

1 **Spatial density estimates of Eurasian lynx (*Lynx lynx*) in the French Jura and Vosges**

2 **Mountains**

3

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14

15 **Abstract**

16

17 Obtaining estimates of animal population density is a key step in providing sound  
18 conservation and management strategies for wildlife. For many large carnivores however,  
19 estimating density is difficult because these species are elusive and wide-ranging. Here, we  
20 focus on providing the first density estimates of the Eurasian lynx (*Lynx lynx*) in the French  
21 Jura and Vosges mountains. We sampled a total of 413 camera trapping sites (with 2 cameras  
22 per site) between January 2011 and April 2016 in seven study areas across seven counties of  
23 the French Jura and Vosges mountains. We obtained 592 lynx detections over 19,035 trap  
24 days in the Jura mountain and 0 detection over 6,804 trap days in the Vosges mountain. Based  
25 on coat patterns, we identified a total number of 92 unique individuals from photographs,

26 including 16 females, 13 males and 63 individuals of unknown sex. Using spatial capture-  
27 recapture (SCR) models, we estimated abundance in the study areas between 5 (SE = 0.1) and  
28 29 (0.2) lynx and density between 0.24 (SE = 0.02) and 0.91 (SE = 0.03) lynx per 100 km<sup>2</sup>.  
29 We also provide a comparison with non-spatial density estimates and discuss the expected  
30 discrepancies. Our study is yet another example of the advantage of combining SCR methods  
31 and non-invasive sampling techniques to estimate density for elusive and wide-ranging  
32 species, like large carnivores. While the estimated densities in the French Jura mountain are  
33 comparable to other lynx populations in Europe, the fact that we detected no lynx in the  
34 Vosges mountain is alarming. Connectivity should be encouraged between the French Jura  
35 mountain, the Vosges mountain and the Palatinate Forest in Germany where a reintroduction  
36 program is currently ongoing. Our density estimates will help in setting a baseline  
37 conservation status for the lynx population in France.

38

## 39 **Introduction**

40

41 Obtaining estimates of animal population density is a key step in providing sound  
42 conservation and management strategies for wildlife [1]. For many large carnivores however,  
43 estimating density is difficult because these species are elusive and wide-ranging, resulting in  
44 low detection rates [2]. To deal with these issues, non-invasive techniques, such as camera  
45 trapping and DNA sampling, are increasingly used [3]. These non-invasive techniques  
46 generate data that can be analyzed with capture-recapture methods to estimate densities [4].

47 Standard capture-recapture models for closed populations [5] have long been used to  
48 estimate animal abundance and density, including many large carnivores [6,7]. However,  
49 when converting abundance into density, density estimates are highly sensitive to the size of  
50 user-defined area assumed to reflect the effective sampling area [8]. In addition, individual

51 heterogeneity on the detection due to spatial variation in the distance of home ranges to the  
52 sampling devices may lead to biased density estimates [5]. Spatial capture-recapture (SCR)  
53 models deal with these issues by explicitly incorporating spatial locations of detections [9–  
54 12], and they are increasingly used to estimate densities of large carnivores [13–18].

55         Here, we focus on the threatened Eurasian lynx (*Lynx lynx*) in the French Jura and  
56 Vosges mountains (see [19] for a map of its distribution in Europe; see also  
57 <https://www.lcie.org/Large-carnivores/Eurasian-lynx> for recent updates). As in many regions  
58 of western Europe [20], lynx were extirpated from France between the 17<sup>th</sup> and 20<sup>th</sup> centuries  
59 due to habitat degradation, persecution by humans and decrease in prey availability [21].  
60 Shortly after their initial reintroduction in Switzerland in the 1970s [22], lynx naturally  
61 increased their range and started recolonizing France by repopulating forests on the French  
62 side of the Jura [21]. Reintroductions also occurred in the French Vosges mountain between  
63 1983 and 1993 with the perspective of establishing a population there [23]. The species is  
64 listed as endangered in the IUCN Red list and is of conservation concern in France due to  
65 habitat fragmentation, poaching and collisions with cars and trains. Currently, the French  
66 population of lynx is restricted to three mountain ranges, the Vosges, in northeastern France,  
67 the Jura and the Alps, with little connectivity between them most likely due to human-made  
68 linear infrastructures. While the Northern Alps are slowly being recolonized with lynx mostly  
69 coming from the Jura [24], the Jura holds the bulk of the French lynx population. In contrast,  
70 the lynx presence in the Vosges mountain remained stable following the reintroductions and  
71 then, has been continuously decreasing since 2005 [25].

