

1 **Adaptive niche-based sampling to improve ability to find rare and**
2 **elusive species: simulations and field tests**

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21 **Summary**

22 1 Sampling efficiency is crucial in order to overcome the data crisis in biodiversity and to
23 understand what drives the distribution of rare species.

24 2 Adaptive niche-based sampling (ANBS) is an iterative sampling strategy that relies on
25 the predictions of species distribution models (SDMs). By predicting highly suitable
26 areas to guide prospection, ANBS could improve the efficiency of sampling effort in
27 terms of finding new locations for rare species. Its iterative quality could potentially
28 mitigate the effect of small and initially biased samples on SDMs.

29 3 In this study, we compared ANBS with random sampling by assessing the gain in terms
30 of new locations found per unit of effort. The comparison was based on both simulations
31 and two field surveys of mountain birds.

32 4 We found an increasing probability of contacting the species through iterations if the
33 focal species showed specialization in the environmental gradients used for modelling.
34 We also identified a gain when using pseudo-absences during first iterations, and a
35 general tendency of ANBS to increase the omission rate in the spatial prediction of the
36 species' niche or habitat.

37 5 Overall, ANBS is an effective and flexible strategy that can contribute to a better
38 understanding of distribution drivers in rare species.

39

40 **Keywords:** adaptive monitoring, niche-based sampling, sampling efficiency, species
41 distribution model, rare species, low detectability

42 **Abbreviations**

43 SDM: Species Distribution Model; ANBS: Adaptive Niche-based Sampling; GAM:
44 Generalized Additive Model

45

46 **Introduction**

47 Species communities are usually composed of a few common species and many rare species
48 (Chase, 2013). Rare species can play major functional roles in ecosystems despite their low
49 abundance (Mouillot et al., 2013; Jousset et al., 2017). Understanding the factors that contribute
50 to the distribution of rare species is thus important to understand ecosystem functioning, assess
51 extinction risks and guide conservation actions (Soulé, 1983; Grenyer et al., 2006). However,
52 the conservation status of rare species is often difficult to determine because data on
53 distributions, abundances and trends are lacking at multiple scales (Bland, Collen, Orme, &
54 Bielby, 2014).

55 Characterizing the spatial distribution of a species relies on records of the locations where the
56 species is present or absent. Yet for rare species, huge efforts may be required to collect
57 presence data using traditional spatial sampling methods (Yoccoz, Nichols, & Boulinier, 2001).
58 As time and funding are limited resources, sampling efficiency is crucial to gain a better
59 understanding of the distribution drivers of rare species (Possingham, Andelman, Noon,
60 Trombulak, & Pulliam, 2000; Nichols & Williams, 2006).

61 Methodological alternatives to random sampling schemes are available (Albert et al., 2010). In
62 many species, and more specifically in rare species, it may be relevant to optimize sampling
63 schemes by using prior information about the distribution of the focal species to guide future
64 sampling efforts (Albert et al., 2010). For instance, adaptive sampling prioritizes the sampling
65 of sites adjacent to recorded occurrences (Thompson, 1990). Adaptive sampling is particularly
66 suitable for spatially aggregated species (Thompson, 1990); however, rare species are not

67 always spatially aggregated. Based on niche theory, we can expect that the locations occupied
68 by a species share a certain number of biotic and abiotic components (Pulliam, 2000). A
69 species' realized niche, i.e. the environmental conditions in which the species persists (e.g.,
70 Kambach et al., 2019), can be assessed with species distribution models (SDMs). These models
71 rely on spatial presence/absence data to predict the presence probability of a species as a
72 function of environmental variables (Guisan & Thuiller, 2005). Predictions from SDMs can
73 then be used as a basis to stratify a sampling scheme (i.e. niche-based sampling, Guisan et al.,
74 2006). In niche-based sampling, locations that are environmentally similar to those where the
75 species has been previously recorded are prioritized for sampling, so this strategy can be
76 considered an adaptive sampling method that is transposed in the environmental dimensions.
77 In the iterative version of niche-based sampling, called adaptive niche-based sampling (ANBS),
78 a first SDM is fitted using the available data and is used to drive sampling strategy, then
79 subsequent SDMs are fitted iteratively by including new data. Niche-based sampling provides
80 an interesting opportunity to improve sampling efficiency for many species – particularly rare
81 species – and ANBS is expected to enhance this improvement (Guisan et al., 2006; Le Lay,
82 Engler, Franc, & Guisan, 2010).

83 Species distribution modelling is considered robust for a small amount of recorded data, i.e. 10
84 to 20 occurrences (Elith et al., 2006; van Proosdij, Sosef, Wieringa, & Raes, 2016). However,
85 one must remember that to accurately identify relevant drivers of a species' distribution is
86 greatly limited when using a low number of records, for example, by the precision of estimated
87 parameters such as the slopes of the response curves (Wisiz et al., 2008; Galante et al., 2018).
88 A small number of true presences and absences will also inflate the potential influence of any
89 spatial bias in available occurrence data, which can strongly influence SDM predictions (Lobo
90 & Tognelli, 2011). When initial data are scarce, a sampling design that provides not only new
91 presences, but also new absences in informative environmental contexts for the model, is

92 therefore of critical interest. With its ability to guide prospection towards areas evaluated as
93 highly suitable and its iterative aspects (multiple sampling and successive modelling iterations),
94 ANBS could also mitigate the impact of initial spatial bias on SDM predictions (Singh, Yoccoz,
95 Bhatnagar, & Fox, 2009).

96 Niche-based sampling is increasingly used in ecology and conservation studies (Stirling,
97 Boulcott, Scott, & Wright, 2016). We reviewed the 462 studies that referred to Guisan et al.,
98 2006 (according to Google Scholar in January 2019), and found that only 32 implemented this
99 method with field sampling, of which 5 compared niche-based sampling to other methods by
100 comparing the number of presences recorded per unit of effort. In these 5 studies, niche-based
101 sampling was evaluated as performing better for 9 out of 11 species tested (Singh et al., 2009;
102 Williams et al., 2009; Le Lay et al., 2010; Edvardsen, Bakkestuen, & Halvorsen, 2011;
103 Aizpurua et al., 2015). Singh et al. (2009) reported the potential of this method to reduce the
104 effect of bias in the initial dataset; Aizpurua et al. (2015) also noted that compared to expert
105 sampling, new locations found with niche-based sampling were less dependent on existing
106 knowledge of spatial distribution.

107 Despite its recognized potential to improve sampling efficiency in ecology (e.g. Le Lay et al.,
108 2010; Rhoden, Peterman, & Taylor, 2017), we found that only two studies reported more than
109 one modelling and sampling iteration in the field (i.e. the ANBS method). These studies
110 (Rinnhofer et al., 2012; Cook et al., 2019) confirmed the value of an iterative approach by
111 ground validating models with subsequent field data, a major benefit of ANBS. However,
112 whether similar modelling and sampling performance would be produced with random
113 sampling was never assessed.

114 To this end, the aim of our study was to assess the gain in new locations found per unit of effort
115 using ANBS compared to random sampling. The comparison was based on simulations and two

116 real case studies. We used simulations to explore the relevance of ANBS in different spatial
117 and ecological contexts of rarity (more or less specialized virtual species). Based on the
118 literature on SDM, we expected the niche of a very specialized species to be more easily
119 identifiable, and thus ANBS to be more efficient for these species, assuming that some of the
120 environmental variables constraining the niche are known. However, depending on the spatial
121 configuration of the area and the abundance of a species, the same niche may lead to very
122 different numbers of sites occupied locally. Very low prevalence of the focal species may lead
123 ANBS to fail at identifying the most suitable areas due to a general lack of new presence
124 location findings. Most SDMs are based on presence locations as well as information about
125 available environmental conditions in the study area, known as ‘background’ or ‘pseudo-
126 absence’ data (see e.g. Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). We explored the
127 benefit of using pseudo-absences and assessed the impact of bias in the initial datasets,
128 expecting that spatial bias may lead to sampling a reduced part of an environmental range,
129 decreasing the ability of ANBS to improve species prevalence in the new data.

