04	-0.0013
<i>Carduelis citrinella</i> (730)	-0.0019	-0.0407
<i>Certhia brachydactyla</i> (449)	-0.001	-0.0068
<i>Certhia familiaris</i> (984)	0.0012	-0.0321
<i>Chloris chloris</i> (668)	0.0071	0.1904
<i>Cinclus cinclus</i> (1887)	-5e-04	-0.0223
<i>Coccothraustes coccothraustes</i> (486)	-0.0031	-0.272
<i>Corvus corone</i> (1745)	-0.0016	-0.0549
<i>Corvus corone cornix</i> (187)	-0.0052	-0.0928
<i>Corvus monedula</i> (152)	-0.0061	-5e-04
<i>Cyanistes caeruleus</i> (1892)	1e-04	-0.0823
<i>Delichon urbicum</i> (734)	5e-04	0.1054
<i>Emberiza cia</i> (1548)	-5e-04	0.0086
<i>Emberiza cirrus</i> (202)	0.0024	0.0605
<i>Emberiza citrinella</i> (1734)	-0.0012	-0.0128
<i>Emberiza hortulana</i> (134)	0.0097	0.2859
<i>Erithacus rubecula</i> (3354)	-0.0013	-0.0195
<i>Ficedula hypoleuca</i> (273)	-5e-04	0.0073
<i>Fringilla coelebs</i> (5447)	-0.0011	-0.0236
<i>Fringilla montifringilla</i> (551)	0.0031	-0.2194
<i>Garrulus glandarius</i> (2201)	2e-04	0.0014
<i>Hirundo rustica</i> (642)	0.0073	0.0208
<i>Lanius collurio</i> (834)	0.0065	0.2762
<i>Linaria cannabina</i> (1369)	-0.0021	0.0514
<i>Lophophanes cristatus</i> (2160)	-2e-04	-0.0279
<i>Loxia curvirostra</i> (1890)	0.0013	-0.0489
<i>Lullula arborea</i> (321)	3e-04	0.0426
<i>Luscinia megarhynchos</i> (376)	-0.0094	0.1224
<i>Monticola saxatilis</i> (566)	0.006	0.1575
<i>Montifringilla nivalis</i> (999)	0.0014	-0.1305
<i>Motacilla alba</i> (1088)	-0.0024	0.0163
<i>Motacilla cinerea</i> (697)	-0.0032	0.0632
<i>Motacilla flava</i> (144)	-0.0051	0.1618

<i>Nucifraga caryocatactes</i> (2275)	0	4e-04
<i>Oenanthe oenanthe</i> (2263)	-6e-04	0.129
<i>Parus major</i> (3165)	2e-04	-0.0695
<i>Passer domesticus</i> (947)	-0.001	-0.0128
<i>Passer montanus</i> (209)	-0.0014	-0.0342
<i>Periparus ater</i> (3595)	4e-04	-0.0424
<i>Petronia petronia</i> (197)	-0.0036	0.0778
<i>Phoenicurus ochruros</i> (4183)	-1e-04	0.0478
<i>Phoenicurus phoenicurus</i> (668)	-0.0015	-0.0212
<i>Phylloscopus bonelli</i> (1668)	-4e-04	0.0714
<i>Phylloscopus collybita</i> (2944)	-0.0031	0.0105
<i>Pica pica</i> (1061)	0.0026	-0.0426
<i>Poecile montanus</i> (2433)	0.0013	-0.0437
<i>Poecile palustris</i> (774)	0.0036	-0.1009
<i>Prunella collaris</i> (1775)	0.0014	-0.0971
<i>Prunella modularis</i> (1386)	-0.0047	-0.0339
<i>Ptyonoprogne rupestris</i> (1695)	0.001	0.0746
<i>Pyrrhula pyrrhula</i> (1816)	9e-04	-0.0381
<i>Regulus ignicapilla</i> (686)	-0.004	-0.0081
<i>Regulus regulus</i> (1030)	0.002	-0.0646
<i>Saxicola rubetra</i> (944)	0.0027	0.2046
<i>Saxicola rubicola</i> (313)	0.0021	0.1124
<i>Serinus serinus</i> (736)	-7e-04	0.1231
<i>Sitta europaea</i> (1841)	-0.0027	-0.0289
<i>Spinus spinus</i> (848)	1e-04	-0.1358
<i>Sturnus vulgaris</i> (353)	0.005	0.0386
<i>Sylvia atricapilla</i> (1904)	-0.0034	0.0182
<i>Sylvia borin</i> (576)	-0.0041	0.1405
<i>Sylvia communis</i> (143)	0.0193	0.2733
<i>Sylvia curruca</i> (753)	0.0049	0.1386
<i>Tichodroma muraria</i> (1318)	-0.0019	-0.0576
<i>Troglodytes troglodytes</i> (2903)	-1e-04	0.0162
<i>Turdus merula</i> (2938)	6e-04	-0.0262
<i>Turdus philomelos</i> (1209)	-5e-04	-0.0198
<i>Turdus pilaris</i> (1270)	-0.0012	-0.1565
<i>Turdus torquatus</i> (1665)	-8e-04	-0.0144
<i>Turdus viscivorus</i> (2585)	0.0014	-0.0779