72         Despite their conservation status, little information on abundance and density of lynx  
73 in France exist. In this study, we used SCR and standard capture-recapture models to provide  
74 the first estimate of lynx abundance and density using camera-trap surveys implemented in

75 the French Jura and Vosges mountains from 2011 to 2016. Based on these results, we discuss  
76 research and management priorities for the effective conservation of lynx in France.

77

## 78 **Methods**

79

### 80 *Ethics statement*

81 We used non-invasive methods for data collection, which did not involve manipulation or  
82 handling of any living organism. Therefore, approval from an animal ethics committee was  
83 not required. Cameras were set on public or private forests with the permission of local  
84 authorities or local owners, respectively. We advertised the study and the presence of camera  
85 traps to the local stakeholders and the public visiting the areas. In agreement with French  
86 legislation, we deleted photos permitting the identification of goods or people.

87

### 88 *Study area and sampling design*

89 The study area encompassed three counties of the French Jura mountain, namely Ain, Doubs  
90 and Jura and four counties of the Vosges mountain, namely Vosges, Haut-Rhin, Bas-Rhin and  
91 Moselle (Figure 1). Elevation ranged from 163 and 1,718 m above sea level in the Jura  
92 mountain and from 104 to 1,422 m in the Vosges mountain. The human population density  
93 was 88 per km<sup>2</sup> in the Jura mountain and 170 per km<sup>2</sup> in the Vosges mountain. Forests cover  
94 50% on average of the Jura mountain [26] and 70% of the Vosges mountain [27]. Sampling  
95 occurred over 6 years, between January 2011 and April 2016, mostly in winter and spring,  
96 with surveys lasting between 2 and 4 months. We considered two study areas in 2011, 2014  
97 and 2015, three study areas in 2013 and one study area in 2012 and 2016 through camera  
98 trapping (Figure 1).

99

100 [Figure 1 about here]

101

102 We divided each study area into a grid of 2.7 x 2.7 km cells applying a systematic  
103 design where one out of two cells was sampled [28], hence ensuring that at least one camera  
104 trap was set in each potential lynx home range (between 100km<sup>2</sup> and 250km<sup>2</sup>, see [29]). To  
105 maximize detectability, we set (non-baited) camera traps in forested habitats, based on  
106 previous signs of lynx presence and on local knowledge, at optimal locations where landscape  
107 and terrain features were likely to channel lynx movements on more predictable paths (on  
108 forest roads, hiking trails and to a lesser extent on game paths) [30]. Camera were settled on  
109 within a single session design continuously during 60 days between February and beginning  
110 of March with little variation between sites.

111 At each trapping location, we set two Xenon white flash camera traps (models:  
112 Capture, Ambush and Attack; Cuddeback, WI, USA) with passive infrared trigger  
113 mechanisms to photograph both flanks of an animal. We checked camera traps weekly to  
114 change memory cards, batteries and to remove fresh snow after heavy snowfall. Based on  
115 unique coat patterns, we identified individual lynx on photographs [31]. The recognition of  
116 individual was computer-induced, not fully automated. We used the Extract-compare ©  
117 software that compares the lynx spot pattern with a library of previously extracted pattern and  
118 proposes potential matches according to a score  
119 (<http://conservationresearch.org.uk/Home/ExtractCompare>). The observer can confirm the  
120 lynx identification or not and browse through the highest-ranking proposed matches. The final  
121 decision is made by the observer based on an additional visual examination of the entire photo  
122 set for this particular lynx. Pictures for which no match was found with the software were  
123 visually checked against our entire photo library. Only when the match is undeniable is the  
124 individual recorded as a match, otherwise it was recorded as a new individual. All captures

125 that do not fit automated or associated visual confirmation with no doubt, because of a poor  
126 picture quality (e.g. blurry, overexposed), were classified as “unconfirmed” and excluded  
127 from the analyses. We recorded the date, time, sex whenever possible, and location of each  
128 photographic capture of a lynx. During the time of year our study took place, juvenile lynx (<  
129 1 year old) can still be with their mother [32]. In our analysis, we retained only independent  
130 lynx, i.e. adult lynx or emancipated individuals based on physical characteristics or previous  
131 knowledge of their age or status (from photographic evidence). We defined a capture occasion  
132 as 5 successive trap nights [30], dissociating trapping events from individual photo to avoid  
133 pseudo-replications.