130 In addition to these simulations, we tested ANBS versus random sampling in the field (in the
131 Pyrenees National Park) to study the distribution of two rare species: the rock thrush *Monticola*
132 *saxatilis* and the white-winged snowfinch *Montifringilla nivalis*. The rock thrush is specialized
133 on a part of the rock cover gradient, but we were not able to formulate a strong hypothesis about
134 the spatial occurrence of the snowfinch. We expected ANBS to identify more new locations per
135 unit of field effort than random sampling, especially for the rock thrush.

136

137 **Material & methods**

138 *Study area*

139 The field study was carried out in the western Pyrenees (Fig. 1); this area was also used as the
140 basis for simulating the virtual species distributions. The Pyrenees Mountains form a natural
141 border between France and Spain, with a climate ranging from Atlantic to Mediterranean. The
142 study area covered 160x70 km, with elevations varying between 115 and 3320 m above sea
143 level, which creates a strong bioclimatic gradient (Körner, 2007). Habitats are mostly forests,
144 open grasslands and rocky habitats; the grasslands extend at the lower elevations as a result of
145 livestock grazing (Mazier et al., 2009).

146

147 *Virtual species distribution*

148 We simulated eight virtual species distribution patterns in open alpine landscapes, combining
149 two scenarios of niche width, two scenarios of species abundance, and two regions with
150 contrasting landscapes in the study area (Fig. 1). The first region was rocky and high in
151 elevation, in the central part of the mountain range, and the second region was lower in elevation
152 and more forested, in the western Pyrenees. We selected four environmental variables, all
153 assumed to influence breeding habitat selection: rock cover, solar radiation flux, mean daily
154 precipitation in June and mean daily temperature range in June (from Worldclim, Fick &
155 Hijmans, 2017). The complete calculation for solar radiation is described in Appendix 2.

156 We obtained different niche widths by modulating species response curves to the four
157 environmental variables selected ('virtual species' package: Leroy et al., 2016; see Appendix 1
158 for the code with response function parameters, as well as Fig. S5). To simulate distribution,
159 we multiplied the presence probability associated with the species' response to each of the four
160 variables at each pixel (when a part of a gradient was avoided by the species, it was avoided
161 whatever the favourability regarding other variables, see Fig. S5). Probabilities were
162 transformed to a presence/absence dataset using a fixed threshold of 0.6 for every scenario, and
163 all occurrences in forest habitats were eliminated.

164 At this stage, the prevalence of the virtual species above the 0.6 threshold was 100%, which
 165 was considered an ‘abundant’ species scenario. We also generated ‘scarce’ species scenarios,
 166 for which only 20% of the cells were occupied above the 0.6 threshold. Some species may not
 167 occupy all favourable sites in an area, for many biological reasons independent of the
 168 environmental niche (e.g. sociality, competition avoidance, antagonistic intraspecific
 169 interactions, etc.). This led to four scenarios in each region (Fig. 1): wide niche/abundant
 170 species (WA), wide niche/scarce species (WS), narrow niche/abundant species (NA), and
 171 narrow niche/scarce species (NS).
 172

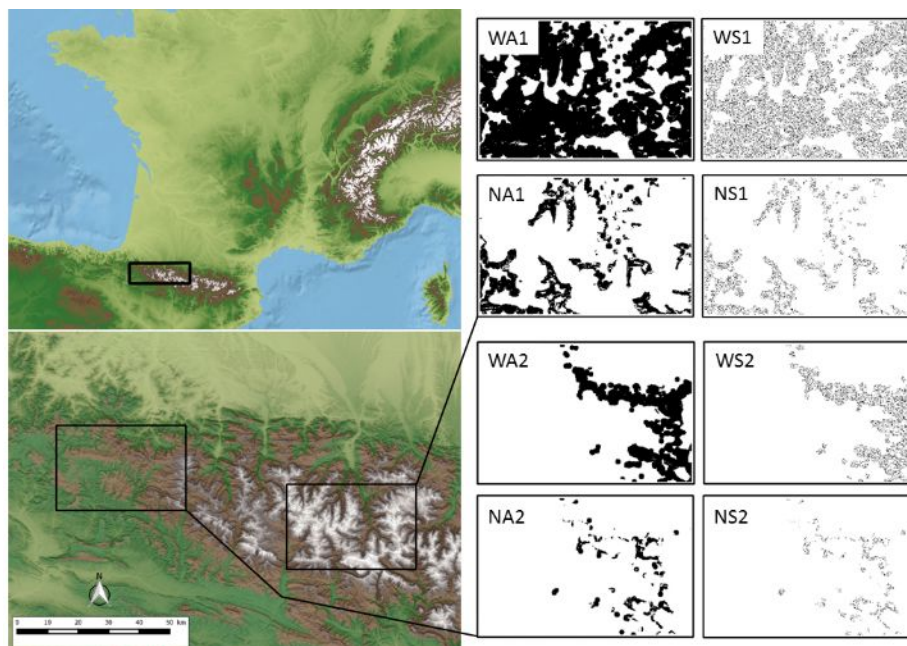


Figure 1: Top left: The study area was located in the western Pyrenees. Bottom left: Two regions were selected for the virtual tests: the western area (1) was at lower altitude, and the central area (2) at higher altitude, with more extended rocky areas. Right: virtual species distributions generated for the two regions and four scenarios: WA = wide niche, abundant species; WS = wide niche, scarce species; NA = narrow niche, abundant species; NS = narrow niche, scarce species.

173 *Field study: species and environmental variables*

174 For the field study, the entire area presented in the bottom left panel of Fig. 1 was considered.
175 The two focal species were the rock thrush, a long-distance migrant that lives in rocky
176 grasslands (Del Hoyo, Elliot, & Sargatal, 1992), and the snowfinch, a mountain specialist
177 adapted to cold conditions that exhibits elevational migration between breeding and non-
178 breeding seasons (Brambilla et al., 2016). In the rock thrush nests can be as close to each other
179 as 50 m, but foraging territories are not shared (Grangé et al., 2015). In the snowfinch, breeding
180 pairs can be solitary or can aggregate in small ‘colonies’. Both species forage a few hundred
181 metres around the nest (Grangé et al., 2015; Brambilla et al., 2016).

182 We selected five environmental variables to model rock thrush and snowfinch distribution in
183 the study area. Rock cover was obtained from CESBIO (Inglada et al., 2017) was considered
184 as a proxy for natural breeding site availability, and for low productivity areas (high rock cover
185 values). The percentage of forests and open habitats covering a 300 meters buffer around each
186 pixel was calculated, merging different habitat classes from the CORINE land cover inventory
187 (Büttner, 2014). We extracted the number of days with snow cover in June from the output of
188 a gap-filling algorithm applied to MODIS snow products for the Pyrenees mountains during the
189 2000–2015 period (Gascoin et al., 2015). Calculation for solar radiation is described in
190 Appendix 2. The data was transformed to 100-m resolution by downscaling for lower resolution
191 variables (snow cover), or by resampling and calculating the mean of values for higher
192 resolution variables.