Table 8 – List of species removed from the habitat preference clustering based on the estimated mean parameters associated with the 6 spatial covariates corresponding to the first 6 axes of the principal component analysis detailed in Appendix 3.

Species (Occurrences)	Reason
<i>Acanthis flammea</i> (464)	1 significant covariate
<i>Acrocephalus palustris</i> (138)	2 significant covariates
<i>Bombycilla garrulus</i> (146)	131 occurrences in 2005
<i>Carduelis citrinella</i> (730)	2 significant covariates
<i>Cinclus cinclus</i> (1887)	Poor AUCs
<i>Corvus monedula</i> (152)	1 significant covariate
<i>Emberiza cirlus</i> (202)	1 significant covariate
<i>Emberiza hortulana</i> (134)	1 significant covariate
<i>Ficedula hypoleuca</i> (273)	2 significant covariates
<i>Fringilla montifringilla</i> (551)	1 significant covariate
<i>Luscinia megarhynchos</i> (376)	1 significant covariate
<i>Motacilla cinerea</i> (697)	Poor AUCs
<i>Passer montanus</i> (209)	2 significant covariates
<i>Sylvia communis</i> (143)	2 significant covariates

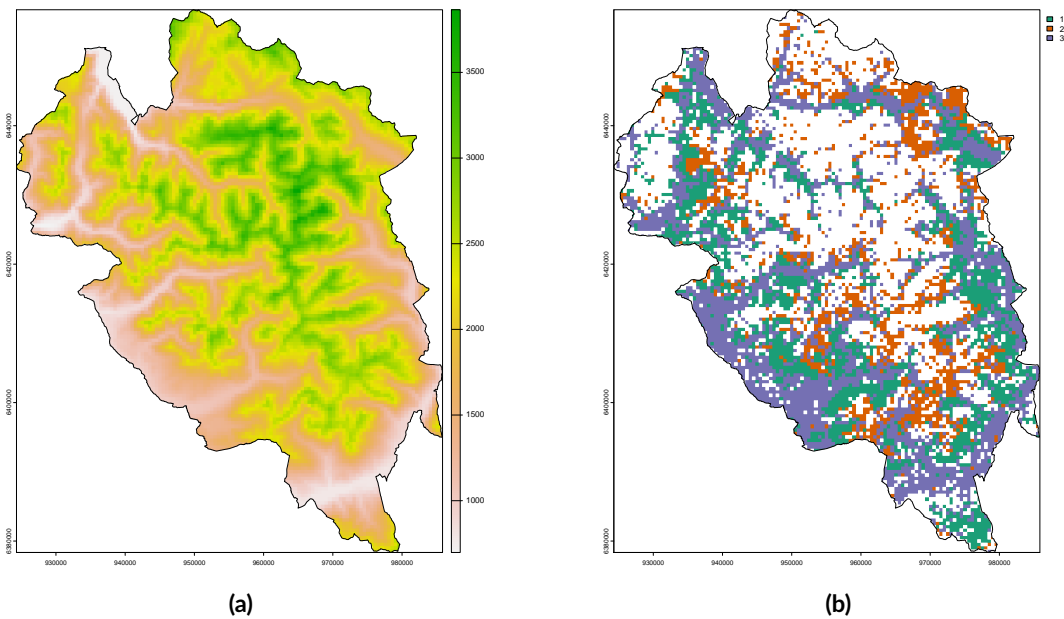


Figure 14 – a) Map of elevation in the Écrins National Park on a 500m×500m regular grid. b) Map of clusters with the highest occurrences on a 500m×500m regular grid. The highest number of occurrences is computed from the 63 classified species: the 77th ones with more than 100 occurrences, excluding the species listed in Table 8. Cluster 1 is associated with forest species, Cluster 2 with high-elevation species, and Cluster 3 with species in the valleys.

7. Fonctionnal Principal Component Analysis

Table 9 – Scores associated with harmonics of the FPCA. The first harmonic is associated with species overrepresented in winter while the second is associated with species overrepresented in summer. The species are categorized by their main migratory status within the territory of the Écrins National Park, as provided by experts from the park

Species (Occurrences)	Winter	Summer	Migratory status
<i>Acanthis flammea</i> (464)	2.65	0.3	Resident