134

### 135 *Spatial capture-recapture analyses*

136 We used spatial capture-recapture (SCR) models to estimate lynx densities [4]. In contrast  
137 with standard (non-spatial) capture-recapture models, SCR models use the spatial locations of  
138 captures to infer the activity center (or home range) of each individual. We assumed that  
139 individual encounters are Bernoulli random variables with individual- and trap-specific  
140 detection probabilities. More precisely, the detection probability  $p_{ij}$  of an individual  $i$  at trap  $j$   
141 is assumed to decrease as the distance ( $d_{ij}$ ) from its activity center increases according to a  
142 detection function. We used the half-normal detection function,  $p_{ij} = p_0 \exp(-d_{ij}^2/(2\sigma^2))$ ,  
143 where  $p_0$  is the probability of detecting an individual when the trap is located exactly at its  
144 center of activity and  $\sigma$  is the spatial scale (or movement) parameter that controls the shape of  
145 the detection function. For one of the two study areas in the French Jura mountain in years  
146 2011 and 2013, we detected only a few individuals (see the columns Doubs in Table 1). To  
147 increase the effective sample size, we combined the data from the two sampling areas using  
148 common detection and spatial parameters for both areas, while estimating density separately  
149 (e.g., [33]). We defined a state-space, i.e. the area encompassing all potential activity centers

150 of the observed individuals, by building a grid that buffered outermost camera trap locations  
151 by 15 km (corresponding to at least  $2\sigma$  [4]) with a resolution of 1.5 km (or pixels of area 2.25  
152 km<sup>2</sup>). We fitted SCR models in the maximum likelihood framework using the R package  
153 oSCR [34,35].

154 For comparison, we also estimated abundance using standard (non-spatial) capture-  
155 recapture models [5]. We dropped the spatial information and considered only the detections  
156 and non-detections for each individual. We considered two models, M0 in which the detection  
157 probability is the same for all individuals, and Mh in which the detection probability varies  
158 among individuals. We fitted standard models in the maximum likelihood framework using  
159 the R package Rcapture [36]. We estimated density as the ratio of estimated abundance over  
160 an effective trapping area (ETA). ETA was estimated by adding a buffer to the trapping area  
161 equal to the mean maximum distance moved (MMDM) or half of it (HMMDM). We  
162 calculated the MMDM by averaging the maximum distances between capture locations for all  
163 individuals detected at more than one site.

164

## 165 **Results**

166

167 We collected data from 413 camera trapping sites (2 camera traps were set per site) resulting  
168 in 25,839 trap days (Table 1). In total, we identified 92 lynx over 532 detection events in the  
169 Jura mountain, including 16 females, 13 males and 63 individuals of unknown sex. The  
170 number of detections per individual was 2.6 on average and varied from 1 up to 11. In  
171 contrast, we collected no lynx photo in the Vosges mountain, therefore we did not proceed  
172 with analyses for this area.

173

174

[Table 1 about here]





200 estimates across landscapes. Our study is yet another example of the potential of combining  
201 SCR methods and non-invasive sampling techniques to estimate abundance and density for  
202 elusive and wide-ranging species, like large carnivores [13–18].

203         When examining densities across study areas in the French Jura mountain, we found  
204 spatial variation between the three counties, with Doubs area having the lowest densities, Ain  
205 the highest densities, and Jura intermediate densities. Our density estimates were of similar  
206 magnitude to other lynx populations in Europe: 1.47 and 1.38 lynx / 100 km<sup>2</sup> in the  
207 Northwestern Swiss Alps [13], 0.58 (Štiavnica mountains) and 0.81 individuals / 100 km<sup>2</sup>  
208 (Velká Fatra National Park) in Slovakia [37] and 0.9 individuals / 100 km<sup>2</sup> in the Bavarian  
209 Forest National Park in Germany [38].