193

194 *Flowchart*

195 The main goal and procedure were very similar for simulations and field studies (Fig. 2). We
196 compared the number of occurrences obtained by unit of effort based on random sampling and
197 on ANBS sampling. As we wanted simulated ANBS scenarios to be as simple as possible,

198 sampling probability was only proportional to the predicted probability of species occurrence
199 obtained from SDMs at the previous iteration. To prevent gathering spatially aggregated
200 information in the field surveys, the probability of a point x_i to be sampled was $\Pr(x_i) = F \times D$,
201 where F was the predicted probability of species occurrence estimated by a distribution model,
202 and D was the distance to the nearest known occurrence of the species (both scaled between 0
203 and 1). For the field surveys, we performed two ANBS iterations for the rock thrush and one
204 for the snowfinch. In simulations, we performed 12 ANBS iterations, and each sampling
205 scenario was simulated 100 times using different initial points, chosen according to different
206 scenarios.

207 The data collected with ANBS were used to evaluate the quality of the spatial predictions from
208 previous iterations of SDMs. The simulations also permitted to assess the benefit of using
209 pseudo-absences, and the impact of bias in the initial dataset. The initial datasets were made up
210 of 10 occurrences randomly selected in the virtual species distribution for ‘no bias’ scenarios,
211 or in the warmer 10% of the ‘temperature range’ variable for ‘bias’ scenarios (Fig. 2). For
212 ‘pseudo-absence’ scenarios, 1000 pseudo-absences were randomly selected for the first SDM
213 and each iteration, which corresponds to a higher number of pseudo-absences than has been
214 recommended in recent studies, but often occurs (Barbet-Massin et al., 2012). For ‘no pseudo-
215 absence’ scenarios, only measured absences were used for modelling; 5 absences were
216 randomly selected to perform the first model. Of the 10 new locations sampled at each iteration,
217 7 locations were selected randomly in the optimal area determined by the SDM (above a 0.6
218 threshold of predicted probability of species occurrence) and 3 locations were selected
219 randomly under this same threshold. Sampling outside the optimal area is important to better
220 model favourability along its entire gradient, and is needed in particular to limit omissions.

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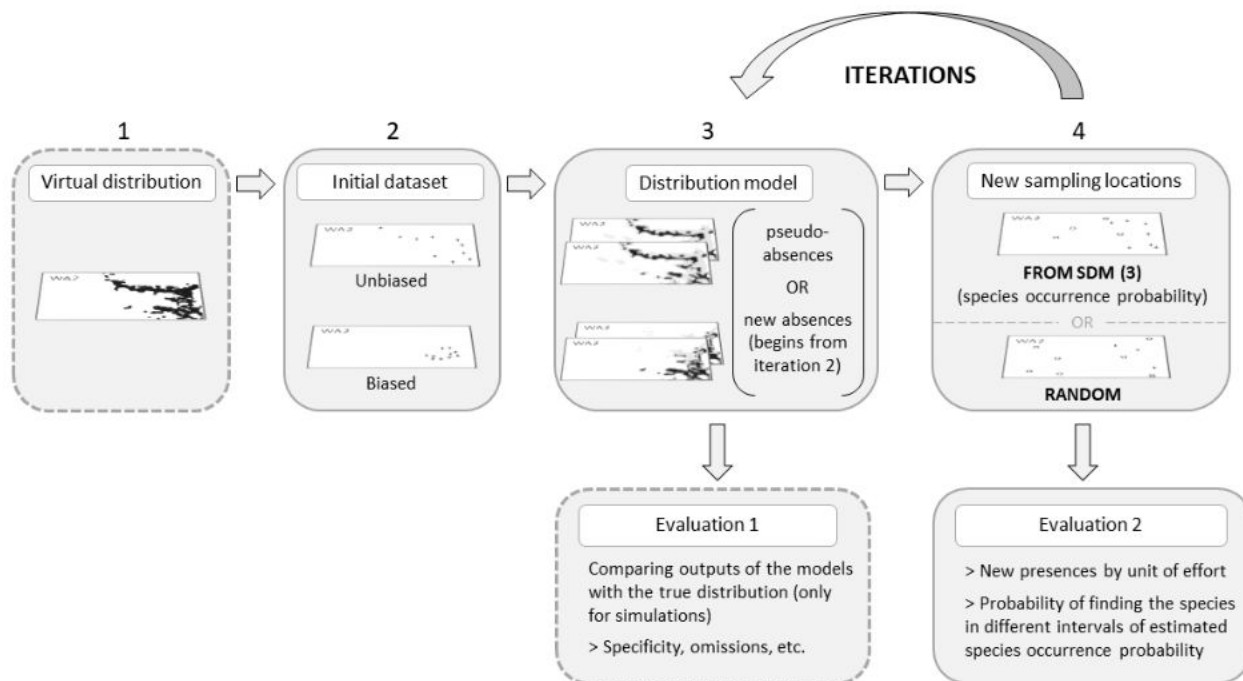


Figure 2: Work flow to test the efficiency of ANBS. Boxes with a dotted outline (stage 1 and evaluation 1) are specific to simulations; the others were performed for both simulations and field case studies. 12 iterations were simulated for each scenario during simulations.

222

223

224 *Species distribution models*

225 For all virtual scenarios and field surveys, SDMs were fitted using generalized additive models
 226 (GAMs) with a logit link and a binomial distribution (Hastie & Tibshirani, 1987). The
 227 probability P of contacting the species was given by:

$$228 \text{Logit}(P) = b_0 + f_1(X_1) + \dots + f_m(X_m)$$

229 Where b_0 is the intercept and the functions f_1 through f_m are smoothing splines for the covariates
 230 X_1 to X_m . These functions were estimated using the gam function in library 'biomod 2' in R
 231 (Thuiller, Georges, & Engler, 2013). Models were not structured following the process used to
 232 simulate species' presence (response probabilities were multiplied). This choice was made to
 233 provide a realistic simulation analysis, as modelling from environmental variables is usually
 234 structured differently than the biological mechanisms involved in generating species

235 distribution (Gaston, 1996; Araújo & Guisan, 2006; Elith & Leathwick, 2009; Buckley et al.,
236 2010). These models do not account for imperfect detection, thus we assumed that we modelled
237 the probability of finding the species. The spatial output from the GAMs provided a predicted
238 likelihood of species occurrence for each pixel of the study area.

239

240 *Initial knowledge and distribution models for the field study*

241 For the rock thrush, based on a 300x300-m grid (Boria, Olson, Goodman, & Anderson, 2014),
242 we filtered 220 opportunistic occurrences supplied by the Pyrenees National Park and the Adour
243 Pyrenees Ornithological Group, as well as 28 presences and 381 absences from random point
244 counts supplied by the national mountain bird monitoring scheme (STOM). For the first SDM,
245 we used 200 pseudo-absences instead of real absences in order to obtain spatially balanced sets
246 of absences and numerically balanced absences versus presences (Barbet-Massin et al., 2012).
247 We set aside 30% of the data for model evaluation, and estimated response curves for 100
248 models based on 10 different sets of pseudo-absences on which we fitted models for 10 different
249 trained datasets. Since many additional ‘true’ absences were found during the first field session,
250 the second distribution model for the rock thrush was fitted without pseudo-absences, with 100
251 different trained datasets. For the snowfinch, the first SDM using ANBS was fitted one year
252 later, so this model benefitted from supplementary data extracted from transects on the rock
253 thrush. The rest of the procedure was identical to that of the second iteration for the rock thrush,
254 with different amount of data (n=64 opportunistic locations, n=16 snowfinch presences and 393
255 absences from the STOM, and an additional n=11 snowfinch presences and 896 absences from
256 transects conducted for the rock thrush).

257

258 *Field method*

259 In the field, an observer had to reach a 300x300-m area defined around the sampling points
260 selected by the sampling procedure. The journey to reach this area was left to the observer's
261 discretion. Along transects, visual and acoustic observations of the focal species were recorded.
262 For the rock thrush, 25 transects were monitored in 2016 after an initial SDM, and 30 in 2017
263 after a second iteration of the model. For the snowfinch, 28 transects were monitored in 2017
264 after one SDM. We also performed 40 random transects in the area between 2016 and 2017.