<i>Acrocephalus palustris</i> (138)	0.77	-0.57	Breeding migratory
<i>Aegithalos caudatus</i> (1599)	2.02	-1.13	Resident
<i>Alauda arvensis</i> (1068)	-4.67	-2.61	Breeding migratory
<i>Anthus spinoletta</i> (1934)	0.22	0.55	Breeding migratory
<i>Anthus trivialis</i> (1292)	-9.92	0.19	Breeding migratory
<i>Bombycilla garrulus</i> (146)	NA	NA	Wintering
<i>Carduelis carduelis</i> (1549)	1.15	-0.57	Resident
<i>Carduelis citrinella</i> (730)	1.63	-0.38	Resident
<i>Certhia brachydactyla</i> (449)	0.99	-0.56	Resident
<i>Certhia familiaris</i> (984)	0.94	-0.63	Resident
<i>Chloris chloris</i> (668)	1.66	0.86	Breeding migratory
<i>Cinclus cinclus</i> (1887)	NA	NA	Resident
<i>Coccothraustes coccothraustes</i> (486)	0.85	-3.22	Resident
<i>Corvus corone</i> (1745)	1.04	-0.6	Resident
<i>Corvus corone cornix</i> (187)	1.78	-0.23	Resident
<i>Corvus monedula</i> (152)	0.72	-0.75	Resident
<i>Cyanistes caeruleus</i> (1892)	1.46	-0.76	Resident
<i>Delichon urbicum</i> (734)	-3.29	2.17	Breeding migratory
<i>Emberiza cia</i> (1548)	1.04	0.11	Resident
<i>Emberiza cirrus</i> (202)	1.78	-0.08	Resident
<i>Emberiza citrinella</i> (1734)	0.42	0.91	Breeding migratory
<i>Emberiza hortulana</i> (134)	1.88	1.29	Breeding migratory
<i>Erithacus rubecula</i> (3354)	0.72	0.41	Resident
<i>Ficedula hypoleuca</i> (273)	-3.13	9.91	Breeding migratory
<i>Fringilla coelebs</i> (5447)	1.02	0.2	Resident
<i>Fringilla montifringilla</i> (551)	2.12	-1.67	Wintering
<i>Garrulus glandarius</i> (2201)	1.2	-0.41	Resident
<i>Hirundo rustica</i> (642)	-1.74	5.23	Breeding migratory
<i>Lanius collurio</i> (834)	2.03	1.75	Breeding migratory
<i>Linaria cannabina</i> (1369)	1.08	-0.43	Resident
<i>Lophophanes cristatus</i> (2160)	1.28	-1.79	Resident
<i>Loxia curvirostra</i> (1890)	1.71	-0.89	Resident
<i>Lullula arborea</i> (321)	-0.86	-1.1	Breeding migratory
<i>Luscinia megarhynchos</i> (376)	-13.95	-2.51	Breeding migratory
<i>Monticola saxatilis</i> (566)	0.08	1.21	Breeding migratory
<i>Montifringilla nivalis</i> (999)	1.4	-0.73	Resident