210         While [13] and [37] used SCR models, [38] used standard capture-recapture models  
211 with HMMDM to estimate densities, which makes them difficult to compare [39]. Indeed, in  
212 other carnivore studies, the use of HMMDM also produced similar density estimates to SCR  
213 models [13], while in others, including ours, the SCR estimates were closer to the MMDM  
214 estimates [2] or intermediate between the MMDM and HMMDM estimates [40]. When  
215 looking at reference values for densities across the distribution range of the species, it may be  
216 biologically meaningful to use the MMDM density estimate as a reference as it covers the  
217 whole potential of animal movements. On the other hand, because SCR models make space  
218 explicit whereas standard model-based densities are sensitive to the definition of the effective  
219 sampling area, we recommend the use of SCR models to estimate lynx densities. Our lynx  
220 density estimates might suffer from potential sources of bias that need to be discussed. First,  
221 the period of sampling is important to account for when setting up camera trap surveys [41].  
222 We conducted our survey outside the dispersal period, during the lynx mating season  
223 (February-March mostly). We did so to avoid capturing transient individuals and to increase  
224 detectability because of high lynx activity and relatively reduced human activities [31].

225 However, some individuals might have moved in and out of the study areas, especially males  
226 who cover greater distances during the mating season. Whereas the presence of non-resident  
227 individuals can affect the calculation of (H)MMDM, and in turn density estimated with  
228 standard capture-recapture models, SCR density estimates were found to be robust to the  
229 presence of transient individuals [42]. Second, males have larger home ranges than females  
230 [13], which leads to heterogeneity in the SCR model parameter estimates. Because there were  
231 too few males and females identified and lots of individuals with unknown sex, sex-specific  
232 SCR analyses [43] produced unreliable abundance and density estimates (results not shown).  
233 If detection heterogeneity is ignored in capture-recapture models, abundance is  
234 underestimated [44], therefore our density estimates are probably biased low and should be  
235 considered as a conservative metric. The determination of sex could be improved by i)  
236 combining the photographic surveys with genetic surveys, ii) conducting deterministic  
237 surveys over several years (e.g., [13]), iii) conducting an opportunistic camera trapping survey  
238 all over the years and setting camera trap at fresh lynx kills, iv) setting infrared flash camera  
239 traps capable of taking burst of images in rapid sequence at marking sites regularly used by  
240 the lynx (e.g., [45]). Last, we did not detect any individuals in the Vosges mountain, even  
241 though the sampling effort was similar to that implemented in the Jura mountain (Table 1).  
242 This finding is likely to be representative of the current critical situation of the lynx in the  
243 Vosges mountain.

244 We envision several perspectives to our work. First, while density estimates are of  
245 primary interest for conservation, understanding the mechanisms underlying trends in  
246 abundance is required to make sound conservation decisions [1]. SCR models have been  
247 extended to open populations [46] and can be used to estimate demographic parameters  
248 (survival, reproduction) of large carnivores [47]. Unfortunately, because of logistic  
249 constraints, we could not sample the same areas over several years, which precludes a

250 standard application of these models. A solution may lie in the combination of the data we  
251 collected through systematic camera-trap surveys with additional data in the SCR framework,  
252 such as occupancy data [48] or opportunistic camera-trap data [49]. Second, in addition to  
253 traffic-induced mortality and conflicts with human activities, the expansion of lynx  
254 populations is limited by habitat fragmentation [50], hence the need to assess connectivity  
255 with other populations [51]. SCR models can be used to quantify landscape connectivity by  
256 replacing the Euclidean distance between camera traps and home range centers by the  
257 least-cost path [52,53]. For lynx, this will require setting up traps across a gradient of habitat  
258 types, not only forested habitats, so that resistance to movement can be estimated.

259 In conclusion, our lynx density estimates for the French Jura mountain complement  
260 nicely the estimates recently provided for the Northwestern Swiss Alps [13]. The use of  
261 camera-trapping coupled with SCR models in both France and Switzerland was the result of a  
262 cooperation between the two countries with the perspective of a transboundary monitoring  
263 [54,55]. This approach would prove useful to accurately estimate densities in other areas  
264 where habitats and prey availability might differ, and overall lynx detectability varies. Also,  
265 collecting and adding movement data from GPS-collared lynx would be useful [49,56] to try  
266 and infer the connections between subpopulations.