265

266 *Model evaluation methods: simulations*

267 In the simulations, we compared the two sampling techniques with paired comparisons. We
268 calculated the absolute difference in new occurrences 'n' found at each iteration 'i' between
269 ANBS 'A' and random sampling 'R' (e.g. for scenario X: $n^{AXi} - n^{RXi}$), and the relative
270 difference as a percentage (e.g. for scenario X: $100 (n^{AXi} - n^{RXi}) / n^{RXi}$). In a second step, we also
271 performed paired comparisons between scenarios with or without initial bias, and with or
272 without pseudo-absences (Barbet-Massin et al., 2012). Based on a fixed 0.6 threshold, we
273 compared the specificity of model predictions (true negative rate) as a metric of the ability to
274 identify unsuitable areas, and we also compared omissions (false negative rate), as this kind of
275 error can be critical in conservation contexts. We additionally compared the AUCs. For these
276 evaluation metrics, we calculated the mean of the individual differences for each of the 100
277 repetitions of each scenario.

278

279 *Method comparison and model evaluation with field data*

280 In the field case studies, we compared the number of new occurrences found by the different
281 sampling methods as a function of sampling effort (in days) using a log-linear model (Poisson
282 distribution and log link). We also tested the quality of SDM predictions by modelling the
283 probability of recording the presence of the focal species at a visited cell, as a function of

284 favourability predicted by the distribution model (binomial distribution GLM, logit link,
 285 favourability split into a factor of four equal classes between 0% and 100%). We only
 286 considered cells that overlapped a transect trajectory by more than 100 m.

287 All analyses were conducted using R 3.3.1 (R Development Core Team, 2016) with the ‘raster’
 288 package (Hijmans et al., 2014) to deal with spatial data, and ‘biomod2’ for SDMs (Georges &
 289 Thuiller, 2013).

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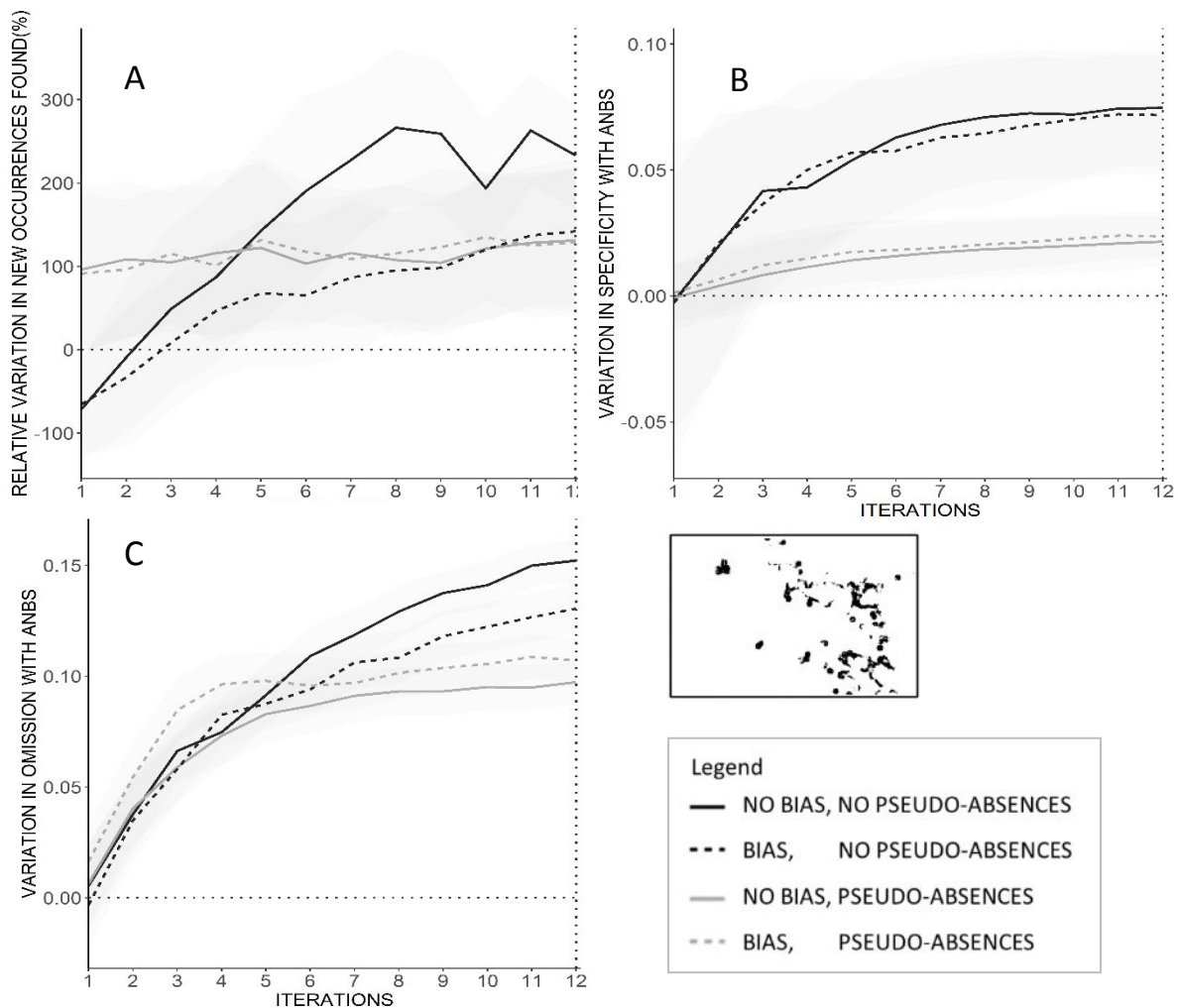


Figure 3: All panels show paired comparisons between the performance of ANBS and random sampling. The horizontal dotted line that intersects 0 corresponds to the value of the random sampling scenario for the different metrics at each iteration. Panel A: Relative difference in new occurrences found with ANBS compared to random sampling for the NA2 scenario (narrow niche, abundant species, region 2). Panel B: Difference in specificity of species distribution models. Panel C: Difference in omissions (bottom left). The grey areas indicate the 5th and 95th quantiles calculated from 100 simulations.

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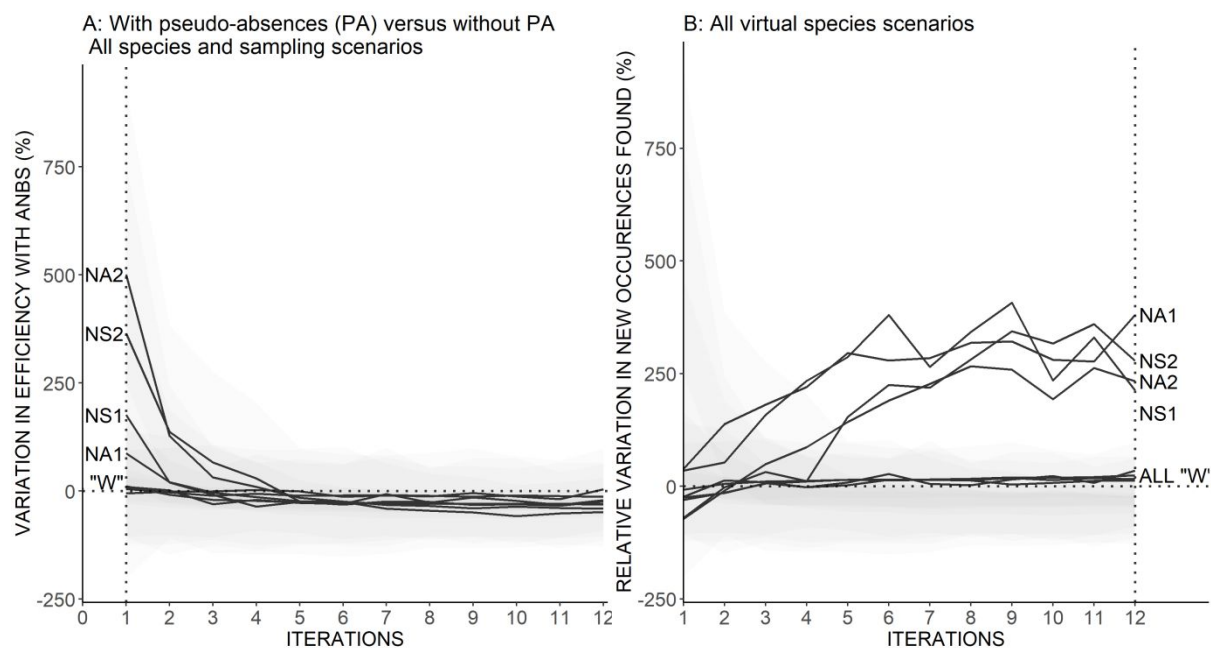