<i>Motacilla alba</i> (1088)	1.04	1.56	Breeding migratory
<i>Motacilla cinerea</i> (697)	NA	NA	Resident
<i>Motacilla flava</i> (144)	-3.02	0.21	Breeding migratory
<i>Nucifraga caryocatactes</i> (2275)	-2.61	-3.66	Resident
<i>Oenanthe oenanthe</i> (2263)	-6.52	-1.11	Breeding migratory
<i>Parus major</i> (3165)	1	-0.63	Resident
<i>Passer domesticus</i> (947)	1.47	-0.36	Resident
<i>Passer montanus</i> (209)	1.18	-0.57	Resident
<i>Periparus ater</i> (3595)	0.96	-0.66	Resident
<i>Petronia petronia</i> (197)	0.84	-0.64	Resident
<i>Phoenicurus ochruros</i> (4183)	0.62	0.91	Breeding migratory
<i>Phoenicurus phoenicurus</i> (668)	1.3	-0.41	Resident
<i>Phylloscopus bonelli</i> (1668)	-13.44	-1.74	Breeding migratory
<i>Phylloscopus collybita</i> (2944)	-0.82	3.58	Breeding migratory
<i>Pica pica</i> (1061)	1.52	-0.48	Resident
<i>Poecile montanus</i> (2433)	1.36	-0.67	Resident
<i>Poecile palustris</i> (774)	1.04	-0.59	Resident
<i>Prunella collaris</i> (1775)	1.21	-0.73	Resident
<i>Prunella modularis</i> (1386)	0.05	1.54	Resident
<i>Ptyonoprogne rupestris</i> (1695)	-0.63	1.47	Breeding migratory
<i>Pyrrhula pyrrhula</i> (1816)	1.49	-0.88	Resident
<i>Regulus ignicapilla</i> (686)	0.68	0.53	Breeding migratory
<i>Regulus regulus</i> (1030)	1.42	-0.87	Resident
<i>Saxicola rubetra</i> (944)	1.7	1.26	Breeding migratory
<i>Saxicola rubicola</i> (313)	1.6	0.25	Breeding migratory
<i>Serinus serinus</i> (736)	1.07	0.13	Breeding migratory
<i>Sitta europaea</i> (1841)	1.71	-1.13	Resident
<i>Spinus spinus</i> (848)	1.99	-1.15	Resident
<i>Sturnus vulgaris</i> (353)	-1.41	-2.53	Resident
<i>Sylvia atricapilla</i> (1904)	-0.15	2.25	Breeding migratory
<i>Sylvia borin</i> (576)	0.35	1.86	Breeding migratory
<i>Sylvia communis</i> (143)	1.41	0.58	Breeding migratory
<i>Sylvia curruca</i> (753)	-4.8	2.74	Breeding migratory
<i>Tichodroma muraria</i> (1318)	1.63	-0.52	Resident
<i>Troglodytes troglodytes</i> (2903)	1.08	-0.38	Resident
<i>Turdus merula</i> (2938)	0.94	-0.59	Resident
<i>Turdus philomelos</i> (1209)	0.28	1.46	Resident
<i>Turdus pilaris</i> (1270)	2.11	-2.43	Resident
<i>Turdus torquatus</i> (1665)	1.34	-0.43	Breeding migratory
<i>Turdus viscivorus</i> (2585)	0.94	-0.63	Resident