267 The case can be made for monitoring the return of the lynx in the French Alps. Indeed,  
268 small-scale camera-trapping surveys and opportunistic observations are currently active and  
269 producing signs of lynx presence. However, the lack of a coordinated and intensive sampling  
270 effort prevents us from being able to estimate abundance and density and inferring trends.

271 In contrast, the situation in the Vosges mountain is alarming with no individuals  
272 detected over the study period. Because the Vosges mountain are located between the French  
273 Jura mountain and the Palatinate Forest in Germany where a reintroduction program is  
274 ongoing (program LIFE13 NAT/DE/000755), the lynx colonization in the Vosges mountain

275 remains possible both by the north and the south. Incidentally, two cases of lynx dispersal in  
276 the Vosges mountain from neighboring mountains have been recently observed ([57];  
277 program LIFE13 NAT/DE/000755). To ensure the detection of lynx in the Vosges mountain,  
278 we recommend reinforcing collaborative monitoring by involving all field stakeholders and  
279 enhancing communication on the species signs of presence.

280 In this context, obtaining accurate and comparable lynx densities will be crucial to  
281 closely monitor population trends at the national scale and inform management policies for  
282 the effective conservation of the Eurasian lynx in France.

283

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299 *d'images* magazine. This study could not have been conducted without authorizations from  
300 and agreements with municipalities, environmental managers and owners.

301

### 302 **Author contributions**

303 OG wrote the paper and all co-authors commented on the manuscript. OG and SG analyzed  
304 the data. AL, CD, EG, EM and SG coordinated the study designs, the data collection and  
305 interpretation, with help from FZ for setting the experimental design in the Jura mountain.

306

### 307 **Data accessibility**

308 The Eurasian lynx is an endangered species with high conservation stakes. Interactions with  
309 human activities are problematic and lead to poaching and anthropogenic pressures. Providing  
310 accurate information on lynx locations can be detrimental to the conservation status of the  
311 species. As a consequence, the original data could not be shared.

312

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489 **Figures**

490

491 **Figure 1: Map of the study area in the French Jura and Vosges mountains.** The study  
492 area encompassed seven counties (Ain, Jura and Doubs in the Jura mountain and Vosges,  
493 Haut-Rhin, Bas-Rhin and Moselle in the Vosges mountain) that were monitored through 418  
494 camera trapping sites (298 in the Jura mountain and 115 in the Vosges mountain; two camera  
495 traps were set per site), each within a 2.7 x 2.7 km cell. The inset map represents the French  
496 counties (grey borders), the counties that were considered in the study (black borders), the  
497 Jura mountain (green shaded area) and the Vosges mountain (red shaded area).

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501 **Figure 2: Lynx (*Lynx lynx*) density maps in the French Jura mountain.** The density scale  
502 is in lynx per 2.25 km<sup>2</sup> (pixel resolution is 1500m x 1500m). We obtained the estimated  
503 abundance in each map by summing up the densities in each pixel altogether. Yellow is for  
504 low densities, green for medium densities and blue for high densities; the density scales are  
505 specific to each map. Note that the interpretation of these plots as density maps is subject to  
506 caution (see the vignette “secur-densitysurface” of the SECR R package [58]).

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**Table 1: Main characteristics and results of the lynx camera-trap survey carried out in a) the French Jura mountain and b) the French Vosges mountain.**