Figure 4. Panel A: Relative difference in new occurrences found between ANBS pseudo-absence scenarios versus ANBS no pseudo-absence scenarios (the horizontal dotted line that intersects 0 corresponds to the value in new occurrences found with ANBS without pseudo-absences). Panel B: Relative difference in new occurrences found between ANBS and random sampling (the horizontal dotted line that intersects 0 corresponds to the value in new occurrences found for the random sampling scenario). Species scenarios refer to wide (W) or narrow (N) niche width, abundant (A) or scarce (S) species; '1' refers to the central Pyrenees and '2' to the western Pyrenees. All 'W' scenarios led to similar outcomes. The grey areas indicate the 5th and 95th quantiles calculated from 100 simulations.

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298 **Results**

299 *Virtual species distribution: method comparison*

300 In all narrow niche (N) scenarios, whatever the geographical context, initial bias, or use of
301 pseudo-absences, the number of new occurrences found increased during the first 6–7 iterations
302 of ANBS and then stabilized (Fig. 4B, Fig. 3A), in the best case reaching a 300% mean
303 improvement over random sampling (see Fig. S1 for the 32 paired comparisons). In wide niche
304 scenarios, ANBS did not perform worse than simple random sampling, but failed to increase
305 the number of new occurrences, whatever the context (Fig. 4B), except for an average 25%
306 increase in occurrences found for scenarios with no initial bias or pseudo-absences (see Fig.
307 S1).

308 Without pseudo-absences, spatial bias in the initial dataset reduced by 30% the ability of ANBS
309 to improve the number of records, even after 12 iterations (Fig. S4). When modelling with
310 pseudo-absences, there was no impact of initial spatial bias on the efficiency of ANBS (Fig.
311 4A). Although the ability of ANBS to increase species prevalence compared to random
312 sampling was clearly improved when using pseudo-absences in initial models, the mean gain
313 in new occurrences found was almost null after five iterations (Fig. 4A).

314 Through iterations, the ANBS procedure increased both specificity and omission rate compared
315 to random sampling in all scenarios (Fig. S1; e.g. Fig. 3). We found no general pattern for AUC
316 (Fig. S3); however, models with 1000 pseudo-absences led to a 0.1 lower AUC compared to
317 other models in cases of wide niche/abundant species.

318

319 *Field test: method comparison*

320 In the rock thrush survey, one day of field work based on ANBS increased the number of new
 321 locations found by $\approx 200\%$ after two iterations (Fig. 5) compared to random point counts and
 322 random transects. In the snowfinch survey, one day of field work based on ANBS increased the
 323 number of new locations found by $\approx 25\%$ compared to random transects after one iteration.

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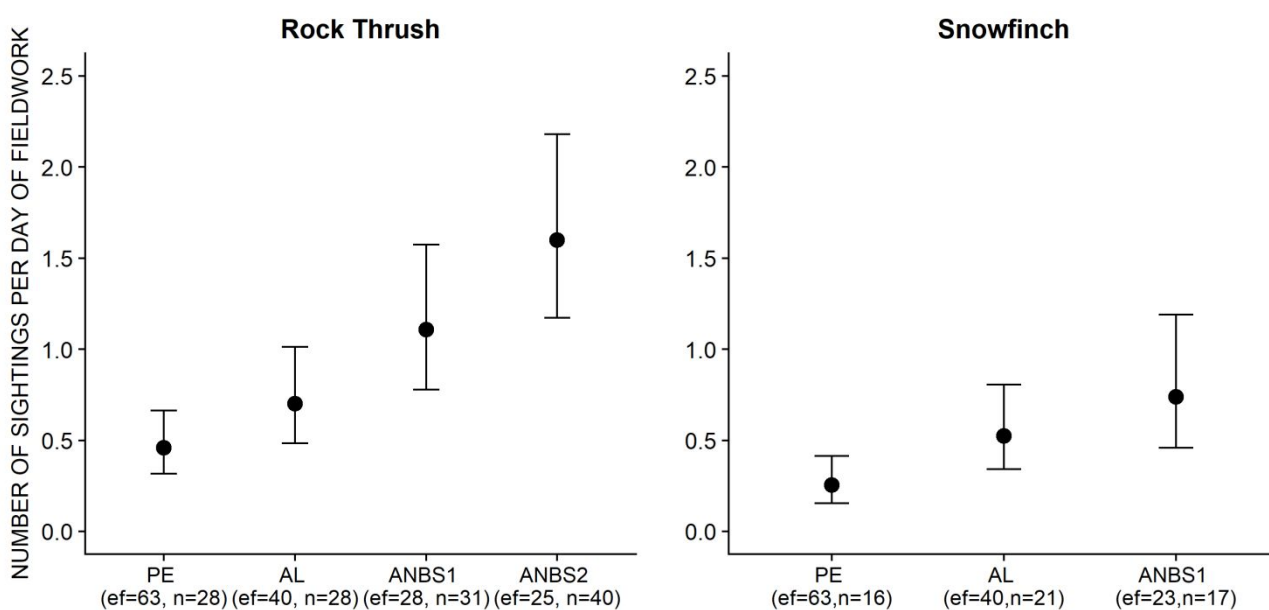


Figure 5: Field sampling scenario comparison: mean number of individuals detected per day of field work with the 95% CI for each sampling technique. PC: random point counts; RT: random transects; ANBS 1 & ANBS 2: adaptive niche-based sampling iteration 1 and 2. ef: effort in days of field work; n: number of occurrences for the focal species. Left: rock thrush, 2 iterations of ANBS; right: snowfinch, 1 iteration of ANBS.

326

327

328 *Evaluation of model output with standardized surveys*

329 In the rock thrush survey, the probability of finding new occurrences increased in areas
 330 classified as most favourable based on the previous iteration model (Fig. 6). The probability of
 331 finding the species in areas classified as less favourable (25–50% and even 0–25%
 332 favourability) slightly increased in both species with iterations (Fig. 6).