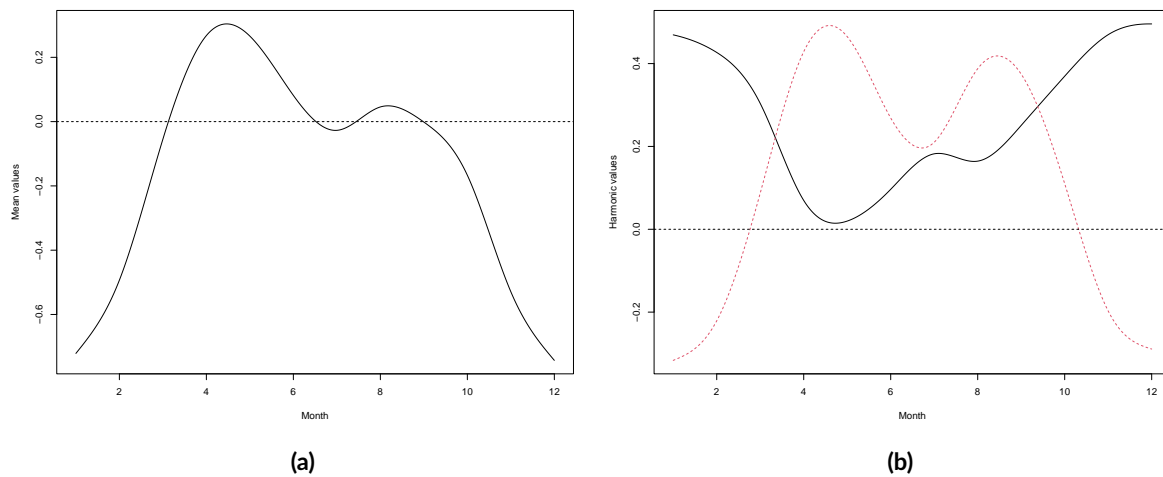


Figure 15 – Figure 15a displays the mean component of the spatial means of the month-dependent spatio-temporal Gaussian field W_i^m . Figure 15b displays the first two harmonics from the Functional Principal Component Analysis (FPCA) of the spatial means of the month-dependent spatio-temporal Gaussian field W_i^m . The black curve represents the first harmonic, explaining 61% of the variance in intra-annual variations. The red dotted curve represents the second harmonic, explaining 22% of the variance in intra-annual variations.

8. Inter-annual trends

Table 10 – Trends in relative abundance (RA) computed by the STOC and in target-group relative abundance (TGRA) in the Écrins National Park (ENP) for the period 2001-2019. The trends are expressed as percentage of variations, as developed in the section “Materials and Methods – Validation and post-processing – Inter-annual effects”. Credibility intervals are provided. The last column contains the differences between the median of these two metrics.