<b>a. Year/County</b>	2011/Doubs	2011/Jura	2012/Jura & Doubs	2013/Doubs	2013/Ain & Jura	2014/Ain	2015/Ain
<b>Period of trap activity</b>	Jan-Apr	Feb-Apr	Feb-Apr	Feb-Apr	Feb-Apr	Feb-Apr	Feb-May
<b>Number of active camera traps</b>	48	66	148	44	142	118	30
<b>Number of trapping days (average/area)</b>	63	59	69	63	58	59	99
<b>Number of capture occasions<sup>i</sup></b>	15	15	17	14	13	13	21
<b>Number of detections</b>	22	42	130	25	117	158	38
<b>Number of detected individuals</b>	4	9	21	6	19	23	10
<b>Number of females, unknown, males</b>	1, 1, 2	1, 7, 1	2, 14, 5	1, 4, 1	2, 13, 4	4, 16, 3	2, 8, 0
<b>Number of detections / ind: mean, min, max</b>	3, 2, 4	2.8, 1, 6	2.5, 1, 10	2.7, 1, 6	3.6, 1, 11	3.3, 1, 9	2.2, 1, 5
<b>b. Year/County</b>	2013/Haut-Rhin & Vosges		2014/Bas-Rhin & Moselle		2015/Bas-Rhin & Moselle		2016/Bas & Haut-Rhin
<b>Period of trap activity</b>	Dec-Jan		Feb-Apr		Feb-Apr		Feb-Apr
<b>Number of active traps</b>	60		50		60		60
<b>Number of trapping days (average/area)</b>	52		59		57		59
<b>Number of detections</b>	0		0		0		0

<sup>i</sup>A capture occasion is defined as 5 successive trap days.

**Table 2: Lynx abundance and density estimates obtained from spatial and non-spatial capture-recapture analyses of camera-trapping data collected in the French Jura mountain.** Densities are provided in number of lynx per 100 km<sup>2</sup>. For 2011 and 2013, parameters of the spatial capture-recapture model ( $p_0$  and  $\sigma$ ) are common to both areas in each year. Acronyms are defined in the footnote<sup>i</sup>.

<b>Year/County</b>	2011/Doubs	2011/Jura	2012/Jura-Doubs	2013/Doubs	2013/Ain-Jura	2014-Ain	2015-Ain
<b>SCR abundance (SE)</b>	5 (0.1)	12 (0.1)	29 (0.2)	7 (0.1)	21 (0.1)	29 (0.2)	12 (0.1)
<b>SCR density (SE)</b>	0.24 (0.02)	0.44 (0.02)	0.67 (0.02)	0.36 (0.02)	0.54 (0.02)	0.91 (0.03)	0.64 (0.03)
<b><math>p_0</math> logit scale (SE)</b>	-2.94 (0.24)		-2.01 (0.20)		-2.57 (0.20)		-3.01 (0.42)
<b><math>\sigma</math> log scale (SE)</b>	8.89 (0.14)		8.54 (0.08)		8.95 (0.06)		8.97 (0.19)
<b>M0 abundance (SE)</b>	4 (0.7)	9 (0.7)	21 (0.6)	6 (0.3)	19 (0.8)	23 (0.7)	11 (1.2)
<b>Mh abundance (SE)</b>	5 (1.7)	10 (1.8)	25 (2.8)	7 (1.2)	25 (4.1)	28 (3.6)	11 (1.2)
<b>MMDM (km)</b>	9.1	16.2	8.9	9.1	18.2	13.6	12.1
<b>ETA with MMDM (km<sup>2</sup>)</b>	1991	2930	3089	1171	4954	2936	1549
<b>M0 density MMDM (SE)</b>	0.31 (0.05)	0.31 (0.02)	0.68 (0.02)	0.51 (0.02)	0.38 (0.02)	0.78 (0.02)	0.71 (0.08)
<b>Mh density MMDM (SE)</b>	0.39 (0.13)	0.34 (0.06)	0.81 (0.09)	0.60 (0.10)	0.50 (0.08)	0.95 (0.12)	0.70 (0.08)
<b>ETA with HMMDM (km<sup>2</sup>)</b>	697	1491	2111	659	2673	1668	753

<b>M0 density HMMDM (SE)</b>	0.57 (0.10)	0.60 (0.05)	0.99 (0.03)	0.91 (0.05)	0.71 (0.03)	1.38 (0.04)	1.46 (0.16)
<b>Mh density HMMDM (SE)</b>	0.72 (0.24)	0.67 (0.12)	1.18 (0.13)	1.06 (0.18)	0.93 (0.15)	1.68 (0.21)	1.43 (0.16)

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<sup>1</sup>Acronyms used: ETA is for Effective Trapping Area, MMDM for Mean Maximum Distance Moved, HMMDM for Half Mean Maximum Distance Moved, SCR for spatial capture-recapture, M0 for the (non-spatial) capture-recapture model with homogeneous detection probability, Mh for the (non-spatial) capture-recapture model with heterogeneous detection probability and SE for standard error.