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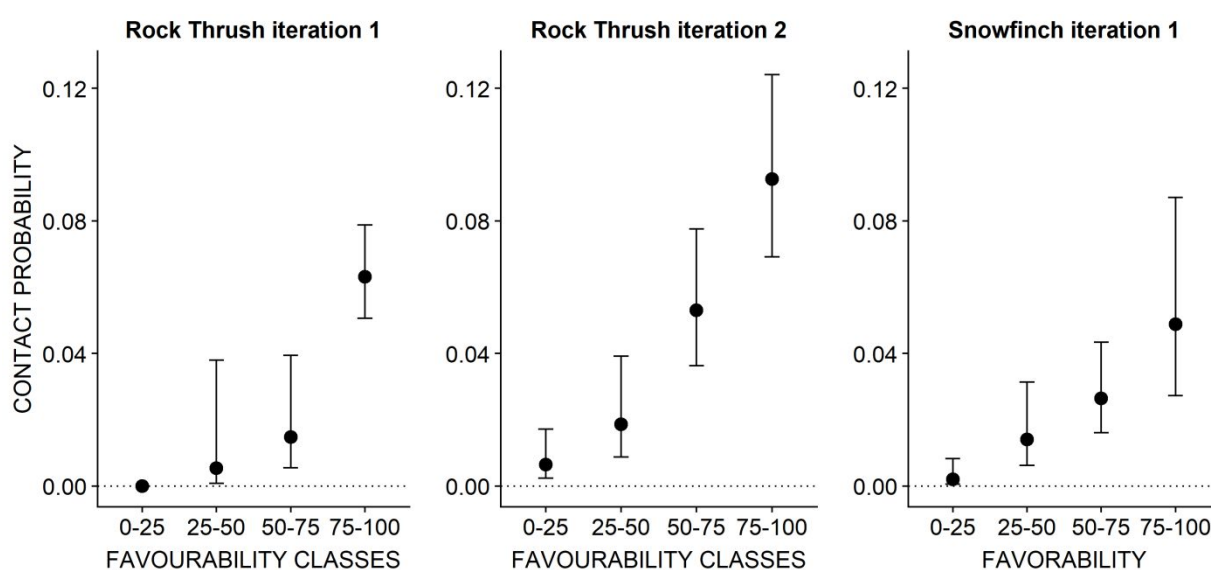


Figure 6: Evaluation of the species distribution models based on field data. Probability for the species to be sighted in sampled 300-m grid cells as a function of cell favourability (predicted by the distribution model and transformed in four equal classes).

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338 Discussion

339 Our results show that ANBS can be effective at improving detection of rare events. This ability
 340 persists in different scenarios of rarity, bias or spatial configuration, even with a small initial
 341 dataset (n=10). They also show that ANBS increases the specificity of SDMs compared to
 342 random sampling, at the cost of omissions at the margins of ecological ranges. Lastly, we found
 343 that ANBS is sensitive to bias in the initial dataset, but pseudo-absences help to mitigate the
 344 impact of initial bias. However, a large number of pseudo-absences restricts the efficiency of
 345 ANBS, as this limits the increase of the true absence ratio (i.e. specificity). The field surveys
 346 confirmed the results obtained from simulations.

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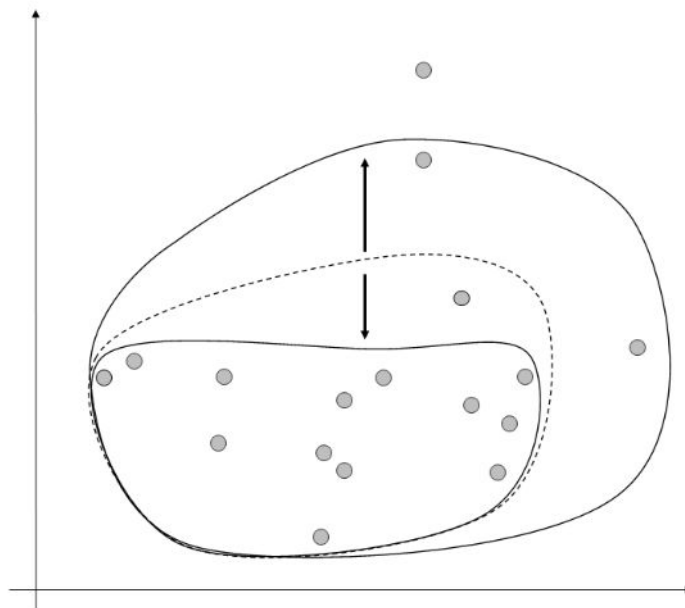


Figure 7: Schematic representation of environmental niche predicted by SDMs with random or ANBS sampling. Axes are environmental gradients effecting species distribution. Shaded circles show environmental conditions for sites where the species is present. Arrows represent the modifications in SDM predictions from the initial model (dotted area) after iterations of ANBS (inner area) and random sampling (outer area).

348

349 Compared to random sampling, ANBS reduces the gradient of ecological conditions that are
350 sampled based on existing knowledge of the focal species, thus ANBS is more efficient for
351 narrow niche species than for wide niche species (Fig. 4B). Interestingly, species rarity and
352 spatial configuration did not influence this result (Fig. S1), mainly because both random and
353 ANBS methods were identically penalized by species scarcity, and identically unpenalized by
354 scarcity of favourable areas (as random sampling was stratified by habitat).

355 By preferentially sampling in occupied parts of the gradients, ANBS lacks precision in range
356 margins (resulting in higher omissions, Fig. 3). Our field surveys confirmed this pattern: after
357 the second ANBS iteration for the rock thrush, the probability of contacting both species
358 increased in classes of low predicted occurrence (Fig. 6). Depending on the context of a study,
359 it may or may not be important to compensate for this tendency: for example, by changing
360 thresholds to minimize omissions. Likewise in long-term monitoring, distribution margins are
361 particularly important to identify, as they may be the first locations to show a response to a
362 change in environmental conditions (Scheele, Foster, Banks, & Lindenmayer, 2017; Papuga,
363 Gauthier, Pons, Farris, & Thompson, 2018).

364 A bias in the initial dataset will lead SDMs to predict suitability and target sampling in a very
365 restricted part of the environmental gradient which is not properly sampled. Further iterations
366 may not overcome this bias if the probability is too low to find the species in another part of the
367 gradient by chance (Fig. S4). Despite this context of severe bias, ANBS still performed better
368 than random sampling in terms of new locations found for specialized species. Another
369 important point is that pseudo-absences strongly reduced the impact of bias: With a small initial
370 set of presence data, large numbers of pseudo-absences will lower the presence/absence ratio
371 in the data. This will lead to a lower true absence ratio (i.e. specificity) in the predictions of
372 spatial models, as shown in Fig. 3B (see all scenarios in Fig. S1). This is an advantage when
373 initial data is biased (Fig. 4A; see also Lobo and Tognelli, 2011), as a smaller effect size for the

374 response to environmental covariates will lead to a more homogeneous predicted probability of
375 species occurrence. Subsequent sampling will thus be less restrictive and allow new
376 occurrences to be detected outside the biased part of the environmental gradient. At the same
377 time, simulations show that lower true absence ratio penalizes models with pseudo-absences
378 compared to models with ‘real’ absence data: Scenarios implemented without pseudo-absences
379 were as good as or better than scenarios with pseudo-absence in iterations 6 to 12 (Fig. 4A; Fig.
380 S1).

381 Results from simulations helped in understanding the results of the two field surveys. In the
382 rock thrush survey, ANBS was more efficient at finding the species than random sampling;
383 moreover, species prevalence increased with ANBS iterations, thus the efficiency of
384 prospections was improved. The addition of standardized data with measured ‘absences’
385 reduced variation in the estimations of responses to environmental variables (Figs S6-S7),
386 which is consistent with other findings (Elith et al., 2006; Lobo & Tognelli, 2011; Leroy et al.,
387 2018). In the snowfinch survey, ANBS only resulted in a 25% increase in new occurrences
388 found per day of fieldwork, and the model’s low specificity revealed a poor ability to identify
389 drivers that really constrained species distribution in the western Pyrenees. This less convincing
390 result demonstrates the necessity of identifying better explanatory variables for snowfinch
391 distribution.