Species (Occurrences)	STOC RA	ENP TGRA	Differences
<i>Acanthis flammea</i> (464)	NA	-5.3 [-28.8, 25.8]	NA
<i>Acrocephalus palustris</i> (138)	-13.8 [-49.8, 47.8]	0 [-1.6, 1.7]	13.8
<i>Aegithalos caudatus</i> (1599)	NA	22.6 [5.9, 42.8]	NA
<i>Alauda arvensis</i> (1068)	-22.6 [-26, -19.1]	0 [-1.7, 1.8]	22.6
<i>Anthus spinoletta</i> (1934)	NA	-11.1 [-24.3, 4.1]	NA
<i>Anthus trivialis</i> (1292)	-19.3 [-27.4, -10.3]	-0.2 [-1.9, 1.7]	19.1
<i>Bombycilla garrulus</i> (146)	NA	NA	NA
<i>Carduelis carduelis</i> (1549)	-30.8 [-36.3, -25]	0 [-1.7, 1.7]	30.8
<i>Carduelis citrinella</i> (730)	NA	-18.1 [-34.8, 1.2]	NA
<i>Certhia brachydactyla</i> (449)	12.6 [4.3, 21.5]	0.1 [-1.7, 2]	-12.5
<i>Certhia familiaris</i> (984)	-9.3 [-43.1, 44.5]	0 [-1.7, 1.7]	9.3
<i>Chloris chloris</i> (668)	90.7 [65.4, 119.9]	11.3 [-10.9, 38.1]	-79.4
<i>Cinclus cinclus</i> (1887)	NA	NA	NA
<i>Coccothraustes coccothraustes</i> (486)	63 [24.8, 112.7]	-0.1 [-1.9, 1.6]	-63.1
<i>Corvus corone</i> (1745)	5.6 [0.8, 10.7]	-25.7 [-39.3, -10.7]	-31.3
<i>Corvus corone cornix</i> (187)	NA	-50.8 [-69.2, -24.1]	NA
<i>Corvus monedula</i> (152)	85.4 [57.5, 118.2]	-12 [-33.9, 17]	-97.4
<i>Cyanistes caeruleus</i> (1892)	14.6 [8.3, 21.2]	0 [-1.9, 2]	-14.6
<i>Delichon urbicum</i> (734)	-23.3 [-33.5, -11.6]	0 [-2, 1.7]	23.3
<i>Emberiza cia</i> (1548)	-45.4 [-68.1, -6.7]	-23.2 [-35, -11.7]	22.2
<i>Emberiza cirrus</i> (202)	-0.2 [-9.5, 10.1]	0.1 [-2, 2.1]	0.3
<i>Emberiza citrinella</i> (1734)	-53.6 [-56.5, -50.5]	-0.2 [-1.7, 1.5]	53.4
<i>Emberiza hortulana</i> (134)	-78.3 [-78.3, -49.2]	-36.2 [-67, 5.7]	42.1
<i>Erithacus rubecula</i> (3354)	-9.2 [-13.1, -5.2]	29.7 [14.8, 45.9]	38.9
<i>Ficedula hypoleuca</i> (273)	19.1 [-47.1, 167.8]	-24.7 [-48.1, 9.1]	-43.8
<i>Fringilla coelebs</i> (5447)	4.9 [2.1, 7.7]	20 [7.6, 31.9]	15.1
<i>Fringilla montifringilla</i> (551)	NA	-34.4 [-51.1, -11.9]	NA
<i>Garrulus glandarius</i> (2201)	23.2 [13.3, 34]	-12.6 [-24.6, -0.9]	-35.8
<i>Hirundo rustica</i> (642)	-25.2 [-30.2, -19.8]	-5.4 [-19.8, 12.3]	19.8
<i>Lanius collurio</i> (834)	-1.7 [-15.8, 14.6]	-8.5 [-24.5, 9.7]	-6.8
<i>Linaria cannabina</i> (1369)	-8.1 [-17.7, 2.7]	0 [-2.1, 2.2]	8.1
<i>Lophophanes cristatus</i> (2160)	-7.8 [-25.6, 14.2]	38 [16.4, 60.4]	45.8
<i>Loxia curvirostra</i> (1890)	-3 [-50.3, 89.5]	-8.2 [-20.5, 6.4]	-5.2
<i>Lullula arborea</i> (321)	-6.3 [-16.4, 4.9]	-60 [-74.4, -40.7]	-53.7
<i>Luscinia megarhynchos</i> (376)	-2.4 [-6.6, 1.9]	0 [-1.8, 1.7]	2.4
<i>Monticola saxatilis</i> (566)	NA	-53.2 [-66.4, -38.5]	NA