Figure 1

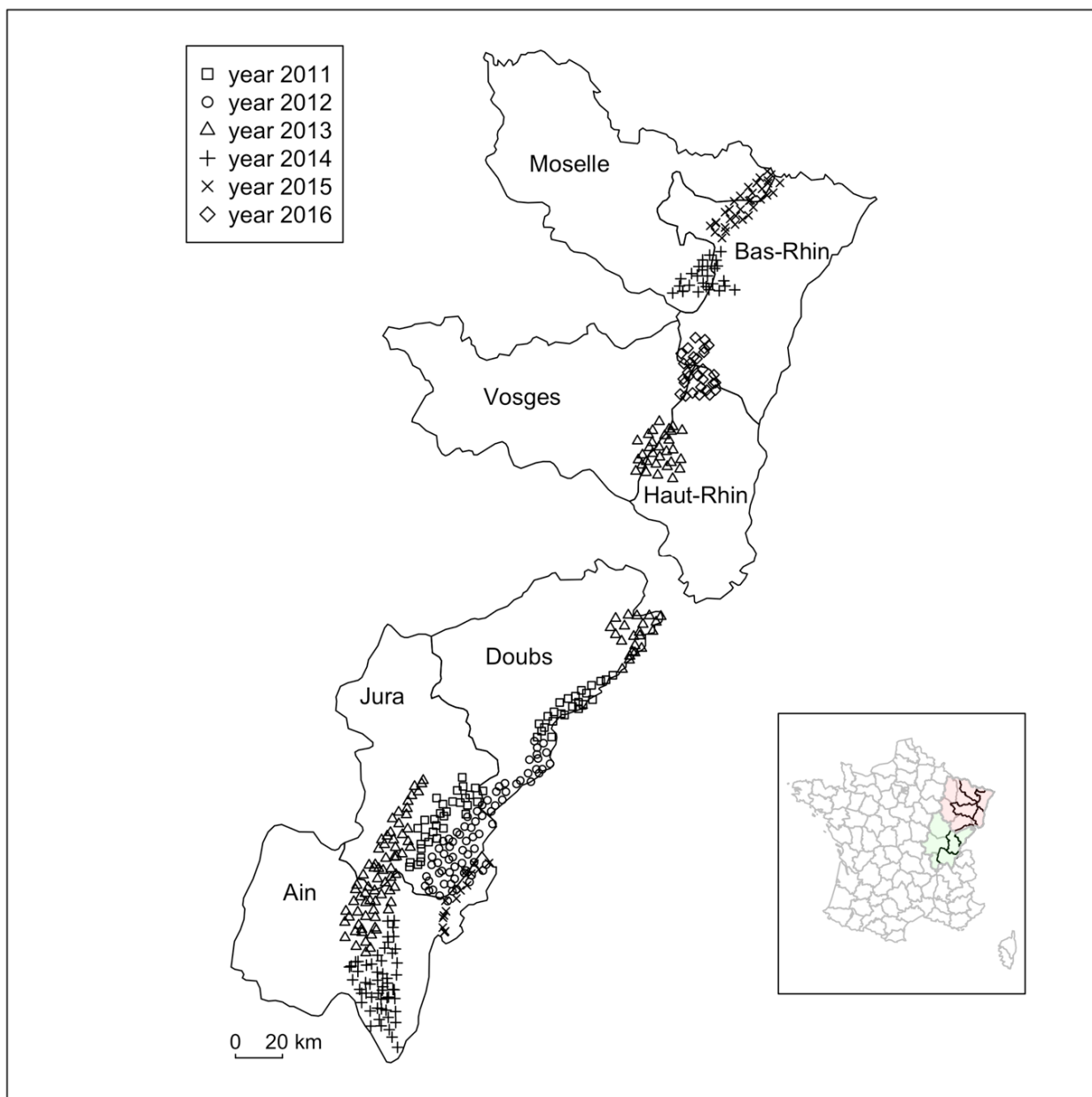


Figure 2