392 Finally, this study was implemented based on a couple of key assumptions about detection and
393 stationarity. First, occupancy and detection were not modelled separately, which may be
394 problematic when detection is heterogeneous in time or space, and particularly if detection is
395 correlated to one of the covariates used in the model. Yet the approach developed here could
396 be extended to deal with detectability after the initial modelling step, which is usually based on
397 a small amount of occurrence data (Kéry, Gardner, & Monnerat, 2010). We also made the
398 assumption that the variables of interest, the environmental covariates and the species’ niche

399 were stable over time. Depending on the temporal scale of the study, species' reproductive
400 parameters, and the temporal resolution of the covariates considered to assess the niche, these
401 assumptions may not be met (Pearman, Guisan, Broennimann, & Randin, 2008). Further
402 development of data filtering, analysis and sampling strategy would be required to account for
403 changes in the ecological systems, especially for invasive species (Pearman et al., 2008; Cook
404 et al., 2019).

405

406 **Conclusion: recommendations for implementing ANBS**

- 407 1) ANBS is a good option for testing a well-supported occurrence hypothesis if environmental
408 data is available. This hypothesis can be inferred from expert or local knowledge, even for
409 data-deficient species. However, without a hypothesis about the species' response to at least
410 one environmental gradient used for modelling, ANBS is unlikely to improve efficiency.
411 Rare species with a large range can benefit from this method if at least one aspect of their
412 niche allows the restriction of spatial sampling.
- 413 2) Spatial or environmental bias in the initial dataset must be accounted for during first
414 iterations through filtering, complementary random surveys, and the use of pseudo-
415 absences.
- 416 3) We recommend using pseudo-absences during the first iterations of ANBS and then
417 removing them when the number and spatial distribution of 'true absences' increases.
- 418 4) Iterations provide the opportunity to ground validate model predictions.
- 419 5) Including distance to existing data in sampling probability can improve the empirical value
420 and spatial coverage of new locations found for the species.
- 421 6) The estimation of species response changes as new data is included through iterations (Figs
422 S6-S7). Thus, we recommend not setting aside biologically significant hypothesized effects

423 during the first iterations of ANBS (which can happen, for example, through an ‘automated’
424 model selection procedure).

425

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431

432

433 **Authors’ contributions**

434 JC, CM, NGY and AB conceived the study and designed the methodology; SD, IN, PF and JC
435 collected data; JC, CM and IN analysed the data; JC led the writing of the manuscript. All
436 authors contributed critically to the drafts and gave final approval for publication.

437

438 **Data accessibility:** Opportunistic data used for initial modelling and count data produced
439 during ANBS process are deposited in the Dryad repository:

440 <https://doi.org/10.5061/dryad.sxksn030m>

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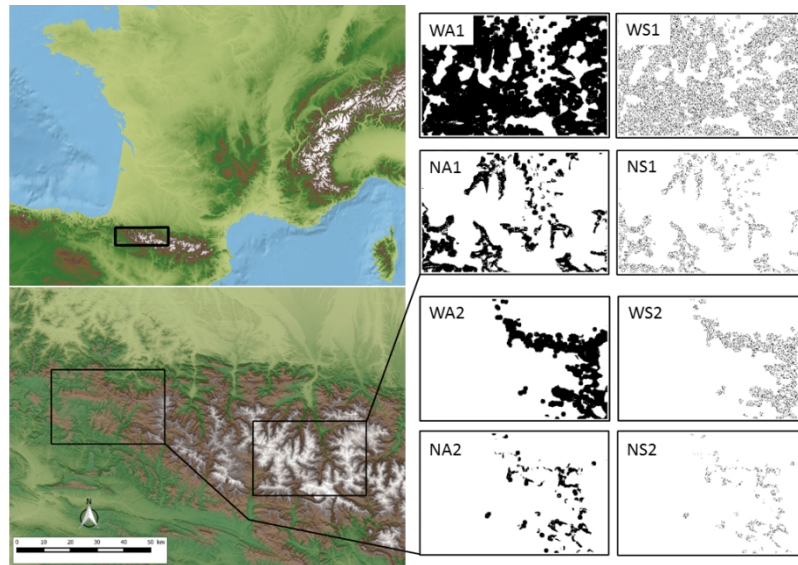


Figure 1: Top left: The study area was located in the western Pyrenees. Bottom left: Two regions were selected for the virtual tests: the western area (1) was at lower altitude, and the central area (2) at higher altitude, with more extended rocky areas. Right: virtual species distributions generated for the two regions and four scenarios: WA = wide niche, abundant species; WS = wide niche, scarce species; NA = narrow niche, abundant species; NS = narrow niche, scarce species.

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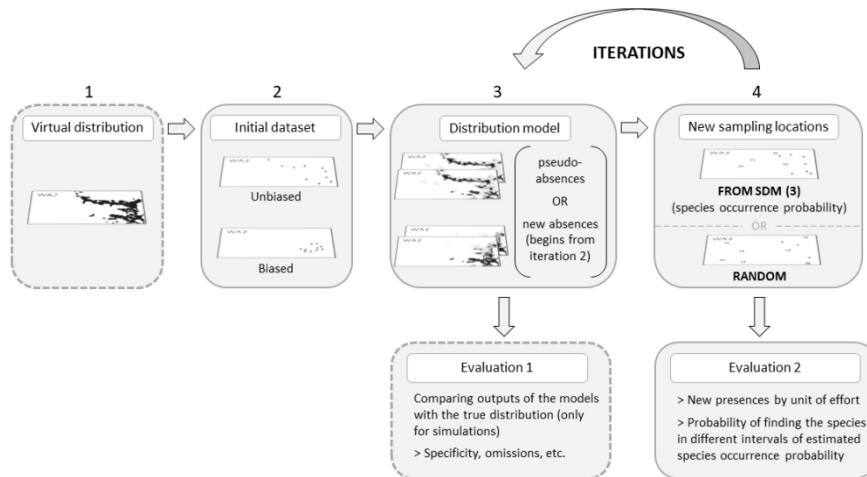


Figure 2: Work flow to test the efficiency of ANBS. Boxes with a dotted outline (stage 1 and evaluation 1) are specific to simulations; the others were performed for both simulations and field case studies. 12 iterations were simulated for each scenario during simulations.

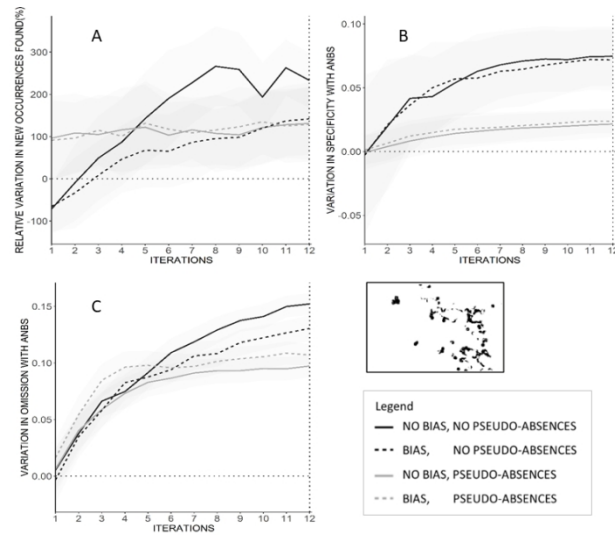


Figure 3: All panels show paired comparisons between the performance of ANBS and random sampling. The horizontal dotted line that intersects 0 corresponds to the value of the random sampling scenario for the different metrics at each iteration. Panel A: Relative difference in new occurrences found with ANBS compared to random sampling for the NA2 scenario (narrow niche, abundant species, region 2). Panel B: Difference in specificity of species distribution models. Panel C: Difference in omissions (bottom left). The grey areas indicate the 5th and 95th quantiles calculated from 100 simulations.