<i>Montifringilla nivalis</i> (999)	NA	-24.7 [-38.4, -7.5]	NA
<i>Motacilla alba</i> (1088)	4.3 [-5.6, 15.3]	-0.1 [-1.7, 1.5]	-4.4
<i>Motacilla cinerea</i> (697)	7.1 [-22.9, 48.9]	NA	NA
<i>Motacilla flava</i> (144)	-13 [-25.7, 1.8]	-62 [-81, -38]	-49
<i>Nucifraga caryocatactes</i> (2275)	NA	-21.5 [-32.6, -8.9]	NA
<i>Oenanthe oenanthe</i> (2263)	13.4 [-42.4, 123.3]	0.1 [-1.8, 1.9]	-13.3
<i>Parus major</i> (3165)	7.4 [3.2, 11.8]	6.5 [-7.6, 21.5]	-0.9
<i>Passer domesticus</i> (947)	-4.6 [-8.9, 0]	-4 [-21.8, 16.9]	0.6
<i>Passer montanus</i> (209)	-60.2 [-68.7, -49.3]	-0.1 [-1.9, 1.8]	60.1
<i>Periparus ater</i> (3595)	1.5 [-11.6, 16.6]	22.9 [10.5, 38.1]	21.4
<i>Petronia petronia</i> (197)	NA	-26.2 [-53.8, 19]	NA
<i>Phoenicurus ochruros</i> (4183)	2.9 [-4, 10.4]	12.2 [0.4, 24.9]	9.3
<i>Phoenicurus phoenicurus</i> (668)	-50 [-53.1, -46.7]	0 [-1.9, 1.8]	50
<i>Phylloscopus bonelli</i> (1668)	52.5 [29.3, 80]	68.1 [39.8, 103.9]	15.6
<i>Phylloscopus collybita</i> (2944)	-11 [-14.3, -7.6]	19 [4.2, 35.9]	30
<i>Pica pica</i> (1061)	14.5 [6.9, 22.5]	0.1 [-1.7, 1.8]	-14.4
<i>Poecile montanus</i> (2433)	-48.8 [-65.9, -22.9]	31.6 [14.2, 52.6]	80.4
<i>Poecile palustris</i> (774)	9.1 [-10, 32.1]	-0.1 [-1.8, 1.9]	-9.2
<i>Prunella collaris</i> (1775)	NA	-26.6 [-38, -13]	NA
<i>Prunella modularis</i> (1386)	-26.5 [-32, -20.6]	0.1 [-1.7, 1.8]	26.6
<i>Ptyonoprogne rupestris</i> (1695)	NA	-0.1 [-1.9, 1.9]	NA
<i>Pyrrhula pyrrhula</i> (1816)	-33.2 [-46.5, -16.4]	-12 [-26.1, 1.9]	21.2
<i>Regulus ignicapilla</i> (686)	79 [54.5, 107.3]	168.7 [92.5, 285.5]	89.7
<i>Regulus regulus</i> (1030)	-43.7 [-51.6, -34.4]	0 [-1.6, 1.8]	43.7
<i>Saxicola rubetra</i> (944)	-60.3 [-72.8, -42.1]	0 [-1.7, 1.8]	60.3
<i>Saxicola rubicola</i> (313)	-22 [-28.8, -14.5]	-32.1 [-52.8, -8.4]	-10.1
<i>Serinus serinus</i> (736)	-41.7 [-46.5, -36.6]	-0.1 [-1.8, 1.9]	41.6
<i>Sitta europaea</i> (1841)	1.3 [-9.2, 12.9]	0 [-2, 1.8]	-1.3
<i>Spinus spinus</i> (848)	NA	3.1 [-21.7, 35.1]	NA
<i>Sturnus vulgaris</i> (353)	22.4 [12.4, 33.2]	-0.1 [-1.9, 1.6]	-22.5
<i>Sylvia atricapilla</i> (1904)	29.6 [25.9, 33.4]	70.6 [45.3, 103.8]	41
<i>Sylvia borin</i> (576)	-32.7 [-39.4, -25.2]	-18.3 [-37.4, 6.6]	14.4
<i>Sylvia communis</i> (143)	-12.5 [-17.9, -6.8]	0 [-1.9, 1.7]	12.5
<i>Sylvia curruca</i> (753)	-7.5 [-31.7, 25.3]	0.2 [-1.6, 2]	7.7
<i>Tichodroma muraria</i> (1318)	NA	-41.5 [-51.6, -28.1]	NA
<i>Troglodytes troglodytes</i> (2903)	-20 [-22.9, -17.1]	11.1 [-2.1, 26]	31.1
<i>Turdus merula</i> (2938)	7 [3.9, 10.2]	8.7 [-6.3, 25.1]	1.7
<i>Turdus philomelos</i> (1209)	-0.9 [-5.9, 4.3]	30.9 [7.5, 61]	31.8
<i>Turdus pilaris</i> (1270)	-32.4 [-65.5, 32.8]	-42.1 [-54.7, -25.2]	-9.7
<i>Turdus torquatus</i> (1665)	NA	0 [-2, 2.3]	NA
<i>Turdus viscivorus</i> (2585)	-0.2 [-9.8, 10.5]	-7.1 [-14.6, 1.8]	-6.9