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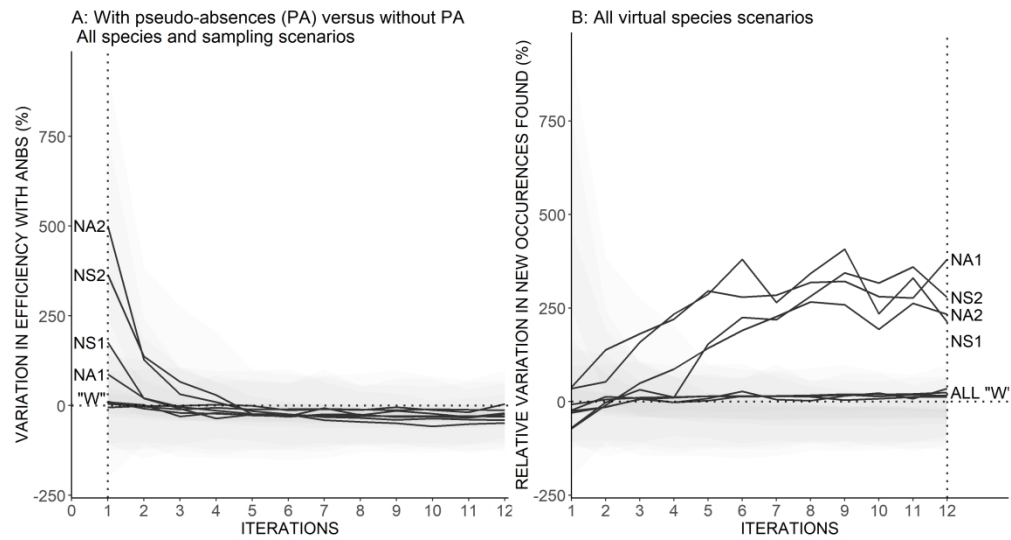


Figure 4. Panel A: Relative difference in new occurrences found between ANBS pseudo-absence scenarios versus ANBS no pseudo-absence scenarios (the horizontal dotted line that intersects 0 corresponds to the value in new occurrences found with ANBS without pseudo-absences). Panel B: Relative difference in new occurrences found between ANBS and random sampling (the horizontal dotted line that intersects 0 corresponds to the value in new occurrences found for the random sampling scenario). Species scenarios refer to wide (W) or narrow (N) niche width, abundant (A) or scarce (S) species; '1' refers to the central Pyrenees and '2' to the western Pyrenees. All 'W' scenarios led to similar outcomes. The grey areas indicate the 5th and 95th quantiles calculated from 100 simulations.

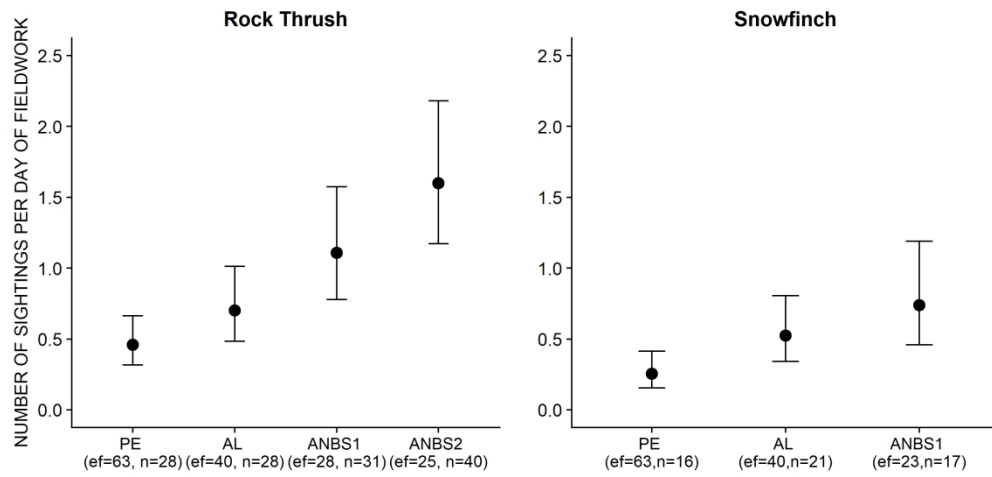


Figure 5: Field sampling scenario comparison: mean number of individuals detected per day of field work with the 95% CI for each sampling technique. PC: random point counts; RT: random transects; ANBS 1 & ANBS 2: adaptive niche-based sampling iteration 1 and 2. ef: effort in days of field work; n: number of occurrences for the focal species. Left: rock thrush, 2 iterations of ANBS; right: snowfinch, 1 iteration of ANBS.

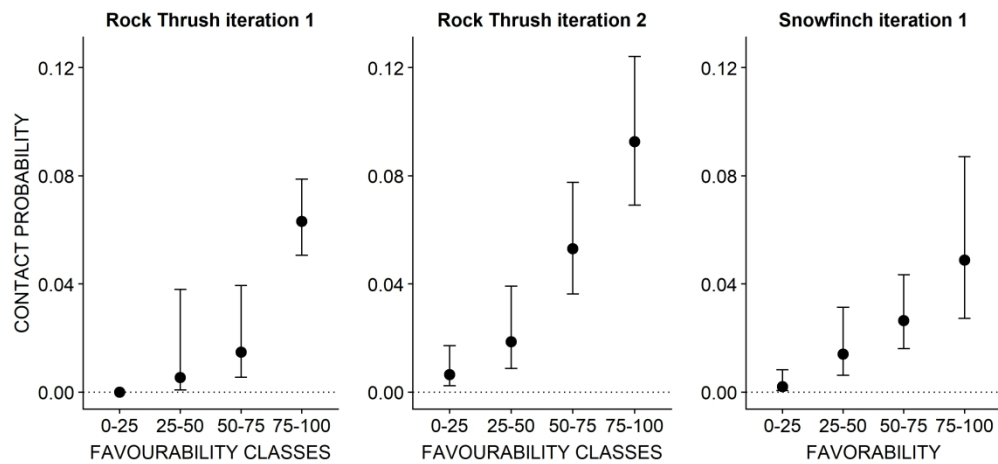


Figure 6: Evaluation of the species distribution models based on field data. Probability for the species to be sighted in sampled 300-m grid cells as a function of cell favourability (predicted by the distribution model and transformed in four equal classes).

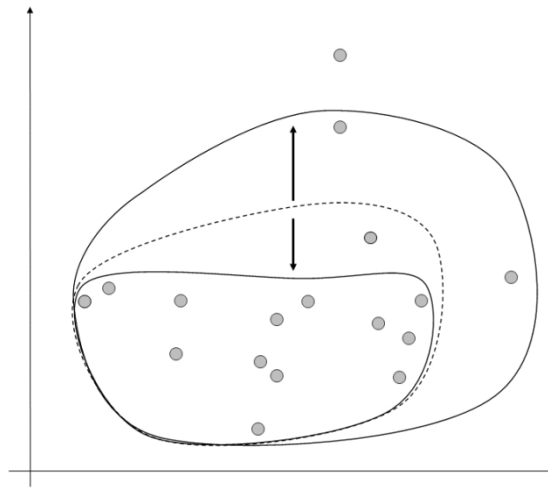


Figure 7: Schematic representation of environmental niche predicted by SDMs with random or ANBS sampling. Axes are environmental gradients effecting species distribution. Shaded circles show environmental conditions for sites where the species is present. Arrows represent the modifications in SDM predictions from the initial model (dotted area) after iterations of ANBS (inner area) and random sampling (outer area).